
Sources and consequences of intraspecific trait variation in movement behaviour

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Declaration of Authorship

I hereby declare to have prepared this dissertation independently under the commonly accepted help of my supervisors. All direct or indirect sources used are given as references. All contributions of co-authors are acknowledged. This thesis has not been submitted to any other university or institution before.

Potsdam, Alexander Benedikt Milles

You're all individuals!
Brian, Monty Python's Life of Brian

Abstract

Variation in traits permeates and affects all levels of biological organisation, from within individuals to between species. Yet, intraspecific trait variation (ITV) is not sufficiently represented in many ecological theories. Instead, species averages are often assumed. Especially ITV in behaviour has only recently attracted more attention as its pervasiveness and magnitude became evident. The surge in interest in ITV in behaviour was accompanied by a methodological and technological leap in the field of movement ecology. Many aspects of behaviour become visible via movement, allowing us to observe inter-individual differences in fundamental processes such as foraging, mate searching, predation or migration. ITV in movement behaviour may result from within-individual variability and consistent, repeatable among-individual differences. Yet, questions on why such among-individual differences occur in the first place and how they are integrated with life-history have remained open. Furthermore, consequences of ITV, especially of among-individual differences in movement behaviour, on populations and species communities are not sufficiently understood. In my thesis, I approach timely questions on the sources and consequences of ITV, particularly, in movement behaviour. After outlining fundamental concepts and the current state of knowledge, I approach these questions by using agent-based models to integrate concepts from behavioural and movement ecology and to develop novel perspectives.

Modern coexistence theory is a central pillar of community ecology, yet, insufficiently considers ITV in behaviour. In chapter 2, I model a competitive two-species system of ground-dwelling, central-place foragers to investigate the consequences of among-individual differences in movement behaviour on species coexistence. I show that the simulated among-individual differences, which matched with empirical data, reduce fitness differences between species, i.e. provide an equalising coexistence mechanism. Furthermore, I explain this result mechanistically and, thus, resolve an apparent ambiguity of the consequences of ITV on species coexistence described in previous studies.

In chapter 3, I turn the focus to sources of among-individual differences in movement behaviour and their potential integration with life-history. The pace-of-life syndrome (POLS) theory predicts that the covariation between among-individual

differences in behaviour and life-history is mediated by a trade-off between early and late reproduction. This theory has generated attention but is also currently scrutinised. In chapter 3, I present a model which supports a recent conceptual development that suggests fluctuating density-dependent selection as a cause of the POLS. Yet, I also identified processes that may alter the association between movement behaviour and life-history across levels of biological organization.

ITV can buffer populations, i.e. reduce their extinction risk. For instance, among-individual differences can mediate portfolio effects or increase evolvability and, thereby, facilitate rapid evolution which can alleviate extinction risk. In chapter 4, I review ITV, environmental heterogeneity, and density-dependent processes which constitute local buffer mechanisms. In the light of habitat isolation, which reduces connectivity between populations, local buffer mechanisms may become more relevant compared to dispersal-related regional buffer mechanisms. In this chapter, I argue that capacities, latencies, and interactions of local buffer mechanisms should motivate more process-based and holistic integration of local buffer mechanisms in theoretical and empirical studies.

Recent perspectives propose to apply principles from movement and community ecology to study filamentous fungi. It is an open question whether and how the arrangement and geometry of microstructures select for certain movement traits, and, thus, facilitate coexistence-stabilising niche partitioning. As a coauthor of chapter 5, I developed an agent-based model of hyphal tips navigating in soil-like microstructures along a gradient of soil porosity. By measuring network properties, we identified changes in the optimal movement behaviours along the gradient. Our findings suggest that the soil architecture facilitates niche partitioning.

The core chapters are framed by a general introduction and discussion. In the general introduction, I outline fundamental concepts of movement ecology and describe theory and open questions on sources and consequences of ITV in movement behaviour. In the general discussion, I consolidate the findings of the core chapters and critically discuss their respective value and, if applicable, their impact. Furthermore, I emphasise promising avenues for further research.

Zusammenfassung

Die Variation von Merkmalen durchdringt und beeinflusst alle Ebenen der biologischen Organisation, von Individuen bis hin zu Artgemeinschaften. Dennoch wird die intraspezifische Merkmalsvariation (ITV) in vielen ökologischen Theorien nicht ausreichend berücksichtigt. Stattdessen wird oft von Durchschnittswerten der Arten ausgegangen. Insbesondere ITV im Verhalten hat erst in jüngster Zeit mehr Aufmerksamkeit erfahren, als dessen Verbreitung und Ausmaß deutlich wurden. Der Anstieg des Interesses an ITV im Verhalten ging mit einem methodischen und technologischen Sprung auf dem Gebiet der Bewegungsökologie einher. Viele Aspekte des Verhaltens werden durch die Bewegung sichtbar und ermöglichen es uns, interindividuelle Unterschiede bei grundlegenden Prozessen wie Nahrungssuche, Partnersuche, Räuber-Beute-Beziehungen oder Migration zu beobachten. ITV im Bewegungsverhalten kann aus intraindividuellem Variabilität und konsistenten, wiederholbaren Unterschieden zwischen einzelnen Individuen resultieren. Die Fragen, weshalb solche Unterschiede interindividuellen Unterschiede überhaupt auftreten und wie sie mit der Lebensgeschichte ("life-history") zusammenhängen, sind jedoch bislang ungeklärt. Darüber hinaus sind die Folgen von ITV, insbesondere von individuellen Unterschieden im Bewegungsverhalten, für Populationen und Artgemeinschaften nicht ausreichend bekannt. In meiner Dissertation gehe ich aktuellen Fragen zu den Quellen und Folgen von ITV, insbesondere im Bewegungsverhalten, nach. Nach einer Darstellung grundlegender Konzepte und des aktuellen Wissensstandes nähere ich mich diesen Fragen mit Hilfe agentenbasierter Modelle, um Konzepte aus der Verhaltens- und Bewegungsökologie zu integrieren und neue Perspektiven zu entwickeln.

Die moderne Koexistenztheorie ist ein zentraler Pfeiler der Gemeinschaftsökologie, berücksichtigt aber ITV im Verhalten nur unzureichend. In Kapitel 2 modelliere ich ein System zweier konkurrierender, bodenbewohnender Arten mit zentralisierten Streifgebieten, um die Folgen von Unterschieden im Bewegungsverhalten zwischen Individuen auf die Koexistenz der Arten zu untersuchen. Ich zeige, dass die simulierten interindividuellen Unterschiede, die mit empirischen Daten übereinstimmen, die Fitnessunterschiede zwischen den Arten verringern, d. h. einen ausgleichenden Koexistenzmechanismus darstellen. Darüber hinaus erkläre ich dieses Ergebnis mechanistisch und löse damit eine scheinbare Zweideutigkeit der

in früheren Studien beschriebenen Folgen von ITV auf die Koexistenz von Arten auf.

In Kapitel 3 richte ich den Fokus auf die Quellen individueller Unterschiede im Bewegungsverhalten und deren mögliche Integration in die Lebensgeschichte. Die Theorie des "pace-of-life-Syndroms (POLS) sagt voraus, dass die Kovariation zwischen individuellen Unterschieden im Verhalten und der Lebensgeschichte durch einen Zielkonflikt zwischen früher und später Reproduktion vermittelt wird. Diese Theorie hat viel Aufmerksamkeit erregt, wird aber derzeit auch kritisch betrachtet. In Kapitel 3 stelle ich ein Modell vor, das Hypothesen einer neuere konzeptionelle Entwicklung stützt, die eine fluktuierende, dichteabhängige Selektion als Ursache des POLS nahelegt. Ich habe jedoch auch Prozesse identifiziert, die den Zusammenhang zwischen Bewegungsverhalten und Lebensgeschichte auf verschiedenen Ebenen der biologischen Organisation verändern können.

ITV kann Populationen puffern, d. h. ihr Aussterberisiko verringern. So können beispielsweise Unterschiede zwischen Individuen Portfolioeffekte vermitteln oder die Fähigkeit zur Anpassung erhöhen und damit etwa eine schnelle Evolution erleichtern, die das Aussterberisiko verringern kann. In Kapitel 4 gebe ich einen Überblick über ITV, Umweltheterogenität und dichteabhängige Prozesse, die lokale Puffermechanismen darstellen. Angesichts der Isolierung von Lebensräumen, die die Konnektivität zwischen Populationen verringert, können lokale Puffermechanismen im Vergleich zu ausbreitungsbedingten regionalen Puffermechanismen an Bedeutung gewinnen. In diesem Kapitel argumentiere ich, dass Kapazitäten, Latenzen und Interaktionen lokaler Puffermechanismen zu einer prozessbasierten und ganzheitlichen Integration lokaler Puffermechanismen in theoretischen und empirischen Studien motivieren sollten.

Neuere konzeptionelle Einsichten legen nahe, dass Prinzipien aus der Bewegungs- und Gemeinschaftsökologie auf die Untersuchung filamentöser Pilze angewendet können. In diesem Zusammenhang ist es eine offene Frage, ob und wie die Anordnung und Geometrie von Mikrostrukturen für bestimmte Bewegungseigenschaften selektieren und damit eine koexistenzstabilisierende Nischenaufteilung erleichtern. Als Koautor von Kapitel 5 habe ich ein agentenbasiertes Modell der Hyphenspitzen entwickelt. In diesem Modell navigieren die Hyphenspitzen in bodenähnlichen Mikrostrukturen entlang eines Gradienten der Bodenporosität. Durch die Messung von Netzwerkeigenschaften konnten wir Veränderungen des optimalen Bewegungsverhaltens entlang des Gradienten feststellen. Unsere Ergebnisse deuten darauf hin, dass die Bodenarchitektur eine ökologische Nische mit verschiedenen Bewegungs-

optima darstellt.

Die Hauptkapitel werden von einer allgemeinen Einführung und einer Diskussion eingerahmt. In der allgemeinen Einführung umreißt ich die grundlegenden Konzepte der Bewegungsökologie und beschreibe die Theorie und die offenen Fragen zu den Ursachen und Folgen von ITV im Bewegungsverhalten. In der allgemeinen Diskussion fasse ich die Ergebnisse der Kernkapitel zusammen und diskutiere kritisch ihren jeweiligen Wert und gegebenenfalls ihre Auswirkungen. Darüber hinaus zeige ich vielversprechende Wege für künftige Forschungsarbeiten auf.

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Chapter 1

General Introduction

Intraspecific variation of heritable, functional traits, i.e. traits that contribute to growth, survival, or reproduction (Violle et al. 2007), has been recognized as the primary material for evolution since Charles Darwins' "On the origin of species". Yet, replacing intraspecific variation by simplifying mean-field assumptions and averages persisted in ecological theory despite perpetual critics (Bennett 1987; Clark et al. 2011; Denny 2017; Huston et al. 1988; Lomnicki 1978; Williams 2008). Only in more recent years, with the extent of intraspecific trait variation (ITV) becoming more tangible (Albert et al. 2010; Bell et al. 2009), questions in community and population ecology have started to address the role of ITV (Bolnick et al. 2011; Des Roches et al. 2018; Jeltsch et al. 2019; Violle et al. 2012) and behaviour in particular (Sih et al. 2012; Wolf and Weissing 2012).

Many aspects of behavioural variation become apparent via movement. Yet, intraspecific variation in movement behaviour has long been notoriously difficult to study especially at local scales. Thus, ITV in movement behaviour has only recently pertained research agendas (Hertel et al. 2020; Shaw 2020). Given its novelty, our understanding of sources of ITV in movement behaviour is incomplete and we lack sufficient integration with formal theory. In this thesis, I approach these knowledge gaps by synthesising concepts from movement and behavioural ecology with existing theoretical frameworks to study sources and consequences of ITV in behaviour with a special focus on movement.

The rise of movement ecology accompanied the wider adoption of an individual-based perspective on ecological questions in the recent decade. This development is not surprising, as movement is the main way by which individuals visibly interact with their environment (Nathan et al. 2012). The advent of modern tracking devices, biologgers and big-data approaches in ecology (Kays et al. 2015; Nathan et al. 2022; Wilmers et al. 2015) provides unprecedented insights into how movement paths shape individual life-histories via foraging, avoiding predators or searching for mates (Shaw 2020). Furthermore, we can now conceive how individuals act as mobile linkers (Lundberg and Moberg 2003) of genetic material (e.g. diseases; Scherer et al. 2020, neobiota; Jones et al. 2019, nutrients; Subalusky et al. 2015) or processes (e.g. pest control; Rand et al. 2006, pollination; Rands 2014) which scale up to the community level (Costa-Pereira et al. accepted; Jeltsch et al. 2013; Schlägel

et al. 2020). For instance, we now realise that some individuals may disperse over longer distances and that dispersal distance correlated with other behavioural traits (Fraser et al. 2001) resulting in different processes mediated by residents and dispersers (Clobert et al. 2009). As such, by moving away from species averages in favour of ITV in movement behaviour, the predictive capacity and mechanistic understanding of ecology via proper theories is a promising perspective. Yet, given the novelty of the topic, recent theories on how ITV in behaviour arises are currently scrutinised and established theories on community assembly and population persistence mostly neglect this topic. Consequently, the purpose of this thesis, namely contributing to the advancement of these theories, is a timely endeavour.

To introduce my thesis in the following, I first describe its conceptual, theoretical, and methodological basis. To study questions revolving around ITV, it is essential to partition dimensions of variation. Heritable among-individual differences and context- and state-dependent within-individual variability constitute the sources of ITV in movement behaviour (Hertel et al. 2020) with distinct eco-evolutionary consequences (Moran et al. 2016; Wolf and Weissing 2012). To highlight this in more detail, I will first introduce the key concepts and terminology underlying ITV in movement behaviour putting special emphasis on among-individual differences. Whilst within-individual variability has long pervaded ecological research and is somewhat better understood, the causes and patterns of among-individual differences in behaviour are puzzling. I will introduce the pace-of-life syndrome as a central theory that attempts to solve this puzzle (Dammhahn et al. 2018; Réale et al. 2010) and which I examine in chapter 3. Next, I change the focus from causes of among-individual differences to their ramifications. Given the novelty of research into ITV, the main body of formal ecological theory on community assembly and population persistence mostly neglects ITV (Jeltsch et al. 2019; Johnson and Hastings 2022) and, particularly, among-individual differences in movement behaviour (Shaw 2020). I will summarise the more recent perspective on the consequences of ITV at the level of populations and identify seemingly conflicting findings concerning species coexistence which motivated several core chapters of my thesis. After outlining the conceptual and theoretical basis that encompasses the chapters of my thesis, I will introduce agent-based models as a key methodological approach to integrate among-individual differences in movement behaviour with eco-evolutionary processes.

1.1 Sources of intraspecific variation in movement behaviour

Tracking individual movement paths and behaviours in the wild has revealed levels of ITV potentially surpassing levels of interspecific variation (Harrison et al. 2019). Yet, what are the sources of variation in movement behaviour? The movement ecology paradigm (Nathan 2008) implies that differences in movement traits may result from environmental and individual variation. The answers to why, how, and when to move are, thus, composed of a mixture of environmental as well as physiological and behavioural components (Nathan 2008). So, to better understand the nature of ITV in movement behaviour, each of these components requires attention.

The effect of the environmental component depends on the environmental conditions than an individual experiences at a certain location and time. This may include the perceived presence of risks such as predators (i.e. landscape of fear; Laundré et al. 2010), disease (i.e. landscape of disgust; Weinstein et al. 2018) and competitors, terrain resistances (i.e. energy landscapes; Shepard et al. 2013), and resources or mating partners. Some aspects of the environmental state are covered by an unprecedented wealth and accessibility of satellite and reanalysis data (Gorelick et al. 2017) with a fine spatiotemporal resolution. Statistical approaches such as step-selection (Fortin et al. 2005) in connection with improved tracking devices facilitate the identification of relevant characteristics in a dynamic environment. Novel approaches even infer patterns of attraction and avoidance between co-occurring individuals (Schlägel et al. 2019), given the movement of a sufficient proportion of individuals is observed. Further sophisticated approaches like hidden Markov models identify different movement modes (e.g. characterised by step size and turning angles) and the transition between these modes based on environmental characteristics (McClintock and Michelot 2018; Patterson et al. 2009).

Using environmental characteristics only to explain the movement behaviour of a population commonly results in a significant proportion of unexplained variation. Partly, this variation can be explained by the internal state of the individual, such as physiological characteristics that are strongly linked to movement behaviour (Campos-Candela et al. 2019; Goossens et al. 2020). Fundamentally, movement incurs metabolic costs but is also vital to acquire resources. To shed light on individual physiology, biologgers are more frequently used and integrated with environmental characteristics to explain movement patterns. Temperature and heart rate loggers or accelerometers allow the estimation of energy budgets (Wilmers et al. 2015). Such physiological conditions affect the decisions on where to forage, when and

if to migrate and where to disperse to (Chapman et al. 2011; Goossens et al. 2020) resulting in an interplay between behaviour and physiology (Biro and Stamps 2010).

Environmental properties and the internal state, such as the energetic status, are variable over time creating within-individual variability in movement behaviour. Yet, besides within-individual variability, consistent, repeatable among-individual differences (in the following as among-individual differences) are related to the total observed ITV in movement behaviour. Such among-individual differences arise even between clonal individuals raised in controlled environments (Bierbach et al. 2017). While this source of variation has long gone mostly unnoticed (Dingemanse 2017; Dingemanse et al. 2010) there is pervasive evidence of among-individual differences in behaviour across time and contexts (Bell et al. 2009). Dissecting the sources of variation is crucial, for instance, to evaluate the buffer capacity due to adaptive plasticity within generations and evolution along generations in populations (Dingemanse et al. 2022; Moran et al. 2016; Wolf and Weissing 2012). Among-individual differences, also coined "animal personalities" or, in movement ecology, "spatial personalities" (Stuber et al. 2022b), recently pervaded research agendas in movement ecology (Hertel et al. 2020; Nathan et al. 2022; Schlägel et al. 2020; Shaw 2020; Spiegel et al. 2017; Stuber et al. 2022b).

1.2 Taking it personally: consistent among-individual differences in movement behaviour

Among-individual differences in movement behaviour encompass multiple traits commonly measured in standardised tests (Carter et al. 2013; Réale et al. 2007). Such standardised tests revealed relations between space-use and other behavioural traits. Dispersal syndromes, for instance, describe a covariation between dispersal properties and aggression, boldness, or sociability (Clobert et al. 2009; Cote and Clobert 2007; Cote et al. 2010; Duckworth and Badyaev 2007). For instance, individuals of Trinidad killifish with reduced latency to explore a novel environment (interpreted as boldness) in repeated standardised tests, showed increased dispersal distances (Fraser et al. 2001). Such among-individual differences become especially surprising if one assumes that only one optimal behaviour exists in certain situations. Such findings would then imply suboptimal behaviour which violates a fundamental assumption of central ecological theories (Charnov 1976). The question of why consistent among-individual differences nonetheless exist is subject to current ecological debates (Bell 2017; Sih 2017; Wilson et al. 2019). Before sketching this debate and related questions in more detail, I first introduce key concepts and

terminology from behavioural ecology and highlight studies that form the nucleus of my methodological developments.

To answer questions of sources and consequences of among-individual differences, conceptual and empirical methods are required which dissect the total amount of observed variation into among-individual differences and within-individual variability. Behavioural reaction norms are a key concept to integrate among-individual differences and within-individual variability in behaviour in general (Dingemanse et al. 2010) and movement behaviour in particular (Spiegel et al. 2017). Behavioural reaction norms define how a behavioural expression (e.g. turning angle) changes along an environmental gradient (e.g. resource availability). Among-individual differences are partitioned by three characteristics of behavioural reaction norms (Hertel et al. 2020). First, individuals may differ in the intercept of the behavioural reaction norm, i.e. their consistent average behavioural expression, which is also called the behavioural type. Second, individuals may differ in the slope of their behavioural reaction norms, i.e. may adjust their behaviour with different magnitudes and even different signs along an environmental gradient. Lastly, the individuals may differ in their predictability, which describes how closely their behaviour tracks their reaction norm, and which can be measured by the residuals (Hertel et al. 2020; Westneat et al. 2015). These three dimensions of reaction norms, behavioural type, plasticity, and predictability are heritable aspects of among-individual differences (Dochtermann et al. 2019; Henriksen et al. 2020; Nussey et al. 2005).

Identifying consistent among-individual differences in movement behaviour only from open-field experiments is challenging (Hertel et al. 2020). As animals move, the environmental context and the individual state change (Shaw 2020). Thereby, within-individual variability is implicitly linked to movement and may contribute a large fraction of the total observed variation. Dissecting variation in movement patterns arising either from among-individual differences or within-individual variability (Spiegel et al. 2017) is challenging. Especially for small-scale movements, meaningful inferences are intricate, as individuals cover only small, sometimes non-overlapping sections of environmental gradients (Hertel et al. 2020). Hence, recently claimed high levels of repeatability in multiple movement traits (Stuber et al. 2022b), are to be debated as many studies still conflate sources of variation (Dingemanse et al. 2022; Spiegel and Pinter-Wollman 2022; Stuber et al. 2022a). To adequately approach this question, elaborated study designs are required that include multiple standardised tests of among-individual differences to measure repeatability that accompany tracking. As such, among-individual differences in small-scale movements has only been subject in recent empirical studies (Aliperti et al. 2021; Eccard et al. 2022; Harris et al. 2020; Schirmer et al. 2019; Schirmer et al.

2020; Spiegel et al. 2015). Nevertheless, while we now have advanced conceptually and methodologically to observe the pervasiveness of among-individual differences in movement behaviour, we are still not sure why they exist in the first place and how they are related to other traits.

1.3 Sources of among-individual differences in movement behaviour and their integration with life-history

The observations of among-individual differences across time and contexts have provoked an intriguing question: Why do individuals not align to one optimal behavioural trajectory along an environmental gradient and show consistent differences instead (Dingemanse and Wolf 2010; Sih 2017; Sih et al. 2004; Wolf et al. 2007)? Possible explanations can be broadly categorised in constrained and adaptive evolution (Sih et al. 2004). On the one hand, evolutionary constraints due to genetic pleiotropy (Wolf and Weissing 2012) or costs of plasticity hinder the expression of an optimal behaviour for a given context (DeWitt et al. 1998). Behavioural syndromes, on the other hand, may also provide an adaptive explanation (Biro and Stamps 2008; Réale et al. 2010; Sih et al. 2004; Wolf et al. 2007).

One prominent line of thought for iteroparous species is that a life-history trade-off between early and late reproduction leads to differences in risk-taking and associated behaviours (Wolf et al. 2007). According to the pace-of-life-syndrome (POLS) theory (Réale et al. 2010), behavioural traits covary along a continuum of late reproducing and long-lived individuals (i.e. with a slow pace-of-life) to early reproducing and short-lived individuals (i.e. with a fast pace-of-life). The POLS theory is rooted in r-K selection theory (MacArthur and Wilson 1967; Pianka 1970), but, includes behavioural and physiological in addition to life-history traits and predicts associations between traits also within populations. According to POLS theory, fast-paced individuals should express behaviours that add to current reproduction even at the expense of future reproduction. Behavioural traits associated with the POLS include typical movement traits such as exploratory behaviour, dispersal, and activity. For instance, fast, early-reproducing individuals are considered to be bolder, more active, and superficial explorers with a higher dispersal propensity despite the elevated mortality risk (Dammhahn and Almeling 2012; Fraser et al. 2001; Réale et al. 2010; Wolf et al. 2007).

The broad implications of POLS theory have made it a popular subject in animal (Dammhahn et al. 2018; Réale et al. 2010) and human biology (Del Giudice et al. 2015; Kaplan et al. 2000). The POLS theory provides *a priori* predictions of how life-

history, physiological and behavioural traits should be correlated across hierarchical levels. Furthermore, ecological and evolutionary consequences arise from the POLS theory. For instance, dispersal syndromes generate differences between source and sink populations strongly affecting invasion biology or range dynamics (Cote et al. 2010; Pintor et al. 2009; Sih et al. 2012). Yet, despite the attention from empirical studies, evidence of POLS remains scarce (Bonte and Doherty 2017; Mathot and Frankenhuis 2018; Moiron et al. 2020; Montiglio et al. 2018; Royauté et al. 2018) partly due to a lack of theoretical underpinning (Del Giudice 2020). Therefore, while movement and POLS theory have strong links (Campos-Candela et al. 2019; Le Galliard et al. 2013; Nakayama et al. 2017), we lack a consensus on ultimate causes of among-individual differences in movement behaviour and its correlation with further aspects of ITV. To address this issue in this thesis, I investigate a recent framework that suggests fluctuating density-dependent selection as a universal mechanism driving the evolution of POLS (Wright et al. 2019).

1.4 Consequences of among-individual differences in movement behaviour

Not only the sources of among-individual differences in movement behaviour are an unsolved puzzle to ecologists, but also its ramifications are not sufficiently explored (Shaw 2020). Dissecting the relative contribution of among-individual differences and within-individual variability in movement patterns yields insights into the fate of species and populations under global change (Moran et al. 2016). For instance, if behavioural variation is mainly a result of within-individual variability and not from heritable among-individual differences, the material for selection (“evolvability”; Wolf and Weissing 2012) is small, reducing the speed of evolution. As a consequence, once evolution within a population cannot keep up with the pace of environmental change, rapid extinction events may occur (Simmonds et al. 2020). Among-individual differences, instead, can increase the resistance of a population towards directed environmental change and environmental fluctuations (Bolnick et al. 2003) by mediating portfolio effects (Bolnick et al. 2011; Schindler et al. 2015; Schindler et al. 2010). Among-individual differences in diet or habitat preference reduce the strength of interactions in ecological networks and increase the connectedness (Bolnick et al. 2011). Thereby, if among-individual differences are present, fluctuations in environmental conditions impact individuals non-randomly, thus, mediating a buffer mechanism which reduces extinction risk. These implications of ITV, however, lack an integration with further buffer mechanisms operating at a local scale. To address this issue, in chapter 4, I provide a perspective and a

conceptual framework on the implications of ITV for population persistence and highlight interactions with further buffer mechanisms.

The effect of among-individual differences in movement behaviour extends to the community context (Costa-Pereira et al. accepted; Jeltsch et al. 2013; Schlägel et al. 2020). In general, weaker but diversified interactions between species are thought to foster species coexistence (Bolnick et al. 2011; Sih et al. 2012; Wolf and Weissing 2012). This effect has been demonstrated in simulated predator-prey systems (Moya-Laraño 2011; Schreiber et al. 2011). Yet, it is not well understood how among-individual differences, especially in movement behaviour (Shaw 2020), shape the coexistence of competing species. Several theories exist to explain the coexistence of competing species, whereas each theory stresses different processes (Vellend 2010). Among those theories, Chesson's modern coexistence theory (Chesson 2000a; Chesson 2000b), has a particular appeal as it clearly shows how the relative size of niche and fitness variation mediates stable coexistence and competitive exclusion (Turcotte and Levine 2016). In general, according to the modern coexistence theory, stabilising niche differences increase as intraspecific competition becomes higher and interspecific competition is reduced. If a species invades a community and interspecific niche differences are high, stable coexistence can occur as population size changes and detrimental effects from intraspecific competition are reduced. However, stabilising niche differences may be counteracted if density-independent, average fitness differences between species are high, i.e. equalising mechanisms are absent (Chesson 2000a).

While the dissection of equalising and stabilising mechanisms has advanced community ecology (Barabás et al. 2018), the theory is still lacking a comprehensive integration of among-individual differences (Jeltsch et al. 2019; Johnson and Hastings 2022; Stump et al. 2022). Some modelling studies on the effect of ITV on species coexistence preceded my thesis (Banitz 2019; Crawford et al. 2019; Hart et al. 2016; Uriarte and Menge 2018). These studies, however, generated seemingly contradictory results. Sometimes ITV increased competitive exclusion by reducing stabilising and equalising mechanisms (Hart et al. 2016), in other studies the effect on species coexistence was positive or context-dependent (Banitz 2019; Crawford et al. 2019; Uriarte and Menge 2018). Furthermore, all of the pre-existing studies are on immobile species and none did model behaviour emerging from reaction norms. This evident research gap motivated large parts of my thesis.

1.5 Movement beyond motile organisms: space- searching algorithms in filamentous fungi

In the previous sections, I presented ideas that revolve around the movement ecology of animals (as unitary organisms). Classically, independent (i.e. active) movement is considered a distinct property of unitary organisms. Modular organisms such as plants and fungi are considered immobile, as only their propagules move due to (mainly) external forces. This distinction has recently been challenged by an attempt to integrate modular organisms such as filamentous fungi in the movement ecology paradigm (Bielčík et al. 2019). The movement characteristics of filamentous fungi are subsumed under the term space-searching algorithms. Space-searching algorithms describe in what manner (magnitude, frequency) hyphae branch, turn, and anastomose (i.e. reconnect) based on the environment and species-specific characteristics (Held et al. 2008; Held et al. 2019). Transferring existing theories and concepts from animal movement and behaviour exposes where they apply to other forms of life and where novel developments are required. I contributed to this in a collaborative work by developing an agent-based model of movement behaviour in filamentous fungi. In the following, I will shortly outline what agent-based models are and why they are suitable to study sources and consequences of ITV in movement behaviour, in general.

1.6 Agent-based models to integrate movement with behavioural ecology

So far, I have outlined fundamental concepts of movement and behavioural ecology and knowledge gaps regarding sources and consequences of ITV, particularly, in movement behaviour. Despite methodological advances of *in vivo* approaches, *in silico* approaches are required to inform empirical studies and generate hypotheses in this novel field. Agent-based models (ABMs) are especially suitable to study behavioural processes and their consequences across different levels of organisation (Jeltsch et al. 2013). ABMs are characterised by interacting “unique and autonomous entities” (Railsback and Grimm 2012, p. 10) which are explicitly simulated along with their states. As such, ABMs allow to explicitly simulate within-individual variability and among-individual differences resulting from behavioural reaction norms (Spiegel et al. 2017). More specifically, consistent among-individual differences and local interactions between individuals and their environment can be simulated.

While ABMs have been long identified as a way towards synthesis in ecological theory (Huston et al. 1988), they have also met criticism (Roughgarden 2012). In

contrast to most other modelling approaches, ABMs can rarely be comprehensibly described by a set of equations alone, posing a major challenge in communicating ABMs. Only as definitions and documentation were standardised (Grimm et al. 2006; Grimm et al. 2010; Grimm et al. 2020), ABMs became more widely applied and accepted, for instance, due to their ability to describe complex systems and model ecological patterns from first principles (Grimm et al. 2017; Grimm and Berger 2016; Stump et al. 2022).

The ABMs presented in chapters two and three integrate the movement ecology paradigm and behavioural reaction norms to study the causes and consequences of variation in movement behaviour. I use established scientific software tools to generate the model (NetLogo; Wilensky 1999) and to analyse simulations, perform statistics, and data visualisation (R; R Core Team 2021). All models are complemented by the standard protocol Overview, Design Concepts and Details (ODD; Grimm et al. 2006; Grimm et al. 2010; Grimm et al. 2020). I publicly provided the documentation along with the model code upon publication of the individual chapters.

1.7 Outline of the following chapters

This thesis consists of four core chapters, which are complemented by this general introduction (chapter 1) and a general discussion (chapter 6). I make the role as a coauthor in chapter 5 more explicit, by using the first person plural when discussing the results.

In the **second chapter**, I investigated the consequences of among-individual differences in personality-related movement behaviour on coexistence in an ABM of two ground-dwelling, central-place forager species (Milles et al. 2020). Among-individual differences in movement behaviour were governed by an individual personality trait representing boldness and exploration, reproducing patterns observed in empirical studies (Schirmer et al. 2019). By contrasting scenarios with and without among-individual variation, I demonstrated that ITV in movement behaviour promoted coexistence via an equalising mechanism. Furthermore, I identified a relationship between population densities and the optimal personality trait. This observation stands in correspondence with a recent framework that suggests fluctuating density-dependence as a source of variation in personality traits along the pace-of-life (Wright et al. 2019). Theoretical works on POLS theory are scarce (Mathot and Frankenhuis 2018) and density-dependent selection may be a powerful explanation, hence, this observation provided the substrate for the third chapter.

In the **third chapter**, I test the predictions of the fluctuating density-dependent

selection POLS framework (Wright et al. 2019) by developing an eco-evolutionary ABM of local populations which experience stochastic disturbances (Milles et al. 2022). Individuals are characterised by two evolving traits, that represent foraging movement and allocation of energy to reproduction. I observed that the traits evolved by aligning to a common pace-of-life axis. Slow types with associated traits evolved at higher population densities whereas faster types evolved at lower population densities. This common axis persisted across hierarchical levels, i.e. within and between populations. Furthermore, in line with the prediction, fast populations were characterised by an elevated degree of among-individual differences. This chapter, thus, provides evidence for fluctuating density-dependent selection as a source for the POLS. Yet, the results also nuance core assumptions of POLS theory such as a consistent axis of pace-of-life across hierarchical levels.

In the **fourth chapter**, I zoom out and synthesise how ITV and environments affect local buffer mechanisms (i.e. mechanisms that reduce extinction risk). One essential motivation for dissecting sources of ITV is to assess the adaptive capacity of populations. For instance, if populations maintain high levels of heritable among-individual differences but low levels of non-heritable plasticity, population decline may be buffered from portfolio effects (Bolnick et al. 2011; Schindler et al. 2015; Schindler et al. 2010) and higher evolvability (Wolf and Weissing 2012). I highlight key characteristics of buffer mechanisms including capacities, latencies, and interactions. I conclude that these complexities of local buffer mechanisms necessitate a comprehensive integration of local buffer mechanisms. In this context, I provide a perspective on how individual-based ecology may foster our understanding of local buffer mechanisms and our capacity to predict extinction risks.

The **fifth chapter** is rooted in the idea, that studying mechanisms guiding fungal growth largely overlaps with the movement ecology paradigm (Bielčík et al. 2019). Movement-based niche partitioning as a coexistence mechanism should, hence, also occur in filamentous fungi. While space-searching algorithms are known from small case studies, generalisation and expositions to questions of community ecology are rare. As a co-author, I developed an individual-based model of hyphal movement. In this model, each hyphal tip acts as an autonomous unit in a spatially-structured soil-like environment. Based on the parameter settings, hyphae branch, turn and reconnect (anastomose). Hyphal tips remain interconnected, constituting the emergence of a hyphae network from first principles. In this chapter, we analysed network traits and their variation along environmental and behavioural gradients to infer the role of movement-based niche partitioning in filamentous fungi.

In the **sixth chapter**, I summarise the novel insights achieved in the context of this thesis and address outstanding questions. Specifically, I address the role

of agent-based models in the field of animal personality and movement ecology. Finally, I provide explicit suggestions of how future studies could be designed so that sources and consequences of ITV in movement behaviour can be studied in more detail.

Chapter 2

Intraspecific trait variation in personality-related movement behaviour promotes co-existence

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Abstract

Movement behavior is an essential element of fundamental ecological processes such as competition and predation. Although intraspecific trait variation (ITV) in movement behaviors is pervasive, its consequences for ecological community dynamics are still not fully understood. Using a newly developed individual-based model, we analyzed how given and constant ITVs in foraging movement affect differences in foraging efficiencies between species competing for common resources under various resource distributions. Further, we analyzed how the effect of ITV on emerging differences in competitive abilities ultimately affects species coexistence. The model is generic but mimics observed patterns of among-individual covariation between personality, movement and space use in ground-dwelling rodents. Interacting species differed in their mean behavioral types along a slow-fast continuum, integrating consistent individual variation in average behavioral expression and responsiveness. (i.e., behavioral reaction norms). We found that ITV reduced interspecific differences in competitive abilities by 5 to 35 % and thereby promoted coexistence via an equalizing mechanism. The emergent relationships between behavioral types and foraging efficiency are characteristic for specific environmental contexts of resource distribution and population density. As these relationships are asymmetric, species that were either “too fast” or “too slow” benefited differently from ITV. Thus, ITV in movement behavior has consequences for species coexistence but to predict its effect in a given system requires intimate knowledge on how variation in movement traits relates to fitness components along an environmental gradient.

2.1 Introduction

Modern coexistence theory (MCT) is a central pillar of community ecology (Adler et al. 2007; HilleRisLambers et al. 2012; Letten et al. 2017; Mayfield and Levine 2010; Saavedra et al. 2017; initial developments Chesson 2000a; Chesson 1994; Chesson 2000b; Chesson 2003; Chesson and Warner 1981). Dissecting coexistence mechanisms into stabilizing and equalizing, this theory contributed to a better conceptual understanding of how and why certain sets of species can form stable communities despite competition for resources. Still, inherent of a population-level ecological theory, MCT neglects among-individual variation, although variation around the population mean is likely to modify species interactions (Violle et al. 2012). Only recently, ecologists are increasingly discussing whether and how equalizing and stabilizing mechanisms are induced by intraspecific trait variation (ITV), e.g., for plant communities (Crawford et al. 2019; Hart et al. 2016) and immobile organisms in general (Banitz 2019).

Behavior plays a crucial role in fundamental ecological processes within and between species, such as competition and predation, and may also affect stabilizing mechanisms (Turcotte and Levine 2016). Therefore, incorporating individual variation in behavior into coexistence theory might lead to a better understanding of the mechanisms determining ecological community composition. Generally, individuals vary in their average behavioral expression across time and contexts (i.e., animal personalities) and their responsiveness to environmental variation (i.e., reversible plasticity; Dingemanse et al. 2010), which both define its behavioral type (BT). Although behavior is among the most plastic traits of an individual, intrinsic differences constrain behavioral expressions of each behavioral type. Thus, in a given set of environmental conditions, individuals of a population vary among each other in behavior and this additional level of variation ought to affect interactions between species in ecological communities (Bolnick et al. 2011; Wolf and Weissing 2012).

Movement may be the most promising candidate for studying feedback from individual behavior to species coexistence at the community level because individual movement characteristics along various movement types, including dispersal (Cote et al. 2010) or migration (Found and St. Clair 2019), covary with BTs. More recently, the relevance of BTs for spatial interactions within and between species during daily foraging movement has been recognized (Harris et al. 2020; Schirmer et al. 2019; Schirmer et al. 2020; Spiegel et al. 2015). For example, in bank voles (*Myodes glareolus*) among-individual differences in boldness correlated with individual differences in movement patterns, home range formation, and spatial interactions (Schirmer et al. 2019). Moreover, along a shy-bold continuum for two species of

small rodents, shyer individuals had smaller home ranges and interacted more with competitors than bolder individuals (Schirmer et al. 2020). Whether and how covariation of BTs and foraging movement have consequences for reproduction and mortality at the individual level and also modify structure and dynamics of communities and ecosystems remains largely unstudied (Shaw 2020). Despite innovations in tracking devices (Kays et al. 2015; Wilmers et al. 2015) and individual-based modeling of communities (Grimm and Berger 2016) and movement behavior (Campos-Candela et al. 2019; Spiegel et al. 2017), there still remains a gap between population-level coexistence theory and individual-level movement ecology (Jeltsch et al. 2013; Schlägel et al. 2020).

Studies that contribute to closing this gap should explicitly include landscape features because of the dynamic feedbacks between the spatial distribution of resources and movement of foraging individuals. Moreover, since landscapes are rapidly changing due to anthropogenic effects, we need to gain a mechanistic rather than a correlative understanding (Radchuk et al. 2019a) of how movement patterns may be altered due to environmental change (Tucker et al. 2018), and how intraspecific variation in movement behavior ultimately affects the community structure and dynamics.

Tracking the movements of several species in ecological communities is logistically challenging and became possible only recently with technological advancements for a limited set of species (Baktoft et al. 2015; Krause et al. 2013; Toledo et al. 2014). Individual-based models of movement on a community level provide a powerful *in silico* approach to complement costly and demanding empirical work by contrasting hypothetical scenarios and thereby generating specific testable predictions. In our study, we analyze the effect of among-individual differences in foraging movement behavior (hereafter referred to as intraspecific trait variation, ITV) on between-species coexistence which are characterized by different BTs along the slow-fast continuum. It is not our intention to explore the emergence nor the maintenance of ITV itself in an eco-evolutionary context. Instead, based on empirical studies (Harris et al. 2020; Schirmer et al. 2019; Schirmer et al. 2020; Spiegel et al. 2015), we assume that among-individual differences in movement behavior are an integral characteristic of populations. As a fitness proxy, we focus on foraging efficiency because it ultimately ought to affect reproduction and survival.

On the intra-generational level, we analyze whether ITV in movement behavior reduces differences in foraging efficiency between species, i.e. species-level competitive abilities, and, thus, acts as an equalizing mechanism for species coexistence. Furthermore, we study how foraging efficiency of different BTs is mediated by different kinds of resource distributions.

On the inter-generational level, we analyze whether and how these mechanisms

induced by ITV found on the intra-generational persist by affecting coexistence. Since the equilibrium coexistence, focused on in modern coexistence theory, is difficult to model and an unlikely scenario for natural systems, we quantified species coexistence using a novel approach, coviability analysis (Jeltsch et al. 2019). This approach allows to quantify degrees of temporary coexistence by adapting metrics originating from population viability analysis (Grimm and Wissel 2004) to the community level. Here, we explore whether the effect of ITV found on the intra-generational level affects coviability expressed by the mean time until one species went extinct. We interpreted a higher mean time until one species went extinct as higher coviability and reduced interspecific differences in competitive ability.

Based on the “personality-dependent spatial ecology” framework (Spiegel et al. 2017) and a holistic view of BTs with the two aspects of average behavioral expression and responsiveness (Dingemanse et al. 2010), we implemented BTs on a slow-fast continuum (Réale et al. 2010). In our model, individuals differed in their tendencies to maintain their main movement directions or to turn towards memorized locations where they had previously found resources, with the assumption that those resources would have recovered from past consumption. We assumed that, in a given environmental context, BTs differ along a continuum from shy, responsive, and thorough explorers (slow) to bold, unresponsive, and superficial explorers (fast). In our model, fast individuals rather persist in their main movement direction leading to a more explorative behavior, whereas slow individuals are more responsive to memory and are thereby more restricted to familiar locations.

Specifically, we address the questions (Q1) how behavioral types differ in foraging efficiency under different environmental conditions, (Q2) if and how ITV mediates an equalizing mechanism by reducing interspecific differences in competitive ability, and (Q3) how this mechanism affects temporary species coexistence (coviability analysis) on the inter-generational level.

2.2 Material and methods

We implemented the model in NetLogo 6.1 (Wilensky 1999). The program and a detailed model description, which follows the ODD (Overview, Design concept, Details) protocol for describing individual-based models (Grimm et al. 2006; Grimm et al. 2020; Railsback and Grimm 2019), are available at the Comses.net Models library and in the supplementary materials (A2, A3). Here, we first provide a summary of the basic features and processes of the model and of the basic principles underlying our model. The ODD-specific terms in italics refer to those used in the full ODD protocol.

2.2.1 Model structure

The purpose of our model was to explore the impact of variation in movement features resulting from BTs on foraging in a community of species. The model was not designed to mimic specific species but was motivated by experiments with small, ground-dwelling rodents (Schirmer et al. 2019; Schirmer et al. 2020). Accordingly, we linked the model to observed patterns of movement metrics. The model comprises two types of entities: moving animals and square spatial units (patches). Animals are characterized by a set of state variables of which the most important are their continuous spatial coordinates, their memory of resource patches, the number of resources they gathered, and the parameter α . The latter defines the BT of an individual. The species are defined by different mean values of α . The global parameter ITV is the variation around this species-specific mean and is equal for all species. The key variables of movement that covary with BT, i.e. are mediated by α , are the direction of movement and the persistence of direction (PoD).

We focus on consequences of ITV on foraging efficiency within one foraging season analyzing ecological dynamics. We refrain from including evolutionary dynamics due to the added complexity which would obscure the underlying ecological mechanisms we are focusing on. For the coviability analysis we extrapolate the intra-generation ecological mechanisms to population dynamics, using the simplifying assumption that ITV remains constant (A3 for further details).

The spatial units are characterized by, in addition to their spatial coordinates, the variables fertile, which determines whether or not that spatial unit can grow resources, and resource, which is either 0 or 1. The spatial extent of the simulated toroidal landscape is 250 x 250 units. The size of the spatial units and model world were chosen to allow for the emergence of home ranges. The time steps are defined by the time an animal needs to move the distance defined by the side length of the spatial units, i.e., they move in discrete steps.

Upon initialization, the spatial distribution of the fertile spatial units is defined by the parameters resource cover (proportion of spatial units with fertile = 1) and patchiness (Table 2.1). Patchiness defines the initial proportion of fertile spatial units, which are distributed at random, and then the remaining proportion is distributed adjacent to the existing spatial units until the proportion of fertile patches is equal to resource cover. At high patchiness, the proportion of randomly distributed fertile spatial units is small, and the landscape consists of many large clumps of fertile patches. At low patchiness, most fertile spatial units are distributed randomly and, hence, independently result in many small clumps. In some scenarios, we contrast different levels of patchiness. In these scenarios, we refer to resource distributions with high patchiness as patchy and with low patchiness as random.

Table 2.1: Model parameters chosen for the Latin hypercube sampling (LHS) to link the model data from field experiments. These parameters determine the behavioral types (BTs) and landscape configurations (resource distribution) (a table with all model parameters is in the ODD model description, A3).

State variable	Entity	Range	Description
resource-density	patch	[0,*]	Amount of resources per patch
harvest-rate	patch	[0,**]	Amount of resources extractable per time step
responsiveness	animal]0; 2]	Trait; probability of inter-patch movement based on perceived-current-mean-hr minus current-hr
current-hr	animal	[0,**]	Harvest-rate of local patch
perceived-current-mean-hr	animal	[0,**]	Mean harvest-rate of neighbouring patches (Moore neighbourhood, i.e. eight neighbours)
reproductive investment threshold	animal	[0; 2]	Trait; determines the threshold above which resources are allocated from soma to r-buffer
soma	animal	[0;	Resources available for allocation to maintenance and r-buffer
r-buffer	animal	[0;]	Resources allocated to reproduction. If ≥ 50 (default level), the animal reproduces

Animals are added at random locations, with equal numbers of individuals per species. The distribution of the α -levels within the community is characterized by the number of species and the parameter ITV, which is the one-sided width of a uniform distribution with a species-specific mean α -level (Table 2.1). We chose a uniform distribution, as non-truncated distributions would lead to edge effects and as a uniform distribution maximizes the contrast between different levels of ITV and eases the interpretation compared to other options such as a truncated normal distribution. The parameter ITV is set globally and thus the same for all species.

2.2.2 Basic principles

Following the movement ecology paradigm (Nathan et al. 2008), we simulated the individual movement paths as the outcome of the navigation capacity as well as the internal (decision-making) and external (environmental gradient) states with a fixed locomotory capacity. In our case, we extended the paradigm to establish a continuum of BTs by resorting to two well-established concepts of movement and animal behavior.

First, we applied a modified version of the memory-based movement algorithm that was created by Van Moorter et al. (2009) to establish dynamic navigation based on external factors (resources) that lead to the emergence of home ranges. Such emergence is considered to be a fundamental design concept (Grimm et al. 2010) for simulating realistic movement behaviors (Börger et al. 2008). Animals memorize patches if they provide resources, and at each step, animals evaluate the utility

of the patches. Utility reflects the perceived likelihood that a patch may again provide resources. Fertile patches with no resources grow stochastically with a chance of 1 %, so the chance that a patch provides resources again increases over time and so does the perceived utility of a patch. However, utility decreases at a certain point, which reflects the increased likelihood that a competing individual has exploited the recovered unit (A3 for details). The perceived utility of one patch determines the length of the vector towards this patch and all these individual vectors determine the attraction vector.

Every time step, animals move by the side length of a spatial unit towards the movement direction, which is a continuous coordinate determined by the attraction vector. An animals' attraction vector is determined by the memory of previously visited resources. In our model, the degree to which an animal persists in its current direction relative to the attraction vector towards the memorized patches is the state variable persistence of direction (PoD). The new direction modulated by the PoD is randomized by sampling from the von Mises distribution. If the PoD were at a maximum, the movement would be a correlated random walk. The higher the PoD is, the more an animal tends to explore new, unknown areas instead of returning to the known locations that have provided resources previously.

Second, we coupled the memory-based movement with the behavioral reaction norms (BRN; Dingemans et al. 2010) to integrate the navigation capacity and the internal state of the animal based on the original concepts of Spiegel et al. (2017). The BRN formalizes the average behavioral expression and responsiveness of a particular BT as a relationship between the phenotypic behavior and an environmental gradient (Dingemans et al. 2010). In our model, PoD represents the phenotypic behavior, while the memory feedback represents the environmental gradient and is the length of the attraction vector towards the memorized patches, which results from their utility and location (Van Moorter et al. 2009). We assumed a linear relationship between PoD and memory feedback, which is defined by α and a maximum PoD at zero memory feedback. Here, α determines both the average behavioral expression and the responsiveness and, thereby, the BT (Fig. 2.1).

This dual role of α simplifies the subsequent analyses of the model outputs and accounts for existing evidence that slow BTs (*sensu* Réale et al. 2010) are correlated with a stronger degree of responsiveness to environmental gradients (Mazza et al. 2018; Natarajan et al. 2009; Spiegel et al. 2015). In our study, a certain α -level thus determined a BT along the slow-fast continuum. Higher α -levels referred to shy, more responsive, and more thorough explorers at the slow end of the slow-fast continuum and vice versa. We generalized that BT was a trait and, hence, the intraspecific variation in α -levels corresponded to ITV.

The integration of memory-based movements with BRN allows for realistic,

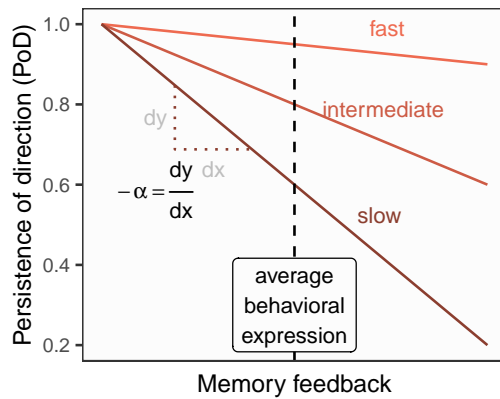


Figure 2.1: The behavioral reaction norm (BRN) is defined as the relationship between the phenotypic behavior (here: persistence of direction, PoD) and an environmental gradient (here: memory feedback). In the model, this BRN is modulated by its slope, the parameter α , which defines a behavior type (BT). The three visualized BTs are part of a slow-fast continuum with shy, thorough explorers at the slow end, where PoD varies more strongly with varying memory feedback, implying high responsiveness. At the fast end, the bold and superficial explorers have the opposite trend: the PoD is barely affected by the memory feedback and remains at a high level, approaching a correlated random walk.

adaptive home ranging behaviors as individuals can compensate for a lack of memorized patches by increasing their PoD and potentially finding new patches. Conversely, it is to be expected that individuals that memorize many high-utility patches would rather not explore unknown areas due to the greater risk for resource loss (Wolf et al. 2007). As a result, the home ranges were larger in landscapes with lower resource cover, which emerged from the adaptive mechanisms in our memory-based movement model rather than being imposed by fixed rules (see Fig. A1.1 for a demonstration).

2.2.3 Model processes and scheduling

In each time step, the entities of the model performed processes according to the submodels, which were scheduled in the following order (Fig. 2.2). First, animals determine the attraction vector towards memorized patches which also defined the memory feedback. Based on their BT and the memory feedback animals determine the PoD and then they move accordingly with some stochasticity. At the new patch, the animals check for resources; if available, they exploit them completely and memorize that patch. The exploited resources fully recover with a probability of one percent at the end of each time step.

If population dynamics are enabled, additional submodels regulate energy costs for reproduction and maintenance that are subtracted from the total amount of accumulated resources. An animal dies if it has no more resources. The likelihood to start breeding depends on the amount of available resources. If an animal is breeding, energy costs increase linearly over time. If the final breeding stage is

reached, an animal creates offspring. The offspring samples the α -level from the species-specific uniform distribution.

For the intra-generational analysis, after a spin-up phase of 1,000 time steps 50 locations of the animals were sampled at equal intervals to calculate home range metrics and the foraging efficiencies of the animals (resources exploited per time step) were recorded. In simulations with population dynamics, the time until one species goes extinct was recorded.

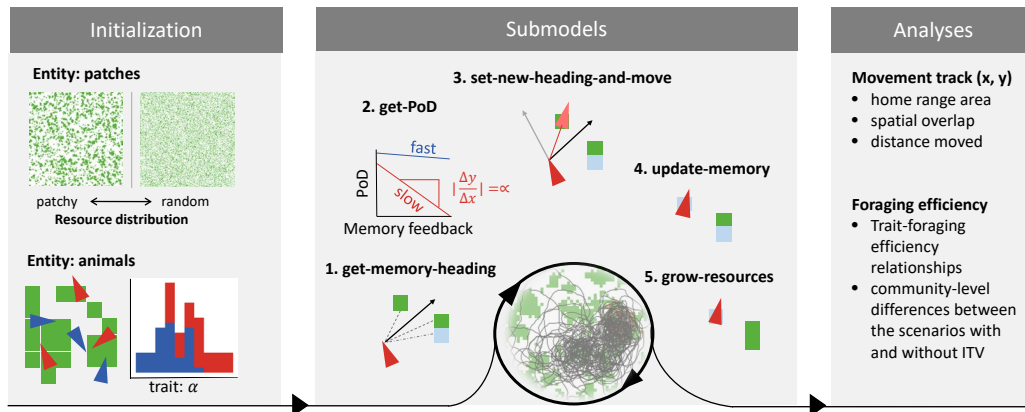


Figure 2.2: Model overview with terminology that refers to the full ODD model description (A3). During initialization, the spatial units, which have resources and animals, are added to the landscape. The BT-composition (α) of the community is defined by the degree of ITV and the number of species and individuals. The schedule of the submodels for the animals (1-4) and patches (5) is described as follow. 1. The evaluation of the memorized patches (green = resource, blue = exploited) and the definition of a memory attraction vector (black arrow), 2. Determination of the persistence of direction (PoD) by the memory feedback (length of the memory attraction vector) and the α -level. 3. Movement in a new direction that was defined by PoD as the degree to which an animal turns to the memory attraction vector. 4. Exploitation of the encountered resource – if any– and the updating and aging of the memory. 5. Growth of the exploited resources with a respective probability of 1 %. The simulation ends after 2,000 time steps, and the output is returned for analysis. If population dynamics are enabled, the simulation ends after 200,000 time steps and energetic costs for maintenance and breeding are imposed via additional submodels (A3 for further details).

2.2.4 Link to data

To ensure that our model reflected a realistic relationship between the movement and BTs, we evaluated the model output with data of BT-related movement metrics of free-ranging individuals of a ground-dwelling rodent species, the bank vole

(*Myodes glareolus*; Schirmer et al. 2019). In a behavioral study of bank voles, Mazza et al. (2018) found a correlation between responsiveness and mean behavioral expression, which we expressed with our configuration of the BRN via the parameter α . This consistency made the dataset well-suited for the following model evaluation.

The purpose of this evaluation was to identify values of key model parameters that lead to realistic movement patterns. We, therefore, used the observations of Schirmer et al. (2019) to calibrate the model. The model was run for a large number of possible parameter combinations and only those combinations were kept which matched the observations. Specifically, we generated 1,000 parameter sets of three parameters that specified the BT composition of the population (ITV, n-individuals, species-1-mean; Fig. 2.2, Table 2.1) and two landscape features (patchiness, resource-cover; Fig. 2.2, Table 2.1). We used Latin hypercube sampling (LHS, Stocki 2005), which is a widely used approach for sub-sampling parameter space in a randomized but systematic way so that all possible interactions between parameters are likely to be captured. With the simulation output of each parameter set, we calculated, in correspondence with the analyses of Schirmer et al. (2019), the kernel areas, kernel overlaps (Calenge 2019; Fieberg and Kochanny 2005; Worton 1989) and total distance moved.

To analyze the match with empirical observations, we scaled the α -levels of each parameter set ($[0, 1]$) and empirically observed the boldness scores ($[-10, 5]$) at the same interval ($[-1, 1]$). We fitted linear models to the simulated and empirical data. We scaled the home range metrics from the absolute to the relative sizes by dividing them by their respective maximum values (see Fig. A1.3). Then, we determined the goodness-of-fit with the normalized root mean squared error (NRMSE), which we calculated for each pair of empirical and simulated movement metrics. For each parameter set, we calculated the sum of the NRMSE-values of these pairs (pooled NRMSE). The pooled NRMSE measured the goodness-of-fit of a parameter set. We chose the quartile of the parameter sets with the lowest pooled NRMSE to determine the parameter distributions and to evaluate the fit of the simulated to observed data. We selected the mean of the parameter distribution of ITV within this top quartile as an estimate of a realistic level of ITV to contrast it with an ITV-level of 0 (no ITV). We did not fix the other parameters as they either had no effect or were changed in the subsequent simulations.

2.2.5 Simulation experiments

Effects of the landscape structure on the foraging efficiency of behavioral types

To test the effect of landscape structure on the foraging efficiency of the different BTs and to determine which BTs are at optimum for a given environment (Q1),

we ran simulations for landscapes with three different levels of patchiness (10, 70, 90) with 40 repetitions (120 repetitions total). As the resource distribution is also modulated by resource cover, we set resource cover to a fixed value (30 %) to avoid effects of this interdependency. In all simulations, one population of 750 animals (results for 375 animals in Fig. Fig. A1.5), each with a α -level sampled from a uniform distribution ranging between 0 and 1, was generated to describe the relationship between the foraging efficiency and the BT via generalized additive models (GAMs). We referred to this relationship as the trait-foraging efficiency relationship (TFE relationship). To explore the trade-offs that constituted the TFE relationship, we analyzed the relationships between BT and the number of resources exploited per clump and the number of different clumps utilized, which together describe the change from superficial to thorough exploration along the slow-fast continuum.

Effect of ITV on differences in foraging efficiency

To analyze the impact of the ITV in the mean BTs on interspecific differences in foraging efficiency, i.e. competitive ability (Q2), we ran simulations with two species. We compared the scenarios with and without ITV. We assigned combinations of mean α -levels for the two species using a 15 x 15 matrix of equidistant values within the range of 0.25 to 0.75, repeating each combination 5 times. The mean α -levels were restricted to this range to avoid edge effects in the ITV scenarios. The degree of ITV determined via calibration with field data was the same for both species and all α -levels. We then compared the foraging efficiency for all combinations of α -levels with and without ITV. To maximize the contrast between BTs, we chose the environmental setting where, based on the previous simulations related to Q1, the TFE relationship indicated the highest differences in foraging efficiency between the BTs which occurred in a scenario with a community of 750 animals in a patchy landscape with a resource cover of 30% (results for random and intermediate resource distribution in Fig. A1.6, Fig. A1.7).

For each combination of α -levels of the 15 x 15 matrix, we calculated the proportion of the resources foraged by a species compared to the total amount of foraged resources. We named this proportion the resource ratio. If the ratio was greater than 50%, we considered the focal species to be superior to its competing species in terms of competitive ability, and if it was smaller than 50%, it was considered inferior to the competing species. By contrasting the ITV scenario and the scenario without ITV, we analyzed how these interspecific differences in competitive abilities were affected by ITV.

Coviability analysis

To test whether mechanisms and patterns found on the intra-generational level persisted if population dynamics were included (Q3), we applied an analysis based on the recently proposed coviability analysis (Jeltsch et al. 2019). We generated 81 combinations of species-specific mean α -levels in a 9 x 9 matrix of equidistant values within the range of 0.25 and 0.75 and analyzed the number of time steps until one of the two species goes extinct. We chose a patchy landscape and a resource cover of 15% and initialized it with 200 individuals for each species. We repeated each combination 5 times with ITV and without ITV, respectively. The degree of ITV was, as in the previous simulations, based on the link to the empirical data. We calculated the mean time to extinction with and without ITV for each combination and analyzed the change in this metric due to ITV. The maximum simulation time was 200,000 time steps.

2.3 Results

2.3.1 Link to data

The linear models fitted to the simulated data ($n = 250$) were mostly within the 95% confidence interval of the linear model of the observed data (Fig. 2.3). For the total distance moved, the linear models of the simulations showed a higher slope than was present in the observed data. Home range overlaps (not scaled) were captured well in terms of proportions, but in some cases the slope was reversed. The parameterization of the parameter ITV returned a value of 0.13 (Fig. A1.8). In general, the model showed a sufficient fit to the observed BT-related movement properties to allow for further inference.

2.3.2 Effects of landscape structure on foraging efficiency of behavioral types (Q1)

The slow-fast continuum of BTs (Fig. 2.1) led to the emergence of corresponding movement patterns (Fig. 2.4, A). We found a hump-shaped relationship between foraging efficiency and BT (TFE relationship; Fig. 2.4, B). The hump resulted from a trade-off between exploiting a few resource clumps thoroughly on the slow end or exploring many clumps superficially on the fast end of the behavioral continuum (Fig. 2.4, B). Slow individuals foraged more resources from single clumps but may have missed available resources in other clumps. As a result, the optimal BT depended on whether resources were distributed in many small clumps (random) or a few large clumps (patchy).

We observed that slow individuals, which relied more on memory, performed

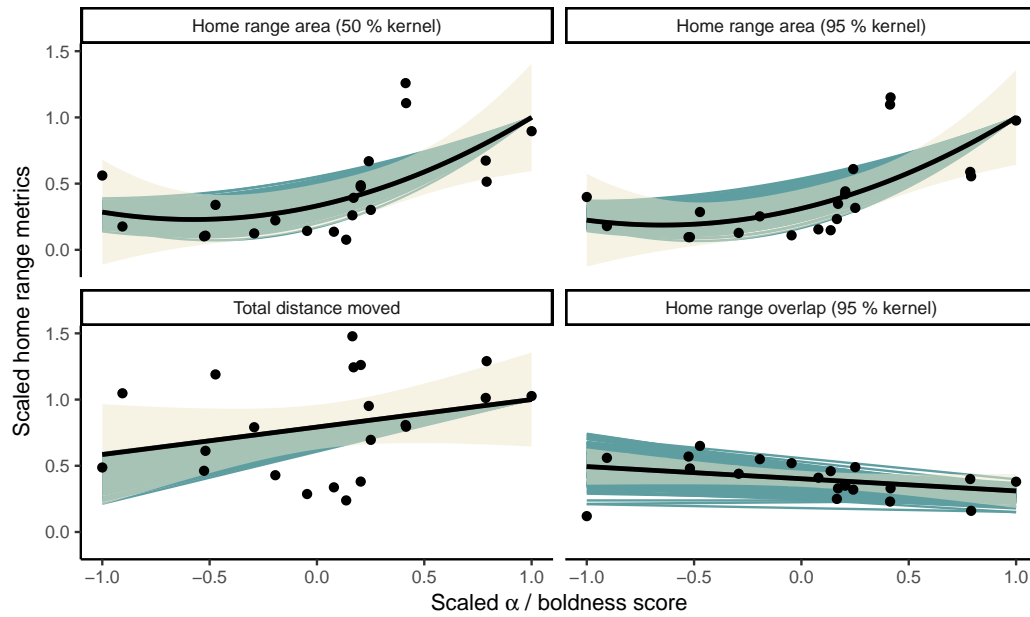


Figure 2.3: Fit of the simulated movement metrics to the empirical data of the free-ranging bank vole individuals (*Myodes glareolus*, Schirmer et al. 2019). The top quartile of simulated parameter sets was selected by using a pooled NRMSE. The fits of the simulated data from the different parameter sets (blue-green) are mostly within the 95 % confidence interval (transparent beige) of the model representing the empirical data (black line and black dots).

better in patchy landscapes. In contrast, in landscapes with a random resource distribution, the bold, explorative behavior of the faster individuals paid off. The finding that slow individuals performed better in patchy landscapes and vice versa for fast individuals held in general. However, the TFE relationships not only depended on resource distribution but also population density. With a reduced number of competing individuals, faster individuals gained an advantage in all tested landscapes (Fig. A1.5).

2.3.3 Effect of ITV on foraging differences between species (Q2)

We interpreted the proportion of resources that were foraged by a species in a two-species community (resource ratio; Fig. 2.5, A) as its competitive ability. Whether a species was superior (resource ratio > 50%) or inferior (resource ratio < 50%) in competitive ability was related to the respective TFE relationship (Fig. 2.4, B). If the mean BT of the focal species was closer to the optimum of the TFE relationship than the mean BT of the competing species, it was superior and vice versa (Fig. 2.5, A). The interspecific differences in the resource ratio (Fig. 2.5, B) were highest if one species was at the fast end of the continuum, which was the least efficient BT in the specified landscape and community structure, while the mean BT of the other species was at the optimum. If both species shared the same trait or, more generally, if their foraging efficiency was at similar levels, as shown by the TFE relationship, the species did not differ in the resource ratio. When comparing percentiles, differences in resource ratio reflect an overall higher foraging efficiency and not just a higher foraging efficiency of some individuals of one species compared to another (Fig. A1.11).

With ITV, the interspecific differences in the resource ratio were reduced, especially if the differences in the scenario without ITV were high (Fig. 2.5, C). If the mean BT of the inferior species was faster (“too fast”) than that of the superior species, the equalization was most pronounced. The slope of the linear model between the interspecific differences in the resource ratio without ITV and the changes of these differences by ITV showed that ITV equalized approximately 15% of the interspecific differences that occurred without ITV (Fig. 2.5, D).

The magnitude of the equalizing mechanism, as mentioned, partly depended on whether the inferior species was “too fast” or “too slow” (Fig. 2.5, C), making the mechanism anisotropic. In a scenario with a random resource distribution (Fig. A1.6), this anisotropy was even more pronounced, and the magnitude of the equalizing mechanism ranged from 5 to 35%.

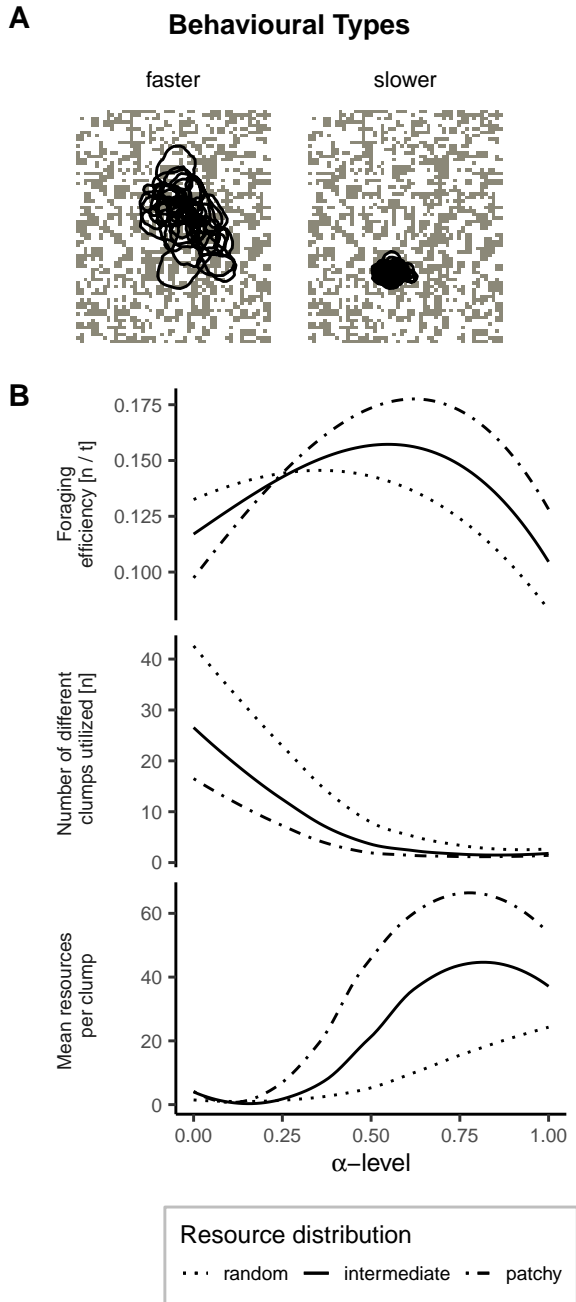


Figure 2.4: Effects of the landscape structure and behavioral types (BT) on the foraging efficiency and resource utilization. A) Examples of the movement patterns that occur at the different ends of the fast-slow continuum of behavioral types that are associated with different levels of boldness, exploratory behavior, and responsiveness. B) The foraging-trait relationship between the foraging efficiency and BT (top), the relationship between BT and the number of different clumps utilized by an individual (middle), and the mean number of resources foraged by the individual per clump (bottom) were fitted for each different resource distribution. We defined a clump as an aggregation of patches (spatial units) that may provide resources that is surrounded by spatial units that never provide resources.

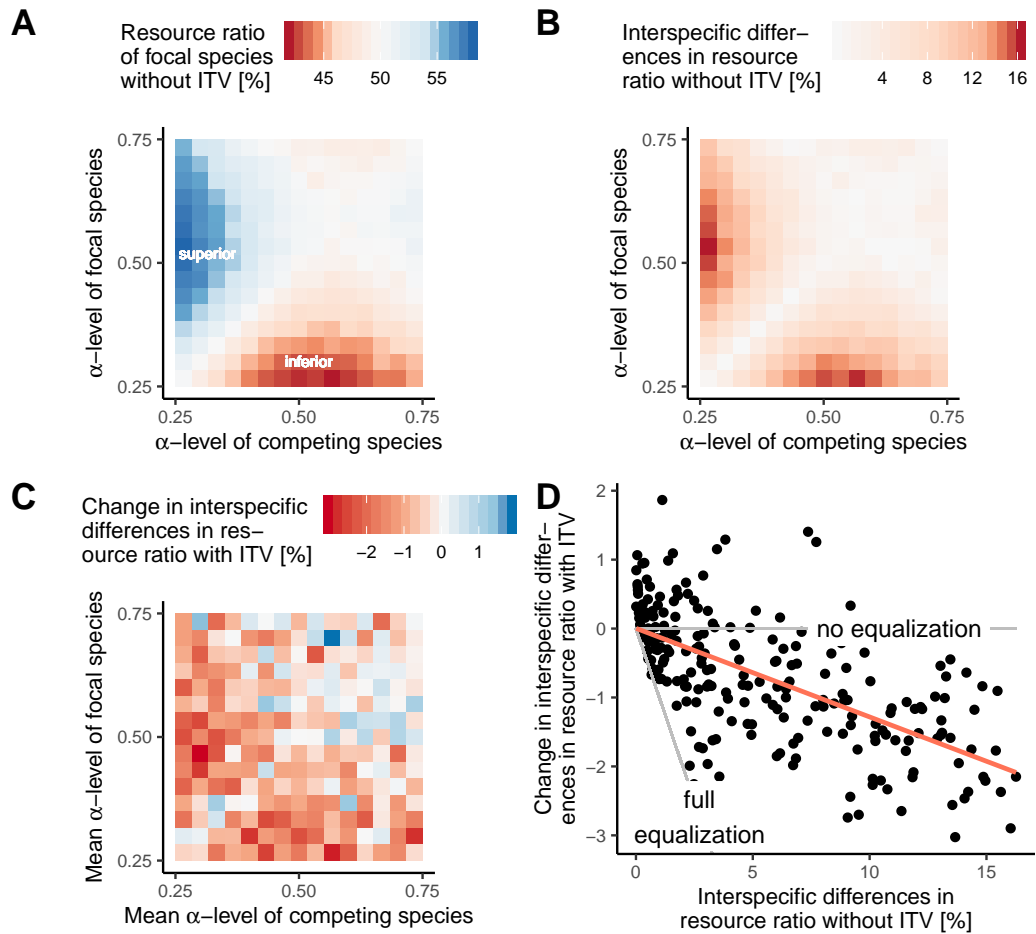


Figure 2.5: Effects of ITV on the differences in foraging efficiency. A) Resource ratio of the focal species depending on the mean BT and the mean BT of a competing species in a scenario without ITV. Depending on the combination of BTs, the focal species is superior (blue), equal (white), or inferior (red) to the competing species. B) Interspecific differences in the resource ratio without ITV. The differences are highest if one species is at the fast end of the continuum and the other is at the optimal level for a specific ecosystem. C) Change in the interspecific differences in the resource ratio due to ITV. BT combinations with high interspecific differences (shown in B) lead to the highest equalization of the differences in foraging efficiency. D) Changes in the interspecific differences in resource ratio as a result of ITV (shown in C) vs. interspecific differences in the resource ratio without ITV (shown in B). The slope of the linear model reflects the strength of the equalizing mechanism.

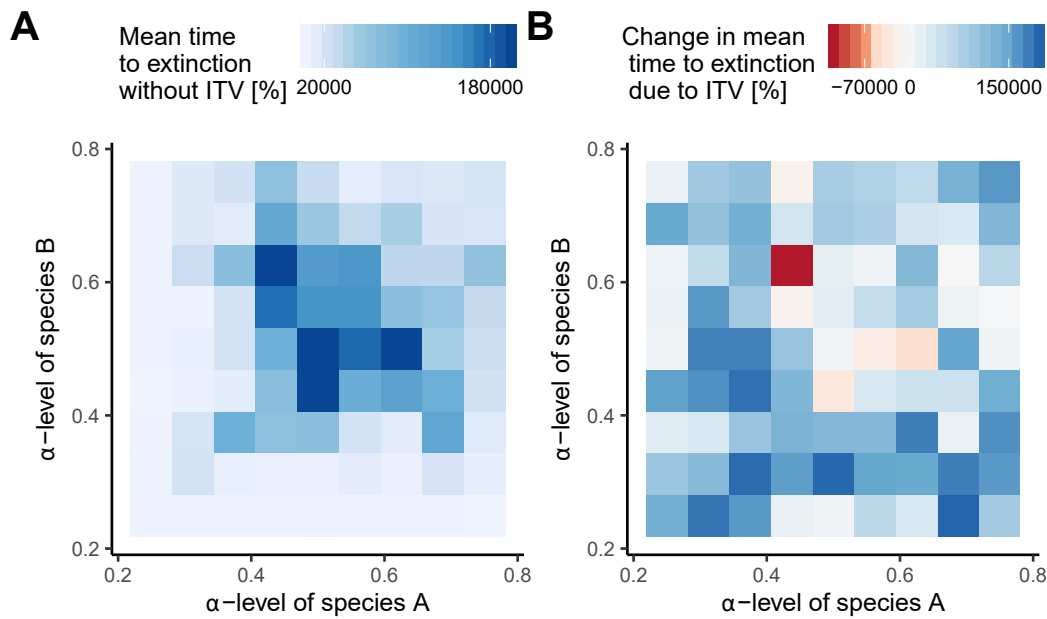


Figure 2.6: Coviability analysis to estimate the effects of ITV in scenarios with population dynamics. A) Distribution of changes in the mean time to extinction without ITV of 9 by 9 combinations of species-specific mean BTs. The maximum simulation time was 200,000 time steps. B) The change in the mean time until one of the two species went extinct from a scenario without ITV to a scenario with ITV.

2.3.4 Coviability analysis (Q3)

We checked how intra-generational mechanisms extend to population dynamics by applying a coviability analysis. We observed highest levels of mean time to extinction of one of the two species, i.e. coviability, if both species shared an intermediate BT (Fig. 2.6, A). Due to ITV, coviability increased especially for communities with one or both species leaning more towards one of the ends of the slow-fast continuum. Thus, ITV increased the diversity of trait combinations that were associated with a higher coviability (Fig. 2.6, B). However, we observe that this effect decreases with increasing mean time to extinction without ITV and eventually becomes negative. Moreover, stochasticity blurs the overall trends in the effect of ITV, which is a common outcome of viability analyses which can be strongly affected by rare but extremely long times to extinction (Grimm and Wissel 2004).

2.4 Discussion

We integrated behavioral reaction norms and memory-based movements in a generic individual-based model to analyze the effects of ITV in movement behavior on the coexistence between species. Based on the alignment of simulated movements with observed relationships between BT and movement metrics, we analyzed the consequences of ITV in movement behavior on interspecific differences in foraging efficiency, which we interpret as differences in competitive ability. Competitive ability was determined by emergent trait-foraging efficiency (TFE) relationship specific for certain resource distributions (Q1). Our study demonstrates that ITV in movement behavior reduced differences in foraging efficiency by 5 to 35%, with 15% on average (Q2). The mechanism prolonged the coexistence of species, particularly in scenarios in which at least one species was maladapted to a given spatial distribution of resources. Therefore, ITV provided an equalizing mechanism that increased the likelihood of stable coexistence of species in communities or, at least, prolonged their temporal coexistence in most cases (Q3). In the following section, we connect our findings to existing studies and examine the general mechanism that drives community-level patterns by contrasting the effect of ITV at different BT-compositions on the equalizing mechanism. Moreover, we discuss how the dynamics reflected in the emergent TFE relationships may affect ecological consequences of BTs in the context of environmental fluctuation and global environmental change.

2.4.1 Foraging efficiency as a proxy for competitive ability

We found that ITV in movement behavior affects the ability to efficiently forage resources. Resource gain, in turn, affects an individual's ability to bear the costs for maintenance and reproduction in simulations with population dynamics. In our model, we focused solely on resource acquisition because it ultimately ought to be positively related to both components of fitness, survival, and reproduction. Certainly, ITV in movement behavior also modulates other ecological processes that affect fitness components, such as predation or energetic demands. Assumptions on the directionality between ITV in movement and fitness costs linked to these processes are less resolved empirically, however. For example, a recent meta-analysis showed that mortality may be lower for risk-taking individuals (Moiron et al. 2020) in contrast to earlier findings (Smith and Blumstein 2008). Similarly, costs of locomotion may be higher for faster individuals, but also memory and other cognitive processes involved in decision-making incur energetic demands (Fagan et al. 2013). To avoid imposing further trade-offs and for parsimony, we kept this generic modelling study simple. Nonetheless, we recognize that the effects of

predation and energetic costs of movement on competitive ability may be crucial and require further investigation.

2.4.2 Drivers of the relationship between foraging gain and behavioral types (Q1)

The central emergent element in our study was the TFE relationship. The hump-shaped relationship that emerged resulted from an inherent trade-off between superficial exploration of many clumps of resource patches and thorough exploration of a few clumps. Shy, responsive, and thorough explorers (slow BTs) performed better in patchy landscapes. In contrast, the bold, unresponsive individuals (fast BTs) had advantages in landscapes with random distributions of resources. These relationships, which were not imposed but emerged from the adaptive movement behaviors of the individuals, correspond with empirical evidence (Dehnhard et al. 2020) and theoretical work (Ritchie 1998).

Community properties also affected the TFE relationship. At lower population densities, the relationship shifted toward favoring faster individuals (Fig. A1.5). This pattern aligns with observations of seasonal variation in boldness at the population level of short-lived common voles (*Microtus arvalis*), which is highest in spring when the population densities are lowest (Eccard and Herde 2013). The shift in the TFE relationship suggests a selection of BTs along the fast-slow continuum in agreement with the density-dependent selection framework proposed by Wright et al. (2019), which generally assumes selection for faster individuals at lower population densities and vice versa. Based on the high level of correspondence with other studies, we synthesize that population density and resource distribution may both affect the selection of specific BTs along the slow-fast continuum in natural systems.

2.4.3 Intraspecific trait variation equalizes foraging efficiency between species (Q2, Q3)

We found that ITV reduced differences in foraging and, hence, competitive ability in most cases and thereby promotes species coexistence via an equalizing mechanism that is induced by the TFE relationships. The mechanism was observable on the intra-generational level and persisted in scenarios with population dynamics by increasing the mean time to extinction (coviability; Jeltsch et al. 2019). The coviability analysis revealed that only in situations with high mean time to extinction of one species, ITV had a negative effect, which can be explained by variation around the optimum of the TFE relationship specific for a certain resource distribution leading to negative returns.

Similar to our findings, Hart et al. (2016) conclude that the shape of the relationship between competitive ability and trait determined the effect of ITV on coexistence. However, they stated that this effect should decrease, not, as in our study, promote coexistence. The reason for these contrasting outcomes lies in the different shapes of the relationships. Hart et al. (2016) assumed a relationship that led to higher gains in competitive ability for the superior species than the inferior species. In our study, a hump-shaped relationship emerged from the inherent trade-off (Fig. 2.4, B) along the slow-fast continuum, with ITV leading to higher gains in foraging efficiency for the inferior species, which corresponded to an equalizing mechanism.

Interestingly, we observed that the equalizing mechanism was anisotropic as the magnitude of gains from ITV for “too slow” and “too fast” BTs could differ profoundly, which was related to an asymmetry in the TFE relationship. This asymmetry may amplify or level out the equalizing mechanism for certain combinations as is observable in the coviability analysis (Fig. 2.6, B). The magnitude of the equalizing mechanism due to ITV in a particular system can, hence, not easily be generalized as it is related to the underlying TFE relationship. Therefore, acquiring knowledge about the determinants of such relationships is of utmost importance for understanding how ITV affects coexistence. In our study, landscape structure, resource abundance, and population density were key determinants for the TFE relationship. Its hump shape persisted under all tested combinations of these determinants, as did the equalizing mechanism. Therefore, we generalize that as long as we observe hump-shaped TFE relationships, ITV should provide an equalizing mechanism for species coexistence that may vary in magnitude, however.

2.4.4 Does intraspecific trait variation decrease niche differences among species?

From the dependence of the TFE relationship on the resource distribution we infer that if environmental contexts differ spatially, the TFE relationship will differ accordingly across space, leading to spatial niches for specific BTs. Spatially structured ITV fosters coexistence for immobile organisms if the trait response to an environmental context differs between species (Banitz 2019). Similarly, empirical evidence suggests that interspecific differences in behavior facilitate coexistence among mobile species (Morris et al. 2019). ITV around a mean BT, however, increases the likelihood that individuals of two species will respond similarly. Therefore, ITV could increase niche overlap and compromise coexistence (Hart et al. 2016). We did not explicitly analyze the effect of ITV on niche differences, and hence, its potential to act as a stabilizing mechanism requires further investigation.

2.4.5 Evolutionary component of intraspecific trait variation and its effect on coexistence

As a first step our model's purpose was to mechanistically analyze ecological consequences of a given level of ITV on interspecific differences in competitive ability. Therefore, for simplicity we assumed a constant degree of ITV. However, a fully-fledged analysis of the effect of ITV on species coexistence will ultimately have to include mechanisms maintaining intra-specific variation in ITV (i.e., intra-specific variation of fitness) and, hence, needs to test how temporal fluctuations in ITV affect species coexistence.

For example, in an inter-generational, i.e. evolutionary, context some BTs will be better foragers in certain environments than other conspecifics leading to higher reproductive rates of these individuals. If BTs are assumed to be heritable and the optimum BT remains constant throughout the simulation, only individuals around the optimal BT could prevail in long-term and ITV would deteriorate. In such scenarios, the initial ITV and the related equalizing mechanism may foster adaptation or prolong coexistence. It might, however, also be unrealistic to assume that a certain BT remains optimal over time, as environments, both biotic and abiotic, are changing. The fact that ITV in BT has been widely observed suggests that strong mechanisms exist that keep ITV within a certain range. Future studies should thus include heritable BTs and explore the maintenance of ITV in constant and changing environments.

2.4.6 Relationship between environmental change and intraspecific trait variation

Since ITV in movement behavior can affect both the stabilizing and equalizing mechanisms, it links movement ecology and biodiversity research (Jeltsch et al. 2013; Schlägel et al. 2020). The strong influence of landscape structure on the TFE relationship suggests a vital role of landscape dynamics and land-use change on the eco-evolutionary dynamics of BTs and, hence, ITV. In addition to fluctuations in population density (Wright et al. 2019), the persistence of ITV could be induced by fluctuations in the environment leading to varying selection pressures that may temporally favor slower or faster organisms.

Furthermore, TFE relationships could help to explain the observed shifts in movement activity that are likely to be associated with changes in the resource distribution (Jones et al. 2014; Miranda et al. 2013; Prange et al. 2004; Tucker et al. 2018). If there was a directed change in the resource distribution from random to patchy, we would expect a shift from faster to slower BTs and a reduction in movement activity, which is observable on different scales. Such inferences have to be

made with great caution, though, as anthropogenic disturbances may alter patterns of resource distributions that benefit faster BTs (O'Farrell et al. 2019). Nonetheless, the mere possibility of changing environments altering the composition of BTs and related movement behavior should gain more attention in studies of global change. Many ecosystem functions, such as seed dispersal, trophic interactions, and disease vectors, are tightly linked with movement properties, and these movement properties, again, covary with BTs.

2.5 Conclusions

Our study suggests that ITV in movement behavior promotes coexistence via an equalizing mechanism that mitigates 5 to 35% of the differences in foraging efficiency, i.e. competitive ability, between species that would be present in a scenario without ITV. The emerging relationship between foraging efficiency and behavior type, which we named trait foraging efficiency (TFE) relationship, induced this mechanism. The direction and magnitude of the effect of ITV on spatial niche differences and thereby the stabilizing mechanisms, however, needs further clarification. We observed an equalizing mechanism in foraging efficiency in generic populations. This mechanism also persisted as the coviability increased due to ITV in most cases. Based on these insights, reducing the level of abstraction and studying the effect of ITV on coexistence of certain species in future empirical or modelling work appears promising.

Our results highlighted that the shape and dynamics of the TFE relationship within each species vary with landscape structure and community composition. Therefore, predicting the influence of ITV on species coexistence requires an intimate knowledge of the relationships between the focal trait and the competitive ability, in general, in different environmental settings. The drivers that underlie such relationships could be identified empirically by assessing parameters such as foraging or reproduction for different behavioral types in manipulated environments. It is worthwhile to investigate these general drivers as they have a direct impact on how ITV affects community dynamics and coexistence.

However, predicting such relationships and their dynamics is challenging as it requires clarification of the persistence of BTs and ITV in general. Heritability, learning, and stochasticity, which control persistence, are not well understood regarding movement ecology (Sutherland et al. 2013). To address this knowledge gap, it is challenging but also highly necessary to improve the integration of in silico modelling to in vivo experiments.

2.6 Additional information

Acknowledgements

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Conflicts of interest

There is no conflict of interest.

Statement of Authorship

M performed the modelling work and analyzed the output data. The concept and design of the model was revised by all authors. AM wrote the first draft, and all authors contributed substantially to revisions.

Data accessibility

The model will be made publicly available on COMSES.net and is supported by an extensive overview, design and details (ODD) protocol. The simulation output will be made available on request. The scripts for analysis are available on GitHub.

Supplementary material

A1: Additional figures

A2: Model

A3: Model documentation

Chapter 3

Fluctuations in density-dependent selection drive the evolution of a pace-of-life-syndrome between and within populations

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Abstract

The pace-of-life-syndrome (POLS) hypothesis posits that suites of traits are correlated along a slow-fast continuum due to life-history trade-offs. Despite widespread adoption, environmental conditions driving the emergence of POLS remain unclear. A recently proposed conceptual framework of POLS suggests that a slow-fast continuum should align to fluctuations in density-dependent selection. We tested three key predictions made by this framework with an eco-evolutionary agent-based population model. Selection acted on responsiveness (behavioural trait) to inter-patch resource differences and the reproductive investment threshold (life-history trait). Across environments with density fluctuations of different magnitudes, we observed the emergence of a common axis of trait covariation between and within populations, i.e. the evolution of a POLS. Slow-type (fast-type) populations with high (low) responsiveness and low (high) reproductive investment threshold were selected at high (low) population densities and less (more) intense and frequent density fluctuations. In support of the predictions, fast-type populations contained a higher degree of variation in traits and were associated with higher intrinsic reproductive rate (r_0) and higher sensitivity to intraspecific competition (γ), pointing to a universal trade-off. While our findings support that POLS aligns with density-dependent selection, we discuss possible mechanisms which may lead to alternative evolutionary pathways.

3.1 Introduction

Understanding the evolution of syndromes, i.e. pairs or suites of correlated traits, is a recurrent focus of organismal biology (Agrawal 2020). Syndromes may be proximately mediated by either genetic (pleiotropy), endocrine or developmental pathways and be expressed across different hierarchical levels (Sih et al. 2004). The pace-of-life syndrome (POLS) framework (Dammhahn et al. 2018; Réale et al. 2010), and analogous concepts in human biology (Del Giudice et al. 2015; Kaplan et al. 2000) propose a universal trade-off between current and future reproduction as the ultimate cause of the covariation between traits.

Early works identified reproduction trade-offs as a key to understanding life-history evolution (Fisher 1930; Williams 1966). The influential, yet also criticized, r- and K-selection theory (MacArthur and Wilson 1967; Pianka 1970) hypothesizes that population dynamics select for certain life-history strategies. The theory of r- and K-selection, but also other non-exclusive theories of life-history evolution, predict that life-history traits covary (Stearns 1977). This covariation has later been termed “slow-fast continuum” (Stearns 1983). The continuum ranges from longer-lived “slow types”, which mature and reproduce later, to shorter-lived “fast types”, which mature and reproduce earlier. Further conceptual developments integrated physiological traits with the slow-fast continuum, yet, mainly on an interspecific level (Ricklefs and Wikelski 2002). More recently, the study of animal personalities, i.e. consistent inter-individual behavioural differences, sparked questions of its integration with life-history theory (Biro and Stamps 2008; Wolf et al. 2007). For instance, consistently bolder behaviour may increase foraging efficiency yet increase predation risk (i.e. mortality), making it a more suitable strategy for early reproducing fast types (Fraser et al. 2001; Wolf et al. 2007). Based on these considerations and empirical evidence, the POLS hypothesis suggests that the slow-fast continuum should extend to the within-population level and include behavioural traits (Dammhahn et al. 2018; Réale et al. 2010). According to the POLS hypothesis, in addition to life-history and physiological traits, slow types are more responsive (i.e. reactive towards environmental cues; Wolf et al. 2007) and reduce current risks in favour of future reproduction whereas fast types are less responsive and bolder.

The connection between animal personality and life-history theory and its potential to modify ecological interactions and evolutionary processes (Sih et al. 2012; Wolf and Weissing 2012) made the POLS hypothesis a popular subject. Nonetheless, a decade since the POLS hypothesis has been proposed (Réale et al. 2010), empirical evidence supporting it remains limited and partly ambiguous (Dammhahn et al. 2018; Royauté et al. 2018). This ambiguity can be partially explained by the lack

of mechanistic theory that clearly identifies conditions under which POLS would emerge (Dammhahn et al. 2018; Mathot and Frankenhuis 2018). Understanding the emergence of POLS holds the promise to provide heuristic a priori predictions on the interdependency of suites of traits (Cote et al. 2010; Sih et al. 2012).

Only recently, a novel framework suggested that within populations POLS emerge due to fluctuations in population density (Wright et al. 2019). The fluctuating density-dependent selection POLS framework is based on recent expansions (Engen et al. 2013; Engen and Sæther 2017; Lande et al. 2009) of classical r- and K-selection theory (MacArthur and Wilson 1967; Pianka 1970) and empirical evidence (Sæther et al. 2016), which suggests that there is a fundamental trade-off between intrinsic reproductive rate (r_0 , density-independent) and the sensitivity to intraspecific competition (γ , density-dependent). For instance, fast individuals with large clutch sizes experienced stronger negative density-dependent effects than slow types (Sæther et al. 2016). According to Wright et al. (2019), this trade-off between r_0 and γ relates to a trade-off between early and late reproduction which should evoke a POL axis along a degree of fluctuating density dependence. Fluctuations in population density are ubiquitous due to recurrent (e.g., seasonal) or stochastic environmental variation; thus, density-dependent selection may pose a general mechanism for the emergence and persistence of POLS at the within- and between population level (Wright et al. 2019). Here, we test three key predictions of the framework.

First, according to the framework (Wright et al. 2019), low population densities which occur in more severely disturbed environments with associated elevated environmental mortality, should select for shorter reproduction cycles and, thus, favour fast types. Vice versa, slow types would be selected in more stable environments with population density closer to the carrying capacity. Short reproduction cycles of fast-type populations in combination with high environmental mortality would amplify fluctuations in population density. If density-dependent selection gives rise to a POLS, more frequent and more intense density fluctuations selecting for faster types would induce a higher degree of fluctuating selection along the major POL axis, as compared to the more stable conditions at which slow-types are selected. Thus, a second prediction by the framework (Wright et al. 2019) is that fast-type populations show a higher degree of variation in traits, i.e. along the POLS axis. Third, traits selected in slow types at higher (and more stable) population densities, should, in contrast to fast types, facilitate a reduced sensitivity to intraspecific competition (γ ; population density as a proxy for intraspecific competition) in exchange for lowered density-independent, intrinsic reproductive rate (r_0), i.e. there should be a trade-off between γ and r_0 .

So far, theoretical studies have only discussed this framework in the context

of life-history traits (Engen et al. 2020; Wright et al. 2020). Yet, in the context of POLS theory, i.e. explicitly regarding multiple traits not restricted to life-history and across hierarchical levels, also including the within-population level (Mathot and Frankenhuis 2018), the predictions of the framework remain to be tested. Approaching these predictions through empirical studies is cumbersome, as it requires long-term datasets of repeatedly measured life-history traits, behavioural phenotypes and population density. Although empirical and experimental studies are an essential step to test predictions of the density-dependence POLS framework, exploring its utility first by resorting to modelling appears plausible to inform subsequent experiments. Here, we present a spatially explicit agent-based model that integrates two heritable traits: 1) the responsiveness (as reactivity towards environmental cues sensu Wolf et al. 2008) to differences in resource extractability (harvest rates) in the landscape as a fundamental behavioural trait, which is testable in empirical studies ((Eccard et al. 2020; Oudman et al. 2018) and relates to multiple behavioural traits associated with the POLS (Wolf et al. 2008; Zwolak and Sih 2020), and 2) the reproductive investment threshold as a life-history trait representing capital breeding (Stephens et al. 2009). The reproductive investment threshold defines the number of resources an animal stores before allocating resources to reproduction. Our modelling approach allows for associated life-history traits (e.g. life span, number of offspring) and behavioural expressions such as movement rate to emerge from the animals' decision-making.

The heritable traits responsiveness and reproductive investment threshold are related to distinct processes of allocating time and resources. First, individuals allocate their time either to foraging at the current resource patch or to moving to a patch where they can gain resources at a higher harvest rate. Second, animals either allocate acquired resources to current reproduction or store resources to avoid starvation (life-history trait). These traits are reaction norms representing the relationship between decision-making (behavioural trait: moving/foraging; life-history trait: investing/saving resources) and both the external state (perceived resources) and internal state (available stores) respectively. The higher the perceived positive differences of neighbouring resource patches compared to the local resource patch, the more likely an animal will move. If stored resources are sufficiently high, an animal allocates resources to reproduction. We analysed the selection of these traits under different environmental disturbance regimes, which are defined by the frequency and intensity of stochastic (i.e. environmental) mortality leading to distinct population density fluctuations. Disturbance regimes determined the degree of population density fluctuation in a particular environment.

In summary, according to the predictions of the density-dependence POLS framework (Wright et al. 2019), we formulate the following hypotheses: (H1) optimal

levels of responsiveness and reproductive investment threshold covary with the POL along different population densities (intra-population) and degrees of fluctuation in population density (inter-population) forming a POLS due to density-dependent selection, (H2) the degree of variation in responsiveness and reproductive investment threshold traits covaries with the POL as it is linked to the degree of fluctuations in population density, and (H3) a trade-off between r_0 and γ underlies the density-dependent selection of traits associated with the POL, i.e. r_0 and γ covary with the POL.

3.2 Methods

We implemented the model in NetLogo 6.1.1 (Wilensky 1999). A detailed model description, which follows the ODD (Overview, Design concept, Details) protocol for describing agent-based models (Grimm et al. 2006; Grimm et al. 2020; Railsback and Grimm 2019), is available in the supplementary materials (B2). All analyses were done in R 3.6.1 and scripts are publicly accessible at a code repository . Here, we first provide a summary of the basic features and processes of the model and then of the basic principles underlying our model. The ODD-specific terms in italics refer to those used in the full ODD protocol.

3.2.1 Model structure

The purpose of our model was to test three predictions made by the fluctuating density-dependent selection POLS framework (Wright et al. 2019). The patterns to be reproduced by the model are those made by the three predictions.

The model comprises two types of entities: moving animals and square spatial units (patches). Patches are characterized by a set of state variables, mainly resource density and the number of resources a single animal can extract per time step (i.e. harvest rate), which depends on resource density (Table 3.1). State variables of animals comprise their energetic state (resources available in soma, resources allocated to reproduction), their heritable traits reproductive investment threshold and responsiveness, and their perceived environmental state (Table 3.1). Responsiveness defines the reaction to differences in harvest rates between local and neighbouring patches. High values of responsiveness reflect a higher likelihood to respond to resource differences by inter-patch movement. The reproductive investment threshold defines the level above which individuals allocate all resources from soma to reproduction. Patches are defined by their resource density and the harvest rate, i.e. the rate at which these resources can be extracted. The spatial extent of the toroidal landscape is 50 x 50 units.

Upon initialization, a resource density in the range of 8 to 10 is assigned to

Table 3.1: State variables of patches and animals. See ODD (B2) for additional state variables that do not affect the simulation but are relevant to analyse the model.

State variable	Entity	Range	Description
resource-density	patch	[0;*)	Amount of resources per patch
harvest-rate	patch	[0;**)]	Amount of resources extractable per time step
responsiveness	animal]0; 2]	Trait; probability of inter-patch movement based on perceived-current-mean-hr minus current-hr
current-hr	animal	[0;**)]	Harvest-rate of local patch
perceived-current-mean-hr	animal	[0;**)]	Mean harvest-rate of neighbouring patches (Moore neighbourhood, i.e. eight neighbours)
reproductive invest-ment threshold	animal	[0; 2]	Trait; determines the threshold above which resources are allocated from soma to r-buffer
soma	animal	[0;]	Resources available for allocation to maintenance and r-buffer
r-buffer	animal	[0;]	Resources allocated to reproduction. If ≥ 50 (default level), the animal reproduces

each spatial unit. Animals are assigned trait values for reproductive investment threshold and responsiveness sampled from a uniform distribution within the range of reproductive investment threshold [0,2] and responsiveness [0,2], respectively. We chose a uniform distribution, as it represents an uninformative prior for selection (Fig. B1.10 for initially monomorphic population). Preliminary analyses showed that increasing the ranges any further did not affect the results.

3.2.2 Model processes and scheduling

Movement and foraging

Each discrete time step, the same sequence of submodels is executed and state variables are updated after each action. First, animals decide whether to move to another patch or to keep foraging at their current patch (Fig. 3.1). This decision is mediated by an animal’s responsiveness as a reaction norm with the average difference between harvest rates at the current patch and neighbouring patches as the external state, i.e. environmental gradient. In the model, responsiveness defines the scale and shape parameter of a gamma distribution. To decide between moving and foraging, an animal samples a value from its gamma distribution. If the value is lower than the external state (average differences in harvest rates), an animal moves to one of the neighbouring patches. If, instead, an animal forages, it extracts resources based on the harvest rate which follows a saturating type II function. The higher the responsiveness, the lower the sampled values tend to be and, hence, the more likely an animal responds to the external state. Animals assess the resource density of their local patch and surrounding patches only, i.e. gather environmental cues via their foraging and movement decisions.

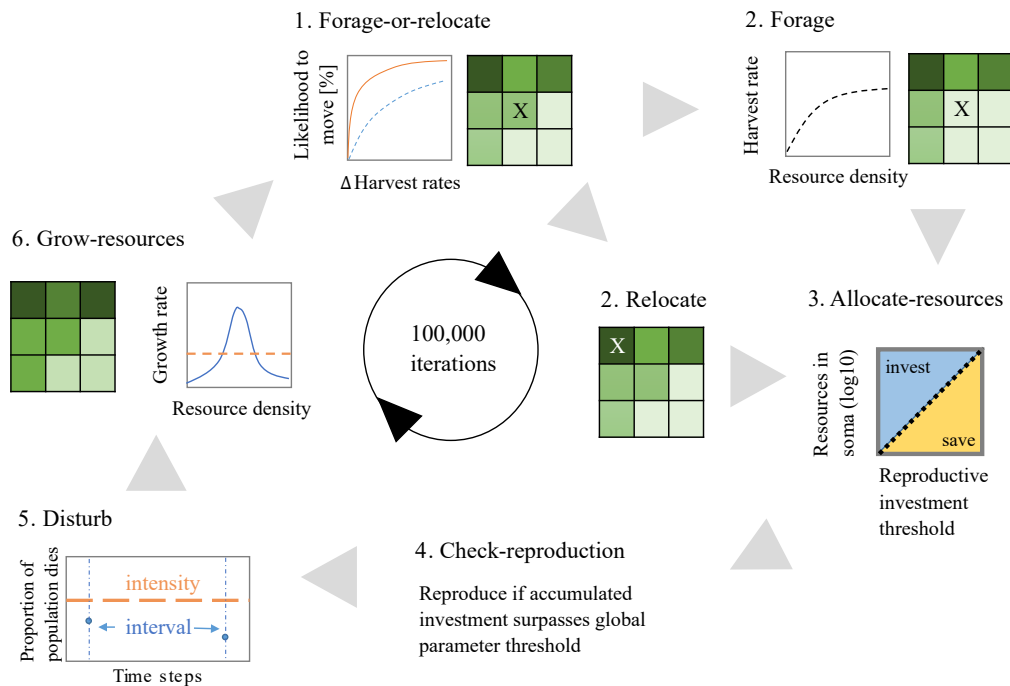


Figure 3.1: Graphical model summary showing submodels and scheduling. 1) Animals decide whether to forage or to relocate based on (A) the difference in harvest rate between the current and the average of neighbouring patches, and (B) their behavioural trait which varies from responsive (orange, solid line) to unresponsive (blue, dashed line). 2) If an animal forages it reduces the resource density at the local patch by the harvest rate which only depends on the patches’ resource density. The animal increases its soma by the same amount. If an animal relocates, it moves randomly to one of the neighbouring patches and will harvest resources only in the next time step; this implicitly represents costs of movement. 3) An animal allocates resources to maintenance (fixed, global parameter). If an animal’s soma drops below 0, it dies. Then, if resources in soma surpass its reproductive investment threshold, an animal invests all excess resources, i.e. the delta between threshold and resources in soma, to reproduction (4) If the accumulated investment to reproduction surpasses a certain level of resources (global parameter, default is 50), an animal reproduces and a new animal is created; it inherits the parent’s responsiveness and reproductive investment threshold, each modified by a globally defined level of stochasticity mimicking empirical heritability of behavioural and life-history traits. 5) With a probability determined by the global parameter disturbance-interval a random proportion of the population with the global parameter disturbance-intensity as upper limit dies due to environmental mortality; this submodel allows to create density fluctuations of different magnitudes. 6) Resource growth: Resource density at each patch increases by the growth rate which is either resource-density-dependent (logistic function shown by the blue, solid line) or resource-density-independent (linear function shown by the orange, dashed line).

We chose the difference in harvest rate between local and neighbouring patches as movement criterion in reference to the Marginal Value Theorem (Charnov 1976). According to the theorem, moving to another patch is beneficial if the harvest rate at the local patch drops below the average of the habitat. We do not assume, however, that animals can assess averages over the entire habitat but only sense the average resource density in the eight neighbour patches. In our model, responsive individuals follow the Marginal Value movement criterion more closely, i.e. forage more “optimally”. The presence of conspecifics is not an explicit movement criterion and multiple individuals may forage at one patch.

If an animal stays on its patch, it reduces the resource density of the patch by its harvest rate and the animal increases its soma by the same amount. If an animal moves to a neighbouring patch, it cannot forage in the same time step. The alternation between local scale foraging and inter-patch movement is a common approach (Spiegel et al. 2017) and supported by empirical studies (Michelot et al. 2017; Pohle et al. 2017).

Resource allocation, reproduction, and trait evolution

In the next submodel, a fixed amount of resources, which is defined by the global parameter maintenance-cost, is deducted from an animal’s soma. If an animal has less than zero resources in soma, it dies. Next, an animal allocates a number of resources from soma to reproduction by which the decadic logarithm soma exceeds the reproductive investment threshold (Fig. 3.1). We chose the decadic logarithm, to resolve lower thresholds with a finer resolution. By doing so, small thresholds can result from selection which would otherwise be obscured by intergenerational variation in traits (i.e. heritability, see below). The higher this threshold, the more resources an animal retains in soma. Ecologically, individuals, thus, represent capital breeders (Stephens et al. 2009; description and results with income breeding see Fig. B1.7). Animals reproduce asexually once an accumulated amount of more than 50 resource units (global parameter) was allocated to reproduction, by placing one offspring at a random location in the landscape. Thus, animals need to allocate resources to prevent starvation but also to advance reproduction. Evolution comes into play by assuming that responsiveness and reproductive investment threshold are heritable: they are sampled from trait-specific normal distributions with parental trait values as mean and global parameters to define the heritability as standard deviation. Heritability (h^2) of each trait was parameterized to fall within the range of average levels of the heritability of life-history and behavioural traits reported by meta-analyses (0.2 – 0.3; Figs. B1.1 and B1.2; Dochtermann et al. 2019; Mousseau and Roff 1987; Stirling et al. 2002). We assumed asexual reproduction to keep the number of parameters low and to investigate the emergence of POLS without

invoking further complexity due to possible sex-specific POL axes (Hämäläinen et al. 2018).

Disturbances

Besides starvation, the model comprises stochastic, environmental mortality due to disturbances as a source of mortality (i.e. we do not assume an effect of age and generations are overlapping). With a probability determined by the global parameter disturbance-interval, a proportion of the population, sampled from a uniform distribution with the global parameter disturbance-intensity as the upper limit, dies (Fig. 3.1). Different disturbance regimes are implemented to modulate density fluctuations and, thus, facilitate the detection of density-dependent selection. The distinct disturbance events as implemented in our model may reflect natural processes, e.g. pulses in abiotic conditions or predation (Bijleveld et al. 2015), disease (Scherer et al. 2020), as well as anthropogenic processes such as pesticide exposures (Debecker et al. 2016; Stark et al. 2004), or fishing events (Law 2000).

Resource growth

At the end of each time step, resource density of patches increases by a fixed amount (Fig. B1.8, I with logistic growth). The harvest rate of a patch depends on resource density of a patch (type II) and is updated upon any changes in resource density either due to growth or foraging (Fig. 3.1). We parameterized resource growth and maintenance cost so that inter-patch movement is required to fulfil energetic demands of reproduction and population density does not increase beyond 1 (see Fig. B1.11 for alternative parameterizations).

Scenarios

Simulations were initialized with a population density of 0.1 animals per patch (i.e. 250 individuals), with traits sampled from uniform distributions of responsiveness [0,2] and reproductive investment threshold [0,2]. Different ranges of traits did not affect the outcome. We ran 12 combinations (i.e. disturbance regimes) of disturbance-interval (100, 125, 150, 200, 300, 500) and disturbance-intensity (50 %, 80 %) with five repeats each (total of 60 simulations, i.e. populations). Simulations ran for 100,000 time steps. In case simulations stopped due to extinction, they were repeated with the same setting (for parameterization see also Table B3.1).

3.2.3 Analysis

Data processing

We analysed the trait distributions of responsiveness and reproductive investment threshold of populations throughout a simulation run. We ignored the initial 10,000 time steps to account for initialization effects. To position individuals along the slow-fast continuum, i.e. to measure the POL, we computed the individual

generation time (T_i) as the average age at reproductive events (Araya-Ajoy et al. 2018):

$$T_i = \sum \frac{a_{gi}}{n_i}$$

With a_{gi} being the age of individual i at the birth of an offspring g and n_i being the total number of offspring of this individual. Higher individual generation times are associated with a slower POL (see B2 for details on how generation time is measured in the model).

To analyse whether fluctuations in population density select different POLs among and within populations, we calculated two metrics for inter- and intra-population analysis. For the inter-population analysis (i.e. among different simulation runs) the coefficient of variation in population density informs about the strength of fluctuations in given disturbance regimes. Higher coefficients of variation correspond to more frequent and/or more intense disturbances. For the intra-population analysis (i.e. within simulation runs), we calculated the mean population density individuals experienced during their life span as a metric of density-dependent selection acting on the individual. We grouped individuals into subpopulations by the decile of this metric such that equal proportions of individuals were in each subpopulation. We applied this grouping to attain a gradient of subpopulations from low to high population density for each population. For each subpopulation, we calculated the median and standard deviation of responsiveness and the reproductive investment threshold as well as their respective behavioural expressions (movement rate, rate of investment to reproduction). In the supplemental material, we show results for a different generation time metric (mean age at reproduction during reproductive events) and the alignment of traits and population density (Fig. B1.16).

Emergence of a pace-of-life-syndrome and its alignment to density-dependent selection (H1)

We checked for the covariation of median traits and their respective behavioural expressions (movement rate, rate of investment to reproduction) in subpopulations with POL (i.e. generation time). We analysed whether this axis of variation covaried with density-dependent selection, i.e. along different levels of population density, and with the degree of population density fluctuations. Furthermore, we analysed whether intra-population and inter-population POL axes were aligned. Therefore, we determined the overall inter-population POL axis via quadratic linear regression (responsiveness as dependent variable, reproductive investment threshold as independent variable). Next, we determined, for each population, the local slope of the inter-population POL axis at the median reproductive threshold of a population and

compared it to the slope (i.e. the regression coefficient of a simple linear regression) of the intra-population POL axis of that population (illustration: Fig. B1.4).

Relation between the degree of phenotypic variation and pace of life (H2)

To test whether greater phenotypic variation occurs in faster populations, we analysed the relationship between generation time and (1) the scaled standard deviation of responsiveness and reproductive investment threshold and (2) the scaled standard deviation of movement rate and rate of investment to reproduction. Standard deviation was appropriate as traits and behavioural expressions were normally distributed at the subpopulation level. We scaled the standard deviation to make variation more comparable between traits.

Trade-off between r_0 and γ along different paces of life (H3)

A higher sensitivity to intraspecific competition (γ) should become more adverse at increasing population densities, i.e. slower types should be selected. We tested whether a trade-off between r_0 and γ occurred by analysing the relationship between reproductive rate and population density for fast-type and slow-type populations.

Robustness analyses

To test whether density fluctuations affect the emergence of POL axes, we analysed simulations without disturbances (Fig. B1.5) and with highly frequent disturbances of low intensity which lead to stable population sizes below the carrying capacity defined by resource growth (Fig. B1.6). Additionally, we varied the parameterization via a one-at-a-time approach with each parameter shifted towards its minimum and maximum value. For all parameter sets, we compared the evolution of responsiveness, reproductive investment threshold and POL under contrasting disturbance regimes (labile vs. stable conditions) with the default parameterization (Fig. B1.11; Table B3.2). We also studied the emergent POL axes if inter-patch movement was not required to reproduce, i.e. maintenance costs were below the resource growth rate and carrying capacity was > 1 (Figs. B1.12, B1.13, and B1.14).

3.3 Results

We found that disturbances drive fluctuations in population density (Fig. 3.2, B), which feeds back on resource density and, thus, harvest rates (Fig. 3.2, A). To test the three key predictions of the fluctuating density-dependent selection POLS framework (Wright et al. 2019), we analysed traits at the level of subpopulations. Subpopulations were grouped by the deciles of mean population density experienced by individuals (Fig. 3.1, B). The term subpopulation always refers to this aggregation level.

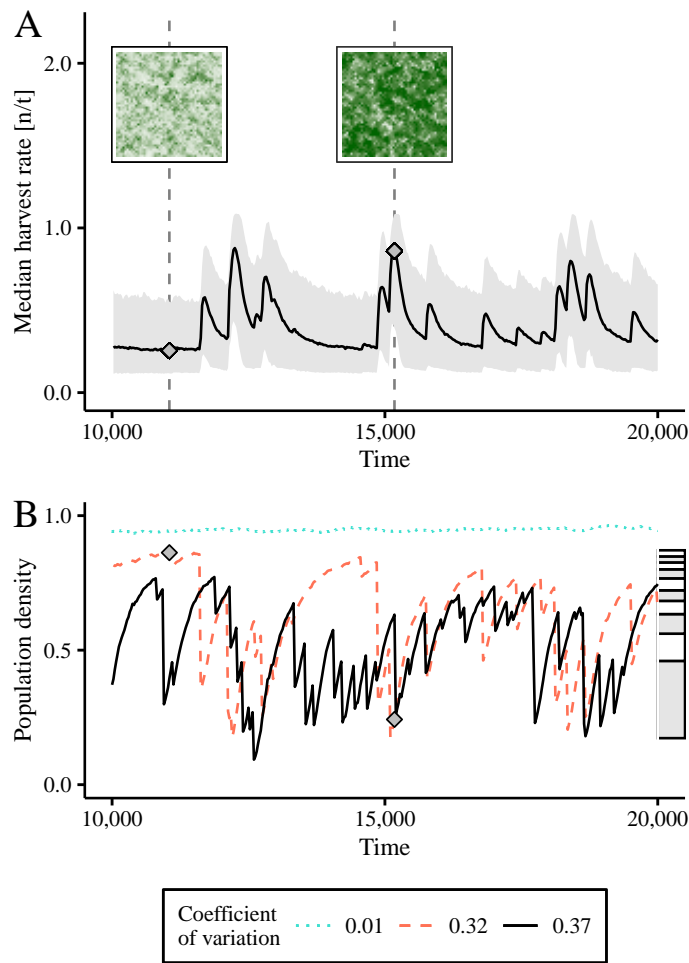


Figure 3.2: Exemplary dynamics of resource and population densities. (A) Median harvest rate over time across the landscape (grey area indicates the interquartile range). Insets show the distribution of resource density across the landscape at maximum and minimum harvest rate with stronger variation (i.e. broader interquartile range) at lower harvest rates. (B) Population density over time for three different degrees of fluctuations in population density indicated by the coefficient of variation. The black line is the same simulation as in panel (A), dotted lines refer to scenarios with disturbance regimes of a lower degree of population density fluctuations. To analyse trait composition due to density-dependent selection, we assigned individuals into subpopulations defined by deciles of population density experienced by individuals (grey and white stripes at the right). Points of low (high) population density correspond to points of high (low) median harvest rate (grey diamond shape).

3.3.1 Emergence of a pace-of-life-syndrome and its alignment to density-dependent selection (H1)

Traits covered only a small fraction of the initial trait space (Fig. 3.3, A). Among populations, responsiveness and reproductive investment threshold were correlated with POL (i.e. generation time) forming an inter-population POL axis (Fig. 3.3, B). Populations composed of responsive foragers with a high reproductive investment threshold were positioned at the slow end, whereas populations composed of less responsive foragers with a low reproductive investment threshold were located at the fast end.

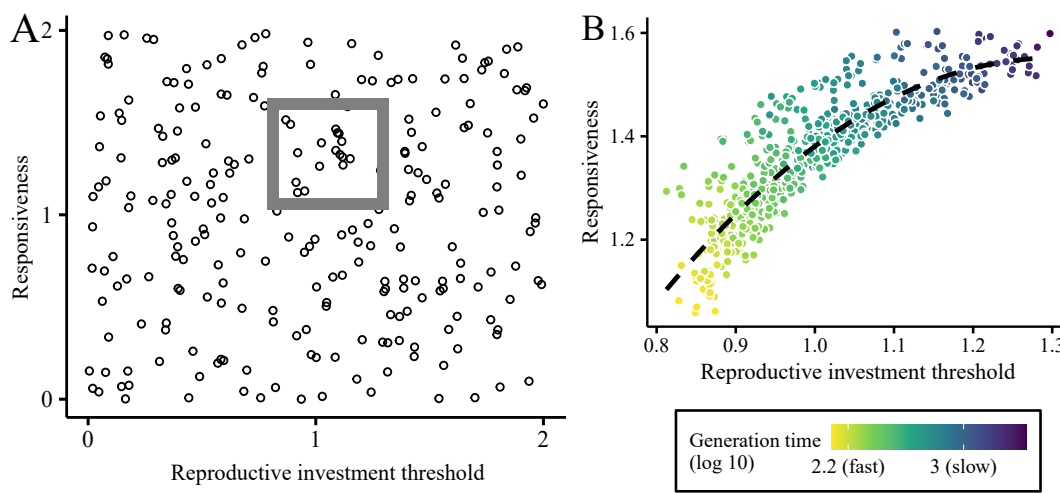


Figure 3.3: Covariation between responsiveness and the reproductive investment threshold across subpopulations that experienced different degrees of population density fluctuations. (A) Initial uniform trait distribution (points) and range of median traits of all simulated individuals in the respective subpopulations after an initial phase of 10,000 time steps (grey rectangle). (B) Emergent median traits in subpopulations ($n = 600$) form a common axis of variation (inter-population POL axes, dashed line), as faster types (generation time, colour gradient), were less responsive and had a lower reproductive investment threshold.

Within and between populations, generation time was positively correlated with population density (Fig. 3.4 A; Figs. B1.6-B1.10). Thus, the intra-population POL axes covaried with different levels of population density and populations arranged along a gradient of different degrees of density fluctuations (Fig. 3.4, B). Movement rate was reduced whereas the rate of investment to reproduction was elevated at lower population densities and higher degrees of density fluctuations (Fig. 3.4, C). While the association between traits was similar across hierarchical levels, intra-population POL axes emerging in severely disturbed environments did not fully

align with the inter-population POL axis (Fig. 3.4, D). If - in robustness analyses - we chose parameters so that carrying capacity increased beyond one individual per patch on average, the POL axes became non-monotonic with selection for lower levels of responsiveness and movement rate in slower types (Figs. B1.12 and B1.13).

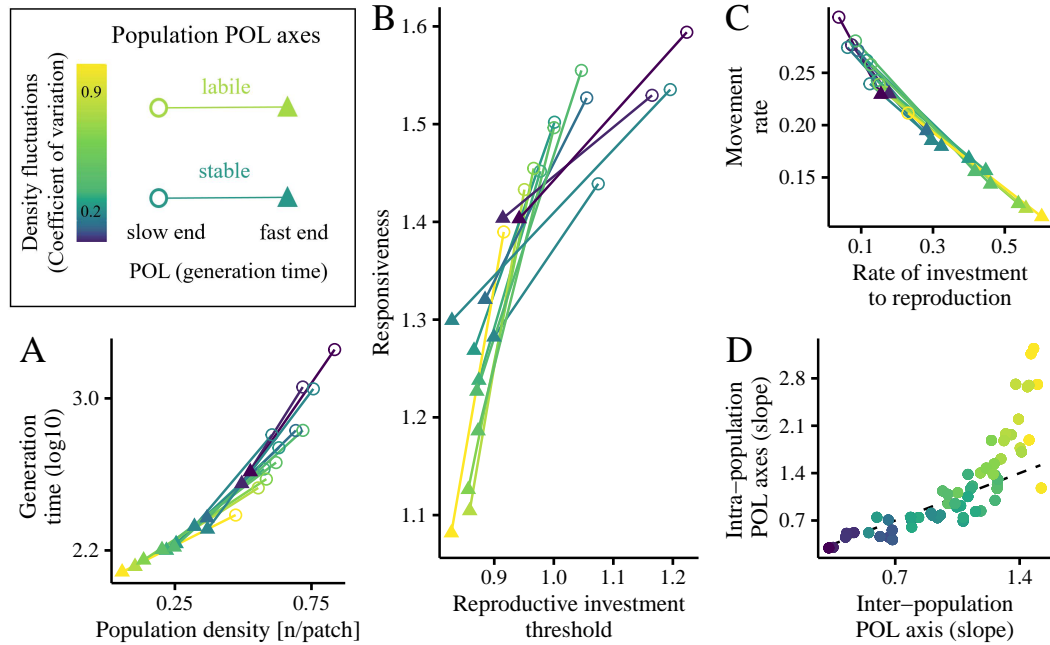


Figure 3.4: Along a gradient of density fluctuations (A), different intra-population POL axes (B) between median responsiveness and reproductive investment threshold and (C) between median rate of investment to reproduction and movement rate emerge. A-C show the slow and fast end (i.e. fastest/slowest subpopulation; ends are distinguishable by shape) of each intra-population POL axes (12 populations, one per unique disturbance regime; Fig. B1.3 shows repeats). (A) The POL (i.e. generation time) of the fast and slow end aligned to population density with the fast type located at lower population densities. (B) Covariation of median responsiveness and reproductive investment threshold along intra-population POL axes and different degrees of density fluctuation (expressed by the coefficient of variation) between population. (C) Covariation of median movement activity (rate of moving instead of foraging) and median rate of resources invested to reproduction along intra-population POL axes along different population densities and degrees of density fluctuation. (D) Comparison between slope of intra-population axes ($n = 60$ populations) and local slope of inter-population POL axis (Fig. 3.3, B). Slopes between hierarchical levels are similar (close to dashed line), yet, differ systematically with disturbance regimes.

3.3.2 Relation between the degree of phenotypic variation and pace of life (H2)

Due to stronger density fluctuations, the degree of trait variation in fast-type populations is predicted to be higher. We related the degree of variation (measured by the scaled standard deviation) in responsiveness and reproductive investment threshold and their behavioural expression (movement rate, rate of investment to reproduction) with POL (i.e. generation time). The degree of variation was negatively correlated with POL for all traits, except for movement rate (Fig. 3.5). Here, slower subpopulations showed a higher degree of variation. So, despite a higher degree of variation in responsiveness, behavioural expression movement rate did not show higher levels of variation, as it was possibly modified by a lower degree of relative variation in harvest rates at lower densities (Fig. B1.14).

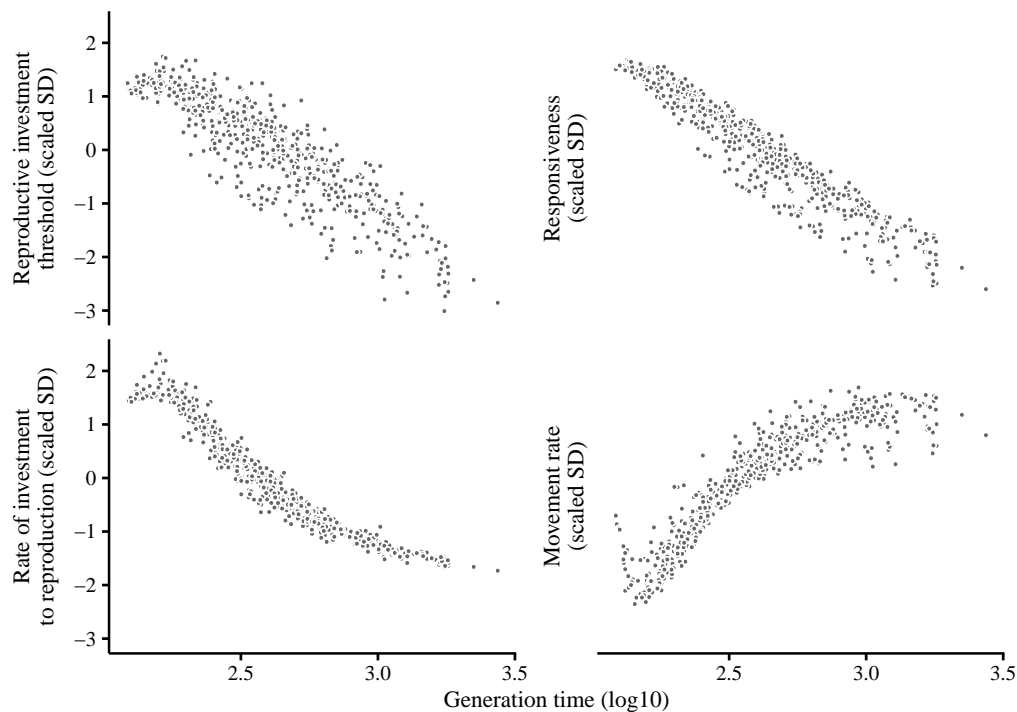


Figure 3.5: Relationships between POL (i.e. generation time) and scaled standard deviation (SD) of median responsiveness and reproductive investment threshold (top) and behavioural expressions (bottom) along different subpopulations (points, $n = 600$). SD was scaled to make traits and behavioural expressions comparable. Fast-type subpopulations show a higher degree of variation in traits and behavioural expression except for movement rate.

3.3.3 Trade-off between r_0 and γ along different paces of life (H3)

Fast types occurred at levels of lower intraspecific competition (low population density), where r_0 mainly defines the reproductive rate, whereas slower types occurred at higher levels of intraspecific competition (high population density) with reproduction rates modified by γ (Fig. 3.6). This pattern pointed to a correlation of generation time (POL) with r_0 and γ ; hence, populations of responsive types with low investment to reproduction, which were associated with a slow POL, have a lower r_0 but also a lower γ , i.e. their reproductive rate was less sensitive to higher population densities compared to populations at the fast end.

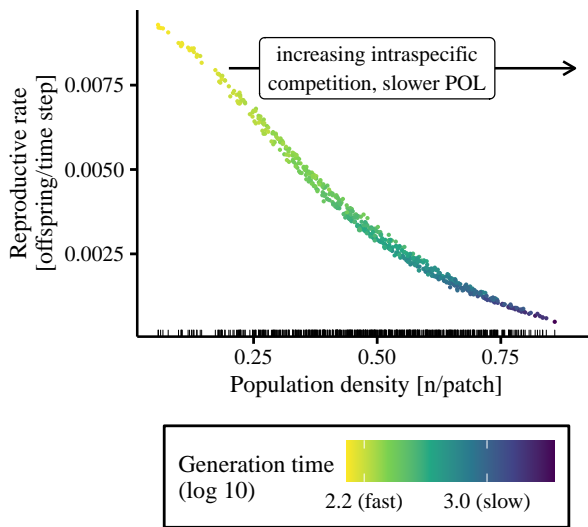


Figure 3.6: Relationship between population density, as a proxy for effects from intraspecific competition, and reproductive rate of subpopulations ($n = 600$) of different POL (i.e. generation time; colour gradient).

3.4 Discussion

In our study, we approached the fundamental question of whether and how observed correlations between suites of traits, i.e. syndromes, may emerge and be maintained by variation in population density which leads to fluctuations in density-dependent selection, as proposed by a novel framework (Wright et al. 2019). We tested three key predictions of the framework using an eco-evolutionary, generic, agent-based model. The parsimonious model design integrates fluctuations in population density via disturbance regimes, foraging, and reproduction, resulting in selection pressures on responsiveness (behavioural trait), reproductive investment threshold (life-history trait), and further traits as emergent properties (Fig. B1.15). Our model supports all tested key predictions by the framework, yet, results highlight potential difficulties

in determining POL axes in real ecological systems. In the following, we discuss these results and the mechanisms induced by population density and its fluctuations that have led to the emergence of POL axes.

3.4.1 Emergence of a pace-of-life-syndrome and its alignment to density-dependent selection (H1)

We found that responsiveness and reproductive investment threshold formed a common axis of variation along slow-fast continua within and between populations; hence, a POLS evolved at two hierarchical levels of biological organization. Selection of responsiveness and reproductive investment threshold are both linked to mechanisms induced by population density and density fluctuations. Density-related variation in behaviour has been demonstrated by several empirical studies. Common voles exhibit seasonal variation in behaviour with bolder individuals in low-density spring populations compared to high-density summer populations (Eccard and Herde 2013). Another prominent examples are western bluebirds where individuals with higher dispersal propensity and aggressiveness are more prevalent in newly founded low-density populations (Duckworth 2006; Duckworth 2008). Duckworth and Aguillon (2015) synthesize that aggressiveness in western bluebirds impairs parental care, which becomes more pronounced in dense populations and, thus, reduces fitness of aggressive individuals. For our simulated populations we can explain the covariation of responsiveness and reproductive investment threshold with the POL along a density gradient by density-dependent fluctuations in mortality risks and resource distributions.

Two sources of mortality exist in the model – density-independent environmental mortality and density-dependent risk of starvation. Density-dependent risk of starvation emerges from patterns of resource use and increases with population density (Fig. B1.18) as resource availability and harvest rates decrease (Fig. 3.2, Fig. B1.14). Individuals with low somatic resources (offspring, individuals with low reproductive investment threshold) are more prone to density-dependent starvation (Fig. B1.18). Hence, as population density increases, individuals with higher reproductive investment threshold can contribute more to population growth (Fig. 3.4, Fig. B1.16).

The effects of population density on the resource layer explain the selection for different levels of responsiveness. As harvest rates decreased with population density, the relative costs (in terms of resources) of moving to another patch instead of foraging in a given patch decreased; consequently, moving required lower positive inter-patch differences to be beneficial. Also, as the coefficient of variation in harvest rates increased with population density (Fig. B1.14), moving to another a

patch became more often rewarding. Furthermore, with elevated population density, increasing interference and exploitation competition favoured an earlier response to more subtle inter-patch differences. These factors contributed to the selection of higher responsiveness and, thus, higher movement rates at higher population densities. This relates to empirical observations of density-dependent movement activity, as intraspecific competition enforces resource scarcity for instance in elephant and opossum populations (Almeida et al. 2015; Young and Van Aarde 2010).

The acquisition of resources – mediated by responsiveness – and the allocation to reproduction – mediated by the reproductive investment threshold – affect the generation time. In line with optimality models, shorter generation times are beneficial in environments with elevated environmental mortality (Engen and Sæther 2016; Michod 1979). As population density increases, slower individuals with reduced allocation to current reproduction can reduce the density-dependent mortality due to starvation and contribute to population growth. Similarly to Araya-Ajoy et al. (2021) environmental mortality limits the maximum range of generation times (Fig. B1.18). Comparing between hierarchical levels, POL axes were overall aligned, yet, differed systematically. The slope of the POL axes (i.e. the variation of responsiveness) was steeper at the intra-population level compared to the inter-population level in more frequently and intensely disturbed environments (Fig. 3.4, D; Figs. B1.7, B1.8, and B1.9). As outlined above, traits aligned to POL axes as environmental properties and population density covaried. Yet, this covariation is not fixed (i.e. differs between environmental contexts) and may, thus, result in POL axes which do not fully align across hierarchical levels. This observation highlights that POL axes between hierarchical levels are not necessarily aligned. Instead, in contrast to most conceptual POLS figures (as in Wright et al. 2019), intra-population POL axes may rather systematically deviate from the major axis at the inter-population level. Another level of complexity is added if environmental patterns do not vary monotonically along a gradient of population density. We parameterized our model based on the assumption that inter-patch movement is required to meet energetic demands for reproduction. Yet, if we relaxed this assumption and population density, i.e. carrying capacity, could increase beyond 1, we observed a shift in foraging regimes. If all patches were – on average – occupied by at least one individual, resources were more homogeneously foraged resulting in a negative correlation of coefficients of variation in harvest rates with population density (opposite to situations with population density < 1). Now, fast types (with lower reproductive investment thresholds) occurring at lower population densities were more responsive and moved more than slower types, resulting in a non-monotonic selection along density gradients.

The integration of traits along a slow-fast continuum, as proposed by Réale et al. (2010), has so far yielded limited evidence (Royauté et al. 2018). Some studies of behavioural correlations along population density gradients, though, have shown correlations of traits such as dispersal propensity and sociability (Cote and Clobert 2007; Duckworth 2006; Duckworth 2008) as well as exploratory behaviour and investment to current reproduction (Nicolaus et al. 2015; Nicolaus et al. 2016), which are in line with POLS theory. Yet, this may not be general (Vanden Broecke et al. 2021) and the presence of non-monotonic responses of environmental properties and interactions to density fluctuations could obscure underlying POL axes in studies of fluctuating density-dependence POLS. Furthermore, non-monotonic POL axes emphasize that conceptual associations between traits along a slow-fast continuum (Réale et al. 2010), may not be taken as a universal prediction. Instead, an intimate knowledge of the study system is required (Agrawal 2020; Montiglio et al. 2018; Royauté et al. 2018).

3.4.2 Relation between the degree of phenotypic variation and pace of life (H2)

In disturbance-free scenarios (Fig. B1.5) traits evolved to high responsiveness and low reproductive investment threshold. With increasing fluctuations in population density, POL shifted to the fast end and the degree of variation in responsiveness and reproductive investment threshold increased. Our observations are, thus, in support of the hypothesis that fluctuations in population density increase the variation in traits. Yet, lowered intraspecific competition at lower population densities may be associated with relaxed selection, which may also contribute to higher degree of trait variation (Fig. B1.17). Furthermore, in case, the environmental variation correlates positively with population density, higher variation in traits (i.e. wider reaction norms) in fast types may not be associated with a higher variation in behavioural expressions. In our study, we observe this case as harvest rates become more similar at low-density conditions. This resulted in differences between patches too small for - on average - less responsive foragers to react to, which lead to a more uniform response. Thus, when testing this prediction based on the variation in a behavioural expression, environmental effects need to be appropriately attributed (Hertel et al. 2020).

Temporal fluctuations in population density as a source of trait variation may have some vital implications for ecological research, as consequences of trait variation scale up to the community level (Bolnick et al. 2011; Sih et al. 2012; Violle et al. 2012; Wolf and Weissing 2012), e.g. by affecting coexistence mechanisms (Banitz 2019; Crawford et al. 2019; Hart et al. 2016; Milles et al. 2020) or mobile link

functions (Brehm et al. 2019; Schlägel et al. 2020; Shaw 2020). Studying the effect of fluctuations in population density on trait variation adds another perspective to anthropogenic effects on trait diversity. For instance, resource provisioning in wildlife management, albeit increasing foraging efficiency and thus fitness, alleviates density fluctuations which may negatively affect trait diversity and its associated functions.

3.4.3 Trade-off between r_0 and γ along different paces of life (H3)

Following the fluctuating density-dependent selection POLS framework (Wright et al. 2019), traits should reflect a trade-off between the sensitivity to intraspecific competition (γ) and intrinsic reproductive rate (r_0). Elevated levels of responsiveness increase the chance to be the first to react to inter-patch differences and, thus, succeed in exploitation competition which becomes more prominent if population density approaches the carrying capacity. Furthermore, a low reproductive investment threshold reduces the density-dependent risk of starvation. So, responsiveness and reproductive investment threshold affect the sensitivity to intraspecific competition (γ), i.e. the observed negative effect of increased population density on reproductive rate. Similarly, lower responsiveness maximizes resource uptake in the absence of competition and a high reproductive investment threshold facilitates a rapid conversion of resources into offspring, i.e. their intrinsic reproductive rate (r_0) increases. Thus, the covariation between responsiveness and reproductive investment threshold along the inter-population POLS axis directly translates into a trade-off between r_0 and γ .

3.4.4 Future directions

We observed a persistent covariation between responsiveness (behavioural trait) and reproductive investment threshold (life-history trait). Yet, In systems where resource availability is not (solely) driven by density in the upper trophic level or where mortality risk from disturbance across the trait space is anisotropic due to trait-dependent adaptive strategies (Mathot et al. 2012), the relationship between these traits may be altered as they do not have a common causal link to population density fluctuations. The identification of mechanisms induced by fluctuations in population density is, thus, vital to formulate testable predictions about the emergence of a POLS and the directionality of the covariation between traits. Such mechanisms may induce a directionality that deviates from the classical association between traits in POLS or to non-monotonic POL axes. In stark contrast to most conceptual figures of POLS (as in Wright et al. 2019), we observed a systematic difference in the slopes of POLS axes between hierarchical levels (inter-

population vs. intra-population level). Slopes of intra-population POL axes in more severely disturbed environments were steeper than suggested by the inter-population POL axis. We could explain this by the distinct effects of population density and fluctuations in population density which act differently across the hierarchical levels. Hence, differences in mechanisms across hierarchical levels and variation in mechanisms associated with population density fluctuations should be accounted for when generating hypotheses to test the fluctuating density-dependent selection POLS framework and the POLS hypothesis in general. This adds to suggestions by other studies (Montiglio et al. 2018; Royauté et al. 2018) that relaxing core assumptions, e.g. by regarding relationships between traits more adapted to the specific context (Montiglio et al. 2018), would allow for more general applicability and may partly resolve the issue of an unclear state of evidence.

Future studies, both *in vivo* and *in silico*, might test the fluctuating density-dependent selection POLS framework in a less generic system with population density fluctuations induced by specific anthropogenic, biotic, or abiotic sources. In our study, environmental mortality imposed on individuals by disturbances was isotropic, i.e. traits did neither mitigate nor amplify the mortality risk during a disturbance event. Yet, individuals with higher responsiveness may reduce their mortality risk as they observe their environment more closely and may, thus, perceive environmental cues of disturbances earlier and react accordingly. Despite the apparent absence of a general relationship between behavioural traits and mortality risk (Moiron et al. 2020), adaptive strategies to reduce mortality risk (Mathot et al. 2012) may be an important element of specific systems. For instance, such adaptive strategies may arise if disturbances become less predictable and may facilitate the persistence of plastic slow types at more severe disturbance regimes (Hämäläinen et al. 2021). This would not only change the relationship between the POL and other traits, but also the general association between POL and density-dependent selection. As a first step, our study provides evidence for the fluctuating density-dependent selection causing a POLS with a null model of interaction between traits and mortality risk; further studies in specific systems with certain sources of density fluctuations will help to further explore limits of the framework and POLS hypothesis itself.

3.5 Conclusions

Our study provides support for key predictions of the fluctuating density-dependent selection POLS framework. Both, at the intra-population and inter-population level, a POLS emerged. The selection of responsiveness and the reproductive investment threshold was mediated by distinct mechanisms induced by population

density (i.e. competition for resources) and fluctuations in population density (i.e. environmental mortality). Due to differences in the expression of these distinct mechanisms the POLS axes did not fully align and, instead, differed systematically between hierarchical levels. This observation nuances hypotheses-making in POLS compared to assuming equal inclination across hierarchical levels. While our study is in support of the framework, further studies may apply predictions to specific sources of population density fluctuations (i.e. disturbance types). Such studies would shed light on whether adaptive strategies, i.e. anisotropic mortality risk across the trait space, or reversible plasticity may alter or even obscure the emergence of POLS along a gradient of density-dependent selection.

3.6 Additional information

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Conflicts of interest

None.

Statement of Authorship

Conceptualization, development, and analysis of the model were done by AM. MD and VG gave feedback on the model development and concepts. AM visualized the results and wrote the first draft. All authors reviewed and edited the draft and contributed substantially to revisions and the final version of the manuscript.

Data accessibility

To reproduce the data and main text/supplemental figures, the analysis scripts and the model code are available at a zenodo repository (Milles 2021). Data is generated via the model code.

Supplementary material

B1: Additional figures

B2: Model documentation

B3: Additional tables

Chapter 4

Buffer mechanisms for population persistence

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Abstract

Assessing and predicting the ability of populations to persist is a central motif of ecological research, for example in species conservation or in the control of invasive species or diseases. Whenever local populations become too small to persist, usually regional mechanisms such as recolonization and rescue effects are explored. However, theory also shows that without mechanisms facilitating local persistence, regional mechanisms cannot unfold. Here we focus on such local buffer mechanisms, i.e. mechanisms that reduce extinction risk. Local buffer mechanisms currently lack an overall integration and an accessible description of how they arise from underlying processes. We therefore provide an overview and synthesis of local buffer mechanisms. We propose two fundamental classes of such mechanisms, dampening and repelling. Dampening buffer mechanisms reduce the risk of stochastic factors on population persistence. They include portfolio effects as well as intraspecific and interspecific interactions. Repelling buffer mechanisms include adaptation and hierarchical filtering which increase population growth rates independent of context. We give examples for dampening and repelling buffer mechanisms and discuss buffer capacities resulting from these mechanisms, interactions among the mechanisms, and latencies (i.e. time until mechanisms become effective) as key characteristics. We argue that buffer mechanisms and their characteristics are fundamental to understand local population persistence. We suggest an individual-based approach, i.e. from pattern-to-process, to study local buffer mechanisms in theoretical modelling and empirical studies.

4.1 Introduction

The question of how populations persist is of great importance in both conservation biology and community ecology. Many populations are threatened with decline due to anthropogenic drivers leading to habitat loss and fragmentation (Almond et al. 2020; Leclère et al. 2020). Furthermore, in most communities, the majority of species have low abundances and may even be locally rare (Dewdney 2017; McGill et al. 2007). To reliably predict and estimate local extinction risks of small or declining populations an intimate knowledge of the mechanisms that allow populations to persist is required. This mechanistic understanding is relevant for species conservation, the management of native and invasive species and the eradication of pathogens.

Metapopulation and metacommunity theory focus on regional persistence mediated by two non-local mechanisms resulting from dispersal: recolonization after local extinction (Hanski et al. 1995), and the rescue effect where the inflow of individuals from source habitats keeps abundances high enough to prevent local extinction in sink habitats (Brown and Kodric-Brown 1977; Dias 1996; Heinrichs et al. 2015). As populations become increasingly isolated due to habitat loss (Ward et al. 2020), these regional mechanisms can contribute less to the resilience of populations (Opdam 1991; Tucker et al. 2018). Moreover, without sufficient local persistence, regional mechanisms cannot fully unfold (Frank and Wissel 2002). Hence, mechanisms locally reducing extinction risk, referred to in the following as local buffer mechanisms, are gaining importance and may in general play a pivotal role for understanding and managing populations and communities.

Buffer mechanisms can, thus, mitigate the impact of global change on biodiversity and may improve the outcomes of conservation policies and the management of natural resources. On the other hand, they can, similar to regional mechanisms (Levins 1969), complicate interventions on invasive species, pest control, or disease eradication. Yet, despite their relevance, we lack a synthesis of local buffer mechanisms and their full incorporation in studies of population viability, species coexistence (Jeltsch et al. 2019) and ecosystem management (Connell and Ghedini 2015).

4.2 Extinction risk and buffer mechanisms

Buffer mechanisms alleviate factors that contribute to extinction risk. In population ecology, several key patterns are associated with the persistence and extinction of populations. Extinction risk increases with stochastic fluctuations in population size as well as reduced carrying capacities of the habitat (Lande 1993). Populations

may be small due to low carrying capacities or to adverse conditions and insufficient recovery.

Smallness can lead to rapid extinction events, especially if Allee effects occur or stochastic fluctuations of population size are pronounced. Such fluctuations may result from population, i.e. demographic, characteristics (e.g. sex ratio, intraspecific variation in survival and reproduction) as well as from spatiotemporally varying environmental conditions (Melbourne and Hastings 2008). Although factors affecting extinction risk have widely been explored in theoretical ecology and population viability analyses, buffer mechanisms have, despite their potential pivotal role, rarely been addressed explicitly (Cardillo and Meijaard 2012; Grimm et al. 2005; Jeltsch et al. 2000; Nimmo et al. 2015). In particular, how the interplay of different local buffer mechanisms may reduce extinction risk requires thorough investigation (Dibner et al. 2019).

Existing knowledge on local buffer mechanisms is currently scattered across domains of research such as niche and coexistence theory, behavioural and landscape ecology, evolutionary biology and research on priming effects. In this synthesis, we, hence, propose basic classes of local buffer mechanisms which can be further divided into subclasses. Each subclass of mechanisms comes with certain properties such as whether they occur with a latency or whether they are limited in their operation by certain capacities. In the following sections, we first introduce the two basic classes and then propose subclasses along with their properties. Finally, we emphasize the role of interactions between local buffer mechanisms and propose ways to study local buffer mechanisms using models and empirical approaches.

4.3 Two classes of local buffer mechanisms

Buffer mechanisms operate by reducing the impact of environmental fluctuations on population abundance and thereby alleviating extinction risk, especially in small populations (Grimm et al. 2005) or by preventing populations from becoming too small in the first place. In general, there are two different perspectives of buffer mechanisms. Most often, buffer mechanisms have been described as a dampening force, i.e. as a force that reduces temporal variation in a variable such as population size (Grimm et al. 2005). Yet, some authors have also considered the perspective that buffer mechanisms repel an ecological system from entering a different state (DeAngelis and Waterhouse 1987; Jeltsch et al. 2000), including repelling a population from extinction. To integrate these two perspectives on buffer mechanisms, we distinguish dampening and repelling mechanisms as two basic classes of local buffer mechanisms (Fig. 4.1).

Dampening mechanisms reduce the impact of stochastic factors on population

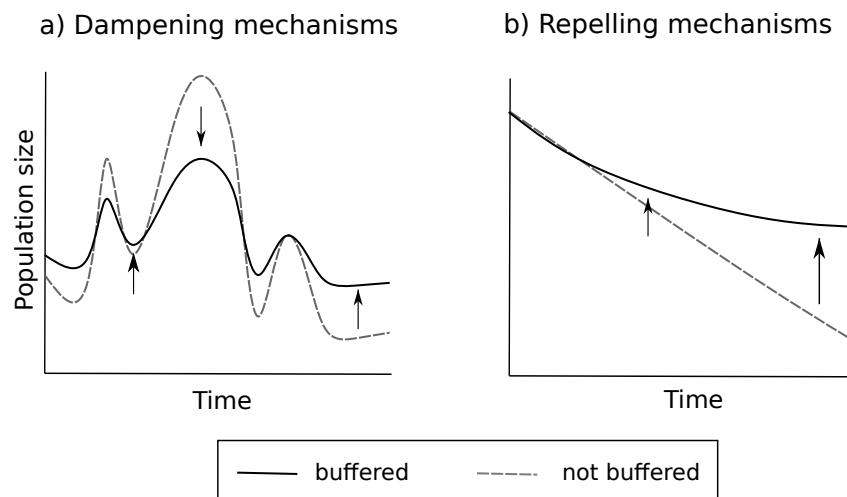


Figure 4.1: The two basic classes of local buffer mechanisms. A) Dampening buffer mechanisms mitigate environmental stochasticity and are characterised by a context-dependent optimum B) Repelling mechanisms operate by increasing population growth rate under adverse conditions and the relationship between their magnitude and effect on population persistence is monotonic. Repelling mechanisms may become stronger over time or as the population approaches lower densities.

size and, thus, persistence. Among-individual variation in niche traits (traits related to the location at a niche-axis; Stump et al. 2022) is one source of dampening mechanisms. With among-individual variation in niche traits, it becomes more likely that at least a subpopulation can perform well under temporally fluctuating environmental conditions (portfolio effect; Bolnick et al. 2011; Schindler et al. 2015). Yet, at a certain magnitude, among-individual variation in niche traits may start to reduce persistence (Crawford et al. 2019), for instance, as some subpopulations' traits never match with the actual environmental conditions. All sources of dampening mechanisms have in common that their effect on population persistence is context-dependent.

Repelling mechanisms, in contrast to dampening mechanisms, monotonically increase population persistence with their magnitude. Repelling mechanisms mainly operate by increasing population growth rate under adverse conditions. Adaptive within-individual variation, such as behavioural changes under adverse conditions is one example of a repelling mechanism. The more adaptive within-individual variation becomes, the more can adverse conditions and their detrimental effect on population size be buffered. We suggest that these two classes are general and

their distinction is useful to understand and predict population persistence and to conceptually guide efforts to conserve threatened or eradicate ecologically or socio-economically harmful populations. In fact, many conservation measures facilitate buffer mechanisms such as by improving habitat quality or adding genetic diversity to a population. By exploring interactions and capacities of buffer mechanisms we highlight research gaps and caveats in managing and studying population persistence. In the following, we introduce subclasses of dampening and repelling mechanisms and highlight their key properties and conditions at which they become relevant.

4.3.1 Dampening buffer mechanisms

Dampening mechanisms reduce the detrimental effect of fluctuations in environmental conditions on population persistence. Dampening mechanisms have a context-dependent optimum, i.e. increasing the magnitude of their underlying processes does not necessarily monotonically increase population persistence. Dampening mechanisms can be subdivided based on whether they act through portfolio effects or interactions within and among species.

Portfolio effects

The portfolio effect, best summarised by “not putting all eggs in one basket”, describes how non-correlated or negatively correlated (i.e. asynchronous) population dynamics in a diverse (meta-)community dampen the variation of the total abundance of that community (Koellner and Schmitz 2006). Yet, the portfolio effect can operate on all scales of biological organisation where context-dependent functional (i.e. fitness-affecting) variation between entities (species, populations, individuals) occurs. At the population level, in some contexts, individuals with certain traits may perform worse and decline, in other contexts the individuals with the same certain traits may perform better and increase whereas others decline (Fig. 4.2 a). This asynchrony in population dynamics may result from two primary factors, environmental heterogeneity and among-individual variation in niche traits (i.e. traits with context-dependent optimum; Fig. 4.2 b).

Table 4.1: Overview of local buffer mechanisms. Some references point to findings on a regional level, yet, we would also expect analo-gous results on a local scale.

Class	Subclass	Cause	Latency	Reference
Dampening	Portfolio effects	Environmental heterogeneity	Pre-existing, immediate	Suggitt et al. 2011, Scheffers et al. 2014, Rytteri et al. 2021
		Among-individual variation in niche traits	Pre-existing, immediate	Schindler et al. 2010, Acker et al. 2014
Repelling	Frequency- and density-dependent interactions	Within-species interaction	Pre-existing, Immediate or induced and delayed	Reed et al. 2013
		Among-species interaction	Pre-existing, Immediate or induced and delayed	van Baalen et al. 2001
		Within-individual variation	Induced, potentially delayed	Mckee et al. 2007, Gribben et al. 2009, Wright et al. 2010, Doak and Morris 2010, Watts and Thompson 2012
Repelling	Adaptation	Microevolution	Induced, delayed	Freeman and Byers 2006, Jørgensen et al. 2009 Nunes et al. 2014
		Site quality	Pre-existing, Immediate	Gill et al. 2001, DeAngelis and Waterhouse 1987
		Among-individual variation in quality	Pre-existing	Payo-Payo et al. 2018

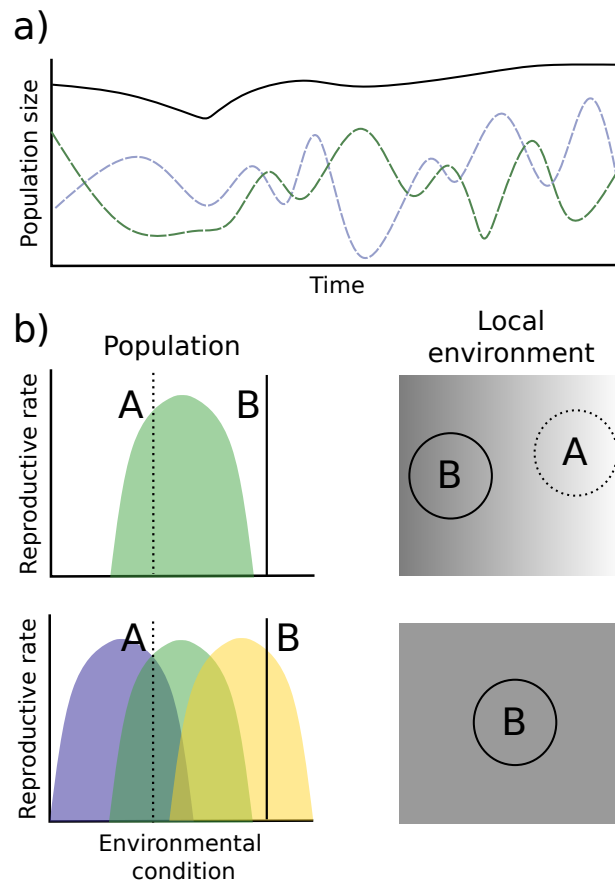


Figure 4.2: Dampening buffer mechanisms due to portfolio effects a) Due to the classical portfolio effect, fluctuations in subgroups of a population (dashed colored lines) are asynchronous, resulting in a dampened population trend curve (solid, black line). b) Besides stochastic factors (such as demographic stochasticity), the different dynamics in subgroups may result from two different factors. First, environmental heterogeneity, as represented by different environmental descriptors of location A and B (upper right panel), retains some part of the local environment within the niche of the monomorphic population (upper left panel). Second, due to among-individual variation in niche specialisation, lower panel, a subgroup of a population can contribute to population growth in absence of environmental heterogeneity.

Environmental heterogeneity In a homogeneous environment, the environmental conditions are either within or outside of a species-specific niche. In a heterogeneous environment, the likelihood that at least some locations overlap with the species-specific niche increases. For instance, butterflies may posit their eggs at warmer and colder locations within a patch. To successfully develop, larvae need to grow in phenological synchrony with their local host plant. For larvae at colder locations (northward slope) phenological synchrony is more likely at above-average spring temperatures and less likely at below-average spring temperatures compared to larvae at warmer locations (flatland; Rytteri et al. 2021). As always some subgroup can successfully grow and develop, the population and inter-annual variability as well as prospective climate change effects are buffered (Rytteri et al. 2021).

Environmental heterogeneity is currently intensively studied in the context of climate change, as it allows populations to persist in otherwise lethal environmental conditions (Scheffers et al. 2014; Suggitt et al. 2011). Scheffers et al. 2014, for instance, found a decrease in the occurrence of lethal temperatures by an order of two magnitudes due to microhabitat features. Buffer mechanisms due to environmental heterogeneity, in general, result from interactions between multiple environmental properties such as microhabitat features and weather (Rytteri et al. 2021; Scheffers et al. 2014).

Among-individual variation in niche traits Among-individual variation in niche traits refers to differences in traits that affect the location of an individual on a niche axis (Fig 2, b), i.e. traits with a context-dependent performance (Stump et al. 2022). Niche traits differ from context-independent hierarchical traits which do not affect location on a niche-axis. These two types of traits have recently been shown to have contrasting effects for species coexistence (Stump et al. 2022) and, as we show here and in a later section, also mediate different buffer mechanisms. Niche traits may result from ontogeny, genetic diversity or maternal effects. In theoretical studies, among-individual variation in life-history traits (asynchronous breeding) increases population persistence by facilitating the survival of some offspring in face of discrete perturbations (Acker et al. 2014; Iwasa and Levin 1995). Simulation studies show that, depending on the timing of the discrete perturbations, either early or late offspring survive more likely (Acker et al. 2014; Iwasa and Levin 1995), thus, representing a portfolio effect which mitigates environmental stochasticity.

While the ecological relevance of among-individual variation has gained more attention lately (Bolnick et al. 2011; Des Roches et al. 2018; Violle et al. 2012; Wolf and Weissing 2012), empirical studies clearly demonstrating portfolio effects

due to among-individual variation are still relatively rare, especially on the local scale. On a regional level, among-individual variation in time spent in fresh water and the ocean (life-history trait) of sockeye salmon resulted in asynchronous population dynamics (Schindler et al. 2010). Disentangling effects of environmental heterogeneity and among-individual variation sometimes becomes difficult (Abbott et al. 2017), in particular, on the local scale. As these two sources of portfolio effects differ in their interaction with other causes of buffer mechanisms (see section 4.4), it is crucial to study among-individual variation niche traits at a local scale empirically.

While portfolio effects are mostly considered beneficial to population persistence (Bolnick et al. 2011; Schindler et al. 2015), modelling studies suggest that high amounts of among-individual variation may be detrimental to population persistence (Crawford et al. 2019). Hence, the optimal magnitude of among-individual variation in niche traits to act as a buffer mechanism depends on the specific context.

Frequency- and density-dependent interactions

Interactions among and within species change with the total abundance (i.e. density) and the relative abundance of a species in a community (i.e. frequency). Relationships between frequency or density and these interactions pervade the most fundamental concepts of ecology and provide key explanations for persistence and coexistence. These relationships suggest that if populations change in size, increase and release of interactions may limit this change, i.e. induce a dampening mechanism. In the following, we summarise some aspects of these relationships on interactions within and among species.

Within-species interactions Negative density-dependence occurs if population growth rates decrease as population density increases and is an outcome of competitive interactions. Strong conspecific negative density-dependence may cause small population sizes (Comita et al. 2010), yet, it is also a mechanism that increases population persistence. Stronger limitation by conspecifics than by heterospecifics is a fundamental mechanism of species coexistence theory (Adler et al. 2007). While stronger limitation by conspecifics reduces equilibrium sizes, stochastic factors are dampened by strong responses in growth rates towards equilibrium sizes (Yenni et al. 2012). As such, stronger limitation by conspecifics is possibly a common characteristic of persistent, low-abundance species (Yenni et al. 2017). Yet, if equilibrium sizes are too small (for instance due to environmental degradation), Allee effects may occur. Therefore, the optimal level of self-limitation in rare population should depend on the specific contexts.

The buffering effect of competitive release has, for instance, been shown in a

population of great tits which experienced a climate change-induced phenological mismatch with its prey, such that only a part of the population could successfully reproduce (Reed et al. 2013). While this resulted in reduced offspring numbers (Reed et al. 2013), the reduced number of offspring relaxed competition and increased offspring survival, which prevented population decline. This implies, vice versa without a phenological mismatch, a larger proportion of a population can reproduce, yet, elevated intraspecific competition reduces offspring survival overall dampening the effects of match and mismatch. While intraspecific competitive release is expected to be quite universal it can interact in a variety of ways with other buffer mechanisms.

Among-species interactions Density-dependent and frequency-dependent processes are not limited to effects of intraspecific competition but also extend to interspecific interactions. Antagonistic interactions (such as predation, infection, parasitism) may change if predators alter their diet as certain prey populations get small and become harder to detect or require costly specialization (positive switch; Baudrot et al. 2016). Simulations models show that positive prey-switching enhances the persistence of predator and prey populations (Baalen et al. 2001). Related processes can be assumed for mutualistic interactions. For instance, if a focal population declines and becomes less frequent than its mutualistic partner, individuals of the focal population may engage in stronger mutualistic interactions potentially increasing growth rates. It is important to note, that these relationships are not general (Baudrot et al. 2016), hence, it is necessary to study the relationship specific for a system to assess whether density- or frequency-dependent interspecific interactions are a source of a dampening buffer mechanism or whether they may even catalyse population decline.

4.3.2 Repelling buffer mechanisms

The second class of buffer mechanisms increase population persistence by mitigating the effects of adverse conditions due to more adaptive populations (adaptation) or high-quality sites and individuals (hierarchical filtering). In contrast, to dampening mechanisms, there is not a general context-dependent optimum for these mechanisms to increase population persistence.

Adaptation

An important subclass of repelling mechanisms are adaptive processes which can slow down or even revert population decline. Adaptive processes mediating a buffer include within-individual variation in traits in response to adverse biotic and abiotic conditions as well as buffering via microevolution (Fig. 4.3). While

evolution, in general, implies optimisation of fitness and, thus, a buffer mechanism, we here focus on evidence of microevolution with patterns of local adaptation within relevant time scales.

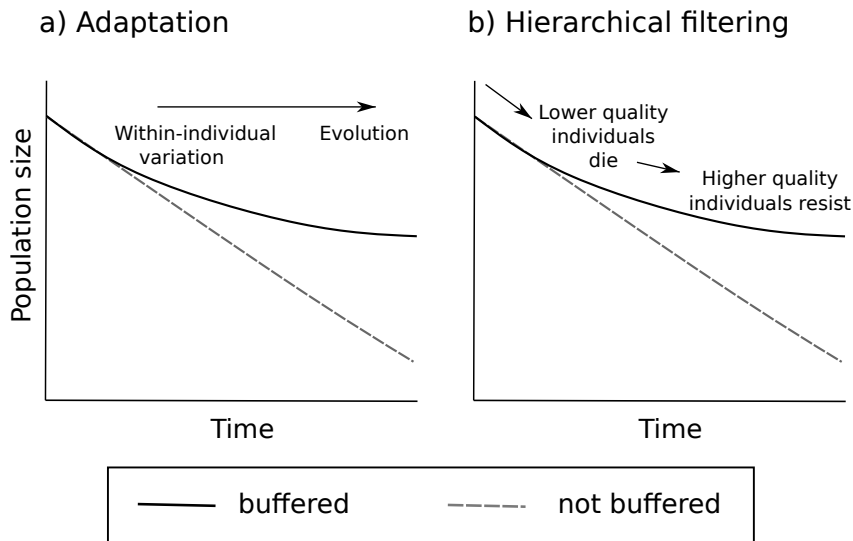


Figure 4.3: Two different types of repelling buffer mechanisms exist. a) Adaptation may occur immediately or after some time period of sampling environmental cues via within-individual variation as well as via microevolution. b) Hierarchical filtering occurs if there is a clear context-independent optimum in locations (i.e. differences in site-quality) or individual quality.

Within-individual variation Adverse abiotic or biotic conditions may be buffered due to adaptive within-individual variation in traits. Altered traits may relate to morphology, behaviour, physiology or life-history (Sergio et al. 2018) and changes may either be reversible or irreversible. For instance, invasive seagrass causes detrimental hypoxic conditions for bivalves (*Anadara trapezia*), which cope with these adverse conditions by burying less deeply which increased survival rates to pre-invasion levels (Wright et al. 2010). Due to this buffer mechanism, invaded populations, which were originally thought to face extinction (Gribben et al. 2009), instead persisted (Wright et al. 2010). In another case, multiple life-history traits change towards the warmer edge of a tundra plant species, with survival and recruitment decreasing, yet growth increasing. This anti-correlation of vital rates ultimately buffers populations at the edge of a species range (Doak and Morris 2010). An example of adverse biotic conditions is the presence of predators. Mussel populations, for instance, may increase shell thickness in response to the presence

of endemic predators, however, the same populations fail to respond equally to an invasive species (Freeman and Byers 2006). This highlights that buffer mechanisms due to within-individual variation is sometimes limited by the ability of individuals to sense changing environmental conditions and respond accordingly (Mathot et al. 2012; Oro 2020).

Microevolution In the previous example case (Freeman and Byers 2006), naïve mussel populations failed to respond to an invasive predator. Yet, 15 years after the invasive species first occurred, mussel populations were able to respond to the invasive predator species as they did towards the endemic predator species which increased population growth rates (Freeman and Byers 2006). The reason behind this buffer mechanism is presumably microevolution within affected populations, which has been recorded in several species and for several traits. For instance, microevolution of life-history traits in response to adverse conditions is known for fish species, which evolved generation times and adult body sizes adapted to fishing techniques being used (Jørgensen et al. 2009; Law 2000). The speed at which microevolution can mediate a buffer mechanism scales with the heritability of functional traits, the standing level of among-individual variation in these traits and their mutation rates, the selective pressure, as well as generation times. As such, the evolvability of a population is intertwined and limited by the magnitude of other buffer mechanisms such as portfolio effects due to among-individual variation in niche traits. In summary, if a novel stressor occurs, within-individual variation and microevolution may accumulate and both contribute to alleviating the rate of population decline (Fig. 4.3; Chevin et al. 2010; Lande et al. 2009). Yet, whether buffering due to adaptation may suffice depends on how novel, rapidly occurring and extreme a stressor is (see Box 1).

Hierarchical filtering

Besides asynchronous dynamics of subgroups of a population with certain subgroups performing better or worse under particular circumstances (i.e. portfolio effect), there may also be subgroups that perform consistently (i.e. context-independent) better, i.e. are of higher quality (Fig. 4.3, Fig. 4.4). Subgroups of lower quality should be more severely affected by adverse conditions than subgroups of higher condition. As such, under adverse conditions high-quality subgroups should create a “floor” for population decline from which populations can recover (DeAngelis and Waterhouse 1987). The higher the overall quality of subgroups, i.e. the higher the magnitude of this buffer mechanism, the less are adverse conditions reflected in population trends and the higher or more firm the “floor” becomes. We

name this repelling buffer mechanism hierarchical filtering, as it becomes apparent if there is a context-independent hierarchy resulting in high and low quality subgroups. Hierarchies can result from variation in site quality and among-individual variation in quality.

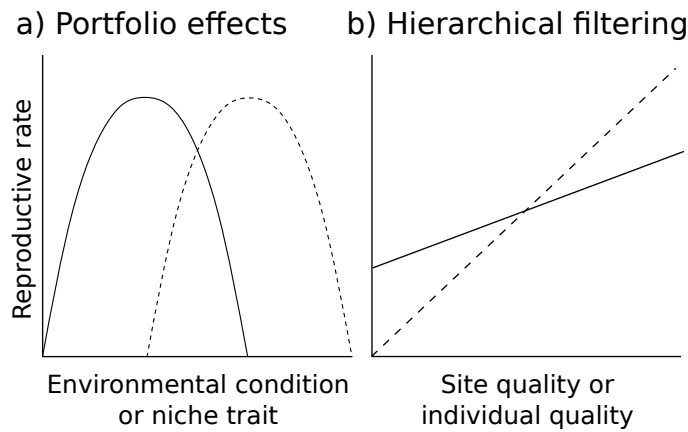


Figure 4.4: Differences between hierarchical filtering and portfolio effect. a) Portfolio effects result from context-dependent optima (solid vs dashed line) of an environmental property or a niche trait. As an outcome, the subpopulation with higher fitness is not fixed. B) In contrast, hierarchical filtering results from context-independent ranking between individuals due to differences in their quality or the quality of the location they inhabit. With context (dashed vs solid line), only the differences between ranks may change, for instance facilitating reproduction at low-quality sites.

Site quality First, differences in site quality (i.e. “better and worse” locations) can confer hierarchical filtering, which most prominently has been discussed in terms of “safe sites” or “refuges”. DeAngelis and Waterhouse 1987, hypothetically formulate that safer sites should result in relatively lower mortality compared less safe nest sites. Assuming that site safety has no relevant trade-offs, there is no difference in mortality under less adverse conditions. Hence, if there are more safe sites and the magnitude of the buffer mechanism is higher, there is no context-dependent optimum site safety but “the more the better” (Fig. 4.4).

Studies at the regional level, for instance, found that bird populations at low-quality sites express phases of strong declines whereas populations at high-quality sites remained stable at high levels of population size (Gill et al. 2001). At a local scale, hierarchical filtering due to variation in site quality is more evident in immobile species (Lloret et al. 2012; Lloret et al. 2004; Suarez et al. 2004) or during life

stages with reduced or no motion capacity (resting stages, hibernation, nestlings). Improving this buffer mechanism is, explicitly, the basic idea of conservation schemes improving nest and resting sites (Fortel et al. 2016; Printz et al. 2021; Wesolowski 2007).

Among-individual variation in quality Hierarchical filtering may also occur due to among-individual variation in quality (i.e. hierarchical traits; Stump et al. 2022). Quality does not affect the niche position of an individual but affects its ability to withstand adverse conditions. In many species, young individuals show higher mortality rates (Payo-Payo et al. 2018) resulting in disproportionate loss of young individuals due to adverse conditions while older individuals can persist and contribute to population growth. In modern coexistence theory, these effects are also described as temporal storage effects. Inter-individual differences in quality can occur due to the stochastic outcome of moving and foraging. Individuals starting with the same conditions may end with different amounts of acquired resources, leading to some individuals being able to endure adverse events whereas other parts of the population will show high mortality. So a ranking between individuals may occur due to contest competition, stochastic effects and environmental heterogeneity. While a buffer mechanism resulting from individuals ranked by acquired resources is ephemeral, safe nest sites may persist for longer time series and buffer populations over a series of severe winters (see Box 1).

4.4 Interactions of buffer mechanisms

Different buffer mechanisms may be linked to the same sources or may interact with one another. Studying these interactions is highly relevant to identifying the impact of separate buffer mechanisms and to inform attempts to predict a population's fate. As we cannot cover all of the particularities of interactions, we, instead, point exemplary to interactions of among-individual variation in niche traits with further sources of buffer mechanisms.

While among-individual variation in niche traits can mediate a dampening portfolio effect, it may also negatively contribute to population persistence. This may occur due to excess degrees of among-individual variation (Crawford et al. 2019) but also due to interactions with density-dependent processes. For instance, variation in phenological traits (mate search, breeding) increases population persistence under stochastic perturbations (Iwasa and Levin 1995), yet, in small populations, where higher degrees of variation becomes detrimental to persistence as mate finding success reduces (Calabrese et al. 2008), i.e. amplify Allee effects.

Box 1: Lurking extinction? Capacity of buffer mechanisms

Global change causes gradual shifts in mean environmental conditions as well as increases in climate variability resulting in more frequent, intense, and often abrupt adverse extreme events (Samaniego et al. 2018; Schär et al. 2004). The contribution of different local buffer mechanisms to population persistence depends on the abruptness, intensity, as well as the pre-occurrence of other adverse conditions. Some buffer mechanisms, such as (micro-)evolution and morphological plasticity, cannot contribute if extreme events occur too abruptly or are too novel in character (Stegen et al. 2017). In other instances, within-individual variation may be triggered by a series of similar adverse events, as experience and morphological changes prime the population (Freeman and Byers 2006; Wright et al. 2010). Conversely, buffer mechanisms may also degrade and be exhausted over subsequent phases of adverse conditions. For instance, buffering due to hierarchical filtering where some individuals have excess resources cannot occur if individuals have spent their excess resources in previous phases of adverse conditions.

It is self-evident that any buffer mechanism is limited, yet, when will buffer capacities be exhausted or exceeded and when may they suffice? Recent studies on phenological asynchrony highlight that buffers mediated by portfolio effects (Abbott et al. 2017; Rytteri et al. 2021) and adaptation (Radchuk et al. 2019b; Simmonds et al. 2020) only have certain capacities. Portfolio effects due to environmental heterogeneity can, in principle, only operate as a buffer mechanism up to the point where no combination of, for instance, microhabitat features and weather (Rytteri et al. 2021; Scheffers et al. 2014) matches with a species' niche. Once the environmental change outpaces microevolution and novel conditions lead to a full mismatch, populations at higher trophic levels can go rapidly extinct (Simmonds et al. 2020). Populations may thus be buffered until capacities are exceeded and sudden declines occur. Such sudden events, also known as regime shifts, are still difficult to predict (Morozov et al. 2020), hence, studying buffer capacities may help to shed light on this topic. In general, given the current pace of global change, it appears likely that novel environmental conditions may increasingly exceed the capacity of buffer mechanisms. Accordingly, many studies addressing certain buffer mechanism conclude that the mechanism will not suffice to mitigate ongoing global change (Radchuk et al. 2019b; Rytteri et al. 2021; Simmonds et al. 2020). Yet, studies seldom represent all local buffer mechanisms, making it difficult to assess the ultimate effect of global change.

Conversely, in larger populations, among-individual variation in niche traits may alleviate intraspecific competition and, thus, increase population persistence

(Acker et al. 2014; Bolnick et al. 2003; Bolnick et al. 2011). Furthermore, niche traits affect an individuals interspecific interactions, among-individual in niche traits may thus result in more different interspecific interactions (i.e. increased degree) with individuals of a focal population differing in their niche-specific interactions (Bolnick et al. 2011). The increased degree may also induce a dampening mechanism by facilitating mutualistic increase or antagonistic release for some individuals with certain niche traits. Ultimately, heritable among-individual variation in niche traits contributes to evolvability, and thus the ability of populations to adapt to adverse conditions (Wolf and Weissing 2012). In summary, the example of among-individual variation in niche traits makes it clear that there are various ways in buffer mechanisms can possibly interact and that those interactions may either be detrimental or beneficial to population persistence. Not regarding those interactions hinders reliable predictions. In the following, we discuss approaches of how to account for buffer mechanisms, their interactions and capacities in empirical studies and models.

4.5 How to account for buffer mechanisms in empirical studies and models

Several issues in studying the persistence of populations have been identified in recent years. The “tyranny” (Bennett 1987) or “fallacy” (Denny 2017) of averaging is a pervasive issue in ecology as it neglects the importance of variation in traits and environmental conditions for driving population dynamics (Bolnick et al. 2011; Moran et al. 2016; Uchmański and May 1985). Alternatively, amalgamating variation by labelling it as noise obscures the underlying processes and may compromise predictions. A further issue arises from a prevalent focus on long-term equilibria in ecological theory. This focus complicates the analysis of rare species and small populations (Jeltsch et al. 2019) and may miss the prevalence of transient population dynamics (Hastings 2004; Hastings et al. 2018; Morozov et al. 2020). Furthermore, if adverse conditions are immediately buffered resulting in no change of population size, the buffer mechanisms will go unnoticed if only population dynamics are monitored (Connell and Ghedini 2015) while monitoring, e.g., population structure or spatial distribution might have detected a decline in buffer capacity and hence warned for pending sudden collapse. Also proxies of total population size (such as breeding population size) may be misleading as they may obscure the exhaustion of buffer capacities (Katzenberger et al. 2021). To overcome these issues, approaches that observe or represent individuals along with their states, environment, and spatial interactions explicitly, are required. Such approaches allow for the repres-

entation and study of buffer mechanisms in higher detail and can improve the reliability of predictions of the fate of populations as well as inform management.

4.5.1 Empirical studies

Studying buffer mechanisms empirically would likely not necessitate any new methods or approaches. Phenomena as adaptive microevolution, within-individual variations, or density-dependent population growth are established research topics. Yet, empirical examples addressing multiple local buffer mechanisms are rare (Dibner et al. 2019). In other instances, the distinction between sources of portfolio effects could not sufficiently be addressed (Abbott et al. 2017). Substantial advances could be achieved by linking these phenomena explicitly and directly to the questions of local population persistence. Relating the population growth rates to biological and ecological variables could elucidate what mechanisms help populations to persist. That is, research could focus on what population-level biological and ecological shifts coincide with the end or reversal of population decline: Are there changes in relative abundance of life stadia, or rather physiological or physiological change in population? If the change is genetic, is it an establishment of new gene variants, or rather spread of pre-existing variation?

Arguably, this direct experimental approach is available only in species with short generation times. Alternatively, seed production or biomass measurements of plants could be evaluated as potential proxy for population dynamics. The advantage of plants is their sessile life style, enabling to study the interactions between environmental heterogeneity and adverse conditions. Eventually, explicit recognition of buffering mechanisms may help to identify underlying traits. For instance, in species that tend to be locally rare, do they more often express “buffer traits”, such as shorter generation times, high ability for within-individual variation, diversification bet-hedging (Wright et al. 2019) or production of persistent life stadia.

4.5.2 Modelling studies

Ecologists developing or using models should, thus, ask if their models sufficiently represent buffer mechanisms, along with their capacities, latencies, and interactions. Improving the representation of buffer mechanisms demands increased efforts to build ecological models from first principles (Egli et al. 2019; Grimm and Berger 2016; Radchuk et al. 2019a). Studying buffer mechanisms – or a lack thereof – with such approaches will foster understanding of drivers underlying possible global change-induced extinction events (Cahill et al. 2013). Agent-based models can, in principle, fulfil the requirements to study buffer mechanisms as well as their interactions and become especially useful in spatial context which is difficult to

represent analytically. Further modelling approaches such as integral projection models are “individual-based” and have successfully been applied to study the effect of within-individual variation as a buffer mechanism under climate change (Simmonds et al. 2020). Modelling studies accompanying empirical efforts can help elucidating the role of buffer mechanisms and their interactions, by providing a controlled environment.

4.6 Conclusions

Many populations are anticipated to decline for several years before ecological management programs may reverse this trend (Leclère et al. 2020; Sala and Knowlton 2006). It is still unclear which populations may go extinct and which populations will persist. General mechanisms and correlates associated with extinction risk are scarce, and causes of population decline appear mainly to be idiosyncratic (Cardillo and Meijaard 2012). In this article, we argue that there is evidence of important mechanisms that may either increase persistence in small populations or prevent populations from getting too small in the first place. These local buffer mechanisms are so far only insufficiently addressed by current approaches, yet, their synthesis is crucial for adequately considering and analysing them in modelling and empirical studies. While novel modelling and empirical studies for instance point towards limited buffer capacities in face of global change (Rytteri et al. 2021; Simmonds et al. 2020), we lack an assessment of multiple buffer mechanisms as well as their interactions. Hence, further efforts are required to study which role these different mechanisms may play for species persistence. Our article aims to motivate this effort by providing a general view on this topic and by introducing a novel classification which can help alleviating some issues with accessing and applying buffer mechanisms. We defined two categories of buffer mechanisms, i.e. dampening and repelling mechanisms, and exemplary outline how different mechanisms can interact. We outlined a framework for future research of these mechanisms, identified key properties and biological foundations. In summary, such research may greatly help at overcoming current limits in our understanding. Future works could also elaborate on an integration between local and regional buffer mechanisms as well as their interactions. These efforts come with the promise of moving ecological research closer to reliable predictions on the fate of populations.

4.7 Additional information

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Conflicts of interest

None.

Statement of Authorship

AM wrote the first draft and developed the concept. VG provided the initial ideas. All authors reviewed and edited the draft.

Chapter 5

Model of interaction between hyphal movement and micro-structured environments

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Milica Lakovic, Florian Jeltsch & Matthias C Rillig
Status: in preparation
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Abstract

Studies in PDMS (polydimethylsiloxane) microstructures show that fungal ability to navigate micro-environments is based on species-specific traits. Given the micro-scale properties of fungal habitats are themselves variable, a possibility exists that particular species are preferentially adapted to different microstructure architectures. We hypothesize that spatial features of microstructures alone can result in spatial niche partitioning. To test this hypothesis, we developed an agent-based model of hyphal propagation. The model simulates the hyphal growth in microstructure environments, and was developed using current knowledge on hyphal growth, space-searching algorithms, and structure of mycelia at microscopic level. Hyphae simulations were parametrised with varying navigation traits in four different degrees of microenvironment porosity, mimicking the microstructures of soil as an important fungal habitat. We show that hyphal navigation and grow traits can be specifically adapted to forage efficiently in different degrees of porosity.

5.1 Introduction

In living organisms, movement occurs in a myriad of ways and on all levels of organization. This has been traditionally reflected in the division of life sciences into disciplines: cellular biology considers cytoplasmic flow or movement of organelles; physiology studies blood flow; while developmental biology describes changes in body part positions during growth. Movement ecology focuses on the movement of entire organisms and their propagules within the environment when searching for food, suitable habitats, reproduction, or avoiding danger.

However, this traditional distinction of biological movement into different domains of life sciences applies only for motile unitary organisms and propagules of sessile organisms. It becomes problematic once we consider modular organisms such as filamentous fungi. Their bodies are composed of filaments (hyphae) interconnected into a mycelial network. In the form of this network, hyphae forage by growing into new areas, and resource patches are integrated through cytoplasmic transport (Moore et al. 2020). Fungi use these very specific movement means to respond to the universal challenges presented by a heterogeneous environment. In filamentous fungi, the physiological, developmental and ecological functions of movement are not present as distinctive physical phenomena. They are intertwined within the dynamic processes of a filamentous body, and this often leads to the ecological function of movement being rather overlooked by researchers.

The first fungal studies in PDMS landscapes demonstrated inter-specific variability of movement and navigation at the microscale, and evidence suggests that fungal navigation and movement capacities are tightly controlled and evolved as species-specific traits (Hanson et al. 2006; Held et al. 2009; Held et al. 2008). Comparative studies of fungal species showed differences in traits such as branching angle, branching distance, or in responses triggered by the collision with obstacle (e.g. directional memory, sliding, collision-induced branching) (Hanson et al. 2006; Held et al. 2009; Held et al. 2008). The third section of this thesis covers the development and application of an agent-based model (ABM) developed with the aim of studying spatial niche partitioning in microstructures. The first fungal studies in PDMS landscapes demonstrated inter-specific variability of movement and navigation at the microscale, and evidence suggests that fungal navigation and movement capacities are tightly controlled and evolved as species-specific traits (Hanson et al. 2006; Held et al. 2009; Held et al. 2008). Comparative studies of fungal species showed differences in traits such as branching angle, branching distance, or in responses triggered by the collision with obstacle (e.g. directional memory, sliding, collision-induced branching) (Hanson et al. 2006; Held et al. 2009; Held et al. 2008).

Not only do fungi differ in the way they navigate microstructures, but natural

micro-environments are themselves variable. They differ in their architecture, defined here as a composite term involving the degree of porosity and geometric properties of soil particles (Baveye et al. 2018; Wei et al. 2016).

This opens the possibility that particular fungal species express different degrees of adaptation to different architectures, and the spatial features of microstructures alone can modulate fungal community interactions and assembly. One of the important functions of fungal hyphae and mycelium is foraging for new resources (Boddyl 1999). Therefore, we chose foraging ability (defined as the maximum distance the mycelium can reach during the simulation) to demonstrate the potential of our ABM to study the spatial ecology of fungi at the microscale. We simulated the growth of fungi with different movement traits in various degrees of environmental porosity, and analyzed the differences in foraging ability between trait-porosity combinations.

The model has been constructed in NetLogo. This provides a user-friendly environment, which we hope will further stimulate the trait-based approach across research groups studying diverse fungal species. In order to increase the accessibility of the model to the broader audience, we provide a short introduction into individual/agent-based models (ABM), and a detailed model description.

In the following section, we explore the possibility of interspecific differences in hyphal movement to generate spatial niche partitioning, by developing an agent-based model of hyphal propagation. We describe the concept and technical details of our model, developed to achieve a high degree of structural realism, with multiple parameters derived from structural traits of real mycelia and empirical PDMS research (Hanson et al. 2006; Held et al. 2009; Held et al. 2008).

5.2 Methods

Given that application of individual/agent-based modelling (ABM) in fungal ecology lags behind its application in ecology of plants and animals, we provide first a short introduction to its potential and limitations, followed by a detailed description of the model itself, including its code. An advantage of ABMs is that they do not require the individuals and their interactions to be treated as a population-scale, averaged parameters typical of mathematical (analytical) models (Grimm and Railsback 2006; Jeltsch et al. 2019). In ABMs, system behavior is an emergent property of interactions between individuals and their environment. Variability among individuals, local environments and their interactions can be maintained, increasing the ecological realism of the system. Thus, ABMs are particularly useful in systems and research questions where individual variability is expected to play a significant role, or where properties of local interactions and local neighbourhoods

cannot be meaningfully averaged at a higher spatial scale (Grimm and Railsback 2006; Jeltsch et al. 2019). In case of our model, each hyphal tip acts as an individual, independent agent. What follows is that each encounter with microstructure and other hyphae has also its unique outcome, based on spatial variables such as angle of encounter or local density of hyphae.

A disadvantage of ABMs compared to analytical models is that it is not readily evident what are the pathways of emergence, i.e. how exactly the processes at the scale of individual agents lead to the observed patterns at the entire system level. Related to this, ABMs are more complex than analytical models (Grimm et al. 2006; Salecker et al. 2019). To alleviate this downside, the emphasis in publishing the ABMs is on detailed, accessible and transparent descriptions, which in turn should improve the interpretability and reproducibility of the results (Grimm et al. 2006). In following sections, we describe the model in close detail.

5.2.1 Overview, Design Concepts, and Details

Purpose

The purpose of the model is to study whether the species-specific hyphal traits can interact with microstructures to modulate the performance of organism, and lead to the spatial niche partitioning.

State variables and scales

The model world is a simulated soil-like 2D arena. This arena is divided into open space and simulation of soil-like particles. Open space is where hyphae can freely propagate forming mycelium (growth starts from a point in the center). Soil-like particles cannot be penetrated by hyphae and must be avoided upon contact, by means described in previous research in PDSM microstructures (Alekklett et al. 2021; Held et al. 2009; Held et al. 2008).

The movement processes and distribution of soil-like particles are simulated in continuous space (i.e. the movement and particle geometries are not restricted to the grid/patches – the grid only stores local information to make processes more efficient).

The arena is a square with one side measuring 1 to 25 millimeters and can be filled with 2D particles of varying size (parameter maximum-grain-diameter is 5 μm to 500 μm), number and shape. Soil-like particles can be round or rectangular, with their shape being defined by the parameter roundness. With increasing size and number of particles, the porosity is decreasing. Porosity reaches values from 1 (i.e. growth of mycelium in open space without obstacles) to approximately 0.35 (most dense environment in our model). The particles are modelled as enclosed spaces delineated by link-type agents (surface-links).

Except for the surface- links and patches (2D squares, basic building blocks of each NetLogo world (Salecker et al. 2019)), all other key agents belong to the mycelium. From the perspective of movement, fungal hypha can be divided into two compartments: the growing hyphal tip and the posterior static part of hypha (Steinberg 2007). Hyphal tip realizes the growth (i.e. elongation of hypha) and it is here where mechanisms responsible for space searching algorithms (i.e. movement response to the environment) are located. Thus, in our model, it is represented by a moving agent called hyphal-tip. Hyphal-tip generates elements of mature hypha alongside its movement track (see below), detects the surrounding surfaces and hyphae and acts accordingly. The posterior parts of hyphae do not grow, but can engage in the formation of the mycelial network through their role in negative autotropism and anastomosis (hyphal fusion) (Brand and Gow 2009; Fleißner 2012; Fleißner and Serrano 2016).

In our model, mature hyphae posterior to hyphal tips consist of two static agents; (hyphal) nodes and hyphae (link-type agents, i.e. edges, connecting nodes; Fig. 5.1). Hyphal links are static structures upon which the hyphal-tips react in processes of hyphal autotropism and anastomosis (Brand and Gow 2009; Fleißner 2012; Fleißner and Serrano 2016). The nodes are static points where the hyphae branch and anastomose.

The following state variables define how the hyphal-tip produces hyphae in processes related to its movement, reproduction, anastomosis, respond to other hyphae and surface-links of particles: Propagation-speed [$\mu\text{m}/\text{min}$], random-propagation-angle [$^\circ$], lateral-branching-interval [μm], lateral-branching-angle [$^\circ$], anastomosis-probability, autotropism-strength, autotropism-perception-range [μm], autotropism-cone-angle [$^\circ$], collision-branching-threshold [$^\circ$]. Each state variable is described separately in the table of variables (in which also other model variables related to implementation details can be found, C1). Here, we briefly describe the processes of the model.

Process Overview and scheduling

Simulation is initialized as an environment of open spaces and particles delineated by surface-links. At the point of initialization, the simulated organism is a point in the middle of the environment, located at open space area. At this point, there are several initial hyphal-tips (based on the variable n-hyphal-tips, set by the user), connected by hyphae links to the single initial hyphal node. After initialization, the initial hyphal-tips start moving based on the parameters' specification. Each time step, they pass a distance of propagation-speed and generate a hyphal node (unless frequency is reduced by the user). New hyphal nodes connect themselves by hyphae links to the previous node in their respective hypha, and the newest node

is connected on one end to the hyphal-tip that generated it. Hyphal-tips keep track of the distance they passed and at intervals defined by lateral-branching-interval [μm] they generate a new hyphal-tip that adopts new heading in accordance with the value of lateral-branching-angle [$^\circ$]. This new hyphal-tip is connected to the parental hypha in a node, and after a certain retention-time, a new hyphal-tip starts growing and producing its own hypha. All hyphal tips grow in straight lines if random-propagation-angle [$^\circ$] equals zero, or hyphal tips wiggle if random-propagation-angle [$^\circ$] is larger than zero.

The above text describes the growth of hyphae in open environment, when no object is detected ahead of the hyphal-tip for the given time step. As the hyphal-tips move, they interact with two kind of objects: surface-links that represent the surface of soil-like particles, and hyphal links of other hyphae. If a surface-link crosses the movement path, the angle of encounter is calculated. If the angle of encounter is smaller than collision-branching-threshold [$^\circ$], hyphal-tip moves towards the surface of the particle and proceeds sliding alongside of it. If angle of encounter exceeds the collision-branching-threshold [$^\circ$], the hyphal-tip moves towards the surface, splits into two hyphal-tips and these continue sliding in opposite directions.

If a hypha is detected ahead of the hyphal-tip at a distance smaller than autotropism-perception-range-micrometers, the hyphal-tip changes its current heading by the value defined by autotropism-cone-angle and by autotropism-strength. Unless the autotropism-strength is set to zero by the user, the hyphal-tip changes its heading either towards or away from the closest intersection with the detected hypha (i.e. positive or negative autotropism, respectively). If the detected hypha is on collision course with the focal hyphal-tip, then anastomosis takes place with the likelihood given by the value of anastomosis-probability.

The last variable that defines the deterministic part of behavior is the Boolean called (with a question mark) memory?. It determines the behavior of sliding hyphal-tip once the obstacle is passed. We will describe the variable memory? in more detail in the next section.

Stochasticity is introduced in the growth of mycelium via four variables. Random-propagation-angle [$^\circ$] indicates the degree of random wiggling of a hyphal-tip around its heading. For lateral-branching-interval [μm], lateral-branching-angle [$^\circ$], and collision-branching-threshold [$^\circ$] each hyphal-tip grows, moves and reacts with a value that is sampled from the normal distribution around the mean. Both mean value and its standard deviation are set by the user.

Design concepts and rationale for implementation of model mechanisms

In previous theoretical works, hyphal growth has been conceptualized as a form of ecologically relevant movement (Bielčík et al. 2019). This opens the possibility of

fungal growth (i.e. active fungal movement) to impact the foraging ability and spatial niche partitioning of the organism by means similar to those studied in animal communities (Bielčík et al. 2019; Jeltsch et al. 2013; Schlägel et al. 2020). To evaluate the model, we test these expectations. Some of the state variables/parameters of fungal behavior, together with their allowable value ranges, were derived directly from empirical research on mycelium architecture, or fungal growth in PDMS microstructures. These include propagation-speed, lateral-branching-interval, lateral-branching-angle, collision-branching-threshold, and memory?. While the biological relevance and definitions of the first three variables are self-evident, the latter two deserve a closer explanation. Collision-branching-threshold is a hyphal trait first identified relatively recently in PDMS microstructures (Held et al. 2009; Held et al. 2008). In short, species differ in the value of the encounter angle (between hyphal tip and the surface) that decides on whether the tip continues sliding without branching, or it branches apically with two new tips, each exploring opposite directions (Held et al. 2009). In general, the lower the collision angle, the more likely the tip will continue sliding without branching. Yet, the exact threshold value is a species-specific trait. Thus, it is one of the traits we explore for their impact on foraging efficiency.

In case the hyphal tip does not branch following collision, once the end of the obstacle is reached two scenarios are available (Fig. 5.1). It can either continue growing in the direction of sliding, or it can resume the original growth direction prior to collision (Held et al. 2009; Held et al. 2008). The former takes place in species without directional memory (represented as Boolean variable, memory? OFF), the latter in species with directional memory (memory? ON). Principally, it would be possible that exactly the same Boolean variable directs the behavior of hyphal tips created at the point of the collision by apical branching. We chose to not implement this, and all hyphal tips created in collision induced branching remain growing in the direction of sliding, without re-assuming the growth direction of the parental hypha. This decision was made based on observation that the Spitzenkörper in hyphal tips is key for existence of directional memory, while during apical branching the Spitzenkörper is degraded and two new ones are created for each hyphal tip (Held et al. 2019). This likely leads to the loss of the information about the former growth direction.

During the conceptual development of our model, it became clear that there are several hyphal growth traits that have, to our knowledge, not been studied empirically in any detail that would allow for direct parametrisation of the model. These are the degree of hyphal wiggling, the details about anastomosis and about the negative autotropism. While it is beyond any doubt that these three features of fungal biology influence the growth of the hyphae and mycelial architecture

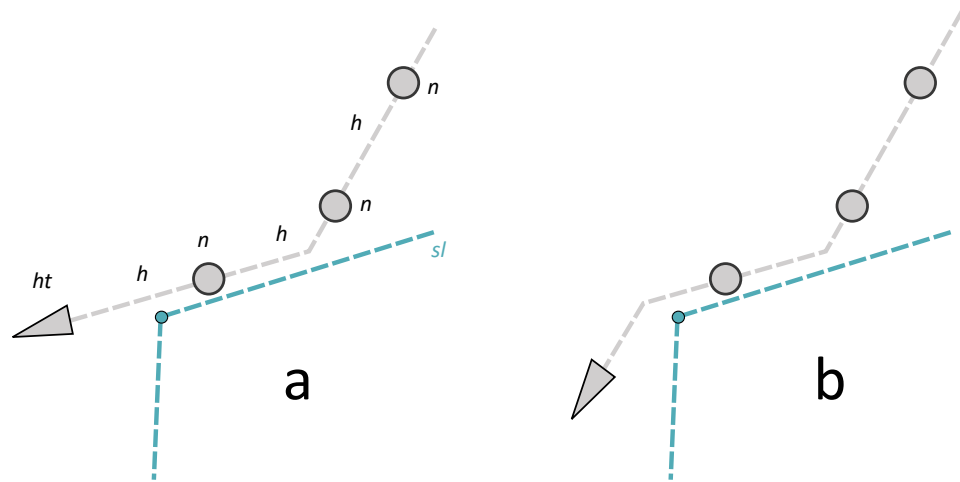


Figure 5.1: Depiction of hyphal directional memory. When the hyphal tip (*ht*) encounters an obstacle (modelled as surface-link: *sl*, green), it starts sliding alongside the obstacle until it reaches its edge. Then it will continue with the new heading in fungi without directional memory (a). In fungi with directional memory it resumes the heading prior to encounter with the obstacle (b). Depicted are also static elements of mature hypha: nodes (*n*) and the links that interconnected them, called in our model simply hyphae (*h*).

(Brand and Gow 2009; Fleißner 2012; Fleißner and Serrano 2016), we did not find any literature attempting to quantify them. Negative autotropism between hyphae of the same mycelium is one of the typical movement- and space- related features in fungi. To our knowledge little is known about the quantitative properties of negative autotropism. For instance, what is the range at which hyphae perceive each other, is the autotropic behavior dependent on spatial parameters of encounter such as angle of approach, or location of hyphae within mycelium? How strong is the autotropic behavior, i.e. to what degree can a hyphal tip be deflected from its original growth trajectory once the other hypha is detected? Given this lack of empirical knowledge, the model interface offers a flexibility in setting up and simulating the properties of negative autotropism. Three autotropism-relevant variables can be manipulated in the interface: autotropism-strength, cone-angle, and perception-range-micrometers. The parameter deciding about the autotropism-strength can be set to a wide range of values, both positive to negative. Before simulations, we tested empirically whether the chosen values resulted in a naturally appearing mycelium (see below).

Similarly, although we know that hyphae do not grow in straight lines and

the degree of wiggling differs among species, we did not have any exact values with which to parametrize the model. We run multiple simulations, observed the patterns, and chose the interval for simulations that appeared to produce natural mycelia.

The likelihood of anastomosis upon encounter can be set anywhere from zero to one, and in our model, it is not influenced by any additional spatial parameter of encounter (i.e. angle of encounter).

Initialisation

The parameter `soil-particles` defines the number of soil particles. Their geometry is defined by the `maximum-grain-diameter` and `roundness` parameters (Fig. 5.2). The number of soil particles is iteratively added to simulation by selecting points that are not already covered by soil particles or in their proximity (i.e. no other soil-particles within a distance of `maximum-grain-diameter` divided by 2). Once such a position is identified, from this center a number of (agent) sampled from a uniform distribution with a range 3 to `roundness` is spawned at that position with random heading. Each agent moves forward by an amount equal to `maximum-grain-diameter` divided by 2. The agents form links (i.e. straight lines or edges) in a clock-wise manner so that they form a closed network. Patches in radius 2 of the links add the link to their `my-surfaces` state variable which later informs the hyphal-tips about possible collision with the surface of a soil particle.

If there are no more locations available the target grain size is divided by two until a number of soil-particles equal to `soil-particles` has been placed. The outer borders of the environment are delineated by 4 edges which are also added to the `my-surfaces` of patches within a radius of 2. These edges limit the growth of the hyphal tips to the experiment area and result in the same behaviour as with regular soil-particles.

Input data

There is no external input of data.

Submodels

This section describes details of submodel `go` and other submodels that submodel `go` calls (Fig. 5.3). Together, they define processes that are carried out by each hyphal tip during each time step. Thus, it generates the growth of the hyphae and simulates the way hyphal tips react to the external environment. The growth of the mycelium is therefore an iterative process of multiple runs of `go` submodels (how many is set by the user).

go The submodel `go` first checks whether the current run (i.e. time step, or tick) is the first one in a given simulation. If so, it calls the submodel `place-initial-nodes`.

Following this, hyphal tips are asked to check their own retention time. Initially,

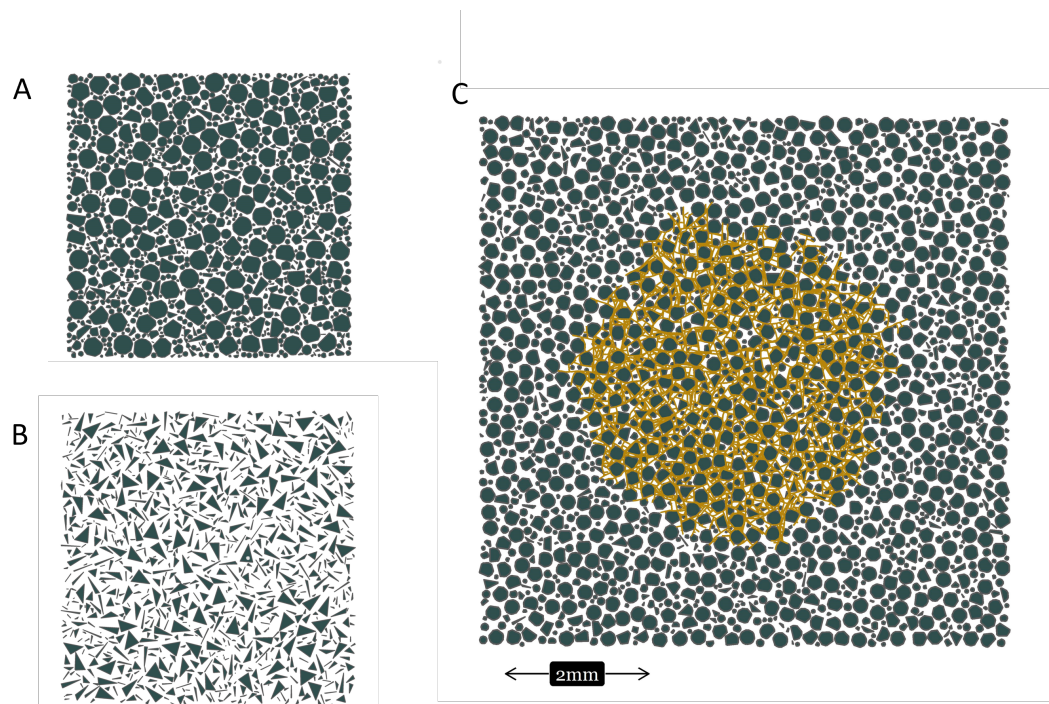


Figure 5.2: Exemplary soil architectures. A) High maximum-grain-diameter and 1,000 soil particles with high roundness (20). B) Equal maximum-grain diameter, yet, lower roundness. C) Lower maximum-grain-diameter resulting in a more homogeneous grain size distribution. Here, the growth of the mycelium after 1,000 minutes is depicted.

at the moment of tip creation retention-time is assigned a negative value that increases with every time step (set retention-time retention-time + propagation-speed). The moment the retention-time is positive, the hyphal tip can start growing.

Thus, if retention-time > 0, the following commands and submodels are run: The hyphal-tip hatches a new node (at each time step, or in intervals prescribed by user by node-frequency).

The new node connects itself with the previous node, asks the parental hyphal-tip to cancel its existing links, and creates a link with the new node.

The hyphal tip further inquires whether it is currently sliding. In case it is not, it checks the presence for another hyphae that could require it to alter the heading, by calling the submodel autotropism. Further in case of no sliding, it adjusts the heading based on its original heading, but with a certain degree of hyphal wiggling. In case of sliding, it is the heading of obstacle that gives the hyphal-tip its own heading.

The new heading is stored as memory-heading and initial momentum is given

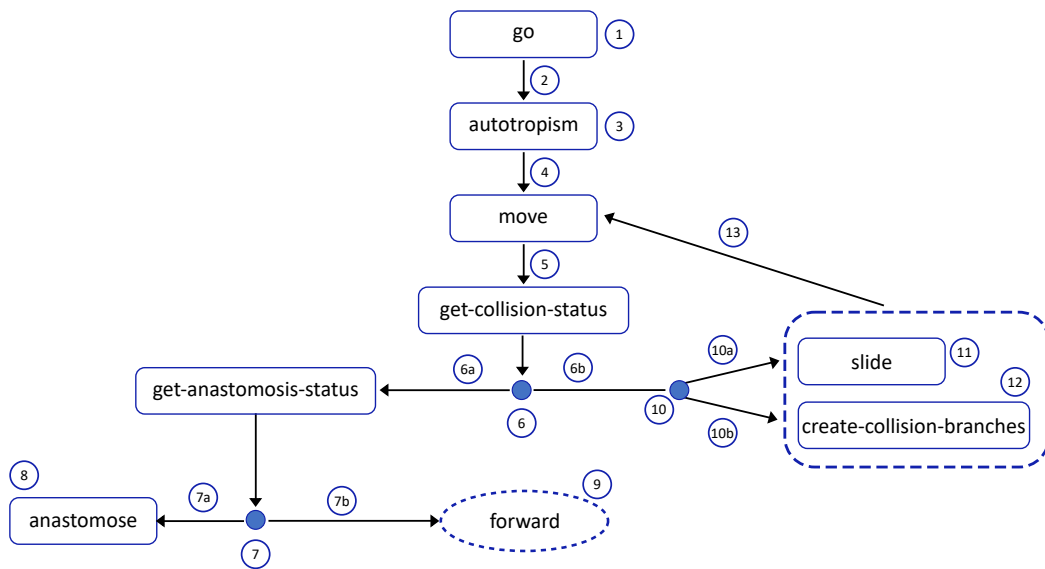


Figure 5.3: Submodels called by the submodel go. Submodel go checks the age of the hyphal-tip and if it is greater than retention-time, submodel go produces the node of the hyphal-tip and a link that connects these two agents (1). It then calls submodel autotropism (2), and autotropism adjusts the heading of the hyphal-tip (3). Subsequently, submodel go calls submodel move (4). Submodel move first calls submodel get-collision-status (5). Get-collision-status checks presence of soil-like particle ahead (6). If the result is negative (i.e. no particle ahead), submodel get-anastomosis-status is called (6a). Get-anastomosis-status checks presence of another hyphae ahead of the hyphal-tip (7). If the result is positive (7a), anastomosis may take place by calling submodel anastomosis, which leads to the disappearance of the hyphal tip (8). If the result of (7) is negative, the hyphal-tip moves forward (9). If the result of the submodel get-collision-status is positive (6b), the angle of the collision (i.e. angle between the soil surface and hyphal-tip trajectory) is compared to the collision-branching-threshold (10). If the collision angle is smaller than collision-branching-threshold (10a), the branching is not induced and the hyphal-tip assumes a new heading alongside the soil surface (11). If the collision angle is above the collision-branching-threshold (10b), the branching is induced. The submodel collision-branching-threshold creates two hyphal-tips in place of the original one, and gives each an opposing direction alongside the surface (12). Thus, either following the submodel slide (11), or following submodel create-collision-branches (12), the hyphal-tip(s) will continue alongside the surface, calling the submodel move and other downstream submodels (13).

the value of propagation-speed. Regardless of the sliding status, the submodel move and its own sub-submodels (e.g. get-collision-status) is called (see below).

The hyphal-tip asks patches in a radius of 2 spatial units to update the agent set

my-nodes by adding the newly hatched hyphal node to it. My-nodes is used in submodels get-collision-status, get-anastomosis-status and autotropism.

Finally, if the hyphal-tip has already travelled the distance larger than the distance between lateral branches, it hatches a new hyphal-tip by calling the submodel create-lateral-branch:

```
if (dist-travelled * spatial-units-conversion-factor) >
  lateral-branching-interval-mean
[
  create-lateral-branch
]
```

place-initial-nodes At the start of the growth simulation (if ticks = 0), the initial node is created by calling the submodel place-initial-node. Initial node is created by a randomly selected initial hyphal-tip (hyphal-tips are already present after the setup submodel).

```
ask one-of hyphal-tips [hatch-nodes 1]
```

Once created, the hyphal-tip that hatched the initial node creates a link to it.

```
create-hyphae-with (turtle-set last-node)
```

Surrounding patches (in-radius 2) are asked to update their my-hyphae variable by including the newly created node.

```
ask myself [set last-node myself]
ask patches in-radius 2
[
  set my-nodes (turtle-set my-nodes [last-node] of myself)
]
```

When simulation begins with multiple hyphal-tips, the remaining tips must be also connected to the initial node. Thus, all hyphal-tips without a link assign status of last-node to the existing initial node, and subsequently connect to it by a link.

```
ask hyphal-tips with [count my-links = 0]
[
  set last-node one-of nodes
  create-hyphae-with (turtle-set last-node)
]
```

At this point, the initialized mycelium consists of one node and n hyphal-tips connected to it by n links. All these agents still have the same location. In order to rule out an erroneous anastomosis event, the submodel place-initial-nodes is

finalized by the hyphal tips making a small forward movement away from their initial position.

```
ask hyphal-tips [fd (1 / spatial-units-conversion-factor)]
```

create-lateral-branch As the hyphal growth simulation proceeds, each hyphal-tip keeps updating the variable of already travelled distance, `dist-travelled`. The submodel `go` is comparing the value of `dist-travelled` with the `lateral-branching-interval`. Once the former is greater than the latter, the `dist-travelled` is reset to zero and the current hyphal-tip hatches a new hyphal-tip and a new node, which are then interconnected by links. That is, a new lateral branch is initiated.

```
if (dist-travelled * spatial-units-conversion-factor) >
  lateral-branching-interval-mean
[
  create-lateral-branch
]
```

In a deterministic scenario, each hyphal-tip would start with exactly zero value of `dist-travelled`. In order to account for stochastic distributions in real mycelia, the actual initial value of `dist-travelled` has zero as its mean value, with `lateral-branching-interval-sd` as the standard deviation around the zero.

```
set dist-travelled random-normal 0 (lateral-branching-interval-sd /
  spatial-units-conversion-factor)
```

In addition to setting the initial value of `dist-travelled`, each newly created lateral branch (a hyphal-tip at this point) adopts an initial heading equal to the heading of parental hypha (submodel `go`: `set heading memory-heading`). In submodel `create-lateral-branch`, this initial heading is then changed to create branching angle. The hyphae branch randomly on left or right side in open space. In case of an obstacle on one side, it will branch on the opposite (free) side.

```
let lateral-branching-angle random-normal lateral-branching-angle-mean
  lateral-branching-angle-sd

ifelse random-float 1 < .5
[
  rt lateral-branching-angle
  get-collision-status
  if not empty? collision-status
  [
    lt 2 * lateral-branching-angle
    set collision-status (list)
  ]
]
```

```
]
[
  ...
]
```

The new hyphal tip needs to be connected to the mycelium (i.e. the model's network of nodes and hyphae links). Thus, in `create-lateral-branch` the parental hyphal-tip also hatches a new node. This new node creates a link with the parental hyphal-tip, with new hyphal-tip, and with the original last-node of the parental hyphal-tip. It is also assigned the status of the current last-node to both hyphal-tips, and the link between the former last-node and parental hyphal-tip is deleted.

```
hatch-nodes 1
[
  create-hyphae-with (turtle-set [last-node] of myself)
  ask myself [ask my-links [die]]
  ask myself [set last-node myself]
  create-hyphae-with (turtle-set myself)
]
```

And for the new tip in regard of interconnecting the link:

```
hatch-hyphal-tips 1
create-hyphae-with (turtle-set last-node)
```

In real hyphae, the lateral branches usually start growing at a certain distance posterior to the leading hyphal tip. For this reason, the submodel ends with setting up a negative value of retention-time of the new hyphal tip.

```
set retention-time -2
```

move In order to limit computational demands, hyphal-tips do not always compute the parameters of possible collision, i.e. `get-collision-status`. Instead, the submodel `move` begins with the hyphal-tip determining whether the collision is possible in the next step. That is, whether the patch of its current location is in vicinity of particle's surface. Only if this is true, it will inquire the details of the surface and potential collision.

```
if [soil?] of patch-here
[
  get-collision-status
]
```

The variable `soil?` is a Boolean that reports true for patches in vicinity of particle's surface, defined in submodel `create-soil-particles`: `ask border-patches [set soil?`

true] The entire rest of the submodel move are two alternatives (`ifelse`) based on the result of the `get-collision-status` inquiry.

```
ifelse not empty? collision-status
```

For cases where the vicinity of soil particle actually leads to the collision in the next step, i.e. the `collision-status` list is not empty, the hyphal-tip moves towards the collision surface and sets the new momentum.

```
let move-towards-surface (distancexy item 0 collision-status item 1
  collision-status) - (2 / spatial-units-conversion-factor)
```

```
set momentum momentum - move-towards-surface
fd move-towards-surface
```

The value of `collision-angle` is calculated from the current growth heading and the heading of the surface, and subsequently compared to the value of `collision-branching-threshold` parameter. That results either in sliding of the original tip, or apical (i.e. collision-induced) branching.

```
ifelse (collision-angle < random-normal
  collision-branching-threshold-mean
  collision-branching-threshold-sd) or sliding-count > 0
[slide]
[create-collision-branches]
```

An alternative scenario unfolds if the `collision-status` either remains empty or returns empty. The submodel move will run with empty `collision-status` if the hyphal-tip is not in vicinity of the particle's surface (the `get-collision-status` is not inquired and the `collision-status` remains empty (`set collision-status (list)`). In addition, there can be cases where the vicinity of soil particle does not lead to the collision in the next step, so the `collision-status` is inquired but returns empty.

In either case, the hyphal-tip not heading for collision with a surface checks for the presence of other hyphae.

```
set anastomosis-status (list)
get-anastomosis-status
```

In case of a sliding tip, the hyphal-tip will wiggle in order to detect potential tips sliding alongside of it. If this returns positive, anastomosis submodel is called.

```
if not empty? anastomosis-status [
  if random-float 1 < anastomosis-probability [anastomose]
]
```

If the hyphal-tip has not anastomosed, it is now facing an open space ahead (i.e. there has been no obstacle, or the obstacle has been reached and hyphal-tip is sliding with the remaining value of momentum). Thus, it moves ahead and updates the value of travelled distance.

```
fd momentum
set dist-travelled dist-travelled + propagation-speed
```

slide Before we describe details of the submodel to slide, let us first outline how this submodel works within the hierarchy of submodels superior to it, namely to move and to go. First, in submodel go the initial value of momentum is set as equal to the value of propagation-speed. In other words, at the beginning of each time step, hyphal tip has its entire movement distance per time step, i.e. propagation-speed available. Subsequently, the submodel go calls the submodel to move.

```
set momentum propagation-speed
move
```

In submodel move, the first part of the momentum is consumed to move towards the sliding surface ahead of the hyphal tip (i.e. through the open space).

```
ifelse not empty? collision-status
[
  set momentum momentum - move-towards-surface
  fd move-towards-surface
]
```

Now the current (remaining) value of momentum is only a fraction of the original propagation-speed and in case the conditions for sliding are met, submodel move calls submodel slide.

```
ifelse (collision-angle < random-normal
  collision-branching-threshold-mean collision-branching-threshold-sd)
or sliding-count > 0
[slide]
[create-collision-branches]
```

In the submodel slide, the hyphal-tip establishes the new heading (see below, the details of slide submodel). Once this and additional operations are run within the scope of the submodel slide, the submodel slide calls back to the move in a loop. Now, the hyphal tip is running again the submodel move, and with its new heading it checks again the presence of obstacles. Assuming (for simplicity) that this time there is no obstacle ahead (neither a hypha to anastomose with), hyphal-tip moves ahead, consuming the remaining fraction of the momentum.

```
fd momentum
```

In summary, above we described how the submodels go, move and slide keep updating the value of momentum during one time-step, in order to realise propagation-speed no matter if the movement takes place in free space, or in collided and sliding hyphal-tip. Analogically, submodels go and move also communicate with submodels create-collision-branches and anastomose.

The submodel slide itself updates the heading of hyphal-tip so it follows the collided surface in the correct direction, it assigns the sliding status to the hyphal-tip (set sliding-count sliding-count + 1), and updates the memory-heading for hyphal-tips without the directional memory, so it is defined by the heading of the obstacle's surface (if not memory? [set memory-heading heading]).

Hyphal-tip adopts the heading from the heading of the surface in three steps: First, the two alternative directions (to the left and to the right, or dir1 and dir2) alongside the surface are defined as either equal to the heading (angle) of the collided surface (i.e. item 2 collision-status), or as its exact opposite.

```
let dir1 ((item 2 collision-status + 180) mod 360)
let dir2 item 2 collision-status
```

Second, values of dir1 and dir2 are used to calculate the angle by which the hyphal-tip needs to alter its current heading in order to align its growth to the surface.

```
let angle1 subtract-headings dir1 heading
let angle2 subtract-headings dir2 heading
```

Third, select the correct new heading (i.e. turn left or right) by comparing the absolute values of turning angle.

```
ifelse abs angle1 < abs angle2
  [set heading dir1]
  [set heading dir2]
```

create-collision-branches Analogical to the submodel slide, also create-collision-branches communicates with its superordinated submodels go and move in order to correctly update the value of momentum. We refer to the description of submodel slide for more details about this hierarchical communication.

The submodel create-collision-branches is called by the submodel move when hyphal-tip is already at its position next to the collision surface.

First, new growth directions alongside the collision surface (to the left and to the right, or dir1 and dir2) are defined as either equal to the heading (angle) of the collided surface (i.e. item 2 collision-status), or as its exact opposite.

```
let dir1 ((item 2 collision-status + 180) mod 360)
let dir2 item 2 collision-status
```

Then the current hyphal-tip is asked to hatch a new node that will later become the new last-node for both new hyphal-tips. This new node connects itself to the previous last-node.

```
hatch-nodes 1
[
  create-hyphae-with (turtle-set [last-node] of myself)
]
```

After this, new hyphal-tips are hatched by the new node and interconnected to it. Each new hyphal-tip assigns the status of last-node to their parental node, and adopt their respective new heading (dir1 or dir2) alongside the surface. Given that directional memory is likely lost after the collision-induced branching, each hyphal-tip takes the current sliding heading as the value of memory-heading (set memory-heading [heading] of self). The submodel to create-collision-branches assigns the sliding status to each new hyphal-tip, and calls back the submodel move (see details of this loop in description of submodel slide).

```
hatch-nodes 1
[
  hatch-hyphal-tips 1
  [
    set heading dir1
    set last-node myself
    create-hyphae-with (turtle-set myself)
    set sliding-count 1
    move
  ]
  ...
]
```

Finally, the submodel cancels the original hyphal-tip and its links.

anastomose Once the get-anastomosis-status returns a positive result, the submodel anastomose is called. At this point, the result of get-anastomosis-status is available as a list of variables with information the hyphal-tip needs to anastomose with the hyphal link ahead of it. This link is item 1 of the anastomosis-status list.

The agent set ends is defined and contains both nodes of the item 1 link.

```
let ends (turtle-set [end1] of item 1 anastomosis-status [end2] of item
  anastomosis-status)
```

Subsequently, ends is used to make sure the link detected by get-anastomosis-

status is not the hyphal-tip's own hypha. This is done by counting how many nodes are left to the item 1 link, once the last-node of the hyphal tip is excluded. Only if the resulting number is 2, anastomosis takes place.

```
let anastomosis-nodes count ends with [ who != ([[who] of last-node] of
  myself)]
if anastomosis-nodes = 2
```

If so, the hyphal-tip hatches a new node, and this node assumes the position of intersection/anastomosis (where hyphal-tip's path intersects with the link to anastomose with). Coordinates are imported from item 0 of the anastomosis-status list. The item 0 itself is a list containing two variables, the x and y coordinate of the intersection point.

```
let is-x (item 0 (item 0 anastomosis-status))
let is-y (item 1 (item 0 anastomosis-status))

hatch-nodes 1
[
  setxy is-x is-y
]
```

The rest of the submodel creates links of this new node, and cancels the old links and the hyphal-tip (which ceases to exist due to anastomosis).

Thus, the new node establishes three links. With the item 1 nodes (ends), and with the last-node of the hyphal-tip.

```
create-hyphae-with (turtle-set [last-node] of myself)
create-hyphae-with ends
```

Finally, the original link between ends and the original hyphal-tip are cancelled.

```
ask item 1 anastomosis-status [die]
die
```

autotropism Submodel autotropism runs several processes analogical or same as submodels get-collision-status and get-anastomosis-status (Fig. 5.4). At the start of the submodel, the agent name active-hyphal-tip is assigned to the hyphal-tip running the submodel. Then it makes a minuscule movement forward, so the possibility of detecting its own hypha is prevented.

```
let the-active-hyphal-tip self
fd (0.0025 / spatial-units-conversion-factor)
```

Further, the variable angles is defined as a list of two items: autotropism-cone-

angle/2 and its inverse value (the value of variable autotropism-cone-angle is set by user). The variable min-dists is defined as a list of two identical variables, perception-range and perception-range, value of which is set by the user. Together, these two two-item lists, angles and min-dists define respectively the perimeter and the range at which the presence of other hyphae is checked in two iterations, first for the right side, then for the left side. The key agent that checks this presence is a probe hatched by the hyphal-tip.

```
let angles list (autotropism-cone-angle/2) (-1 *
  autotropism-cone-angle/2)
let repeat-count 0
let min-dists list perception-range perception-range
repeat 2
[
  let distance-list (list)
  hatch-probes 1
  [
    rt item repeat-count angles
    fd perception-range
    ...
  ]
  ...
]
```

Hence, once the probe is hatched, it turns right or left based on the current iteration and moves forward by the value of perception-range. At its new position, the probe check whether it has crossed any hyphae while moving from the original position. To do so, it first checks whether the patches in vicinity (in-radius 2) of its new location (i.e. patch-here) contain any nodes (i.e. my-hyphal-nodes). These nodes of potentially intersecting hyphae are called the-hyphae-start, from which the last-node of the own hyphal-tip is excluded (to prevent the detection of own hypha).

```
let the-hyphae-start [my-nodes] of patch-here
if member? [last-node] of the-active-hyphal-tip the-hyphae-start
[
  set the-hyphae-start the-hyphae-start with [who != [[who] of last-node]
  of the-active-hyphal-tip
]
```

In the next step, the agent set containing links of all nodes in vicinity (except for the own last-node) is defined. These are potentially intersecting links.

```
let potential-IS-links link-set [my-out-links] of the-hyphae-start
```

If there are any potentially intersecting links, it is checked whether the intersection actually takes place. The probe creates a link to its parental hyphal-tip and then it is checked whether this probe-link intersect with any of the potential-IS-links.

```
if count potential-IS-links > 0
[
  create-probe-link-to myself
  [
    ask potential-IS-links
    [
      let is intersection self myself
      ...
    ]
    ...
  ]
  ...
]
```

If the intersection exists, then the list distance-list is updated. Distance-list is empty if this is first iteration, but might be already filled if this is the second iteration. In updating, the distance from the hyphal-tip to the intersection is added to it.

```
if not empty? is
[
  ask the-active-hyphal-tip
  [
    set distance-list lput distancexy item 0 is item 1 is distance-list
  ]
]
```

Once the distance-list is updated following intersection event, the list min-dists is update as well. While originally it contained two equal values of perception-range, now one of them is being replaced by the distance to the nearest intersection.

```
if not empty? distance-list [set min-dists replace-item repeat-count
  min-dists min distance-list]
```

The iterative part of submodel ends with the probe dying and updating the repeat-count. The hyphal-tip returns to its original position, and a new variable anastomosis-heading is defined with an original value zero.

```
fd (-0.0025 / spatial-units-conversion-factor)
let anastomosis-heading 0
```

The zero value of anastomosis-heading is maintained in two situations. Either

there has been no intersection within the perception range and perception perimeter, or there has been an intersection but on both sides of the perimeter the distance to the intersecting hypha is equal. That is, there is no space to deflect the growth, and in both cases the hyphal-tip continues growing with its original heading.

In case there has been an intersection and there is a possibility to deflect towards the side with either further distance towards the intersecting hypha or no intersecting hypha, the hyphal-tip will be given a new value of anastomosis-heading and deflect by the value based on anastomosis-heading and autotropism-strength.

```
if min min-dists != max min-dists
[
  set anastomosis-heading item position min min-dists min-dists angles
]
rt autotropism-strength * anastomosis-heading
```

get-anastomosis-status In analogy to submodels `get-collision-status` and `autotropism`, `get-anastomosis-status` starts by defining its output as a list (empty at the beginning) and assigning the agent name `active-hyphal-tip` to the hyphal-tip running the submodel.

```
let result (list)
let the-active-hyphal-tip self
```

The hyphal-tip makes a minuscule movement forward, so the possibility of detecting its own hypha is prevented.

```
fd (0.0025 / spatial-units-conversion-factor)
```

In order to detect potential hyphae ahead, a probe is hatched that runs the operations necessary for detection. These operations are first analogical to those in `autotropism`. The probe moves by the distance which the hyphal tip can move in current time step.

```
hatch-probes 1
[
  fd [momentum] of myself
  ...
]
```

At its new position, the probe check whether it has crossed any hyphae while moving from the original position. To do so, it first checks whether the patches in vicinity (i.e. in a radius of 2 spatial units) of its new location contain any nodes. These nodes of potentially intersecting hyphae are called the `hyphae-start`, from

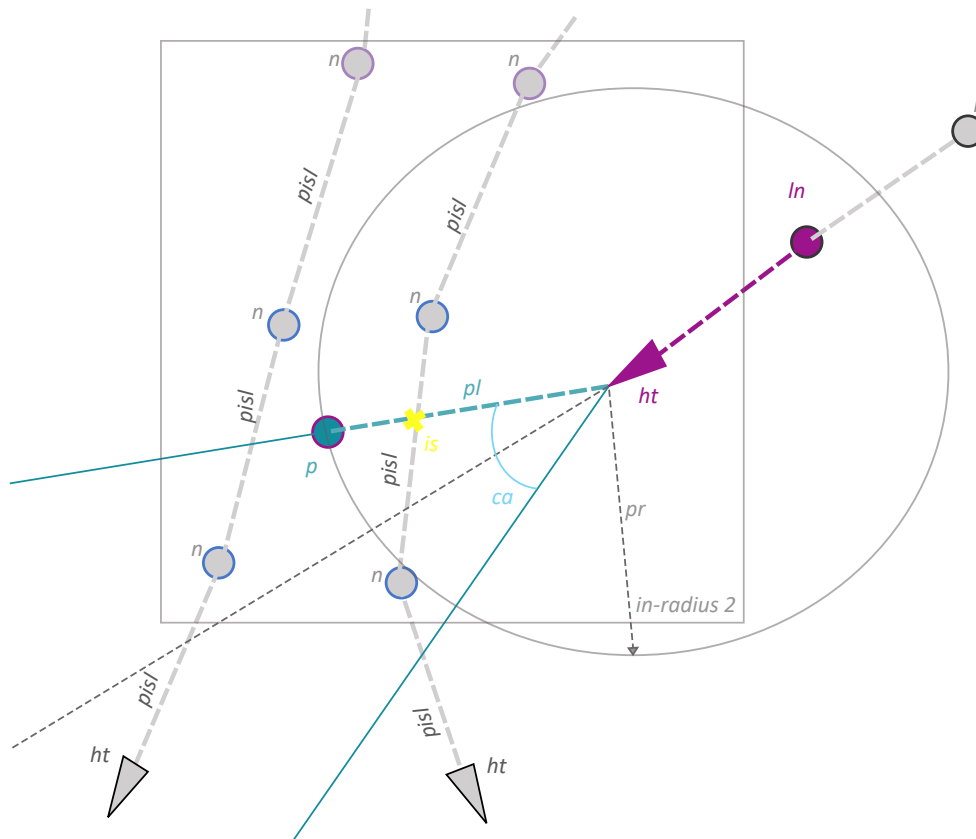


Figure 5.4: Depiction of processes, variables and agents of submodel autotropism, involved in detection of hyphal links ahead by the focal hyphal tip (*ht*, purple). If hyphal nodes (*n*) are present in vicinity of current location (i.e. 2 spatial units), focal hyphal tip hatches a probe (*p*, green) which travels to the point defined by the variables perception-range (*pr*) and cone-angle (*ca*, cyan). The probe creates a probing link between itself and the focal hyphal tip (*pl*, green). If this one intersects with a potential intersection link (*pisl*), an intersection (*is*) is calculated. The last-node of the focal hyphal tip is depicted in purple (*ln*). Similar agents and processes are involved in submodels *get-anastomosis-status*, and *get-collision-status*.

which the last-node of the focal hyphal-tip is excluded (to prevent the detection of its own hypha).

```

let the-hyphae-start [my-hypha-nodes] of patch-here
if member? [last-node] of the-active-hyphal-tip the-hyphae-start
[
  set the-hyphae-start the-hyphae-start with [who != [[who] of
    last-node] of the-active-hyphal-tip]
]

```

In the next step, the agent set containing links of all nodes in vicinity (except for the own last-node) is defined. These are potentially intersecting links.

```
let potential-IS-links link-set [my-out-links] of the-hyphae-start
```

If there are any potentially intersecting links, it is checked whether the intersection actually takes place. The probe creates a link to its parental hyphal-tip and then it is checked whether this probe-link intersect with any of the potential-IS-links.

```
if count potential-IS-links > 0
[
  create-probe-link-to myself
  [
    ask potential-IS-links
    [
      let is intersection self myself
      ...
    ]
    ...
  ]
  ...
]
```

If the intersection is detected, the result list will be updated. The result list will carry the information on x and y coordinates of the intersection point and the intersected link potential-IS-links.

The submodel must ensure that in case of multiple intersections detected for given time step, the hyphal-tip anastomoses with the nearest one and ignores the distant ones. Thus, if the result list is still empty at the moment of detecting the intersection, it is simply filled with intersection coordinates and intersected link. If the result list is already filled at this point, the hyphal-tip is first asked to compare distances to two intersection points and the nearest one is chosen to fill the result list.

```
ask the-active-hyphal-tip
[
  if distancexy item 0 item 0 result item 1 item 0 result > distancexy
    item 0 is item 1 is
  [
    set result (list is myself)
  ]
]
```

At the end of the submodel, the probe is cancelled, the result list is renamed to anastomosis-status list, and the hyphal tip moves back to its original position.

```
[
  [
    ...
    die
  ]
]
set anastomosis-status result
fd (-0.0025 / spatial-units-conversion-factor)
```

Submodel get-collision-status The submodel `get-collision-status` is highly analogous to `get-anastomosis-status`. It also hatches a probe, detects the intersection and fills the result list. The only two differences are: 1) While in `get-anastomosis-status` the potentially intersected links are hyphae in the vicinity of the current probe's patch, in `get-collision-status` the potentially intersected links are those that create surfaces of soil particles.

```
let potential-IS-links [link-set [my-links] of my-surfaces] of patch-here
```

2) The result of `get-collision-status` is a list of three items: The coordinates `x` and `y` of intersection point, and the angle (heading) of `potential-IS-links` (that is the heading of the surface-link to collide with).

```
[set result is]
if length result = 2
[
  set result lput [link-angle] of self result
]
```

5.2.2 Simulations

We simulated multifactorial experiments in environments with five different degrees of porosity: Without spatial constrains (i.e. simulation of growth on plain agar), and with low, intermediate, high and very high porosity. For respective five degrees of soil porosity, the following number of soil-particles was generated: 0, 100, 200, 800, 1200. The experimental arena was 7.5 x 7.5 mm large, simulation time was 1000 minutes. The following soil parameters were chosen: maximum-grain-diameter was 250, and roundness of particles 20. In total, 800 different parameter sets were simulated with 10 repeats each. The following model parameters (i.e. simulated fungal traits) were kept constant for all 8,000 simulations: `n-hyphal-tips` (i.e. number of initial hyphal tips at the start of the simulation), `propagation-speed-micrometers`, `lateral-branching-interval`, `anastomosis-probability`, and all three parameters that define negative autotropism. Below we provide the reasoning for the particular values we chose for these parameters.

Each simulation starts with nine initial hyphal tips. Although actual spores often germinate as a single conidial anastomosis tube (CAT), the initial CAT can branch frequently at an early stage, which can be then approximated as multiple hyphae spreading from nearly a single point (Gabriela Roca et al. 2005). In addition, multiple initial hyphal tips reduce the stochasticity in outcomes based on random spatial constellation of initialized mycelia. For instance, a higher number of initial tips reduces the chances of some areas being unexplored. The mycelia are thus growing in a more symmetrical fashion. That in turn makes mycelia more comparable and it becomes easier to observe the influence of studied growth parameters.

For all simulations, propagation-speed was kept at the value of three micrometers per minute. This is within the range of growth rate in the fungal kingdom, while we do not expect the growth rate to have an impact on the relative ranking of different space-searching algorithms (Alekklett et al. 2021; Morrison and Righelato 2000).

The branching frequency (lateral-branching-interval) was kept constant in order to minimize the effect of different number of hyphal tips in different mycelia on results and interpretations of our simulations. The value was normally distributed around the mean of 100 μm ($M = 100 \mu\text{m}$, $SD = 50 \mu\text{m}$), thus comparable to natural mycelia (Held et al. 2009).

We kept the likelihood of anastomosis at the value one, so each time a hyphal tip encounters a hypha, it is either deflected from it by negative autotropism, or it anastomoses. On the one hand, this may not always happen in natural mycelia (a fraction of hyphal tips that are not deflected will cross the hypha without anastomosing). On the other hand, in natural mycelia a proportion of hyphal tips could be suppressed in their growth by other means, so the higher anastomosis likelihood can compensate for the lack of this function in our model. Indeed, the simulated mycelia have appearance closest to the natural mycelia when the values of anastomosis likelihood are high.

Autotropism parameters were kept constant at a low negative value. This enables negative autotropism typical for hyphae, but also does not prevent the parallel growth of hyphae in narrow channels, observed in natural mycelia (autotropism-strength: -0.05 ; cone-angle: 20° ; perception-range-micrometers: $40 \mu\text{m}$). The following growth parameters were studied for their impact on foraging capacity in different porosities: random-propagation-angle, lateral-branching-angle, collision-branching-threshold, and the presence or absence of spatial memory in hyphal tips.

The parameter random-propagation-angle is one of those for which we do not have direct empirical data. When random-propagation-angle is set to zero, the hyphae grow as straight lines. When too high (three degrees and above), the resulting mycelium does not appear natural either, with many hyphal growth trajectories

collapsing back to the colony center and to the sides. Following observations of multiple morphologies of real and simulated mycelia, we decided to keep the random-propagation-angle at the values of 0.5° , 1° , 1.5° and 2° for our simulations.

Lateral-branching-angle and collision-branching-threshold were kept within ranges comparable to empirical data, with mean values of 25° , 40° , 55° , 70° , and 85° for lateral-branching-angle (Lehmann et al. 2019), and mean values of 45° , 60° , 75° and 80° for collision-branching-threshold (Held et al. 2009; Held et al. 2008). Standard deviation for all values of both lateral-branching-angle and collision-branching-threshold was 10° . Directional memory is a Boolean, in simulations hyphal tip either expresses it or not.

5.2.3 Analyses

We processed the NetLogo output in R to calculate the maximum distance reached by the hyphae from the colony center. For each parameter set, we run ten simulations and calculated the mean value of all ten repeats. To visualize the results, we chose a heat map. The maximum distance reached (area covered) defined the 100% foraging efficiency (Fig. 5.5). Darker colors on the scale represent the respective fractions of this maximum foraging efficiency.

5.3 Results & Discussion

While recent studies showed interspecific variation in space-searching algorithms, ecological consequences for community assembly in micro-structured soils and the associated selection gradients are hardly explored. Our results strongly indicate that the porosity itself, before its effect on other vital environmental variables (i.e. oxygenation or water holding capacity) can be studied as a driver of fungal community assembly. In environments with no obstacles (zero particles), the presence of directional memory after collision did not alter the foraging capacity. This is fully expected, as the trait is only activated by contact with surfaces. Similarly, the trait collision branching threshold had no impact in open space environment. In line with expectations, increasing the hyphal wiggling in open space had an overall negative impact on foraging capacity (i.e. the closer the hyphae are to straight lines, the further they reach). The effect of hyphal wiggling was slightly modulated by the value of branching angle.

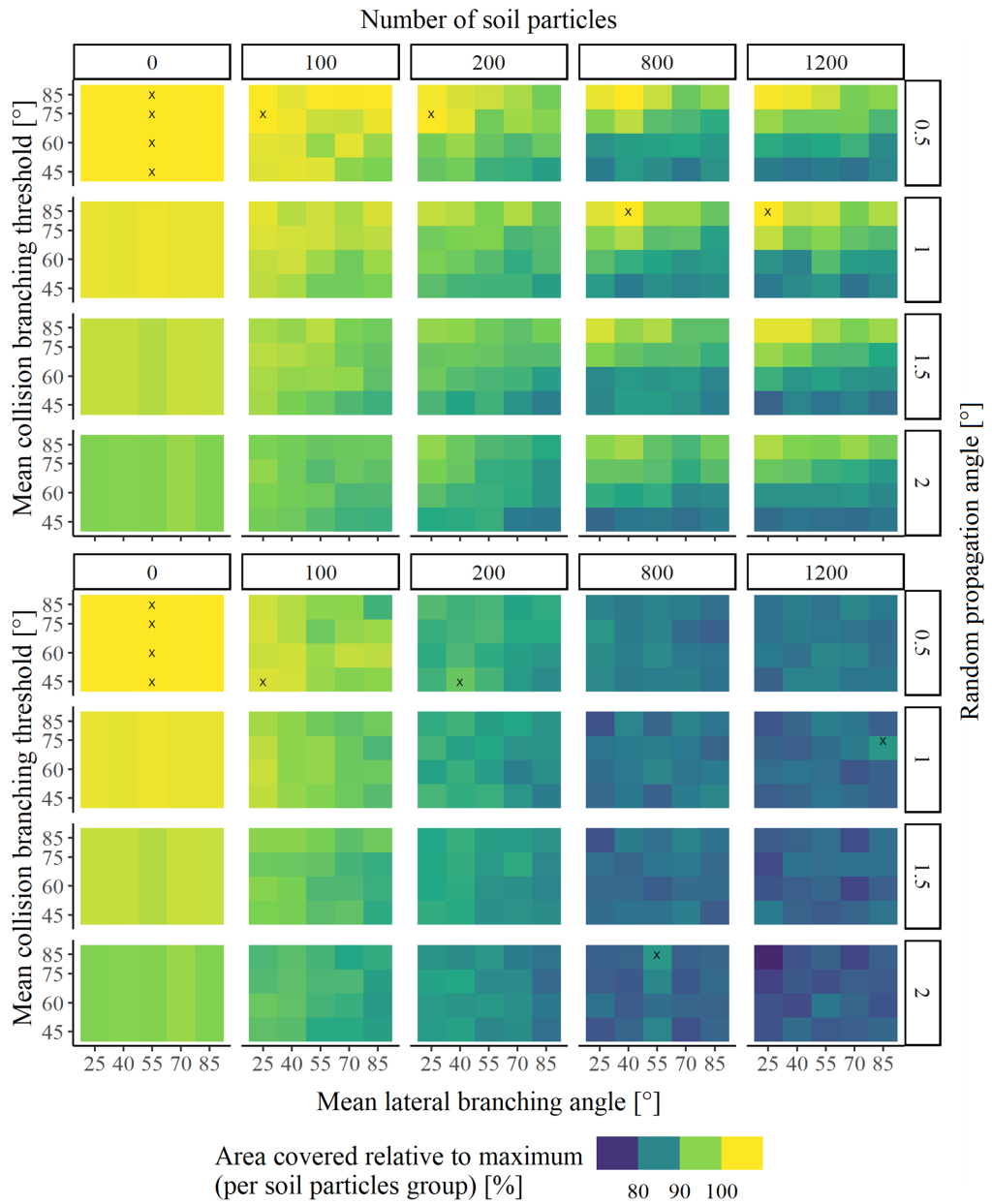


Figure 5.5: Visualization of the foraging capacity in simulated microstructures. In general, presence of directional memory (above) resulted in better foraging capacity (i.e. area covered relative to maximum), as compared to fungi without the directional memory (below). This effect was more pronounced for environments with lower porosity (i.e. higher number of soil particles, columns on the right side).

Overall, increasing hyphal wiggling has a negative impact on foraging capacity in all environments, regardless of porosity. This is unsurprising as in our model, the increased wiggling does not improve navigational capacity of hyphal tip. That is, by investing into a less straightforward growth, in our model the hypha does not collect additional information about its immediate surroundings. In real hyphae this may be different and the trait may have more pronounced and more positive effects on foraging capacity. What is surprising that in spite of the overall pattern described above, for some particular trait value and porosity combinations, increased wiggling actually improved foraging capacity. For instance, at low porosity (1200 particles) the hyphae without directional memory with high branching angle (85°) and a high collision branching threshold angle (75°) perform better at moderately higher wiggling (random propagation angle 1° as compared to 0.5°).

In line with previous research in PDMS microstructures, the directional memory increases the foraging capacity of mycelia across all porosities (Hanson et al. 2006; Held et al. 2011). It interferes with the collision branching threshold in an expected manner. The smaller the collision branching threshold, the less successful directional memory becomes in navigating hyphae through obstacles. The memory can only work if the hyphae slide without branching upon encountering the obstacle, but it is lost if the obstacle encounter triggers a branching event. This can be observed as decreasing foraging capacity as the value of collision branching is decreasing in hyphae with memory. The pattern is most pronounced for higher porosities. Surprisingly, the combination of directional memory with a high collision branching threshold (and to some degree with lower branching angle) can result in high foraging capacity being maintained even in low porosity environment. Thus, it is possible that species with directional memory living in high density soils might be selected towards high collision branching thresholds and low branching angles. In species without the directional memory the lower branching threshold allowed for higher foraging capacity in higher porosities.

Interestingly, outside of the general patterns described above, there are multiple unexpected and not easily interpretable combinations of traits and porosities in which hyphal foraging performed well, indicating further opportunities for degree of porosity acting as an axis of niche partitioning between species of filamentous fungi. For instance, in case of the presence of directional memory, random-propagation-angle = 1° , and collision-branching-threshold = 85° the performance in environment with 800 particles was best for branching-angle = 40° . When the porosity decreased, in environment with 1200 particles the branching-angle = 25° performed better.

In summary, we could explore possible selection gradients on space-searching algorithms across differently micro-structured soils. These novel insights sustain the

view that interspecific variation in space-searching algorithms and environmental heterogeneity in soil architectures mediate niche partitioning. Yet, while spatial extent is a common metric for competitive ability, the trade-offs resulting from different allocation strategies should be studied by including further network metric in a next step (Aguilar-Trigueros et al. 2021).

5.4 Additional information

Conflicts of interest

None.

Statement of authorship

MB wrote the first draft. All authors contributed to the writing of this paper. MB and AM developed the model.

Data accessibility

Model and analysis code will be made available upon publication. Data is generated via the model code.

Supplementary material

C1: Additional table

Chapter 6

General discussion

Intraspecific trait variation (ITV) in movement behaviour is pervasive (Hertel et al. 2020; Shaw 2020) and has broad eco-evolutionary consequences (Clobert et al. 2009; Cote et al. 2017; Jeltsch et al. 2013; Schlägel et al. 2020; Spiegel et al. 2017). Methodological advances now facilitate tracking individuals across vast spatiotemporal scales (Hertel et al. 2020; Kays et al. 2015; Nathan et al. 2022; Wilmers et al. 2015) and inferring the relevance of ITV in movement behaviour as well as its sources. Among-individual differences and within-individual variability constitute ITV in movement behaviour and have distinct eco-evolutionary consequences (Moran et al. 2016; Wolf and Weissing 2012). As identifying among-individual differences in the wild is notoriously difficult (Dingemanse et al. 2022; Hertel et al. 2020; Spiegel and Pinter-Wollman 2022), it was only recently achieved for among-individual differences in local scale movement behaviour (Aliperti et al. 2021; Eccard et al. 2022; Harris et al. 2020; Schirmer et al. 2019; Schirmer et al. 2020; Spiegel et al. 2015). The observation of among-individual differences in movement behaviour challenges ecologists. As among-individual differences violate assumptions of central ecological theories (Charnov 1976; Eccard et al. 2020; Sih 2017) or are just not sufficiently recognised (Grimm and Railsback 2013; Huston et al. 1988; Jeltsch et al. 2019; Johnson and Hastings 2022), we currently lack a coherent knowledge of ultimate sources of ITV in movement behaviour and its consequences (Shaw 2020). The goal of this thesis is to contribute to the advancement of ecological theory, foremost, by applying novel agent-based models to existing ecological theory.

I embarked on the journey of this thesis with one main question in my backpack: how do empirically observed levels of among-individual differences in movement behaviour affect the coexistence of ecologically similar competitors? Modern coexistence theory (Chesson 2000b) does not sufficiently address among-individual differences (Jeltsch et al. 2019; Johnson and Hastings 2022) despite larger augmentations (Barabás et al. 2018). Existing modelling studies on consequences of among-individual differences are on immobile species and have yielded ambiguous results (Banitz 2019; Crawford et al. 2019; Hart et al. 2016; Uriarte and Menge 2018). As such, the effect of among-individual differences in movement behaviour could not be deduced from existing studies.

In the second chapter, I reproduced observed patterns of among-individual differ-

ences (Schirmer et al. 2019) by developing an agent-based model (Milles et al. 2020). I could demonstrate that among-individual differences promote coexistence via an equalising mechanism. I attribute this result to the underlying, hump-shaped, trait-function-relationship (i.e. the relationship between resource uptake and trait). The shape of the trait-function-relationship crucially defines whether among-individual differences facilitate or avert equalising mechanisms, giving a more general explanation to why studies have been ambiguous (Hart et al. 2016; Uriarte and Menge 2018). The concepts, methods, and findings of the second chapter present the nucleus of this thesis from which branches with different directions developed.

While among-individual differences in the second chapter are assumed as given, the third chapter (Milles et al. 2022) tests whether fluctuating density-dependent selection may lead to the evolution of a POLS (pace-of-life syndrome; Wright et al. 2019) and, as such, among-individual differences in movement behaviour and life-history traits. This notion by Wright et al. (2019) promises to fill apparent gaps in the theoretical foundation of the POLS hypothesis (Dammhahn et al. 2018; Mathot and Frankenhuis 2018; Réale et al. 2010; Royauté et al. 2018). By developing a novel individual-based model, I could show that movement and life-history traits covaried along a slow-fast continuum within and between populations. While these findings largely support predictions (Wright et al. 2019), they also nuanced the typical assumption of strictly integrated axes across hierarchical levels. Instead, evolved POL axes within and between populations deviated systematically and may be non-linear. This suggests that assumptions of POLS theory should be relaxed.

The second chapter shows that ITV equalises fitness differences, yet, ITV also reduced coviability (Jeltsch et al. 2019) if both species trait averages were located at the optimum of the function-trait relationship (Milles et al. 2020). Does this imply that ITV is harmful to population persistence? The contrary is normally assumed, as among-individual differences should facilitate niche specialisation which buffers populations (i.e. reduce extinction risk) via the portfolio effect (Bolnick et al. 2011; Schindler et al. 2015; Schindler et al. 2010). In the fourth chapter, I reviewed implications of the portfolio effect and further local buffer mechanisms stemming from among-individual differences, intra-individual variability, environmental heterogeneity, and density-dependence. To advance synthesis of local buffer mechanisms, I grouped mechanisms into two fundamental classes (dampening, repelling) and aimed to make local buffer mechanisms more accessible to empirical and theoretical ecologists. I elaborated on latencies, capacities, and interactions between local buffer mechanisms. I concluded that these levels of complexities require novel methodological and conceptual approaches, for instance, by developing corresponding, spatially-explicit ABMs.

In the fifth chapter, I co-authored a study where questions about the consequences

of variation in movement behaviour for species coexistence were transferred to the realm of filamentous fungi. This study follows a recent effort to introduce the modern coexistence theory and the movement ecology paradigm to fungal ecology (Bielčík et al. 2019; Bielčík et al. unpublished). In this study, we developed an agent-based model to study niche-partitioning via interspecific differences in space-searching algorithms (i.e. active movement). We could determine that porosity in soil-like microstructures constitutes niches, thus, possibly facilitating coexistence of filamentous fungi. As such, this chapter marks a novel application of theory predominantly applied in animal ecology and facilitates testing for the generality of the respective theory.

The further general discussion encompasses a critical evaluation and contextualisation of the individual chapters as well as promising avenues to continue the research outlined in this thesis. Throughout my ongoing academic journey, the scientific landscape has already changed. For some questions, a critical mass of evidence has accumulated, exhibiting distinct patterns which have allowed theory to advance. Thus, if applicable, I will also discuss how my contributions have been received by the scientific community or match with more recent findings.

6.1 The pace-of-life syndrome as a source of among-individual differences in movement behaviour

The link between the occurrence of among-individual differences in movement behaviour and POLS theory (Dammhahn et al. 2018; Réale et al. 2010) has recently been made more explicit (Campos-Candela et al. 2019; Le Galliard et al. 2013; Nakayama et al. 2017). The work in my third chapter demonstrates that fluctuations in density-dependent selection are a potential driver of the evolution of a POLS, which integrates among-individual differences in movement behaviour and life-history. Recently, some additional empirical observations in agreement with the fluctuating density-dependent selection POLS framework (Wright et al. 2019) have been made (Eccard et al. 2022). Yet, synthesis work documents an unclear, ambiguous, integration of life-history traits (fecundity) and competition (Grainger and Levine 2021), as well as survival and risk-taking behaviour (Moiron et al. 2020). These findings have the potential to undermine fundamental assumptions of POLS theory. Possible explanations for these findings range from inconsistent study designs and axes of variation related to risk-taking deviating from assumptions in POLS theory (Moiron et al. 2020) to further, alternative trade-offs such as between parental investment and mating effort (Del Giudice 2020). Yet, despite this unclear state of evidence,

POLS theory is considered a useful heuristic (Del Giudice 2020), which requires more critical evaluation (Montiglio et al. 2018; Royauté et al. 2018).

A more critical evaluation of POLS theory includes testing the predictions of the fluctuating density-dependent POLS framework (Wright et al. 2019) rigorously, as it is considered the "closest attempt" (Del Giudice 2020) to explain causes of POLS. Beyond the predictions tested in chapter 3, the framework by Wright et al. (2019) formulates clear predictions for the integration of the pace-of-life with dispersal. For instance, conditions favouring fast types should also favour higher levels of dispersal leading to greater connectivity between populations. In my thesis, I have so far mainly focused on local, i.e. "station-keeping" (Schlägel et al. 2020), movement. To continue the study of POLS and the sources of among-individual differences in movement behaviour, though, the scope should be increased to include dispersal. In the following subsections, I briefly summarise the recent discussion and findings on the integration of dispersal with life-history and behavioural traits and make explicit suggestions on how modelling could help the field to advance.

6.1.1 Among-individual differences in dispersal and their integration with life-history

Dispersal is a central movement trait in ecological and evolutionary contexts (Bonte and Doherty 2017) as it mediates regional buffer mechanisms (Brown and Kodric-Brown 1977; Hanski 1999) and genetic exchange (Lundberg and Moberg 2003; Schlägel et al. 2019). Findings preceding the POLS hypothesis by Réale et al. (2010) showed a covariation of among-individual differences in dispersal with aggressiveness, sociability, and dispersal propensity (Clobert et al. 2009; Cote and Clobert 2007; Cote et al. 2010; Duckworth and Badyaev 2007). Given the ramifications of dispersal in eco-evolutionary contexts, syndromes of heritable traits including dispersal suggest intriguing consequences such as non-random gene-flow (Cote et al. 2017; Edelaar and Bolnick 2012). Non-random gene-flow, can, for instance, explain rapid range expansions as highly dispersive, less social individuals mainly populate the expanding edge of a species range (Duckworth and Kruuk 2009; Duckworth and Badyaev 2007). According to POLS theory (Réale et al. 2010), this should be a more general phenomenon. As energetic and mortality risks can occur throughout all stages of dispersal (Bonte et al. 2012), slow-type individuals should be more philopatric as they are less sensitive to competition and would avoid the elevated risks (Wright et al. 2019). Yet, although the POLS theory has been extensively studied in recent years, synthesised evidence for an integration of dispersal with the pace-of-life has remained insufficient. In the light of this situation, Bonte and Doherty (2017) recently argued, that dispersal is not generally integrated with other

aspects of life-history and trade-offs. This debate has not been settled and more theoretical work is required to gain a better understanding.

6.1.2 Metapopulation models to study the integration of dispersal with life-history

A promising avenue is to study POLS and the associated relationship between life-history and behaviour by including local movement and dispersal. As dispersal is a complex process consisting of multiple stages (Travis et al. 2012), modelling platforms have been developed to facilitate studies on this topic (Bocedi et al. 2021; Malchow et al. 2021). Yet, currently, resorting to these modelling platforms is not an option as they lack the flexibility of including further heritable traits to study the dispersal in the context of the POLS. Instead, I would suggest extending the model presented in the third chapter of this thesis by adding natal dispersal and among-individual differences in dispersal propensity. In addition to studying the integration of dispersal with life-history, introducing dispersal in the model of the third chapter also serves the purpose of relaxing assumptions to explore conditions at which the evolution of POLS may be hindered. In the original version of the model, each simulation run represented evolution in one population and the POLS between populations was identified by comparing simulation runs with different parameter settings. As such, extending the model (Fig. 6.1) to study POLS and dispersal in a metapopulation context would foster our understanding of the role of dispersal in three key aspects.

A first key aspect includes the outstanding question of whether and when observations in Milles et al. (2022) hold in the context of metapopulations, i.e. populations experiencing different degrees of local competition and which are linked by dispersal. Dispersal may alter the evolution of a POLS in two directions. On the one hand, speciation rates point out that elevated dispersal ability may degrade local diversification due to adaptive divergence (Claramunt et al. 2012; Weeks and Claramunt 2014), on the other hand, non-random gene flow may also contribute to adaptive divergence (Edelaar and Bolnick 2012). By adding dispersal to the model in the first place, these processes could unfold, yet, they may crucially depend on how context and population density modulate dispersal propensity.

A second key aspect would be to address the ongoing debate about how dispersal and life-history are related. As outlined before, higher dispersal movement should be associated with fast-type individuals (Wright et al. 2019). A further expectation is, that given dispersal affects local adaptation (first key aspect) and is associated with the pace-of-life (second key aspect), slow and fast type populations should differ in their connectedness and, hence, the adaptation to local optima (Wright

et al. 2019). Interestingly, in the case of degraded local adaptation due to dispersal, this may also suggest a limiting factor for the selection of more dispersive types mediated by dispersal itself.

A third key aspect would study the role of the spatial structure of slow and fast-type populations, by altering the autocorrelation of disturbance regimes. I would expect that the effect of dispersal on local adaptation and, thus, the observation of the formation of a POLS essentially depends on this spatial structure. With negative autocorrelation, conditions for slow and fast type populations would be spatially close, facilitating the connectivity between these two environments. On the other hand, positive autocorrelation with larger spatial clumps of similar conditions should reduce the connectivity between different environmental conditions and, thus, the effect of dispersal *per se*. In general, studying the evolution of POLS in spatially-explicit contexts may greatly advance our still too limited understanding.

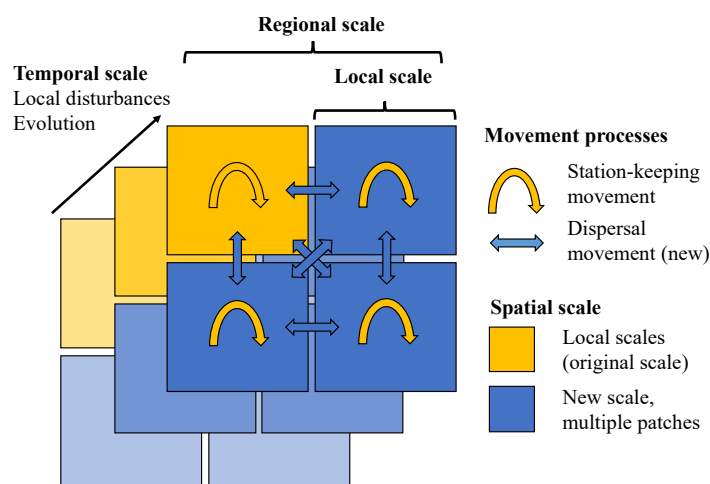


Figure 6.1: Concept of an individual-based model to study the POLS in the context of metapopulations. Processes included in the model of the third chapter (yellow) are augmented by adding dispersal and extending to a regional scale (blue). Patterns of local disturbances and heritable dispersal interact with the mechanisms that have led to the emergence of a POLS in the third chapter.

6.2 Consequences of intraspecific trait variation in movement behaviour for species coexistence

In the second chapter, I observed an equalising (i.e. fitness differences reducing) mechanism due to ITV in movement behaviour (Milles et al. 2020). While it represents the first study on the implications of ITV in movement behaviour in the context of modern coexistence theory (Chesson 2000a; Chesson 2000b), earlier studies investigated the effects of intraspecific variation in non-movement traits

on species coexistence (Banitz 2019; Crawford et al. 2019; Hart et al. 2016; Uriarte and Menge 2018). So far, these results have often been perceived as ambiguous (Stump et al. 2022). In my study, I reasoned the occurrence of an equalising mechanism by an emerging hump-shaped relationship between the trait and foraging efficiency. Variation in the superior species (i.e. which is closer to the optimum to the relationship) and variation in the inferior species reduce the average differences in competitive ability. I explained the contrasting outcome to the widely received study by Hart et al. (2016), by pointing out that they assume a relationship between trait and function that always favours the superior species. This insight has been supported by a recently published novel perspective on ITV and species coexistence.

6.2.1 A novel perspective on equalising mechanisms

Stump et al. (2022) recently proposed a novel framework to synthesise the seemingly contradictory results based on similar considerations of "function-trait relationships". The authors examined 10 different modelling studies and could identify reasons for the otherwise ambiguous outcomes. One major aspect is related to whether the relationship between a trait and function (i.e. performance) in a focal species is concave-up or concave-down. Applying the mathematical rule of Jensen's inequality (Bolnick et al. 2011; Denny 2017), in a concave-up trait-function relationship, ITV increases the average performance compared to a scenario without ITV, whereas ITV in the case of a concave-down trait-function relationship reduces the average performance (Stump et al. 2022). This provides a generalisation of the mechanistic explanation I present in my second chapter, which also revolves around the position of inferior and superior species along with a trait-function relationship. In the second chapter, the superior species was located closer to the optimum of the hump-shaped trait-function relationship, i.e. at a concave-down location. The central role of trait-function relationships affirms my conclusion, that we need to understand and predict trait-function relationships to infer the effect of ITV as an equalising mechanism.

Ecological theory has advanced and can now provide a conclusive explanation for the effect of ITV on equalising mechanisms. Yet, testing this mechanism empirically poses a major challenge. Trait-function relationships can consist of linear, concave-up and concave-down regions and may fluctuate spatiotemporally with population density, community composition, or abiotic conditions. So, certainly, strongly controlled environments with known compositions of trait variations are the most likely next step in empirical studies. This challenging endeavour should be accompanied by next-generation models that give insights into trait-function-relationships and whether they induce an equalising mechanism.

6.2.2 Next-generation models to study population and community level consequences of intraspecific trait variation in movement behaviour

What should next-generation models look like to accompany these challenging empirical studies on population and community level consequences of ITV? Based on their synthesis of 10 existing models of consequences of ITV for species coexistence, Stump et al. (2022) conclude that models applying first principles and multi-trait approaches are needed to answer outstanding questions. While only 3 out of 10 models were ABMs, 2 out of 3 models considered by Stump et al. (2022) as simulating "first principles" are ABMs (Crawford et al. 2019; Milles et al. 2020) and 2 out of 2 models with a multi-trait approach are ABMs (Banitz 2019; Crawford et al. 2019). While both criteria can be met using equation-based models (e.g. lottery models), this substantiates the view that next-generation ABMs are highly suitable to address current research gaps (Grimm et al. 2017; Grimm and Berger 2016). In the following, I consider options to advance models synthesising movement ecology and behavioural ecology to study consequences of ITV in movement behaviour for species coexistence (chapter 2) as well as population persistence (chapter 4).

Next-generation models based on first principles and multi-trait approaches should account for within-individual variability and among-individual differences. So far, the consequences of within-individual variability on equalising and stabilising mechanisms elude generalisation (Girard-Tercieux et al. 2022; Turcotte and Levine 2016). Uncertainty about the consequences can result from a lack in acknowledging among-individual differences. Averaging among-individual differences in plasticity (i.e. slope of reaction norms) by assuming within-individual variability only, removes an ecologically relevant factor. Populations with equal average within-individual variability may strongly differ at the individual levels with strong consequences on niche differences (Bolnick et al. 2011; Crawford et al. 2019) and, thus, stabilising mechanisms.

While the dissection of sources of ITV has become central to the study of animal behaviour, to the best of my knowledge, no modelling study on species coexistence analyses the effects of within-individual variability and among-individual differences along with its three dimensions (predictability, behavioural type, and plasticity). Furthermore, within-individual variability in movement behaviour arising from physiological processes is lacking broader adoption (Campos-Candela et al. 2019; Dingemanse and Wolf 2010). These open flanks in ecological modelling provide a promising ground for future research with intriguing questions. How do the three dimensions of among-individual differences - behavioural type, plasticity, and predictability - contribute to species coexistence? Can, for instance, among-

individual differences in predictability alone - so individuals with the same reaction norms - promote coexistence (Hertel et al. 2021)? How do among-individual differences in plasticity and within-individual variability differ in their consequences?

These intriguing questions could be addressed by modifying the model I developed in the second chapter. Here, the simulated individuals differed in a trait that integrates among-individual differences in behavioural type and plasticity. While this integration is rooted in empirical evidence (Mazza et al. 2018; Natarajan et al. 2009), it may not be general. A promising future development of the model would, thus, be to represent predictability, plasticity, and behavioural type independently.

Further questions remain unaddressed by my modelling approach and require investigation. For instance, I could not address stabilising mechanisms, partly as the simulated landscape did apparently not generate niche variation which is a precondition for stabilising mechanisms to occur. Instead, the global parameter patchiness defines the hump-shaped, i.e. mono-modal, function-trait relationship. To address this issue and to study stabilising mechanisms, a modified version of the model may include different levels of patchiness, i.e. different niches.

Beyond questions of species coexistence, such next-generation models could also help to drive the study of among-individual differences itself. For instance, models explicitly simulating the three dimensions of among-individual differences could be applied to shed light on the conditions at which correlated dimensions, i.e. syndromes, of among-individual differences occur (Hertel et al. 2020). Beyond that, models could allow for further dimensions of among-individual differences, for instance, the plasticity of predictability. Among-individual differences in plasticity of predictability would suggest the individuals switch between routine-like and less predictable behaviour along environmental gradients. Identifying such patterns from empirical data is notoriously challenging as it requires abundant individual movement tracks (Hertel et al. 2021; Hertel et al. 2020). Next-generation models could provide hypotheses on conditions at which such levels of among-individual differences occur.

6.3 Movement ecology - new horizons

Recent perspectives propose a better integration of space-searching algorithms (Hanson et al. 2006), i.e. navigation capacity of fungal hyphae, with the movement ecology paradigm (Bielčík et al. 2019; Nathan 2008) and modern coexistence theory (Chesson 2000a; Chesson 2000b). Applying established ecological theory and concepts to novel fields can identify existing limits in their generalisation. Our initial explorations of community consequences of variation in movement behaviour in

filamentous fungi using an ABM yielded first insights into the selection landscape (i.e. trait-function relationship) of movement traits with regard to foraging. As stated earlier (subsection 6.2.1), trait-function relationships are crucial to determine effects of among-individual differences on species coexistence. The exploration of variation in fungal movement behaviour is currently limited to interspecific differences with ITV being mostly reported as a standard deviation around a species mean. Accordingly, our modelling study is framed in the context of interspecific variation in movement traits.

The model presented in chapter 5 is, in principle, unconscious of the concept of a species. In the context of this thesis, this provokes the obvious question of whether applying concepts from animal behavioural ecology to fungal ecology, would open an untapped, promising field. This may not readily be the case as individual-based ecology encounters one fundamental issue when studying filamentous fungi - the definition of an individual itself is fuzzy and dynamic (Bielčik et al. 2019; Smith-Ferguson and Beekman 2019). Individuals may connect or split and, thus, alternate between phases of competition and cooperation. These dynamics would make it extremely difficult to assess among-individual differences as one would also need to know how many individuals an organism consists of, where the individuals are located, and whether and how the expression of among-individual differences is affected by the composition of an organism. So while, heuristically thinking, the interspecific variation in space-searching algorithms and the principles of evolution suggest that among-individual differences should exist, their actual study currently appears adventurous.

So, while not all concepts in this thesis are readily applicable to filamentous fungi, individual-based approaches to space-searching algorithms may help the field to advance. The study of variation in movement traits has only recently gained traction in fungal ecology and the relation between the network structure of mycelia and space-searching algorithms is largely unknown. In this context, we demonstrate that modelling individual interactions of hyphal tips with their environment provides a viable process-to-pattern approach. To advance in this direction, future studies could compare observed time series of fungal network growth with simulated networks. Network traits provide aggregated information of the network structure with fitness consequences and trade-offs (Aguilar-Trigueros et al. 2021). First, this would facilitate inverse calibration, i.e. the determination of space-searching algorithms using data, which would broaden our knowledge of interspecific differences in space-searching algorithms. Second, if inverse calibration fails, this may identify processes that are not sufficiently understood and require consideration in empirical or theoretical works. This would increase the structural realism of the model and allow us to take advantage of a unique feature

of the model in chapter 5. In contrast to most other approaches, the model explicitly simulates a network where allocation processes could be realistically represented. Yet, for now, representing processes at these more granular levels requires further empirical studies.

6.4 Concluding remarks

The overarching questions of this thesis concern the sources and consequences of ITV in movement behaviour. The recent identification of among-individual differences in movement behaviour (Aliperti et al. 2021; Eccard et al. 2022; Harris et al. 2020; Schirmer et al. 2019; Schirmer et al. 2020; Spiegel et al. 2015; Stuber et al. 2022b) challenges assumptions of central ecological theories (Charnov 1976; Chesson 2000a; Chesson 2000b). In this thesis, I applied ABMs to synthesize current concepts from behavioural and movement ecology to address the lacking integration of among-individual differences in ecological theory.

I found support for currently discussed frameworks to explain the evolution of among-individual differences in movement behaviour and their association with life-history. Based on these insights, I propose ways to relax assumptions in the model and to test the framework more rigorously. In another study, I could demonstrate that among-individual differences in movement behaviour mediate a coexistence-promoting equalising mechanism and highlight the underlying mechanism which contributed to a recent theoretical advancement. I provided a process-to-pattern perspective on buffer mechanisms that mediate population persistence, which is conceptually linked to species coexistence. I identified characteristics of these buffer mechanisms that necessitate individual-based approaches to replace simplifying assumptions in ecological theory. Consequently, I propose next-generation ABMs synthesising behavioural ecology and movement ecology to study consequences of among-individual differences in more detail.

Sources and consequences of ITV in movement behaviour span across scales from behavioural to community ecology and from evolutionary processes to fine-scaled movement decisions. Yet, general ecological theories may be at risk of becoming too implicit to be useful (Vellend 2010) and testable. The application of existing established ecological theory to novel fields, such as animal ecology to fungal ecology, gives insights into their limitations to describe all life. Regarding sources and consequences of ITV in movement behaviour, I could identify relevant mechanisms, yet, their mode of operation remains context-specific. For instance, function-trait relationships help to understand equalising mechanisms, yet, assessing and, let alone, predicting function-trait relationships is highly challenging. Where will theory advance and reduce these dimensions of complexity to form

general, applicable laws, where will we require a "pragmatic view" on ecological theory (Travassos-Britto et al. 2021), and where will idiosyncrasy of real ecological system render any possible generalisation too imprecise to be meaningful (Lawton 1999; Vellend 2010)? Individual-based ecology, as studying how processes result in patterns, represents a promising avenue to escape from the apparent idiosyncrasy.

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A Supplementary material to: Intraspecific trait variation in personality-related movement behaviour promotes coexistence

A1 Additional figures

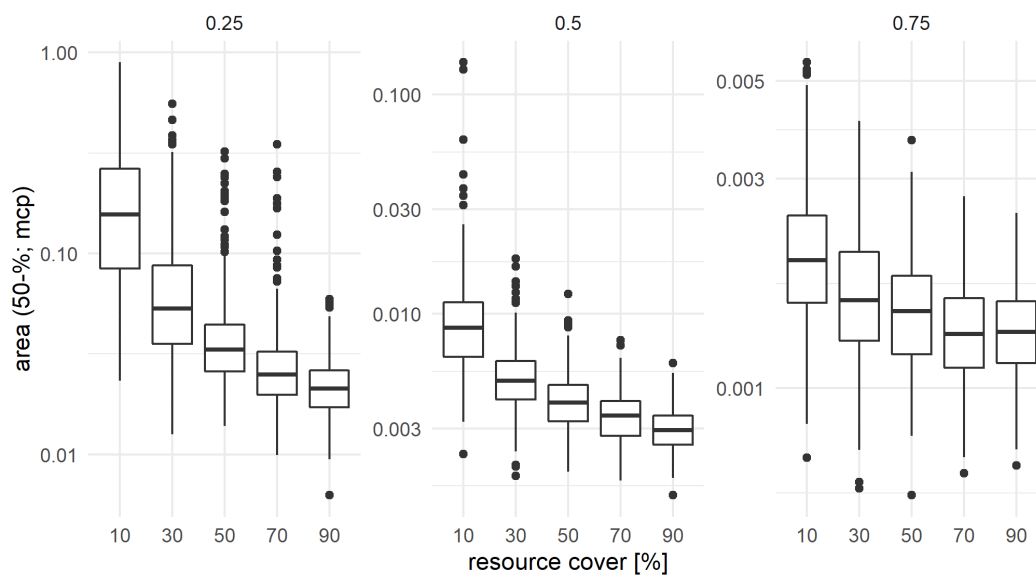


Figure A1.1: Adaptation to different resource coverages via variation in home range size for different behaviour types (0.25, 0.5, and 0.75). Fast (left), intermediate (middle), and slow (right) behaviour types all plastically track changes in resource cover by non-linearly adjusting their home range sizes.

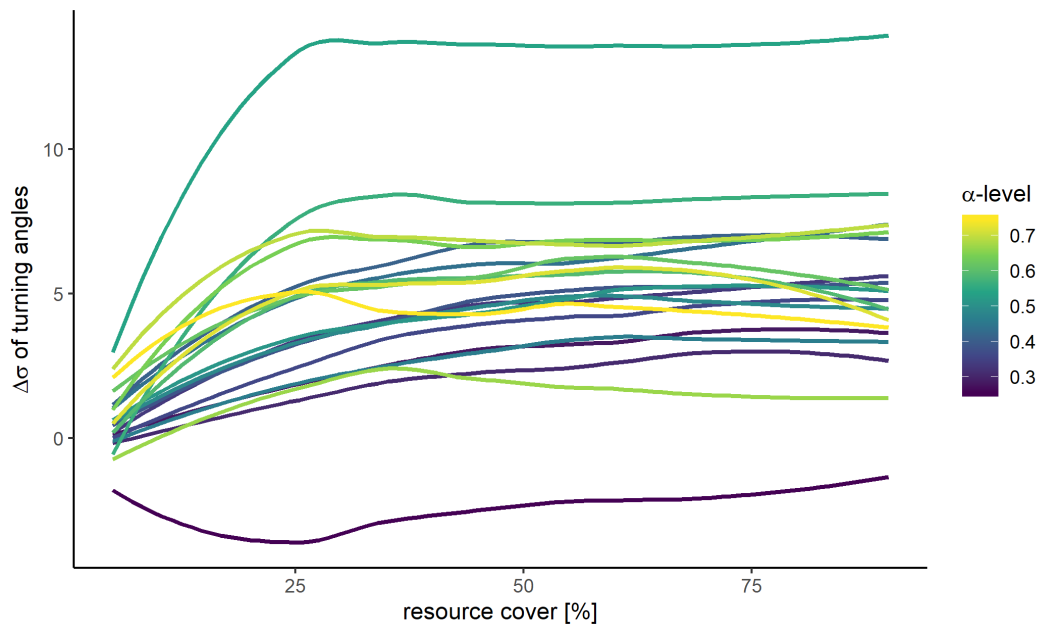


Figure A1.2: Change in standard deviation of turning angles with increasing resource cover. The higher the resource abundance, the less correlated the movement paths become. The strength of the response depends on behaviour type (responsiveness); fast behaviour types respond less especially if increasing from low to intermediate resource cover. Slower behaviour types exhibit a higher responsiveness, however, their response in becoming less correlated eventually saturates at high resource levels. So, despite the higher responsiveness of slower individuals, they do not respond to further changes, which may be due to a stagnation in the number of environmental cues (patches with resources) as their home range size shrinks. Faster individuals may still acquire enough environmental cues (resources) to change their response. See Fig. A1.10 for absolute standard deviation of turning angles for specific scenarios.

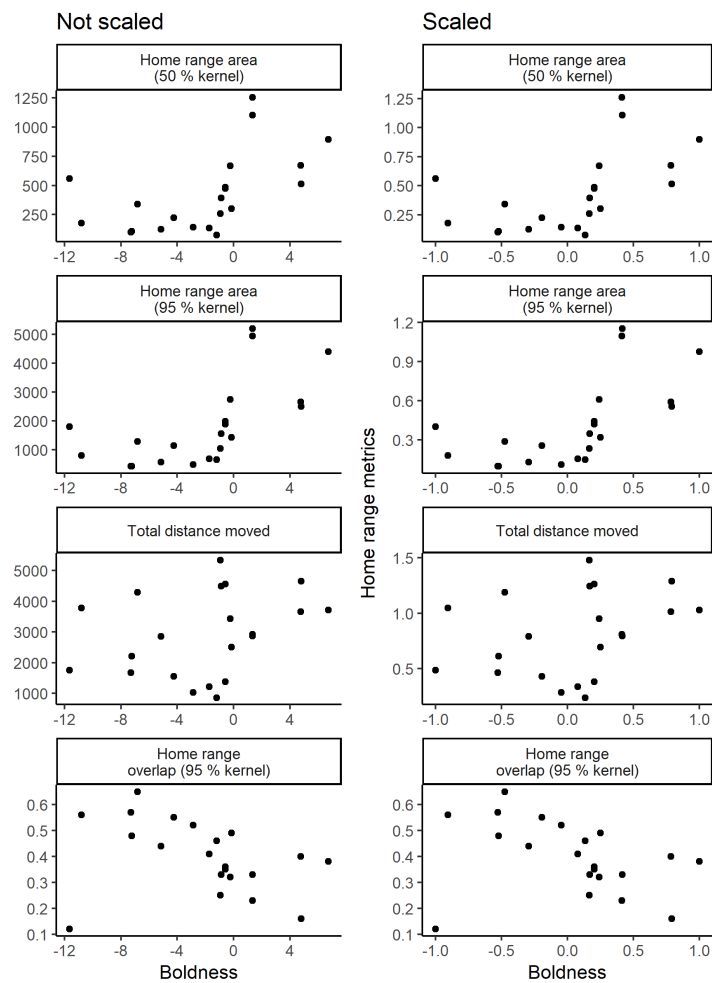


Figure A1.3: Scaled and unscaled data by Schirmer et al. (2019). Scaling changes the observed Boldness Scores to a range from -1 to 1 and the metrics (except for overlap) are divided by the maximum predicted by the linear model. The relative position of data points is preserved. The purpose of scaling is the comparison of simulated and observed data.

We scaled simulated and observed (Fig. A1.2) data to make them comparable. We preserved the relative location of the datasets and only changed the absolute scale. We divided the metrics (except for the mean overlap) by the maximum metric predicted by the linear model (Fig. A1.3).

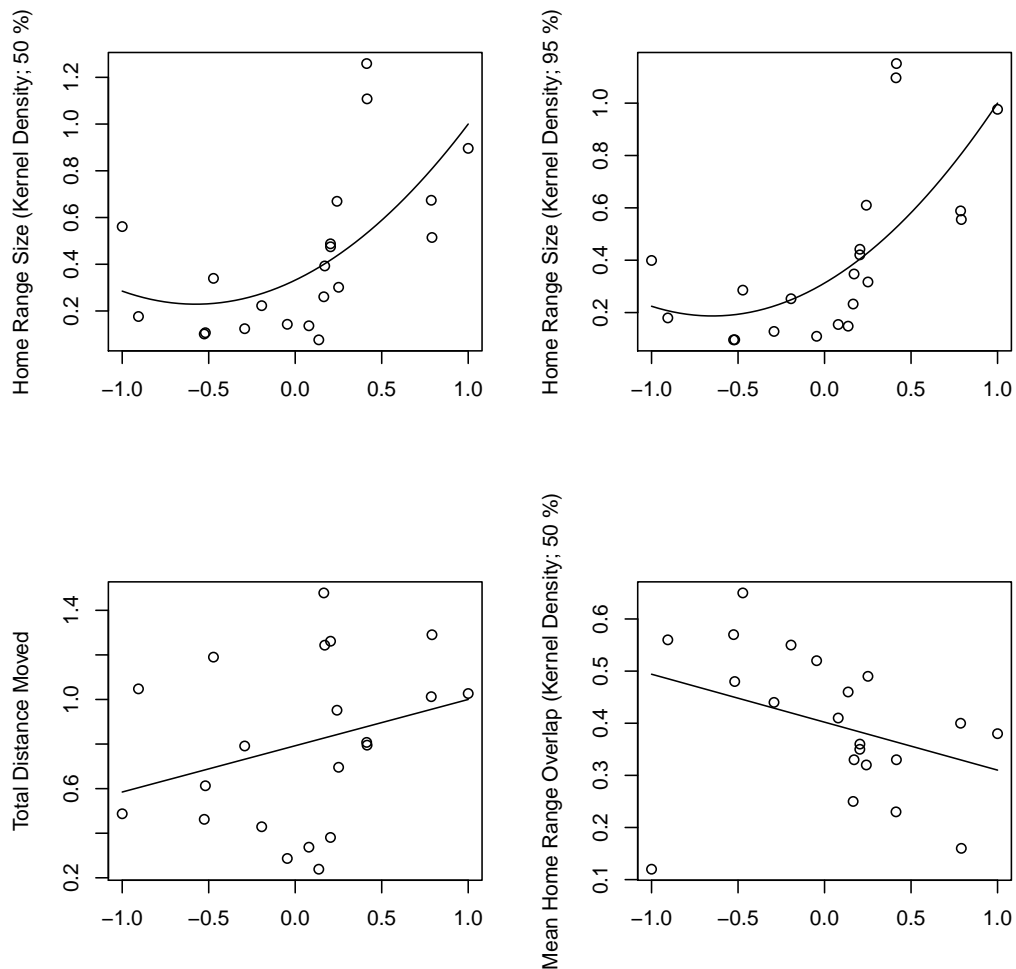


Figure A1.4: Linear Models fitted to the datasets with scaled x and y axis of Schirmer et al. (2019).

We scaled boldness scores and α -levels of each parameter set to range between -1 and 1. The range of α -levels differs between parameter sets. For instance, with trait-mean = 0.3 and ITV = 0.1, α -levels ranges from 0.2 to 0.4, whereas with an ITV of 0.2 they would range from 0.1 to 0.5. To compare each simulation setup with the empirical dataset, we scaled α -levels from different simulation setups to the same scale. Doing so, we could determine whether the output of a simulation setup with ITV = 0.1 or ITV = 0.2 was closer to the observed patterns.

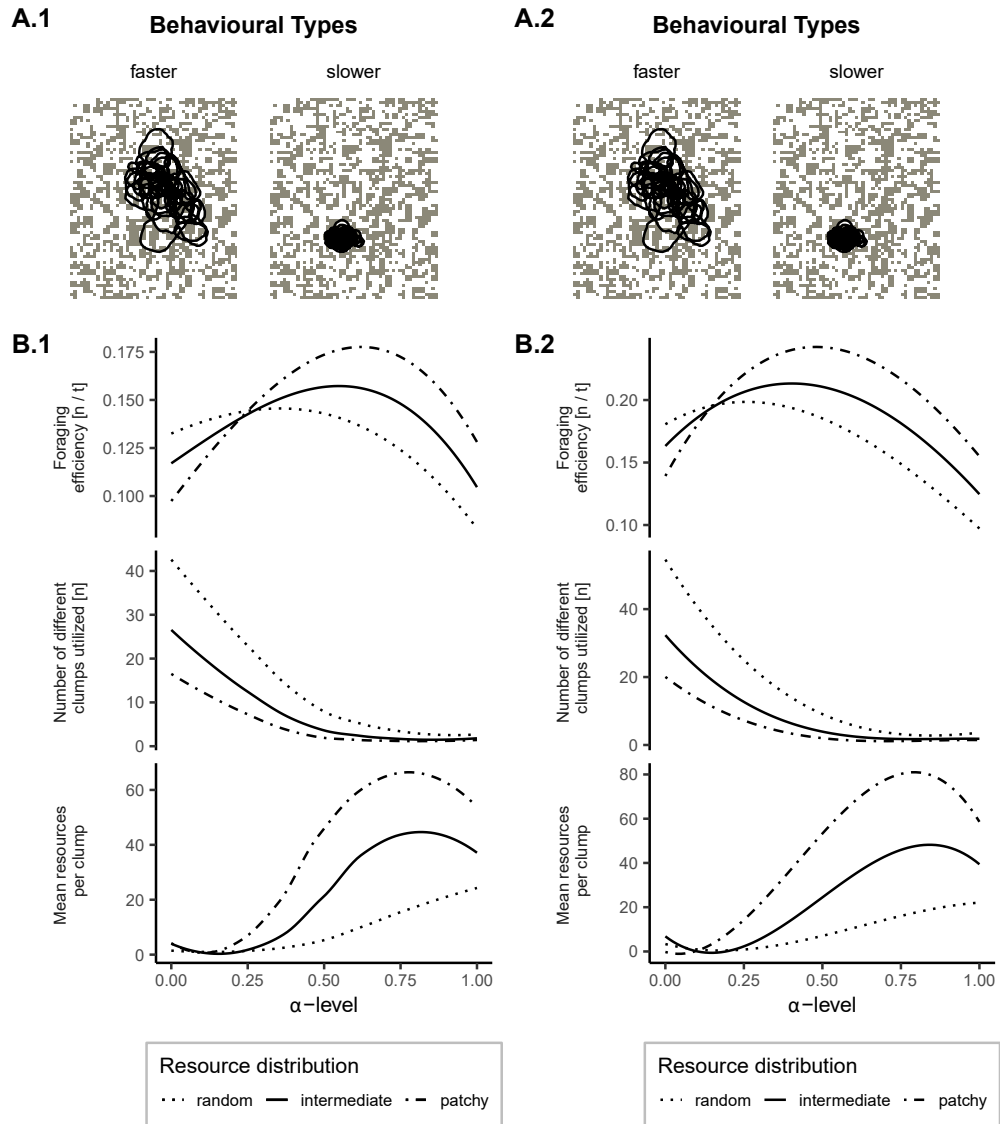


Figure A1.5: Foraging-behaviour-relationship for simulation runs (Scenario 1) with 375 (left) and 750 (right) individuals. The number of competitors affects the location of the optimal landscape-specific behaviour type. With lower competition, bolder behaviour pays off more as exploring other areas becomes more rewarding.

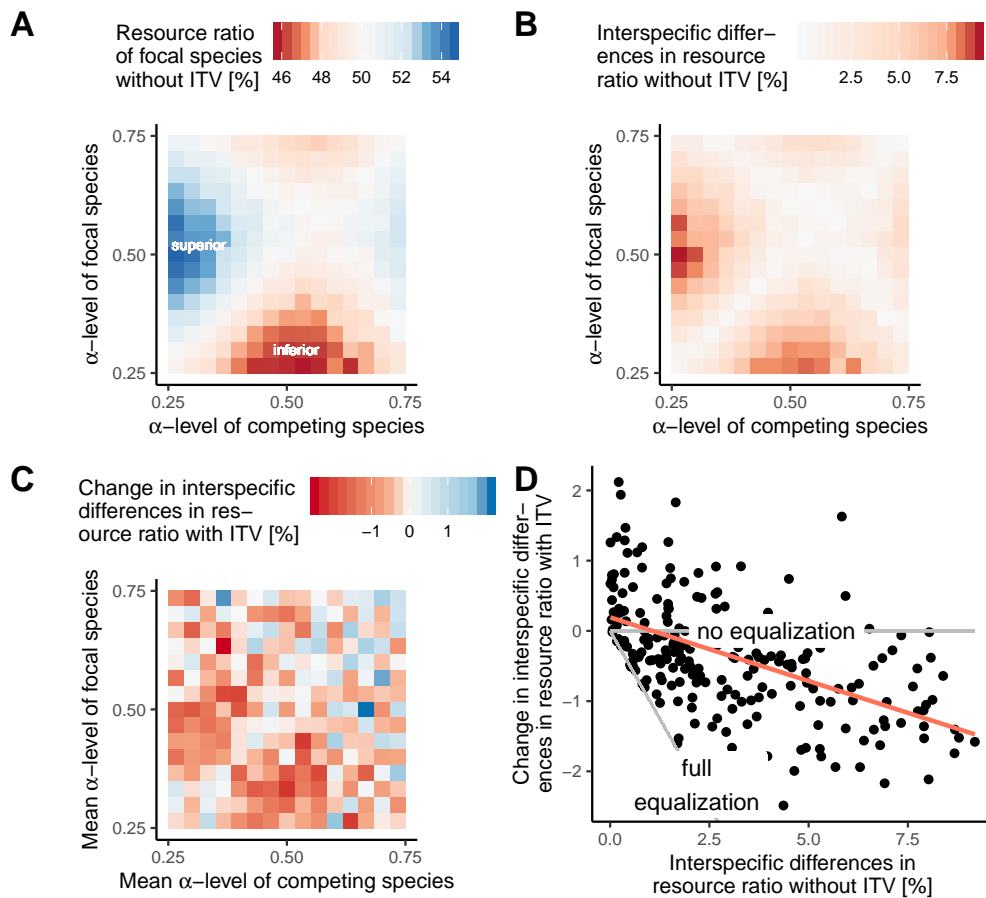


Figure A1.6: Resource ratio of resources a species foraged in relation to the total number of resources both species foraged in a landscape with an intermediate resource distribution. Depending on the combination of BTs, the focal species is superior (blue), equal (white), or inferior (red) to the competing species. B: Interspecific differences in resource ratio without ITV. Differences are highest if one species is at the fast end of the continuum and the other is at the optimum. C: Change in interspecific differences in resource ratio by ITV. Combinations with high levels of interspecific differences in B depict reduced differences due to ITV. D: Change in interspecific differences in resource ratio by ITV (C) in dependence of the interspecific differences in resource ratio without ITV (B). The slope of the linear model reflects the strength of the equalizing mechanism.

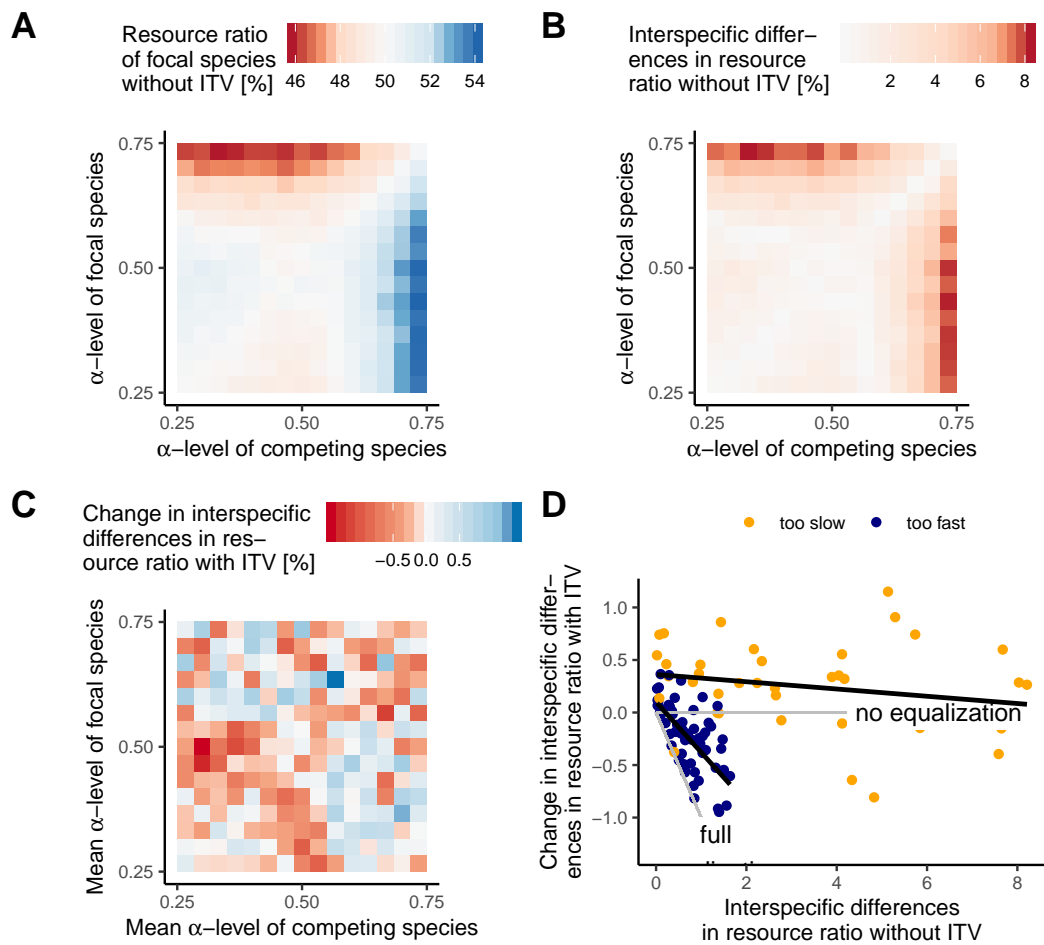


Figure A1.7: Resource ratio of resources a species foraged in relation to the total number of resources both species foraged in a landscape with a random resource distribution. *A:* Depending on the combination of BTs, the focal species is superior (blue), equal (white), or inferior (red) to the competing species. *B:* Interspecific differences in resource ratio without ITV. Differences are highest if one species is at the fast end of the continuum and the other is at the optimum. *C:* Change in interspecific differences in resource ratio by ITV. Combinations with high levels of interspecific differences in *B* depict reduced differences due to ITV. *D:* Change in interspecific differences in resource ratio by ITV (*C*) in dependence of the interspecific differences in resource ratio without ITV (*B*). The slope of the linear model reflects the strength of the equalizing mechanism.

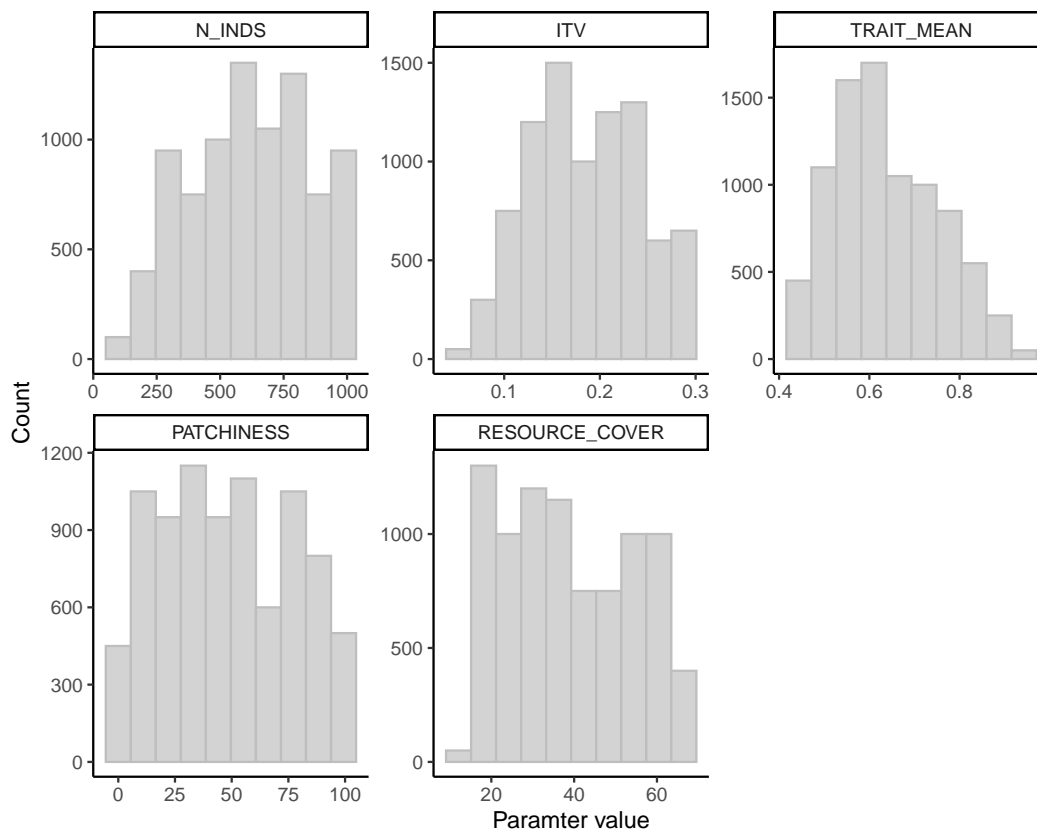


Figure A1.8: Parameter distribution of the top quartile of parameters sets selected with a pooled NRMSE. *ITV* and *TRAIT_MEAN* (which corresponds to *SPECIES-1-MEAN*) are the most restricted to a particular region of the parameter space. The median of the parameter distribution of *ITV* is around 0.13 and was selected for the community analysis. Different levels of *RESOURCE_COVER* appeared with the same frequency in the selected parameter sets. *N_INDS* was not explicitly selected but setting it to 750 individuals appears to be supported by the parameter distribution.

Table A1.1: Summary of settings used for three different simulation types: The Latin Hypercube Sampling (LHS) to perform a global sensitivity analysis and to check the fit to data, a scenario to analyse fitness-trait-relationships in differing landscapes (Fitness-trait-relationship) and a scenario to analyse foraging in a community of species with species-specific mean behaviour types (Community-analysis).

Settings	LHS	Fitness-trait relationship	Community analysis	Coviability analysis
Animals parameter				
species-1-mean	[0, 1]	0.5	[0.25, 0.75]	[0.25, 0.75]
species-2-mean	-	-	-[0.25, 0.75]	[0.25, 0.75]-
ITV	[0.05, 0.3]	0.5	0 (no-ITV), 0.13 (ITV)	0 (no-ITV), 0.13 (ITV)
n-species	1	1	2	2
n-inds	[100, 1000]	750, (375)	750	400
Patches parameter				
resource-cover	[15, 70]	30	30	15 (30 if not patchy)
patchiness	[0, 100]	10 (random), 70 (intermediate), 90 (patchy)	(10, 70), 90	(10, 70), 90
General settings				
max-output	true	false	false	false
max-ticks	2,000	2,000	2,000	100,000
set-this-seed	0	0	0	1 – 100
repetitions	1,000	120	5 x 15 x 15	3 x 9 x 9
Landscape setting				
x-coords	[0, 250]	[0, 250]	[0, 250]	[0, 250]
y-coords	[0, 250]	[0, 250]	[0, 250]	[0, 250]
landscape type	torus	torus	torus	torus

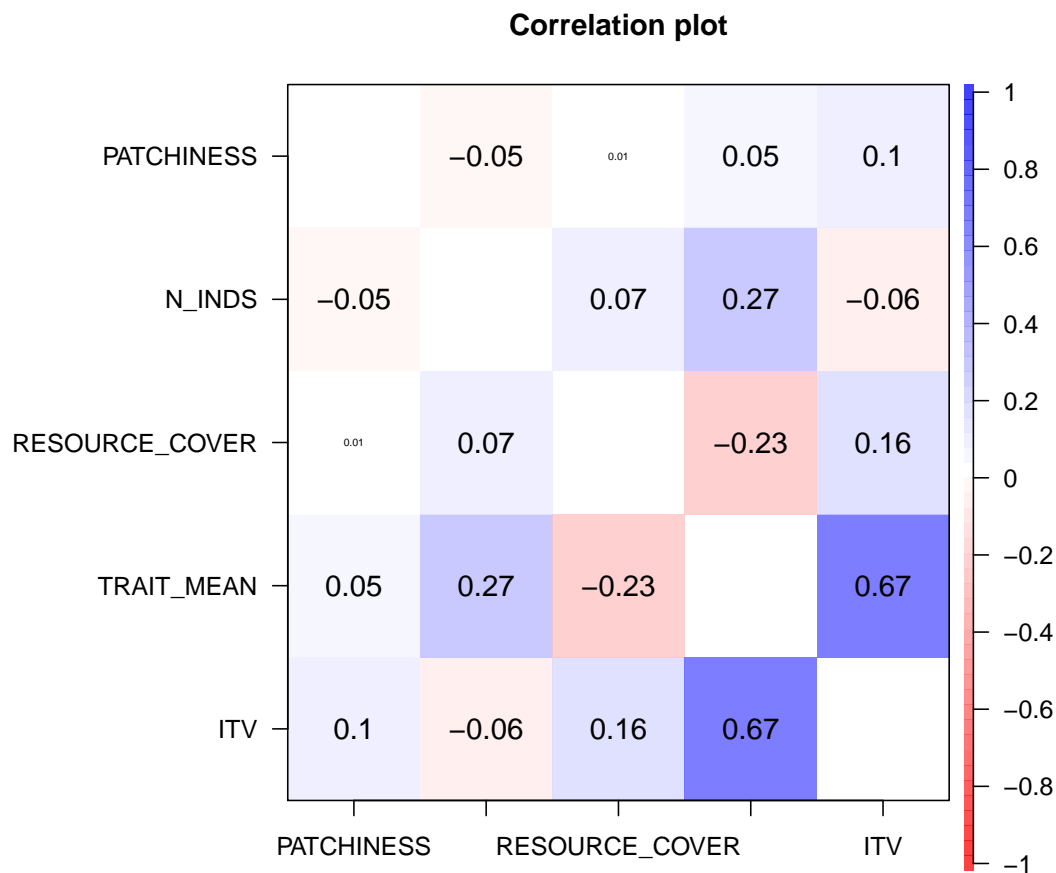


Figure A1.9: Correlation plot of the top quartile of the parameter sets created with LHS and evaluated with the NRMSE. There is a strong correlation between ITV and TRAIT_MEAN. As a consequence, the higher the mean BT of a species, the higher the ITV to fit the patterns observed in the field data. Using the median ITV-level is hence a rough approximation to the real system.

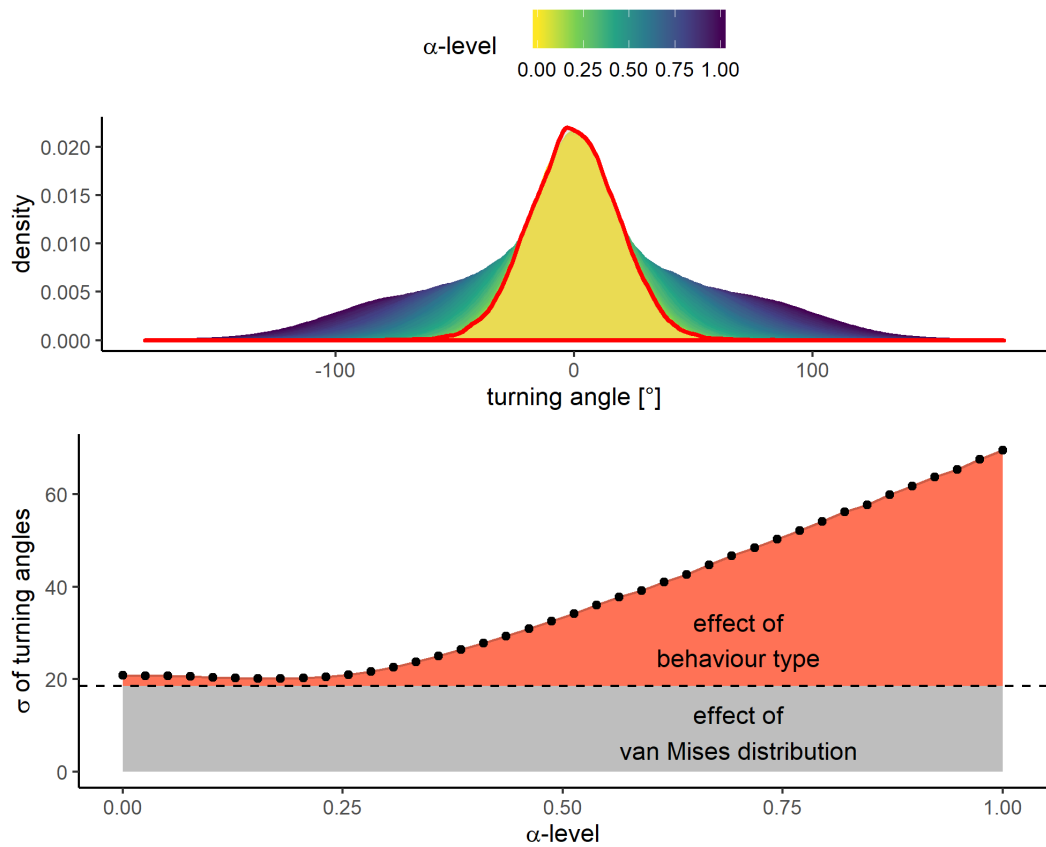


Figure A1.10: Distribution of turning angles and the standard deviation (*sd*) in relation to the specified α -level for exemplary simulation runs with 40 animals in a landscape with random resource distribution. The distribution and the effect of behaviour types depends on the specified scenarios. A: Distributions in comparison with the van Mises Distribution (outlined in red). As expected, the lower the α -level the more the persistence of direction increases and the more the animals perform a movement pattern that is mostly determined by the van Mises distribution. B: Relation between the standard deviation of turning angles and α -level shows a non-linear relationship, as at the fast end, behaviour ceases to have an effect on the distribution of turning angles with standard distribution remaining slightly above the minimum level of stochasticity induced by the van Mises distribution.

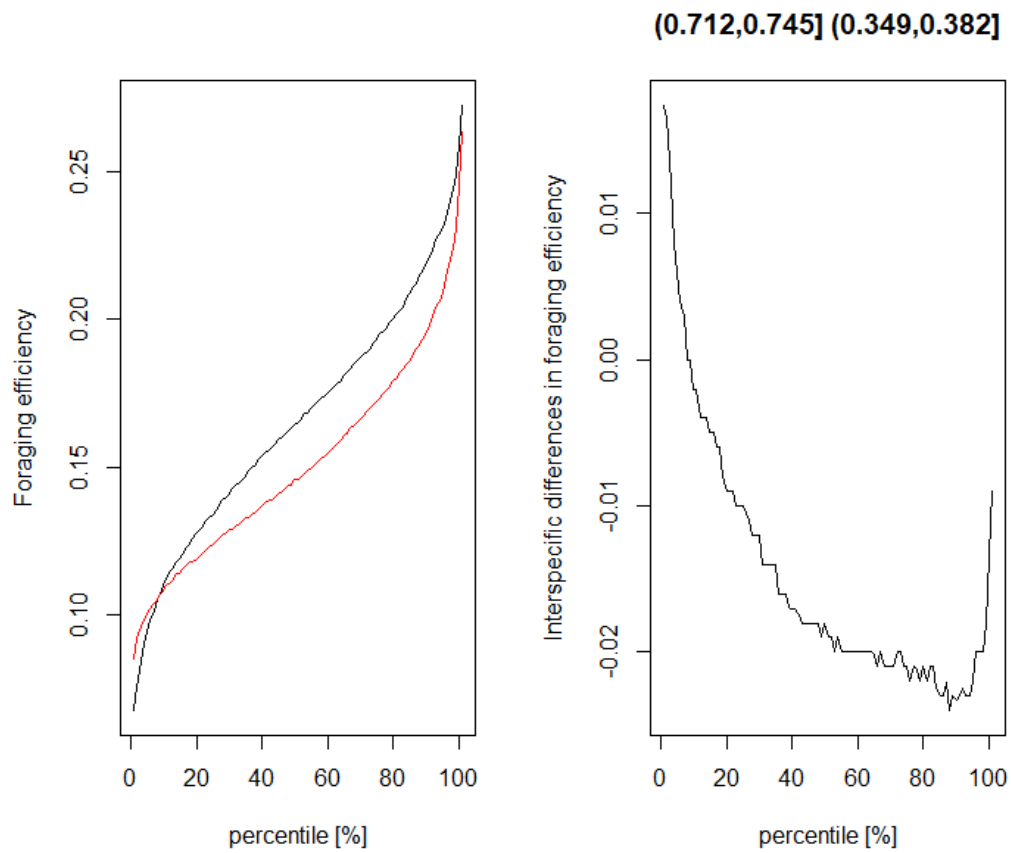


Figure A1.11: Exemplary distributions of foraging efficiency with 1 to 99 % percentile of foraging efficiency for two different species (left) and the differences in foraging efficiency between these species (right) in a scenario with a patchy landscape, The mean BT of one species is between 0.712 and 0.745 and the mean BT of the other species is between 0.349 and 0.382.

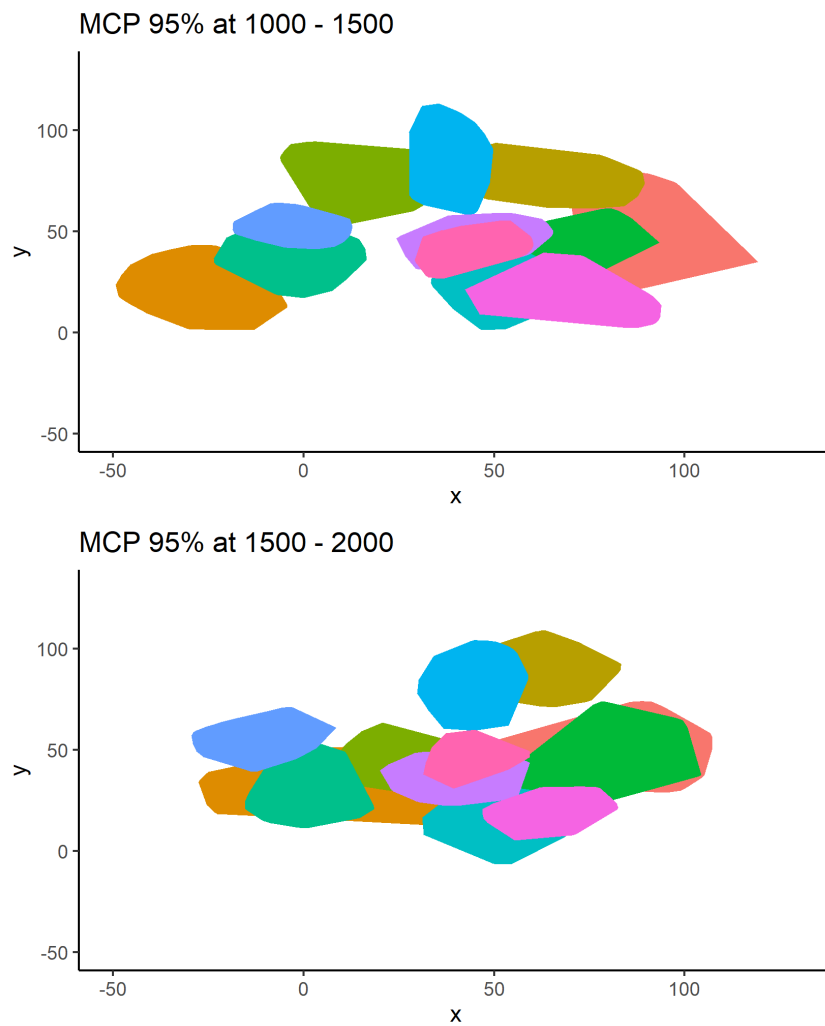


Figure A1.12: Home ranges after the initial 1,000 time steps split in the phases 1000 – 1500 and the phase 1500 - 2000. Certain colors represent the 95-% MCP of an individual. We observe that home ranges do hardly change in position over the course of the simulation, suggesting that home ranges reached some stable state. At an alpha level of zero, stabilization becomes impossible as individuals perform a correlated random walk with no centralizing tendency.

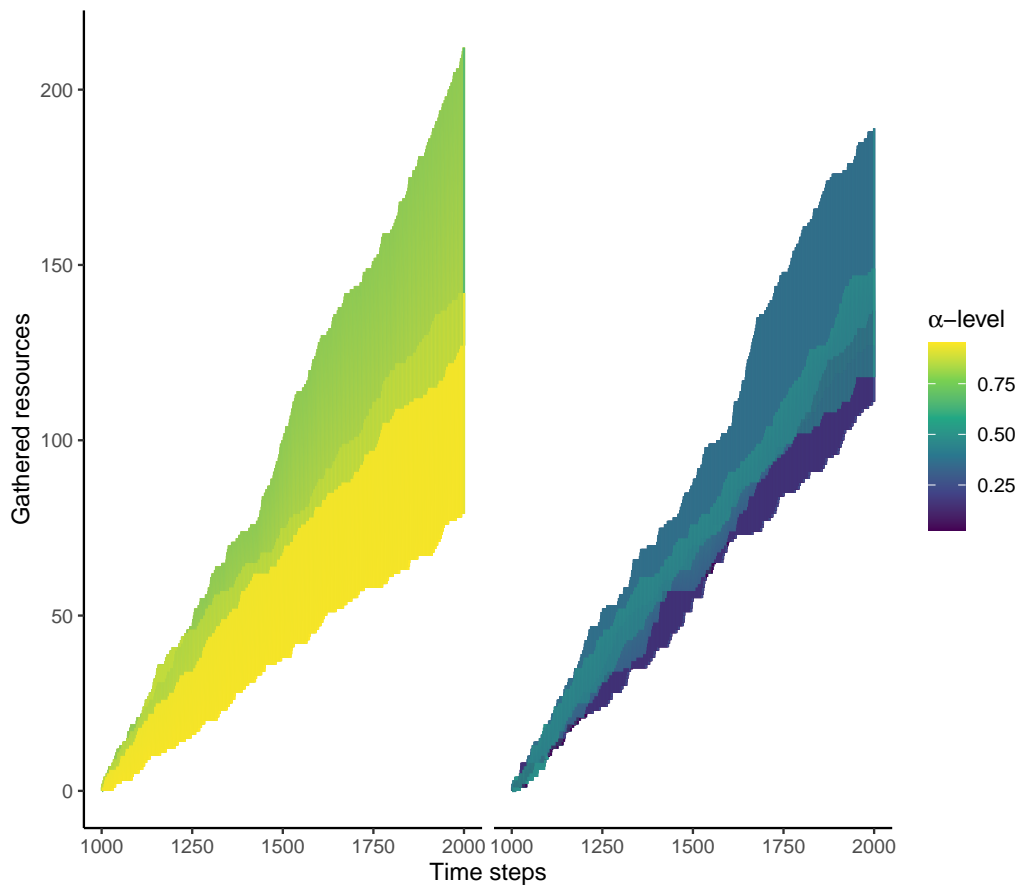


Figure A1.13: Change in gathered resources in the time steps 1000 to 2000 for different alpha levels in one exemplary simulation run in a patchy landscape with 80 individuals. Generally, there is a steady (linear) increase in the amount of gathered resources suggesting a stable situation.

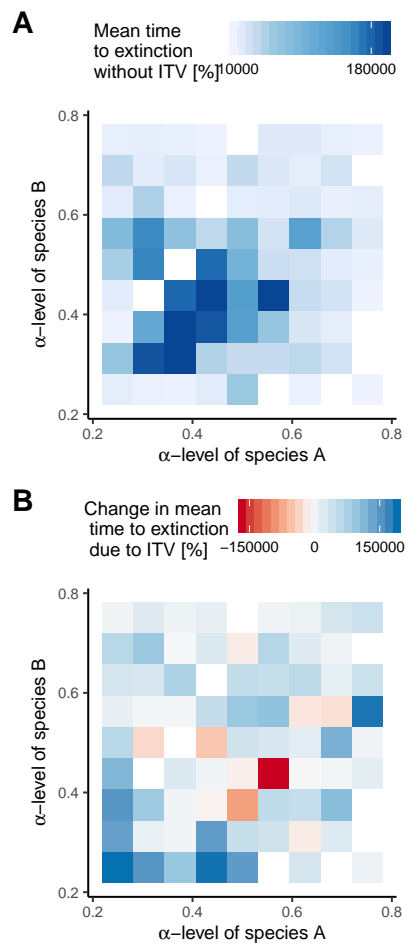


Figure A1.14: Coviability analysis to estimate the effects of ITV in scenarios with population dynamics. The scenario was a intermediate resource distribution and a resource cover of 30%. Resource cover is increased compared to patchy resource distributions to account for the difference in maximum foraging efficiency and to yield similar maximum mean times to extinction. A) Distribution of changes in the mean time to extinction without ITV of 9 by 9 combinations of species-specific mean BTs. The maximum simulation time was 200,000 time steps. B) The change in the mean time until one of the two species went extinct from a scenario without ITV to a scenario with ITV. Overall the pattern is similar to a scenario with a patchy resource distribution, whereas combinations of BTs that are more likely to coexist are generally shifted towards the faster end of the continuum. This is related to the TFE relationship.

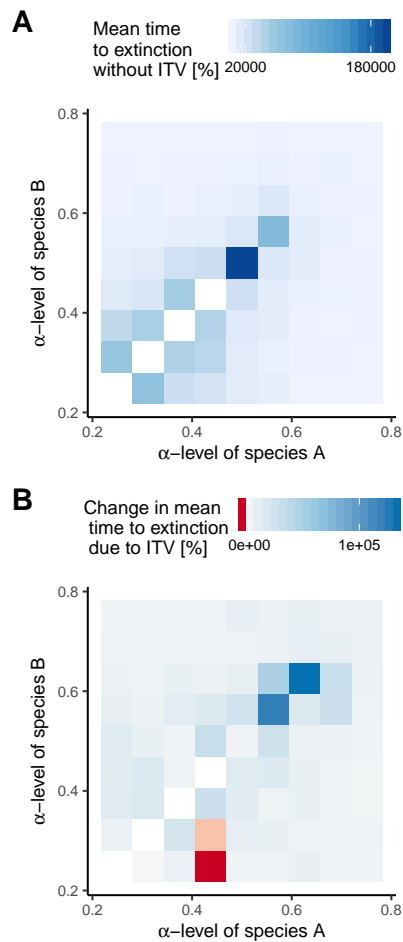


Figure A1.15: Coviability analysis to estimate the effects of ITV in scenarios with population dynamics. The scenario was a random resource distribution and a resource cover of 45%. Resource cover is increased compared to patchy resource distributions to account for the difference in maximum foraging efficiency and to yield similar maximum mean times to extinction. A) Distribution of changes in the mean time to extinction without ITV of 9 by 9 combinations of species-specific mean BTs. The maximum simulation time was 200,000 time steps. B) The change in the mean time until one of the two species went extinct from a scenario without ITV to a scenario with ITV. Overall the pattern is similar to a scenario with a patchy resource distribution, whereas combinations of BTs that are more likely to coexist are generally shifted towards the faster end of the continuum. For landscapes with random resource distributions, the effect seems to be smaller, in general which may be related to the generally smaller interspecific differences in competitive ability. Seemingly, equal BTs have a higher coviability.

A2 Model

The model was written in NetLogo (Wilensky 1999) is made available along with analysis scripts in a zenodo Repository (Milles 2020), on Comses.Net (Janssen et al. 2008), as well as with the published article (Milles et al. 2020).

A3 Model documentation

Basic principles

Our movement model integrates a modified version of a memory-based movement model (Van Moorter et al., 2009) and behavioural reaction norms (BRN, Dingemanse et al., 2010) to explore the emergence of realistic home ranges in a community of species. These two elements of our model are introduced in the following sections as a basis for the subsequent Overview, Design Concepts and Details (ODD, Grimm et al., 2006, 2010; Railsback and Grimm, 2019).

Behaviour reaction norms (BRN) The BRN (Dingemanse et al., 2010) formalizes behaviour as a relationship between an environmental gradient and the behavioural phenotype. In our model, the behavioural phenotype is the persistence of direction (PoD) and the environmental gradient is the strength of the perceived utility of memorized patches (memory feedback). PoD determines the magnitude by which the memory of resource locations (patches) affects the movement direction. The higher PoD, the more an animal turns towards known resource locations.

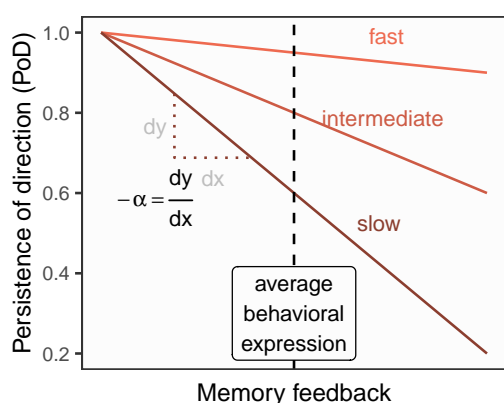


Figure A3.1: Behavioural reaction norm (BRN, Dingemanse et al., 2010) that formalizes the relationship between behavioural phenotypes along an environmental gradient. In our study PoD is the behavioural phenotype and the memory feedback is the environmental gradient as perceived by the individual. Different behaviour types lead to different phenotypic conditions as indicated by the three different linear relationships.

The BRN is modelled as a linear relationship that consists of two elements – the average behavioural expression (e.g. animal personality) and responsiveness (e.g. reversible plasticity) that are both defined by one parameter α . Different α -levels define different behaviour types (BTs). This assumed correlation between these two dimensions of behaviour is backed by empirical evidence (Mazza et al. 2018; Natarajan et al. 2009) and eases the subsequent analysis. The BRN is defined as:

$$PoD = 1 - \alpha * MemoryFeedback$$

We categorize the BTs along a slow-fast-continuum sensu Réale et al. (2010).

Animals with a higher α -level have a higher tendency to rely on their memory and we, hence, define them as shy, responsive and thorough explorers. Animals that rather persist in their current movement direction are thought to be bolder, less responsive and superficial explorers (low α -level). We refer to BT as a behavioural trait and, hence, call the intraspecific variation around a mean BT intraspecific trait variation (ITV).

Memory-based movement In the approach of Van Moorter et al. (2009), animals' decision-making is based on the perceived utility of memorized patches. The perceived utility is the product of reference memory, the working memory and the maximum utility of a patch divided by the distance to that patch. Essentially, the reference memory decays over time mimicking forgetting, whereas the working memory increases hindering the animal to visit a patch that was already recently exploited. The maximum utility is the highest utility value an animal has encountered for a specific patch. Our approach differs slightly from Van Moorter et al. (2009) as the maximum utility (resource) can only be 0, 1. Thereby the product of working memory, reference memory and maximum utility and, hence, the perceived utility would be zero for patches that did not have a resource. Hence, patches with resource 0 do not become part of the memory and the maximum utility as a state variable becomes redundant as it is always 1. Furthermore, the calculation of reference and working memory differs slightly which leads to a difference in parameter settings between our model and the algorithm by Van Moorter et al. (2009) that would lead to the same outcome (for details, see the submodels section below).

In the next step, the perceived utilities are multiplied with the unit vectors of the directions towards the memorized patches to generate attraction vectors. The mean attraction vector is the sum of all attraction vectors. The mean new heading of the animal is a compromise of the current heading and the mean attraction vector. The persistence of direction (PoD) defines the degree to which the animal remains directed towards its current heading.

Van Moorter et al. (2009) add stochasticity with a scale parameter based on the length of the mean attraction vector to represent decision uncertainty. Here we chose a different approach and used the length of the mean attraction vector as the environmental gradient and PoD as the behavioural phenotype sensu Dingemanse et al. (2010) to allow for plastic behaviour and fixed the scale parameter to a certain value. By implementing different relationships between phenotypic behaviour and environmental behaviour via different α -levels, a slow-fast continuum of BTs is generated.

Overview, Design Concepts, and Details

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based and other computational models (Grimm et al., 2006, 2010; Railsback and Grimm, 2019).

1 Purpose The purpose of our model is to analyse the effect of personality-dependent movement behaviour on interspecific differences in competitive ability in foraging and coviability (Jeltsch et al. 2019) and, implicitly, coexistence. The model aims at identifying the role of inter- and intraspecific variations in memory-based movement behaviour for coexistence in multispecies communities. We use the individuals' ability to obtain a certain amount of resources within a certain time frame as a proxy for competitive ability that provides, at the community level, an indicator for coexistence. To consider our generic model realistic enough for its purpose, we linked the emergent movement patterns to home ranges observed in a community of small, ground-dwelling rodents (Schirmer et al. 2019).

2 State variables and scales Entities included in the model are Patches and Animals. Patches are square grid cells characterized by their coordinates and the boolean variable resource 0,1 and the boolean variable fertile 0,1.

Rationale: The value of resource changes from 1 to 0 when visited by animals, whereas fertile remains constant for the whole simulation. Patches with fertile 1 and resource 0 change to resource 1 with a certain probability.

The distribution of fertile and resource is defined by two continuous parameters. Patchiness [0-100 %], which defines habitat heterogeneity, and resource-cover [0-100 %], which is the proportion of patches which are fertile 1. Via set-this-seed, landscape generation can be made reproducible by setting a seed for the random number generator. Low levels of patchiness translate to homogeneous landscapes with random resource distribution and high levels of patchiness translate to heterogeneous landscapes with patchy resource distributions.

Animals are characterized by: parameters alpha ([0, 1]) and the species-specific species-ID ([1 - 2]). Alpha specifies the relationship between the behavioural phenotype PoD (persistence of direction) and the memory-feedback, which specifies how the experienced environment affects movement. Alpha, hence, is the behaviour type (BT) with low values leading to unresponsive, bold, and superficial exploration and high values inducing responsive, shy, and through exploration. The species-specific means alpha is set by the parameters species-1-mean and species-2-mean.

The memory of an animal includes a list of memorized patches (mem-patch), a list of the time (mem-time) since the last visit of a memorized patch, and the number of resources gathered within 1,000 ticks (mem-resources) after a spin-up phase. The utility of elements of mem-patch determined by mem-time and the respective distance constitutes the length of the mean attraction vector (mem-feedback) which

represents the environmental gradient of the behavioural reaction norm (BRN; Fig. A3.1).

Rationale: Animals are assumed to adapt their home ranging behaviour based on their expectations of the availability of resources. Behavioural changes require an environmental gradient to adapt to. In our model, the environmental gradient is defined by the perceived utility and location of memorized patches with resources. Utility and location constitute the length of the mean attraction towards memorized patches which together define the mem-feedback. This feedback increases with the total perceived utility of all patches and the more uniform the direction towards the patches is. The higher the feedback the more an animal expects to gain benefits from returning to memorized patches. Therefore, higher feedback is linked to a higher reliance on memory and, hence, lower the persistence of direction, PoD (details in section 7).

The boolean parameter population-dynamics defines whether animals starve and reproduce. The Boolean state variable breeds defines whether an animal is currently breeding and the continuous variable breeding-stage [0, 3600] defines the stage of the breeding process.

Rationale: Ecologically breeding-stage includes the time from conception to the point where offspring can acquire own resources for the first time. Offspring is only added to the simulation at the end of the breeding process, before its only abstractly represented by an increase in the energetic demand.

Since this is a generic model, the spatiotemporal resolution is not specified, but a single patch should represent a site where a foraging animal finds and exploits resources, i.e. it is specific enough to be distinguished from its surroundings and to be memorized. Accordingly, a time step corresponds to the time to move to and to exploit a patch that has a resource. The spatial extent of the landscape is 250 x 250 patches. The extent of the temporal scale is 2,000 time steps for analysing foraging efficiency and 200,000 time steps a coviability analysis. When analysing foraging efficiency, the first 1,000 time steps are used for initializing the individuals' memories and resource competition dynamics.

Rationale: We chose the extent of the temporal scale to allow for a spin-up phase of the memory algorithm and to sample enough independent, so informative, relocations to analyse the individual home ranging behaviour. We chose the spatial scale to allow for emergent home ranges in a community.

3 Process overview and scheduling In each time step, submodels are performed in the order given below, but the order by which the entities (animals, patches) perform their tasks changes randomly in each time step. The first 1,000 ticks are reserved for initializing the model, so no output is generated during this time. The

submodels are described in detail in ODD section 7. The sequence starts with the submodels for the animals; in the following, bold and underlined fonts indicate names of submodels, while underlined ones refer to variables.

The submodel get-memory-heading calculates a mean heading towards memorized patches (mem-patch) based on a respective perceived utility that is a function of mem-time and the distance to members of mem-patch. The submodel get-PoD returns the current PoD based on the individual's alpha and the recent feedback from memorized locations (mem-feedback). The submodel set-new-heading-and-move returns the new heading as a compromise of the outputs of get-memory-heading, get-PoD, and noise added by a random value sampled from the van-Mises distribution with the scale parameter κ fixed to 10. The animal moves 1 spatial unit in the direction of the new heading.

Rationale: The lower the total perceived utility of patches and the lower α , the higher the PoD. The higher the PoD, the less the new heading changes towards the mean heading of memorized patches and the more the current heading remains.

If no patches have been memorized yet, get-memory-heading and get-PoD are skipped which leads to a correlated random walk determined by the van-Mises distribution.

Depending on whether the animal is on a patch with resource 1 or 0 and whether this patch is an element of mem-patch, different parts of the memory (mem-time, mem-patch, mem-resources) are updated via the update-memory submodel. If the resource of the patch is 1, its resource is set to 0. After the initial spin-up phase of 1,000 ticks, gathered resources are counted via mem-resources to calculate the foraging efficiency which serves as a proxy for competitive ability and, more indirectly, as a proxy for fitness.

If the parameter population-dynamics is true, the submodels do-energetics, attempt-breeding, and create-offspring are activated.

The submodel do-energetics regulates maintenance costs by reducing the value of mem-resources. If breeds is true, also breeding costs are imposed. If mem-resources drops below zero, the animal dies.

If breeds is false, the attempt-breeding submodel is executed. Here, the animal attempts breeding whereas the likelihood to engage breeding depends on the level of mem-resources. The higher mem-resources, the more likely the animal will switch breeds to true.

If the breeding-stage is at its maximum, the animal generates five offspring that share the same species-specific traits (species-mean, species-ID) and are assigned a value of alpha that is sampled from the species-specific uniform distribution defined by species-mean and ITV.

If population-dynamics is true and if there are less than two different species left, save-output is executed.

After all animals performed the previous submodels, patches with resource 0 and fertile 1 perform the submodel grow-resources to reset resource from 0 to 1 with a 1-% chance.

Finally, output is saved. If max-output is true, after the spin-up phase, each tick several observations (e.g. animal location, landscape settings, mem-resources) are written to a .csv-file in the submodel save-output. If max-output is false, save-output is only performed at the end of the simulation.

4 Design concepts We took the following design concepts into account:

- **Emergence.** The movement behaviour emerges from the memory-based movement decisions. The foraging efficiency emerges from the adaptive decision-making, landscape structure, and the indirect interaction between the animals.
- **Adaptation.** Memory-based movement coupled with BRN leads to an adaptive movement behaviour, e.g. via an increase of home range sizes in landscapes of lower resource abundance.
- **Learning.** The home ranges tend to stabilize over time as animals learn about the position of fertile patches.
- **Prediction.** Animals implicitly predict that patches that they (again) visited but had/had no resources will also be favourable/not be favourable in the future.
- **Memory.** Animals memorize patches with resource 1. Memory affects the decision-making as it constitutes an animal's knowledge about the state of the environmental gradient and defines the movement path. Furthermore, animals memorize when they exploited resources from a patch.
- **Interaction.** Indirect competition via shared resources affects an animal's memory and learning. Competitors may exploit resources in patches, which are perceived to be highly favourable as the probability of regrowth. Animals, therefore, affect each other's movement and hence home ranges.
- **Stochasticity.** The initial landscape and the community can be set up randomly. Memory-based movement is randomized by sampling from a van-Mises-distribution. The growth of resources is stochastic. All this stochasticity is used to represent variation caused by factors which are not represented mechanistically in the model.

- **Observation.** The foraging efficiency is the value of mem-resources divided by the number of recorded time steps. In the default setup, the last 1,000 time steps of the simulation were recorded. Optionally, relocations are tracked.

5 Initialization The submodel create-landscape initializes the landscape by distributing resources and fertile to patches according to the settings by the continuous parameters patchiness [0, 100] and resource-cover [0, 100]. This random landscape generation can be replicated by setting a seed for the random number generator using the discrete set-this-seed input parameter [0, 100].

Afterwards, the submodel spawn-animals adds n-inds animals equally divided into n-species species (and hence different species-ID) to the landscape with random initial xy-coordinates. The distribution of behaviour types is defined by ITV and n-species, species-1-mean and species-2-mean. If n-species is 1, the parameter species-1-mean defines the mean behaviour type of that species. If n-species is 2, species-2-mean additionally defines the mean behaviour type of the second species. The initialization consists of the submodels that are more precisely explained in the following:

create-landscape The submodel create-landscape initializes the landscape by distributing resources and fertile to patches according to the settings by the continuous parameters patchiness and resource-cover. So, patchiness multiplied with resource-cover is the initial proportion of randomly chosen patches that have resource 1 and fertile 1. Around these patches, patches with resource 1 and fertile 1 are added until a proportion of patches with resource 1 equal to resource-cover is present. This random landscape generation can be replicated for a certain combination of patchiness and resource-cover by setting a seed using the discrete set-this-seed input parameter [0, 100]. Values from 1 to 100 refer to different seed of the random number generator. If set-this-seed is 0, no seed is set and the landscape generation is not reproducible.

fertilize Subsubmodel of the create-landscape submodel. The variables resource and fertile of a patch are set to 1.

spawn-animals Spawn-animals creates n-inds animals divided into n-species species with their individual properties. The distribution of the individual behaviour type (alpha) is defined by n-species. In any case, alpha is confined to the range of [0, 1]. n-species 1: An equidistant sequence of behaviour types from the minimum (species-1-mean - ITV) to the maximum (species-1-mean + ITV) with a length equal to the number of animals per species is generated. Minimum and maximum are

set to zero or one, respectively, if they are outside the possible range of behaviour types [0,1]. For each species, individuals have a unique alpha value assigned from this sequence. This is repeated for each species.

Rationale: This mode is used to check the relationship of explicitly specified distributions of behaviour types on foraging efficiency at certain population densities and landscapes in single species simulations.

n-species 2: With two species, the mean alpha of one species is set by species-1-mean and of the other by species-2-mean [0.25, 0.75]. There is an equal number of individuals per species. The individual alpha is sampled from a uniform distribution with the species-specific mean as the centre and ITV as the extent in the positive and negative direction. So, the minimum alpha of a species is species-specific mean - ITV and the maximum is species-specific mean + ITV. The assignment of species-specific mean alpha can be made reproducible if set-this-seed is set to a fixed value greater zero.

All state variables related to memory (mem-feedback, mem-time, mem-patch, mem-resources) are empty or zero, respectively. Only if population-dynamics is true, the level of mem-resources is set to 10 to prevent immediate starvation due to maintenance costs.

6 Input data There is no external input of data.

7 Submodels Equations specified below are numbered (“Model equation I”). To link the ODD to the program implementing the model, and the code corresponding to each equation is marked, via comments, by the same label (e.g., “Model equation I”) in the NetLogo program.

get-memory-heading Following Van Moorter et al (2009), the utility of the memory of a given location is a function of temporal and geographical distance. Hence, each memory of a location consists of spatiotemporal information given by mem-time and mem-patch. For a certain memory item i of an animal, the position of the respective patch (p_i) (mem-patch) and the time since the last visit (t_i) (mem-time) are used to calculate the perceived utility U_i . The shortest path $|\vec{ap}|$ between the current position of an animal (a) and p (on a torus, since we use wrapped boundaries) and its length ($|\vec{ap}|$) are calculated. U_i is the product of the decay functions of the working memory (w) and the reference memory (r) with their respective decay rates (d_r) and (d_w) (0.99 and 0.999 as default values) divided by $|\vec{ap}|$.

Rationale: Choosing the values for d_r and d_w might appear arbitrary. In this rationale we reflect why we chose these parameters via some equations which are not part of the model. The absence of competition and forgetting, an optimal perceived utility of a patch should, at constant geographical distance, only be a function of the

Table A3.1: Model parameters.

Entities	Parameter range	Description
Landscape (patches)		
patchiness	0 – 100 [%]	heterogeneity and amount of distributed resources
resource-cover	0 – 100 [%]	
max-pxcor	250 [const.]	size of x-dimension
max-pycor	250 [const.]	size of y-dimension
set-this-seed	0 – 100	set seed for the random number generator during landscape generation
Community (animals)		
species-1-mean	0.0 – 1.0 [continuous]	mean behaviour type, species 1
species-2-mean	0.0 – 1.0 [continuous]	mean behaviour type, species 2
n-species	1 – 2 [n]	number of species
n-inds	1 – 750 [n]	number of individuals
TV	0.0 – 1.0 [continuous]	one-sided width of the uniform behaviour type distribution
Movement algorithm		
rvm-kappa	10 [const.]	scale parameter of van-Mises distribution (higher values = more correlated)
rate-mem-ref	0.99 [const.]	decay of reference memory
rate-mem-work	0.999 [const.]	decay rate of working memory
Miscellaneous		
max-output	true, false	give continuous model output
max-ticks	2000, 100,000	number of simulation steps
population-dynamics	true, false	enable population dynamics
subfolder	string	output folder
Population dynamics (only used if population dynamics is set to true)		
breeding-cost	0.0075 [const.]	increase in breeding cost per 100 time steps
breeding-duration	3600 [const.]	amount of time steps from conception to generating offspring
litter-size	5 [const.]	amount of generated offspring
maintenance-cost	0.18 [const.]	energetic costs per time step

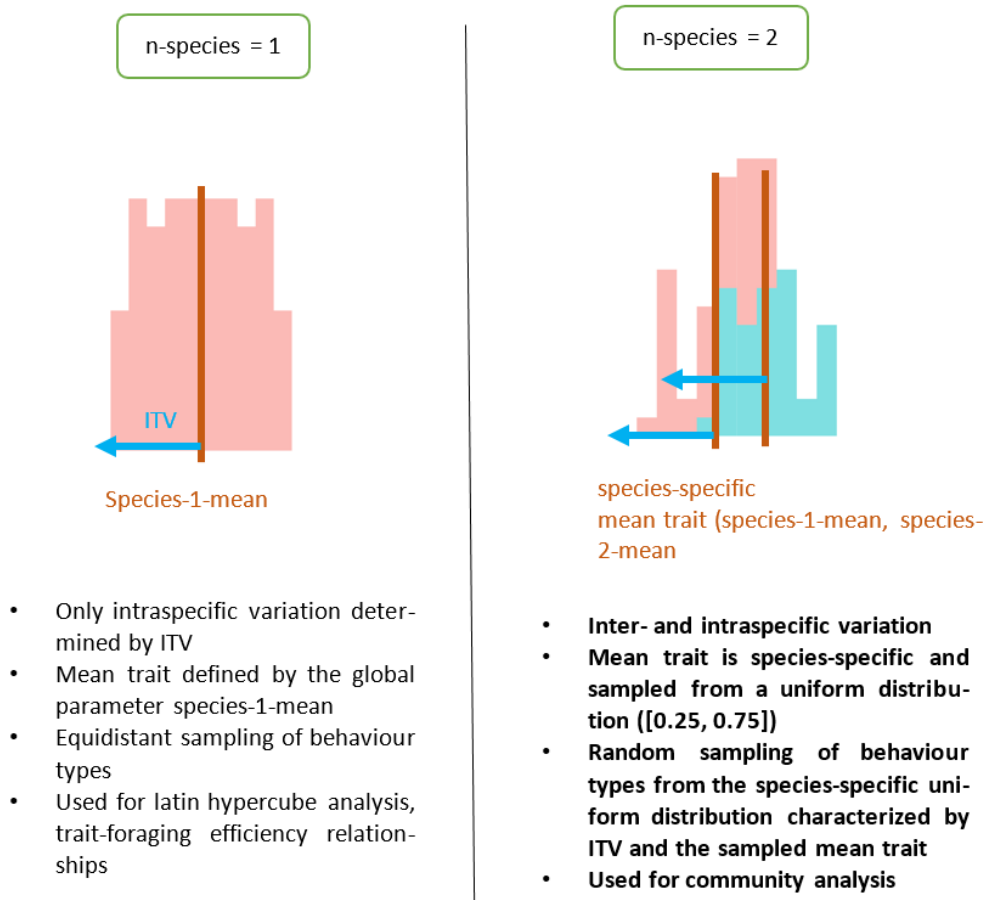


Figure A3.2: Spawn animals procedure.

likelihood that a resource regrow (R). R is a function of the time (t) since a patch has been exploited and the probability of resource growth per time step:

$$R(t, p_r) = 1 - (1 - p_r)^t$$

Competition, as the likelihood that a competitor exploits a known resource patch in the meantime, can be described as a function of the likelihood of regrowth (Fig. A3.4) and the likelihood of a competitor visiting a patch. The likelihood of regrowth per time step (p_r) and the likelihood that a competitor visits a patch (p_c) define the likelihood over time that a competitor exploits a given resource first:

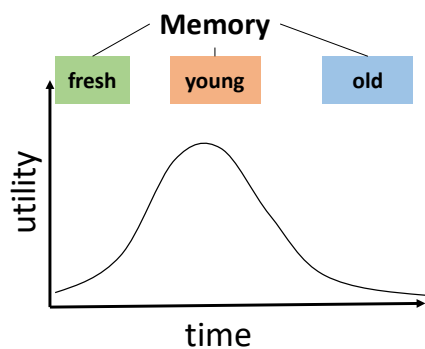


Figure A3.3: The perceived utility as the product of working memory and reference memory assuming the same geographical distance

$$C(t, p_r, p_c) = R * (1 - (1 - p_c)^t)$$

The difference between R and C is the residual likelihood that there is a resource at a certain a patch and a competitor has not exploited it first. This difference could be assumed to be the optimal perceived utility (if not regarding geographical distance to this resource). This optimal perceived utility is hump-shaped at different levels of competition and, thus, reasons the choses parameterization of the memory algorithm via (d_r) and (d_w) even without considering elements such additional as forgetting about the utility of patches. As a side note: one can infer from this observation that at higher levels of competition the penalty from an earlier forgetting about patches is reduced as the optimal perceived utility starts to decrease earlier. The level of competition is likely to vary strongly between patches and individuals, so we cannot infer from these reflections to the actual likelihood that a competitor exploits a resource first. We decided to parameterize the memory algorithm to reach the highest perceived utility after around 100 ticks, which leads to a similar shape as the delta between the likelihood of competition and regrowth.

We modified the calculation of reference and working memory given by van Moorter et al. (2009) by changing it from an iterative approach that requires a specification of the initial reference and working memory to a decay function that only requires the time since the resources were exploited from this patch as the determinant. The initial reference and working memory and the decay rates of van Moorter et al. (2009) can still be parameterized to give return a similar utility function (Fig. A3.5).

$$r(t_i) = d_r^{(t_i)}$$

$$w(t_i) = 1 - d_w^{(t_i)}$$

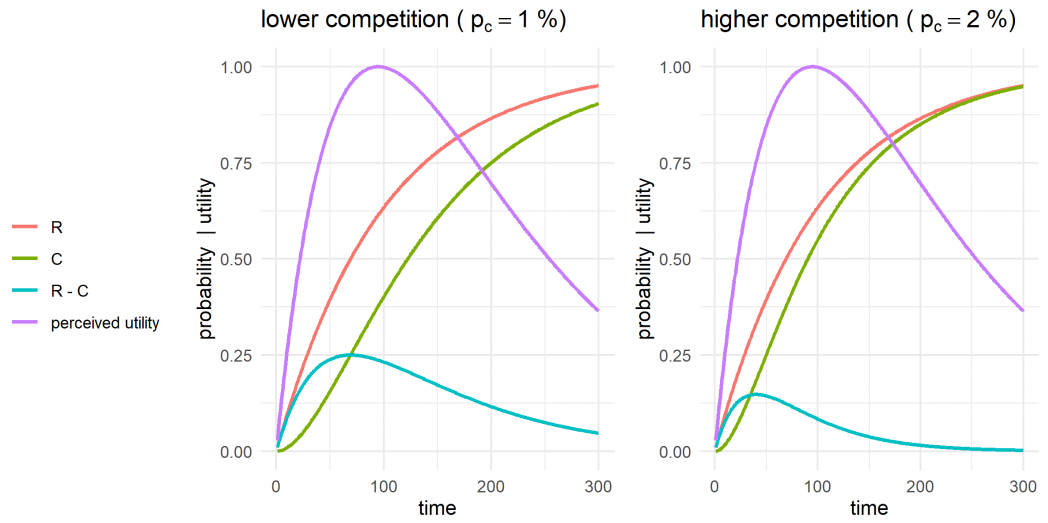


Figure A3.4: The perceived utility (divided by its maximum), the likelihood of growth (R), the likelihood that a competitor exploited the regrown resource first (C), at higher ($p_c = 0.02$) and lower ($p_c = 0.01$) levels of competitor (e.g. population density), and the differences between the likelihood of regrowth and likelihood of competition ($R - C$). For simplicity, we disregard that the likelihood of competition again alters the likelihood of regrowth.

$$U_i = \frac{w(t_i) * r(t_i)}{|\vec{a}\vec{p}|^2} \quad (.1)$$

The mean attraction vector from memory is the sum of all vectors towards memorized patches converted to unit vectors ($\frac{\vec{a}\vec{p}_i}{|\vec{a}\vec{p}_i|}$) and weighted by their utility U_i . To calculate the unit vector, the shortest path towards a memorized location ($\vec{a}\vec{p}$) is determined ...

Rationale: In a toroidal landscape there are multiple straight lines that connect two points, here the location of the animal a and the location of patch p . The shortest path is $\vec{a}\vec{p}$.

... and divided by its length ($|\vec{a}\vec{p}|$) and multiplied with U_i to combine utility and direction. The sum of all memory vectors is the attraction vector from memory \vec{x}_m .

$$\vec{x}_m = \sum_{i=1}^n \frac{\vec{a}\vec{p}_i}{|\vec{a}\vec{p}_i|} * U_i$$

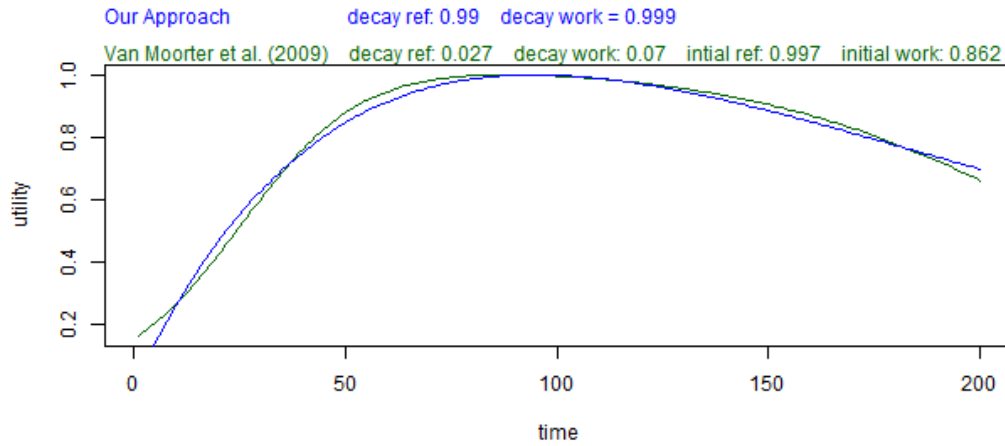


Figure A3.5: Changes in utility due to the two component memory over time in our approach and the approach by van Moorter et al. (2009) can yield similar results, if parameters are set accordingly. Note that the utilities of the different approaches in this example are divided by the maximum.

In the model, the calculation of the equation above is split into 3 lines of code for the x and y component respectively:

$$\frac{\vec{a}\vec{p}_i}{|\vec{a}\vec{p}_i|} \quad (2)$$

$$\frac{\vec{a}\vec{p}_i}{|\vec{a}\vec{p}_i|} * U_i \quad (3)$$

$$\sum_{i=1}^n \frac{\vec{a}\vec{p}_i}{|\vec{a}\vec{p}_i|} * U_i \quad (4)$$

Note that opposing vectors with equal utility would neutralize each other's effect on the mean attraction vector.

get-PoD PoD (Persistence of Direction) defines the behavioural phenotype that depends on the environmental gradient (memory-feedback) and the behaviour type (alpha). The variable mem-feedback x is the 4th root of the length of the attraction vector from memory $|\vec{x}_m|$.

$$x = \sqrt[4]{|\vec{x}_m|} \quad (5)$$

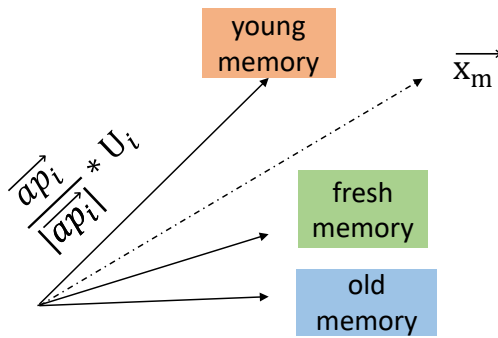


Figure A3.6: Example of the calculation of a mean attraction vector from memory. Opposing memorized patches would neutralize each other and therefore not contribute to the mean attraction vector.

Rationale: The length and direction of the attraction vector from memory results from the perceived utilities and the locations of the memorized patches. If there many patches are memorized, with high utility, memory-feedback is large and vice versa. Furthermore, if memorized patches with high utility are at a certain location instead of randomly distributed around the animal, the memory-feedback is higher as exactly opposing memorized patches neutralize each other and do not prolong the attraction vector. The directivity of the memorized patches affects the memory-feedback. The transformation of the attraction vector from memory by the 4th root serves to adjust the emergent movement behaviour that results from the relationship between alpha and memory-feedback. Without the transformation, memory-feedback would be close to zero and PoD, hence, close to one. Linear transformation of the memory-feedback, e.g. by a factor of 10, leads to higher dynamics in PoD, but the movement pattern did not correspond to the desired central-place foraging. The transformation by the 4th root, however, facilitated central-place foraging without constraining the adaptive effect of the environmental gradient too much (e.g. demonstrated by larger home ranges in resource poor landscapes).

Now, the PoD (behavioural phenotype) is calculated via the behaviour type α and the memory-feedback as environmental gradient (Fig. A3.7)).

$$PoD = 1 - \alpha * MemoryFeedback \quad (.6)$$

Rationale: Animals should adapt their home ranging behaviour based on their expectations of the availability of resources. Behavioural changes require an environmental gradient to adapt to. In our model, the environmental gradient is defined by the perceived utility and location of memorized patches with resources. Utility and location constitute the length of the mean attraction towards memorized patches which is the determinant of the mem-feedback. The feedback is higher the higher the total perceived utility of all patches and the more uniform the direction towards the patches is. The higher the feedback the more an animal expects to gain benefits from returning

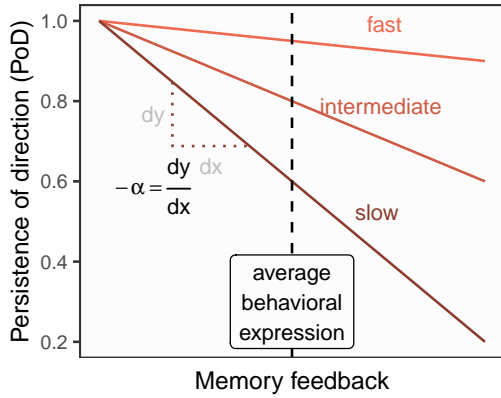


Figure A3.7: Behavioural reaction norm (BRN, Dingemans et al., 2010) that formalizes the relationship between behavioural phenotypes along an environmental gradient. In our study PoD is the behavioural phenotype and the memory feedback is the environmental gradient as perceived by the individual. Different behaviour types lead to different phenotypic behaviours under common environmental conditions as indicated by the three different linear relationships.

to memorized patches. Therefore, a higher feedback is linked to a higher reliance on memory and, hence, lower PoD (details in section 7). The higher the memory feedback and the higher α , the lower is PoD and the higher is the reliance on memory. For the sake of simplicity, the intercept at zero memory-feedback does not vary between individuals and is always 1. The correlation between mean behavioural response and responsiveness is based on existing evidence (Mazza et al. 2018; Natarajan et al. 2009). If the PoD is below 0 it is set to 0.

Rationale: The PoD is fixed to a range of 0 to 1. Individuals with a PoD of 0 turn fully towards the mean attraction vector. Fixing the lower boundary to 0 is therefore necessary. However, drops of PoD to 0 have not been observed in test runs with individuals with an α -level of 1. A PoD of 0 becomes unlikely due to the underlying processes. The higher the PoD gets, the more likely it becomes that an individual will exploit a certain patch resetting the utility function (see. Fig. A3.3) or, if it is not successful at exploiting a patch, the utility will start to decrease.

set-new-heading-and-move PoD and the attraction vector from memory \vec{x}_m determine the new mean attraction vector from memory (\vec{x}_n). Hence, (\vec{x}_n) is a combination of the current movement direction \vec{x}_c and the attraction vector from memory \vec{x}_m weighted by PoD :

$$\vec{x}_n = PoD * \vec{x}_c + (-PoD) * \vec{x}_m \quad (.7)$$

Finally, the direction of \vec{x}_n is slightly randomized by sampling from the van-Mises distribution with the radians of \vec{x}_n as its location parameter and $\kappa = 10$ as the scale parameter (Fig. A3.8)). By moving one spatial unit towards this new direction, the decision-making is completed.

Rationale: The stochasticity induced by the van-Mises distribution should account for effects (i.e. disturbance, barriers) that may alter the movement path generated from memory and are not included in the model.

update-memory After moving, the attributes of the current location (patch) are assessed. If resource on the current patch is 1 and it is not part of the animal's mem-patch yet, the patch is added to the mem-patch list and gets a corresponding entry in mem-time of 0. If the patch is part of mem-patch already, the corresponding mem-time of the patch is reset to 0.

In any of these two cases, resource of the patch gets set to 0.

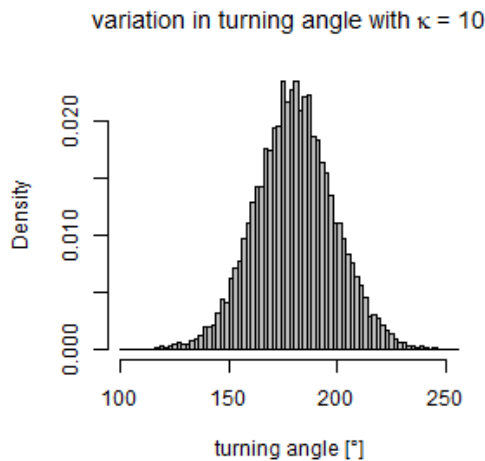


Figure A3.8: Sampled turning angles ($n = 10,000$) with the scale parameter $\kappa = 10$ and location parameter π (180°). The location parameter is arbitrary as it depends on the direction of memorized patches.

Rationale: Patches with resource 0 are not added to mem-patch as their perceived utility would be zero. Only patches with resource 1 affect the memory.

Finally, all entries in mem-time are increased by 1 to account for the aging of the memory.

do-energetics The submodel reduces mem-resources by 0.18 per time step and resembles maintenance costs. *Rationale:* The maintenance costs of 0.18 per time step are derived from mean foraging efficiencies at the optimum of trait-foraging efficiency relationships in a patchy landscape.

If breeds is true, the animal increments breeding-stage by 1. The costs imposed on mem-resources (MR) per time step depend linearly on the breeding-stage (BS):

$$MR_{t+1} = MR_t - 0.0075 * BS$$

Rationale: The model's population dynamics are generically based on to the ecology of small mammals. To account for the increase in body mass during pregnancy and the increase in energy demand by the offspring during lactation, we assume a linear increase in the total energy demand.

attempt-breeding If breeds is false, the attempt-breeding submodel is executed. Here, the animal attempts breeding whereas the likelihood to engage breeding depends on the level of mem-resources. The higher mem-resources, the more likely the animal will switch breeds to true (Fig. A3.9)).

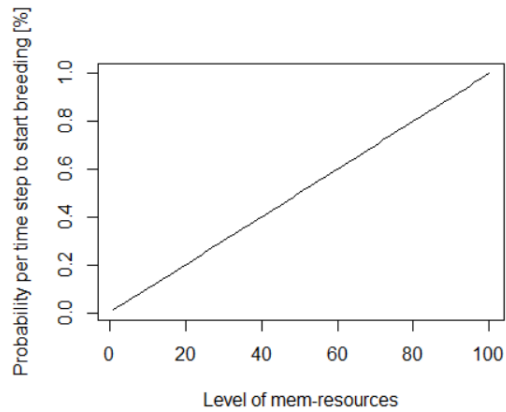


Figure A3.9: Probability per time step to attempt breeding in dependence of the level of mem-resources.

create-offspring If the breeding-stage is at its maximum, the animal generates five offspring that share the same species-specific traits (species-mean, species-ID) and are assigned a value of alpha that is sampled from the species-specific uniform distribution defined by species-mean and ITV. The initial location is the same as the current parental location. All other state variables are set as during initialization of the model.

grow-resources All patches with fertile 1 and resource 0 have 1%-chance to set resource back to 1.

B Supplementary material to: Fluctuations in density-dependent selection drive the evolution of a pace-of-life-syndrome between and within populations

B1 Additional figures

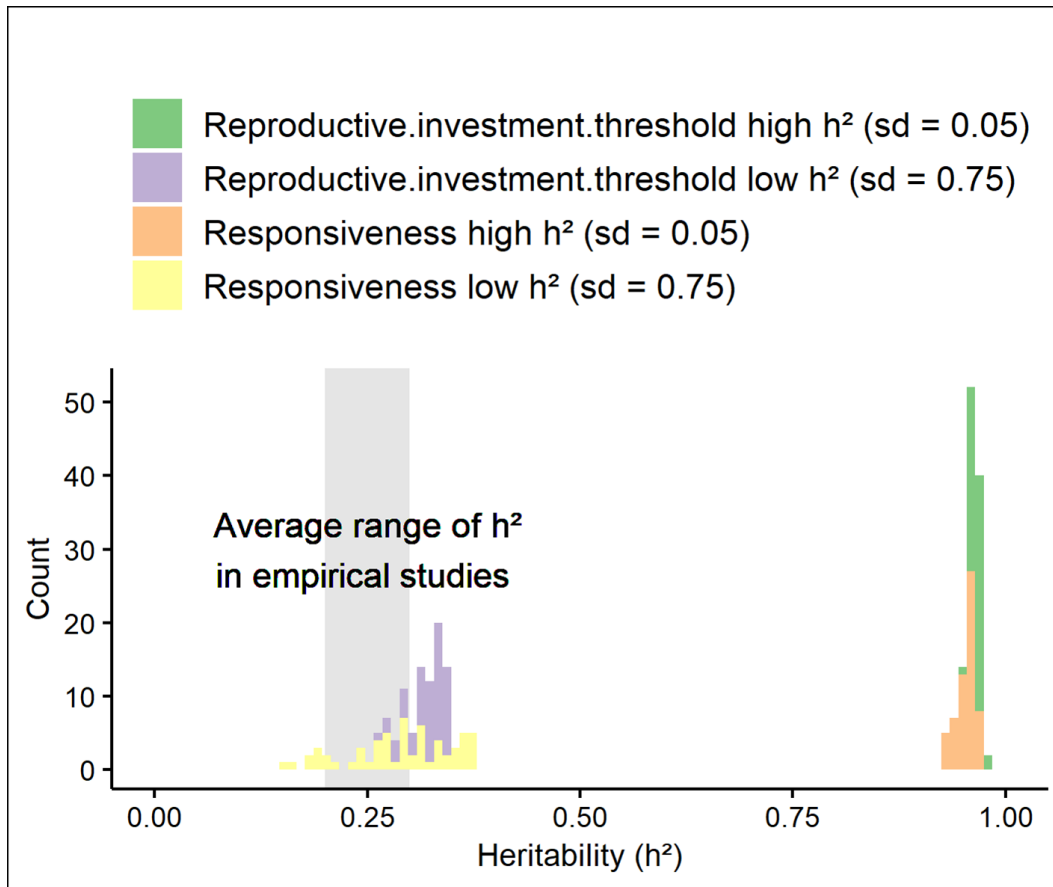


Figure B1.1: Heritability (h^2) of traits with different parameter settings (stochasticity-BT, stochasticity-LH) within populations ($n = 60$ for low and high h^2 , respectively). All other parameters were as described in the main text. The scenario with low h^2 represents the parameterization in described in the main text. These parameters define the standard deviation (sd) of a normal distribution with the parental trait as the mean. Traits of the F1 generation were sampled from this normal distribution. If we chose low levels of stochasticity, traits were more correlated between generations (i.e. h^2 was higher). To achieve realistic levels of h^2 , we chose a standard deviation of 0.75. Heritability was calculated by the coefficient of correlation between traits of parent and offspring.

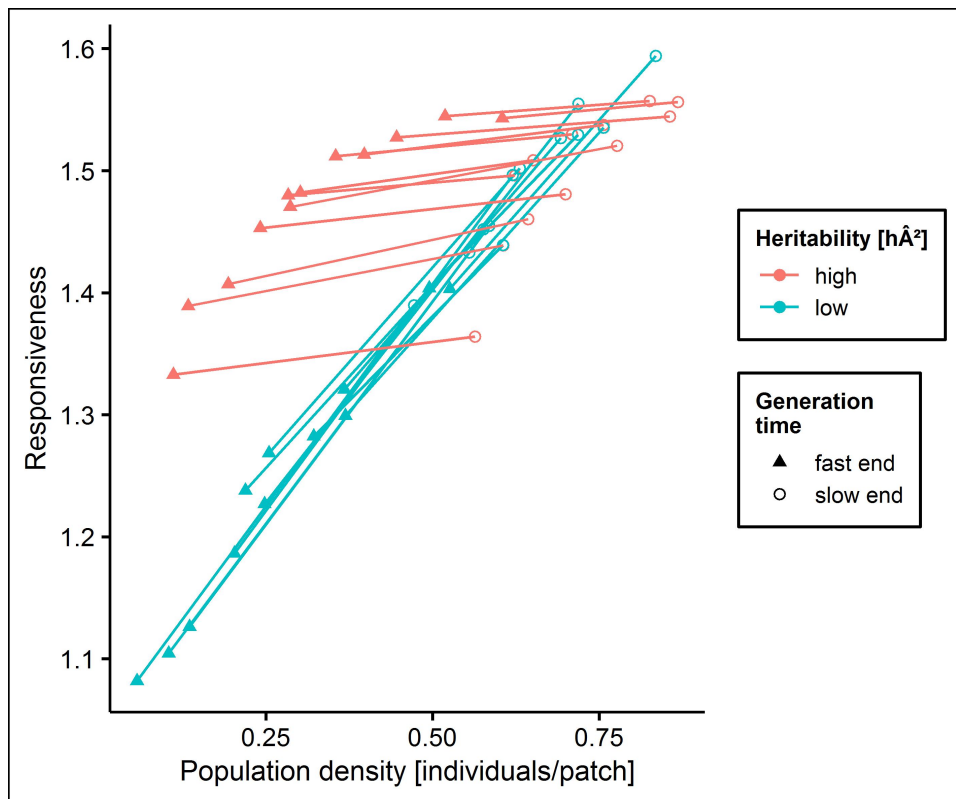


Figure B1.2: Alignment of the trait responsiveness within populations to fluctuations in population density ($n = 24$ populations with two different levels of stochasticity-BT and 12 unique disturbance regimes). At both levels of heritability (i.e. different levels of stochasticity-BT), the slow end of a population selected at higher population densities is associated with higher responsiveness than the fast end. With higher heritability (as in the original manuscript) the responsiveness, however, varies less along fluctuations in population densities as traits are more correlated over time.

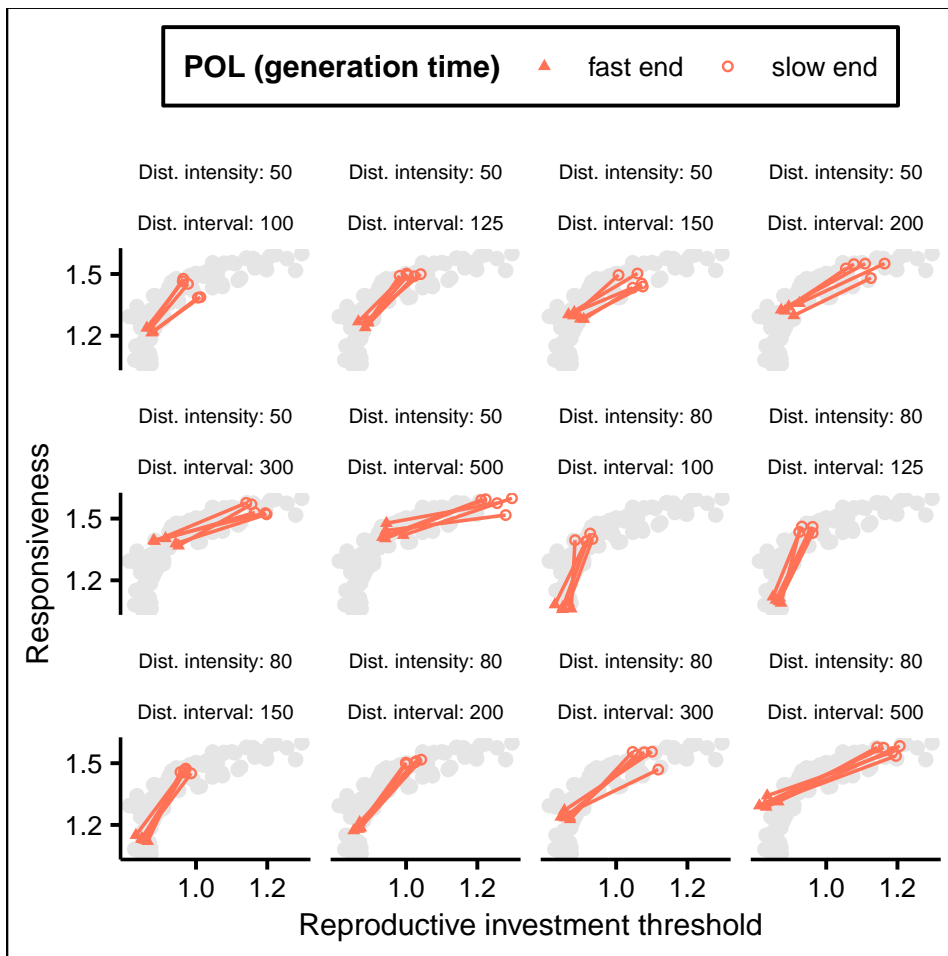


Figure B1.3: Alignment of repeated simulation runs (same dataset as in the main text with 60 populations). Red lines indicate the intra-population POL axes at the same combination of disturbance intensity and disturbance interval (i.e. the same disturbance regime, 5 repeats per disturbance regime). Grey points indicate the fast and slow ends of populations stemming from different disturbance regimes. Overall, intra-population POL axes were well aligned, i.e. there is not much variation between simulation runs in the slope and position of the axes.

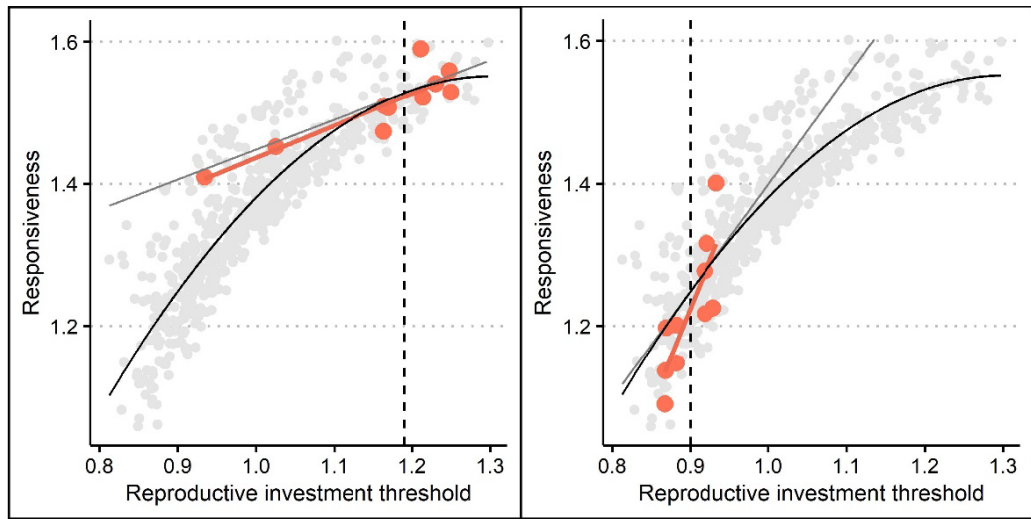


Figure B1.4: Illustration of the comparison of angles (i.e. slopes) of inter-population and intra-population POL axes. Subpopulations are grey dots. For a focal population, we calculated the regression coefficient of the intra-population axes (red line) along its subpopulations (red dots). At the median reproductive investment threshold of the focal population (vertical dashed line), we compared the regression coefficient with the slope of the tangent (dark grey line) of the inter-population POL axes (quadratic linear regression of all subpopulations, black line) at this point. In the left panel, both axes are well-aligned. In the right panel, the intra-population POL axis has a steeper slope.

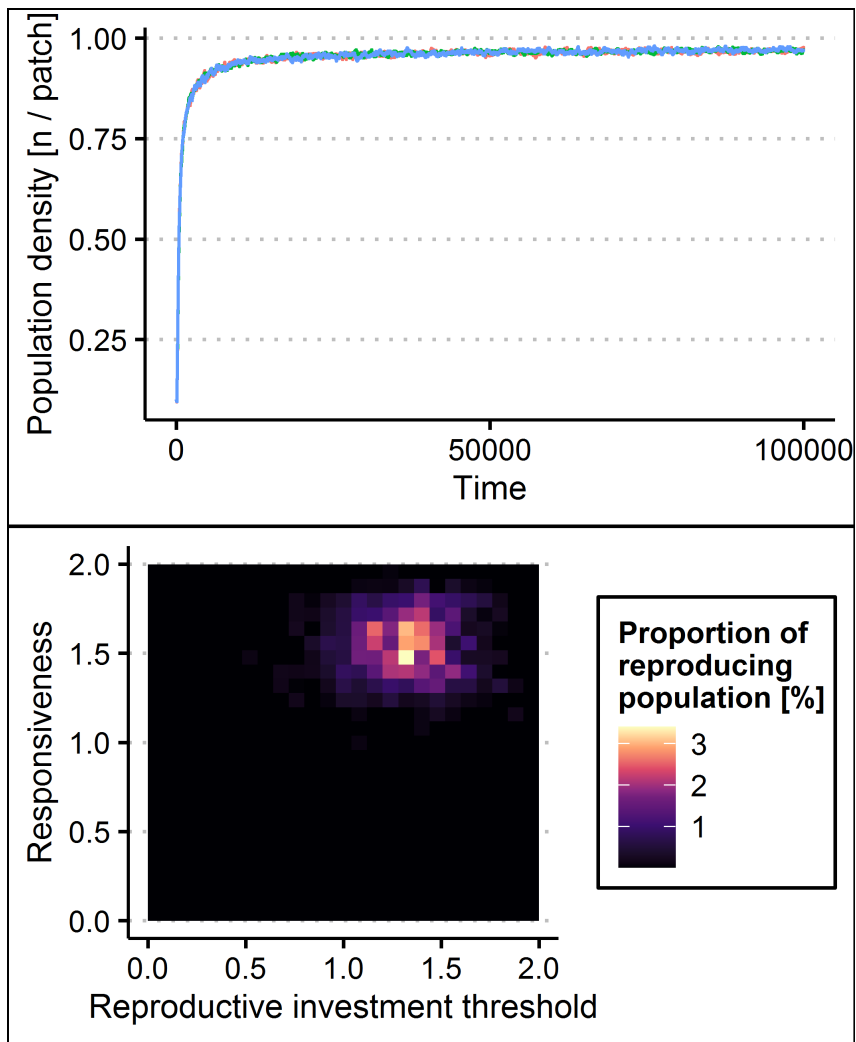


Figure B1.5: Distribution of traits in absence of any environmental mortality after 50,000 time steps (i.e no disturbances, otherwise same parameterization as described in the main text). The traits were normally distributed around a reproductive investment threshold of 1.4, and a responsiveness of 1.6 and were, thus, corresponding to traits selected at the slow end of the inter-population POL axis in the main text.

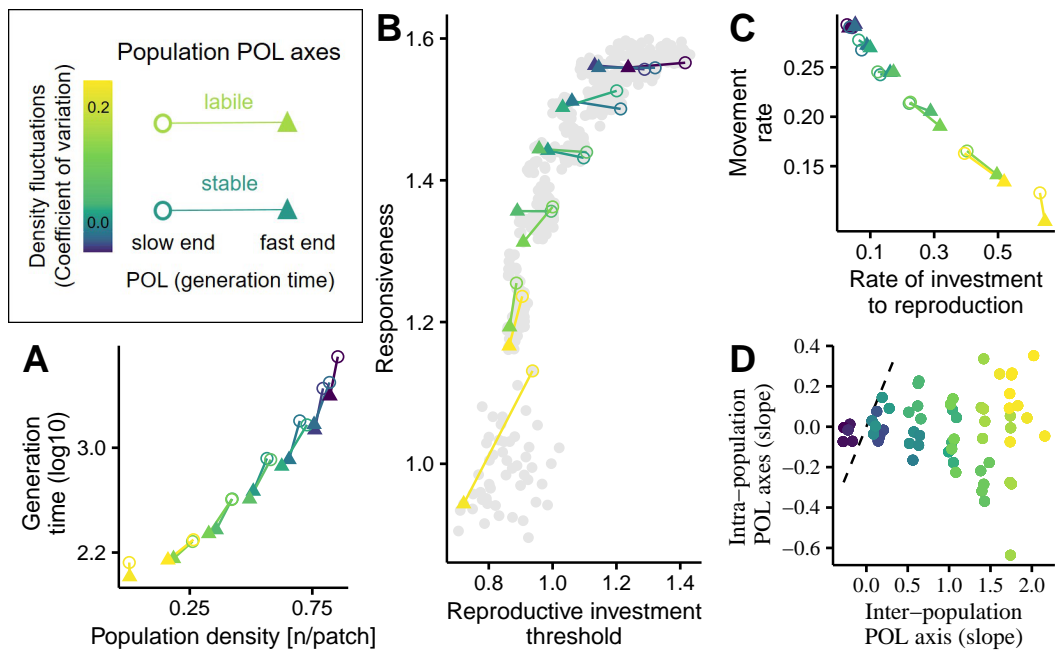


Figure B1.6: Intra-population POL axes in case of more frequent, yet less intense disturbances (otherwise same parameters as in main text). A-C show the slow and fast end (i.e. fastest/slowest subpopulation; ends are distinguishable by shape) of each intra-population POL axes (12 populations, one per unique disturbance regime). In scenarios with more frequent, yet less intense disturbances, population densities hardly fluctuated as indicated by panel A and the lower coefficient of variation (range 0 – 0.2, instead of 0.2 – 0.9). Here, the expectation is that intra-population POL axes are less distinct as there was no (hardly any) gradient of population density along which a POL axis could form. Panel B and C show that - in comparison to the settings described in the main text - slow and fast ends were at more similar positions in the trait space, i.e. POL axes were less distinct at the intra-population level. Grey points in Panel B highlight all subpopulations ($n = 600$) of all simulated populations ($n = 60$). Panel D shows the slopes of intraspecific POL axes vs. slopes expected from the interspecific POL axes. The dashed line indicates positions at which slopes would be equal. Panel D highlights that the slope of intra-specific POL axes varies around 0, whereas the POL axis at the inter-population was similar to the main text results.

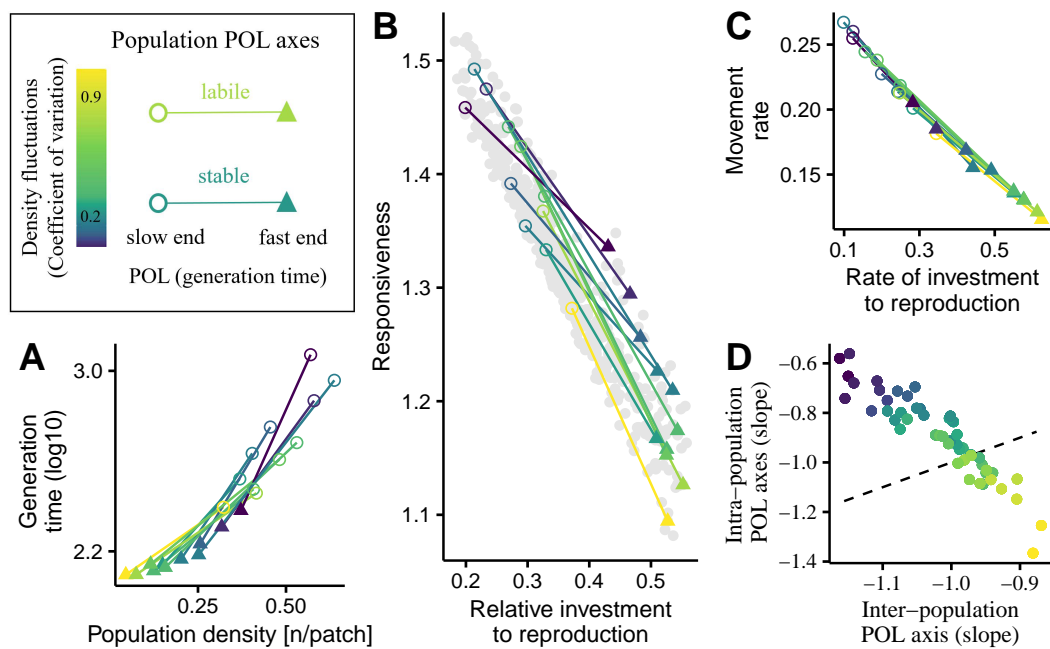


Figure B1.7: Intra-population POL axes with a different life-history trait. As an alternative implementation of the life-history trait, we included income breeding (as the relative investment to reproduction, details see S2 ODD). Parameterizations were other-wise the same as in the main text. A-C show the slow and fast end (i.e. fastest/slowest subpopulation; ends are distinguishable by shape) of each intra-population POL axes (11 populations, one per unique disturbance regime). Simulations did not finish in the most severe disturbance regime (highest intensity, lowest interval), so 11 different disturbance regimes were simulated with 5 repeats (subpopulations of repeats are visualized in Panel B in grey). Associations between POL and population density (Panel A), POL and behavioural expressions (Panel C) as well as POL and responsiveness were as in the main text. Slow types were associated with a lower relative investment (so invest a smaller proportion to reproduction) and vice versa for fast types (Panel B). Panel D shows the slopes of intraspecific POL axes vs. slopes expected from the interspecific POL axes. The dashed line indicates positions at which slopes would be equal. As in the main text, inter- and intra-population axes were systematically misaligned (Panel D), whereas this pattern was even clearer in the case of income breeding. In more stable environments, intra-population POL axes had less negative slopes (i.e. closer to zero) whereas in more labile environments, POL axes were steeper (i.e. more negative).

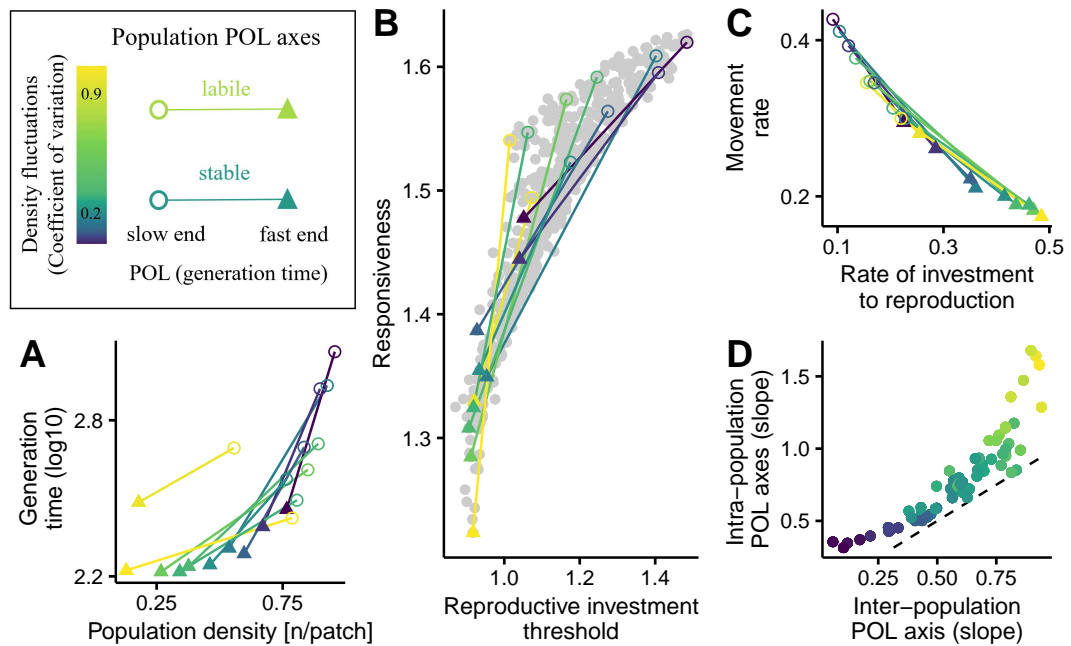


Figure B1.8: Intra-population POL axes with logistic growth (resource-growth-beta-logistic = 0.2, resource-growth-rate-logistic = 0.4, resource-growth-limit = 10). A-C show the slow and fast end (i.e. fastest/slowest subpopulation; ends are distinguishable by shape) of each intra-population POL axes (10 populations, one per unique disturbance regime). Subpopulations ($n = 500$) of all runs (i.e. of all 5 repeats) are hinted in gray in panel B. Populations with parameters disturbance-intervals at 100 and 125 disturbance-intensity = 80% were extinct before 100,000 time steps. Overall the association between POL and population density (Panel A), the association between responsiveness and reproductive investment threshold along the POL axis within populations (Panel B), as well as the association between behavioural expressions along the POL axes (Panel C) remained the same. Panel D shows the slopes of intraspecific POL axes vs. slopes expected from the interspecific POL axes. The dashed line indicates positions at which slopes would be equal. Furthermore, the systematic difference between inter- and intrapopulation POL axes was similar to the main text, with populations at more disturbed, labile environments having a steeper slope in the POL axis (Panel D).

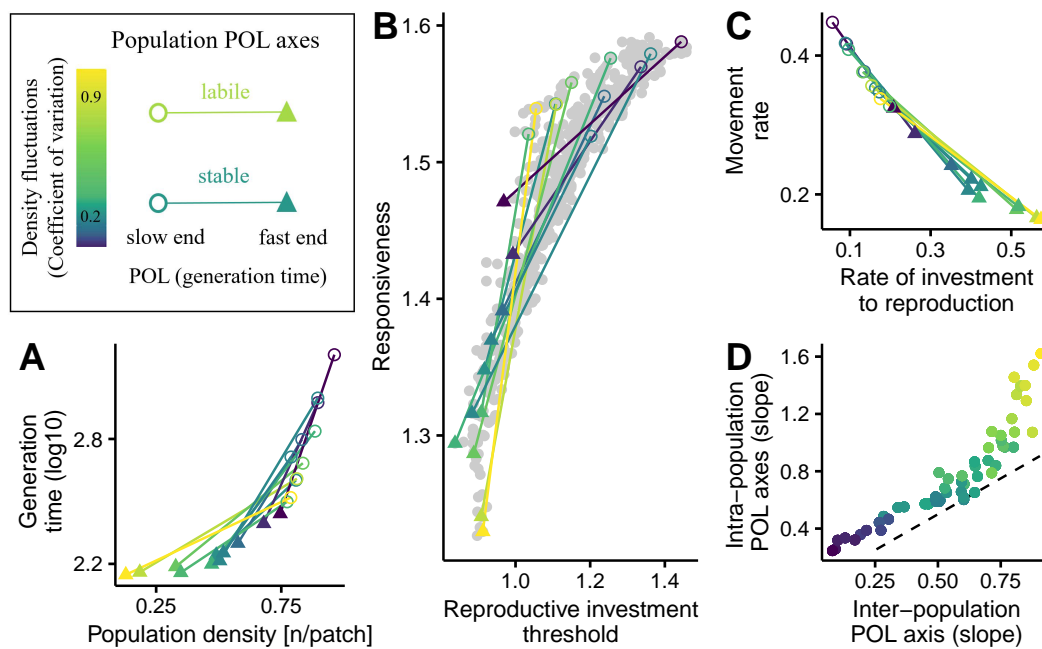


Figure B1.9: Intra-population POL axes with logistic growth (resource-growth-beta-logistic = 1, resource-growth-rate-logistic = 0.2, resource-growth-limit = 10). A-C show the slow and fast end (i.e. fastest/slowest subpopulation; ends are distinguishable by shape) of each intra-population POL axes (10 populations, one per unique disturbance regime). Subpopulations ($n = 500$) of all runs (i.e. of all 5 repeats) are hinted in gray in panel B. Populations with parameters disturbance-intervals at 100 and 125 disturbance-intensity = 80% were extinct before 100,000 time steps. Overall the association between POL and population density (Panel A), the association between responsiveness and reproductive investment threshold along the POL axis within populations (Panel B), as well as the association between behavioural expressions along the POL axes (Panel C) remained the same. Panel D shows the slopes of intraspecific POL axes vs. slopes expected from the interspecific POL axes. The dashed line indicates positions at which slopes would be equal. Furthermore, the systematic difference between inter- and intrapopulation POL axes was similar to the main text, with populations at more disturbed, labile environments having a steeper slope in the POL axis (Panel D).

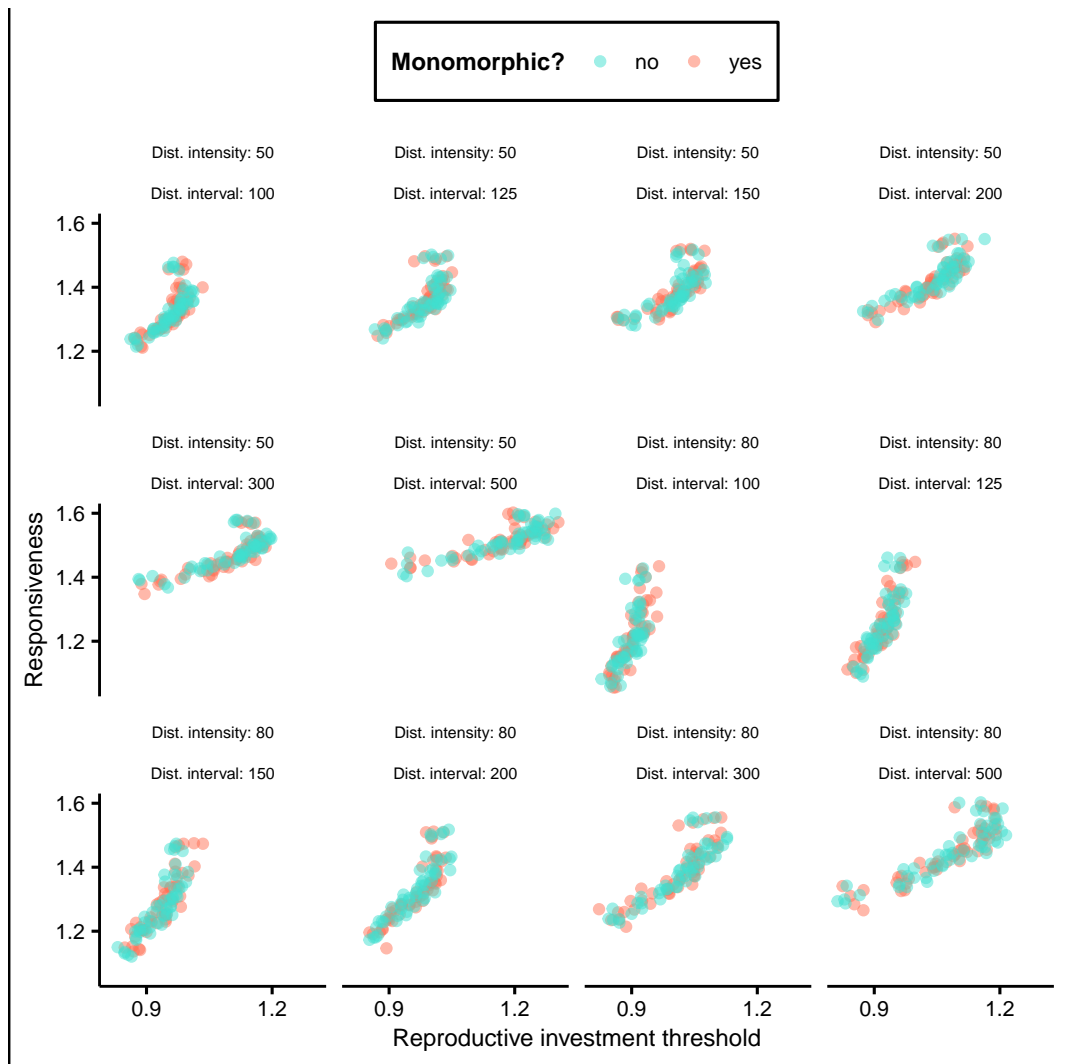


Figure B1.10: Subpopulations with initially monomorphic populations (coral, $n = 600$) and initial traits drawn from a uniform distribution (turquoise, $n = 600$) as in the main text. Parameter settings were otherwise the same as in the main text. Monomorphic populations had a random combination of traits sampled from the trait space, i.e. initial traits differed between runs. Across disturbance regimes, subpopulations align to similar range of traits with a similar pattern of variation within populations. So, the way of initializing the model did not affect the simulation outcome.

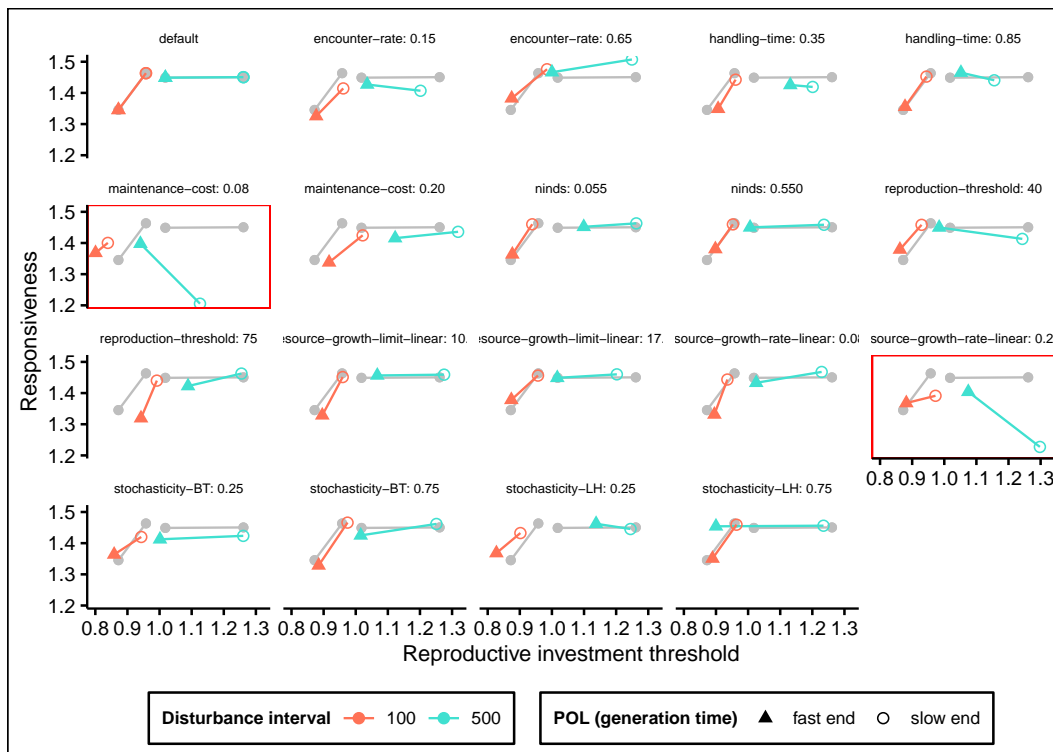


Figure B1.11: We altered parameters that were otherwise kept the same in simulations in a one-at-a-time approach. We choose two different disturbance intervals (100, coral; 400, turquoise) and the same disturbance intensity (50 %) to contrast scenarios with low and high degrees of population density fluctuation. We compared the intra-population POL axes with the outcome under default parameterization (grey). Our expectation was that the association between POL (slow and fast end) as well as between more and less disturbed environments should remain the same across parameterizations while the exact traits may vary. In other words, faster types / populations in more disturbed environments should be less responsive and have a lower reproductive investment threshold. In the case of maintenance-cost equalling 0.08 (highlighted in red) this association changed. Here, the faster type is more responsive than the slow type. Along with growth-rate-linear set to 0.225 (highlighted in red) this resembled a case where our assumption that movement was required to fulfil energetic demands for reproduction (and carrying capacity is ≤ 1) was relaxed. We examine cases where this assumption is relaxed more closely in the following figures.

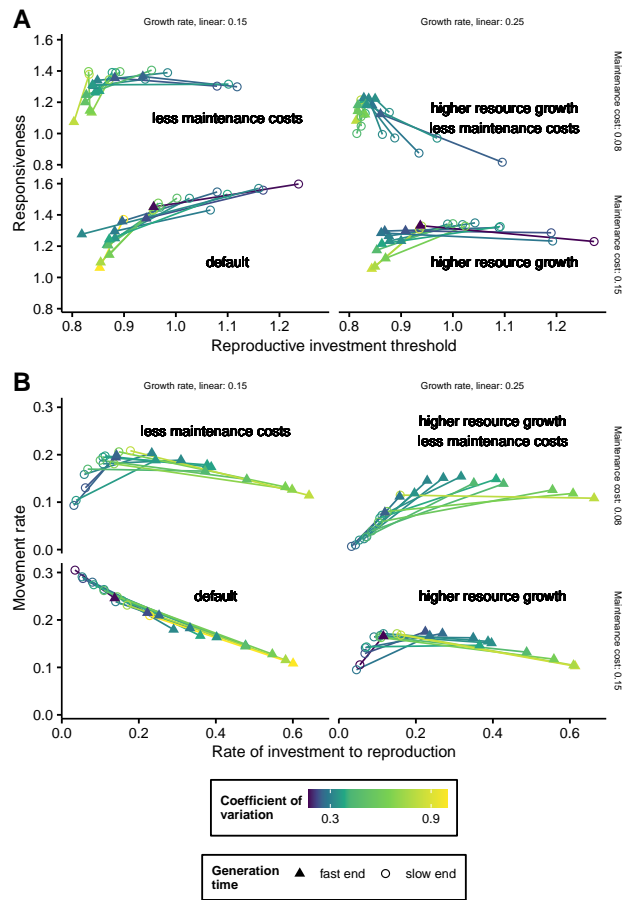


Figure B1.12: Intra-population POL axes as well as the behavioural expression at default and altered parameterizations (relaxed assumption) along different degrees of population density fluctuation. The assumption was relaxed as single patches could now grow resources at a rate above maintenance costs. Compared to the default parameterization, the intrapopulation POL axes exhibited a different association between traits in less disturbed environments (lower coefficient of variation). The fast end was still associated with a lower reproductive investment threshold, yet, in contrast to the default parameterization, the faster type was more responsive (Panel A). Panel B also highlights that the association between the POL and the behavioural expression reversed in these cases, as fast types moved more frequently while slow types strongly reduced their movement rate especially if maintenance costs are reduced and growth rates are increased.

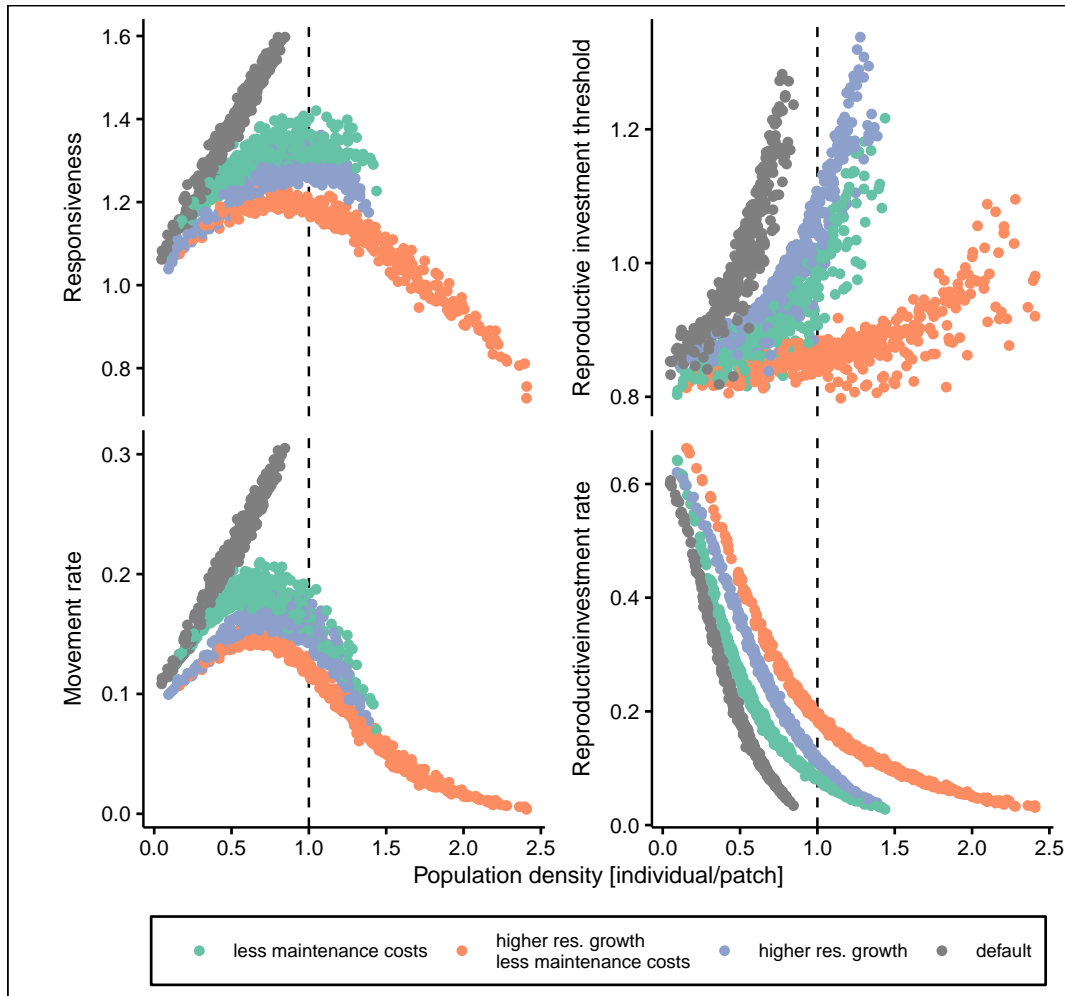


Figure B1.13: Change in traits (responsiveness, reproductive investment threshold) and their behavioural expressions (movement rate, reproductive investment rate) of subpopulations along a gradient of population density. Parameters besides maintenance costs and resource growth rate were as in the main text (i.e. the default scenario). Each disturbance regime (12) was repeated 3 times (resulting in 360 subpopulations per unique parameter combination). As the assumption that movement is required to meet energetic demands of reproduction was relaxed and population density may increase beyond 1, a non-monotonic selection of responsiveness and the associated movement rate became visible. While movement activity and responsiveness monotonically increased in the default scenario, relaxing the assumptions lead to a peak in responsiveness around a population density of 1 (slightly below).

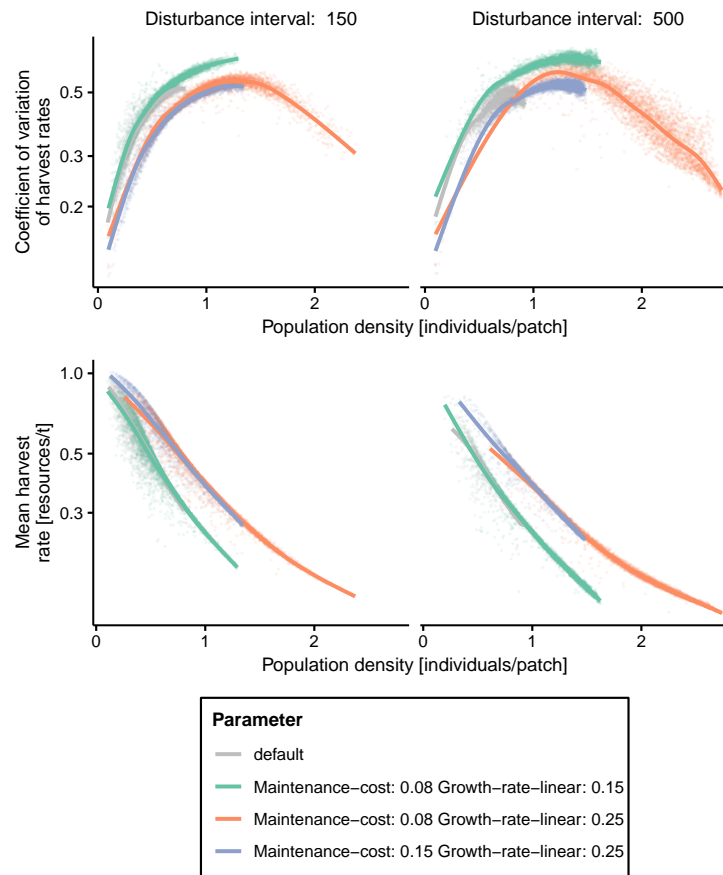


Figure B1.14: Change of harvest rates and variation in harvest rates along a gradient of population density at different parameterization (default and relaxed assumption, 4000 measurements per unique combination of disturbance regime and growth rate as well as maintenance cost). Disturbance intervals were set to 150 and 500 whereas disturbance intensity was fixed to 50 %. All other parameters were set to default (i.e. as in the main text). Whereas the mean harvest rate monotonically declined with population density, the coefficient of variation in harvest rates peaked around a population density of 1 depicting a non-monotonic response once the assumption that movement is required to meet energetic demands for reproduction is relaxed. Higher levels of responsiveness are useful if there is something to gain from moving to neighbouring patches. As the responsiveness (and related movement rate) varies similarly to the coefficient of variation in harvest rates, the non-monotonic response of the environment to changes in population density explains why POL axes forming due to density fluctuations may be non-monotonic. More general, there may not always be a clear variation of traits along a slow-fast continuum.

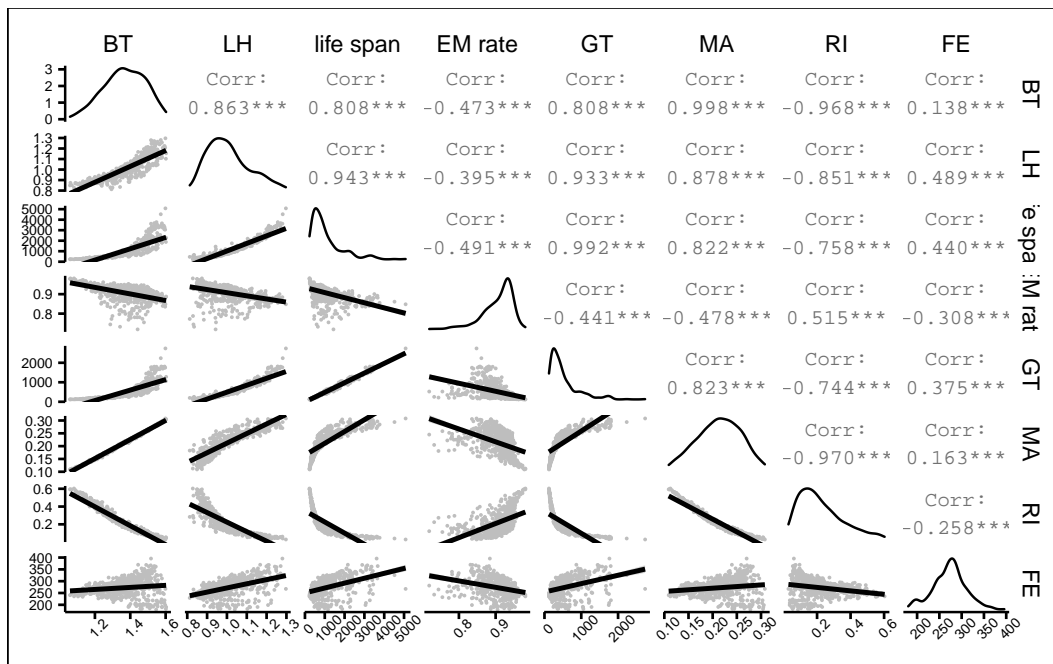


Figure B1.15: Correlogram of emergent traits at default parameterization (i.e. as in the main text). Each scatter plots contains 600 data points. Density of the data points is given on the diagonals. Pearson correlation coefficient is given in the upper corner. All correlations are highly significant (***, i.e. p -value < 0.05). Responsiveness (BT), relative investment to reproduction (LH), life span, environmental mortality rate (EM rate; proportion of deaths due to disturbances), generation time (GT), move-ment rate (MA), rate of investment to reproduction (RI), foraging efficiency (FE, amount of resources per turn, i.e. average harvest rate). The correlation shows, among others, that foraging efficiency is higher in fast-type populations and life span increases in slow-type population.

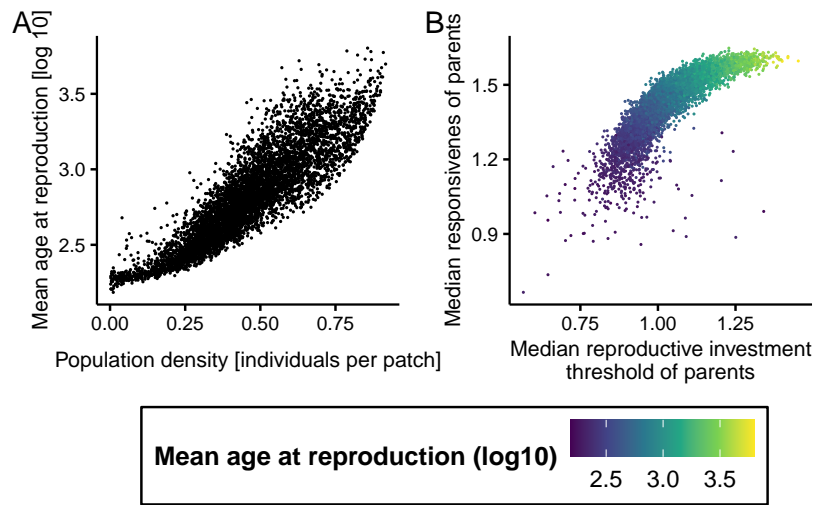


Figure B1.16: Alternative metric of generation time (mean age at reproduction of individuals during reproductive events) and its relation to population density and traits. Simulations were separated into 100 equally-sized reproductive periods and for each of the reproductive periods the mean age of parents at the time of reproduction and the mean population density at the time of reproduction was calculated. A: The mean age at reproduction increases with population density and B: during reproductive periods with individuals of higher age of reproduction, i.e. at higher population density, individuals with higher levels of responsiveness and reproductive investment threshold contribute more to population growth. Overall, the analysis using an alternative metric is consistent with the main text results.

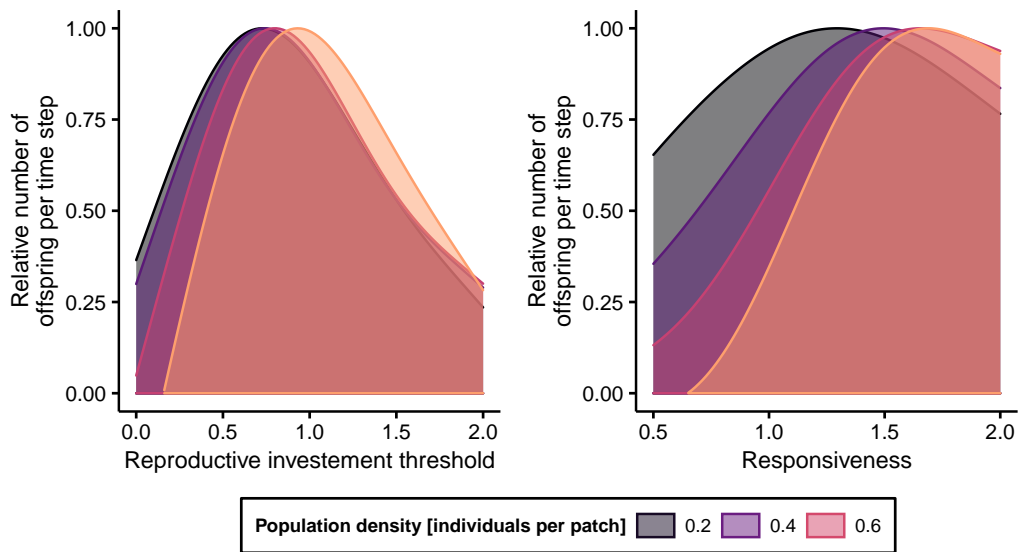


Figure B1.17: Relationship between reproductive investment threshold and responsiveness with the relative number of offspring per time step as a measure of competitive ability. The y-axis is scaled to make peaks comparable. Relationships are fitted by GAMs for different levels of population density using data of all individuals simulated for the main text results. From low to high population density, the peak shifts from lower reproductive investments thresholds and lower responsiveness to higher levels. Overall, selection seems to be more relaxed at lower population densities (indicated by fewer regions with very low relative number of offspring per time step), which coexplains the higher degree of trait variation in fast-type populations.

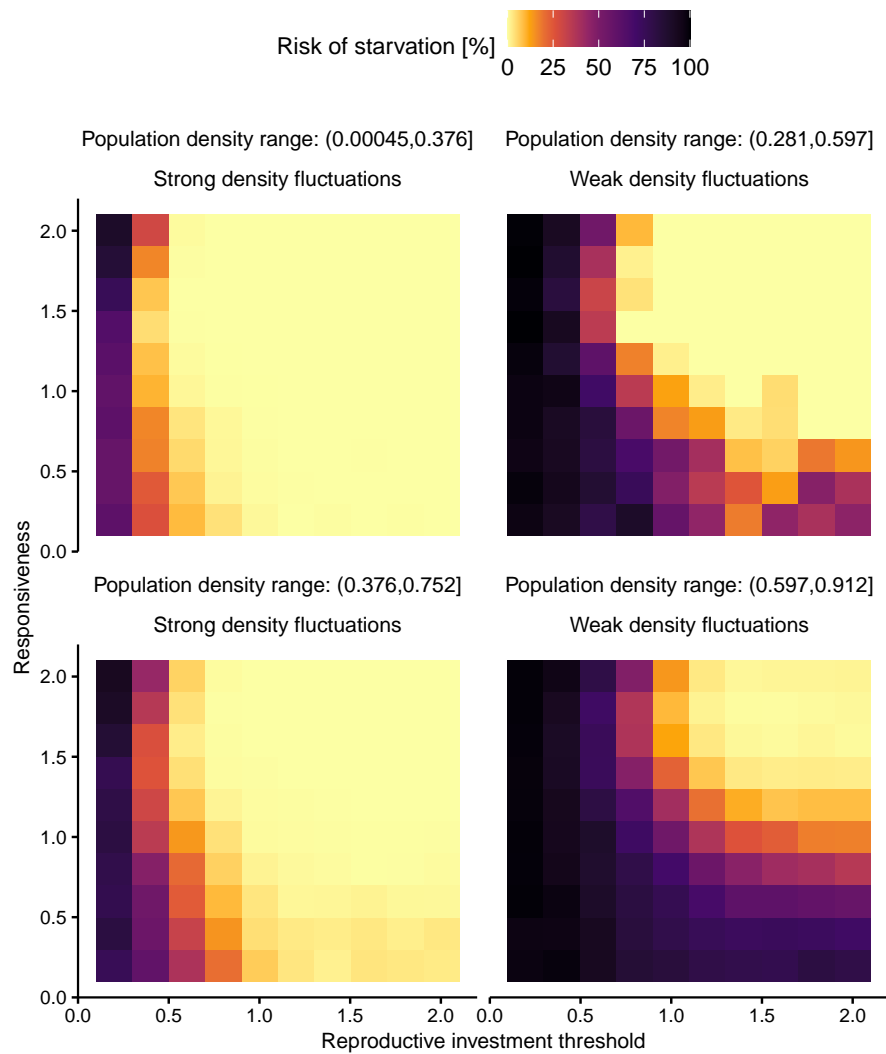


Figure B1.18: Risk of starvation for different levels of population density in two populations (based on all individuals of these populations). One population is characterized by a disturbance regime that induces weak density fluctuations, the other population is characterized by a disturbance regime that induces strong density fluctuations. In both scenarios higher population density amplifies the risk of starvation of individuals with low reproductive investment threshold and unsuitable behavioural foraging strategies. In other words, starvation is density-dependent and individuals that retain more resources and are adapted to resource distributions at higher density can minimize this source of mortality. Comparing between populations, at similar ranges of population density (top right, bottom left), weaker density fluctuations lead to an elevated risk of starvation.

B2 Model documentation

1 Purpose

The purpose of this model is to explore three predictions made by Wright et al. (2019) on density-dependent selection of different paces of life (POL). The addressed predictions state that, (H1) selected behavioural and life history traits covary with the POL along different population densities (intra-population) and degrees of fluctuation in population density (inter-population) forming a POLS due to density-dependent selection, (H2) the degree of variation in behavioural and life history traits covaries with the POL as it is linked to the degree of fluctuations in population density, and (H3) density-dependent selection along the POLS is reflected in a trade-off between r_0 and γ , i.e. r_0 and γ covary with the POL.

We test these predictions by analyzing the selection of behavioural and life-history traits (reproductive investment threshold) of stylized animals moving and foraging in environments that differ in the frequency and intensity of disturbances.

1 State variables and scales

Entities included in the model are patches and animals. Patches are square grid cells characterized by their coordinates and the continuous state variables resource-density and harvest-rate.

Rationale: Resource-density is the density of resources, i.e. the amount of resources per square spatial unit (one patch). Harvest-rate is the amount of resources an animal extracts from a patch and is given by the state variable resource-density of that patch. The harvest-rate curve follows a type II function. At lower densities, the handling time for gathering resources, e.g. vegetation or prey, is higher and therefore harvest-rate, the amount of harvest per time step, decreases.

The growth of resource-density over time is determined by the growth-type (either logistic or linear).

State variables that characterize animals can be categorized by whether they affect movement decisions or the energy budget or whether they only track the state; they are not affecting the animal's behaviour but are used in model analysis.

The rationale underlying the model's structure as defined in Tables B2.1 and B2.2 is described in the legend of Fig. B2.1, which provides a graphical representation of the model and its processes, and in the process overview below.

Since this is a generic model, the spatiotemporal resolution is not specified, but a single patch should represent a site where a foraging animal finds and exploits

Table B2.1: State variables of Patches.

State variable	Static / dynamic	Type	Range	Meaning
resource-density	dynamic	Float	[0, *]	Amount of resources per patch
harvest-rates	dynamic	Float	[0,]	Amount of resources that can be extracted per time step
pxcor	dynamic	Float	[0, 49]	x-coordinate of patch
pycor	dynamic	Float	[0, 49]	y-coordinate of patch

*upper limit determined by parameter resource-growth-limit

resources, i.e. it is specific enough to be distinguished from its surroundings and to be memorized. Accordingly, a time step corresponds to the time required to move between neighbouring patches. The spatial extent of the landscape is 50 x 50 patches. The extent of the temporal scale is 100,000 time steps.

3 Process overview and scheduling

In the submodel forage-or-relocate an animal decides between foraging and moving to another patch. The lower the difference between current-hr the perceived-current-mean-hr and the lower the BT, the lower the probability of triggering the relocate subsubmodel instead of the forage subsubmodel:

- The relocate subsubmodel moves the animal to one of the neighbouring patches. The state variable times-moved is increment by one.
- The forage subsubmodel reduces the resource-density of the patch the animals are located at and increases the soma of the animal by the harvest-rate of the patch. The tracking state variable gathered-resources is incremented by the same amount.

High values of BT represent individuals of higher responsiveness which move earlier due to differences between their current and neighbouring patches, while individuals with lower levels of BT have a lower responsiveness towards differences in resource density and, thus, harvest rates. Still, both types perceive the difference between their current harvest rates and the one they would achieve in the neighborhood, by assessing the average harvest rate of the eight neighboring patches. We, thus, assume that animals base their decision not just on perceived resource density, but on the harvest rate they would expect for a given density. This assumption is fairly realistic as a positive relationship between resource density

Table B2.2: State variables of animals. Upper limit of some state variables depends on the chosen parameterization and simulation time.

State variable	Static / dynamic	Type	Range	Meaning
Movement variables				
BT	static	Float]0; ^a]]	Behavioural trait ^b
perceived-current-mean-hr	dynamic	Float	[0;]	Mean harvest-rate of neighbouring patches (Moore neighbourhood)
current-hr	dynamic	Float	[0;]	Harvest-rate of current patch
ycor	dynamic	Integer	[0; 49]	x-position of the animal
ycor	dynamic	Integer	[0; 49]	y-position of the animal
Energy budget variables				
LH	static	Float	[0; 2]	Life-history trait ^c
soma	dynamic	Float	[0 ^d ;]	Resources available for allocation to maintenance and r-buffer
r-buffer	dynamic	Float	[0;]	Resources allocated to reproduction. At 50, the animal reproduces
Further variables (analysis only)				
age	dynamic	Integer	[0;]	Number of time steps the animal is alive
generation	static	Integer	[0;]	Number of generations since initialization
age-first-reproduction	dynamic	Integer	[0;]	Age at first reproduction
n-offspring	dynamic	Integer	[0;]	Number of offspring (one per reproductive event)
gathered-resources	dynamic	Float	[0;]	Gathered resources (total)
times-moved	dynamic	Integer	[0;]	Times an animal moved between patches
list-age-at-reproduction	dynamic	list of integers		List of ages at which an animal reproduced
who	static	integer	[0;]	Unique animal ID
parental-who	static	integer	[0;]	who of the animal's parent

^aDetermined by the parameter BT-range, ^b Heritable traits that determines probability of inter-patch movement which depends on the harvest-rate difference, ^c Heritable trait that determines the threshold above which resources are allocated from soma to r-buffer, ^d Animals die if soma below 0

and harvest rate is ubiquitously found. Once a decision to relocate is made, we assume that animals are able to explore the neighboring patches more thoroughly and chose the one with the highest harvest rate.

In the allocate-resources submodel animals allocate resources from soma first to maintenance and then to r-buffer. The maintenance cost per time step is fixed. If animal's soma is smaller than 0, it dies. In case of death and if the global parameter create-output is true, the submodel save-output is executed. If an animal's soma is 0 or greater than 0, the amount of resources allocated from the remaining soma to r-buffer is determined by both the value of soma and LH. LH is the reproductive investment threshold and represents capital-breeding. Animals invest all resources exceeding the threshold to reproduction, i.e. animals with low values of LH reserve less for maintenance costs n and thus may need less time to reproduce. Yet, at lower levels of LH, they are more prone to the risk of mortality due to soma values that became negative, representing starvation. In an alternative implementation of LH, animals always invest a relative amount of soma to reproduction, yet, whereby the relative amount is the trait (breeding-type = income-breeding).

The check-reproduction submodel checks whether an animal's r-buffer is above the threshold for reproduction (determined by the reproduction-threshold parameter). In this case, one new animal is created at a random location with BT and LH inherited, with some stochastic variation (determined by the parameters stochasticity-BT and stochasticity-LH), from the parent animal. The state variable parental-who is set to the state variable who of the parent animal. The state variable generation is incremented by one compared to the parental generation. The state variables age-first-reproduction, n-offspring and, list-age-at-reproduction of reproducing animals are updated accordingly and the energy/resources that were used for reproduction is subtracted from r-buffer.

At a probability given by disturbance-interval, the submodel disturb lets a certain random proportion of animals die. The upper limit of this proportion is given by the parameter disturbance-intensity.

Next, in the submodel grow-resources resource-density of the patches is increased by the growth-rate which depends mainly on the parameters growth-type as well as the state variable resource-density. Depending on the growth-type, resource-growth-rate-linear, resource-growth-limit, and resource-growth-rate-logistic determine the growth-rate. Harvest-rate is updated according to the new level of resource-density and depends on harvest-rate-curvature and harvest-rate-factor.

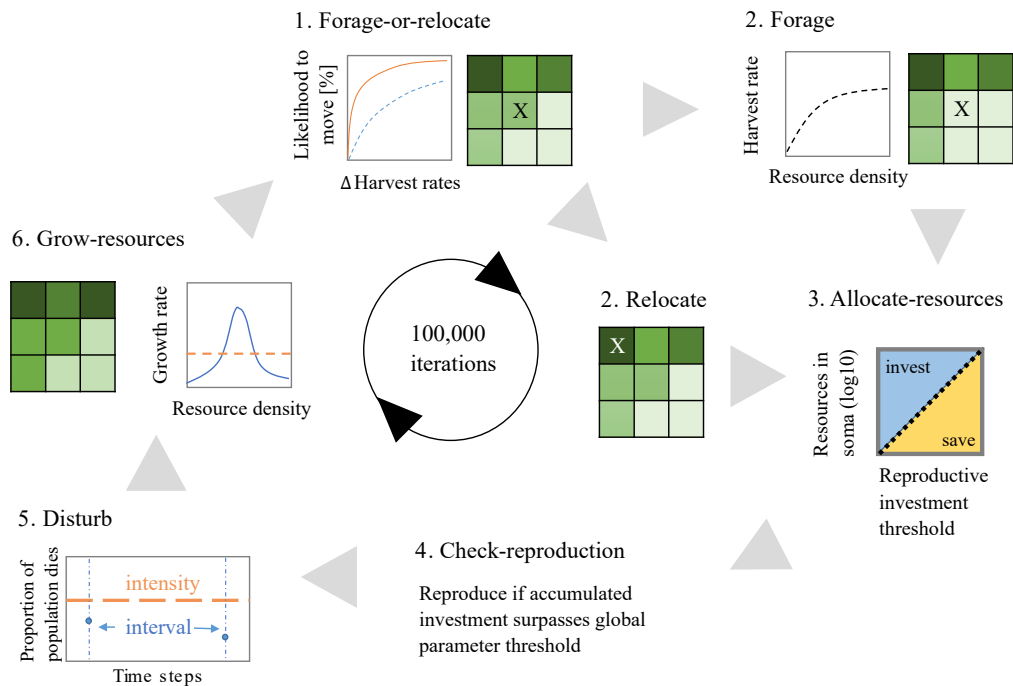


Figure B2.1: Graphical model summary showing submodels and scheduling. 1) Animals decide whether to forage or to relocate based on (A) the difference in harvest rate between the current and the average of neighbouring patches, and (B) their behavioural trait which varies from responsive (orange, solid line) to unresponsive (blue, dashed line). 2) If an animal forages it reduces the resource density at the local patch by the harvest rate which only depends on the patches' resource density. The animal increases its soma by the same amount. If an animal relocates, it moves randomly to one of the neighbouring patches and will harvest resources only in the next time step; this implicitly represents costs of movement. 3) An animal allocates resources to maintenance (fixed, global parameter). If an animal's soma drops below 0, it dies. Then, if resources in soma surpass its reproductive investment threshold, an animal invests all excess resources, i.e. the delta between threshold and resources in soma, to reproduction (4) If the accumulated investment to reproduction surpasses a certain level of resources (global parameter, default is 50), an animal reproduces and a new animal is created; it inherits the parent's responsiveness and reproductive investment threshold, each modified by a globally defined level of stochasticity mimicking empirical heritability of behavioural and life-history traits. 5) With a probability determined by the global parameter disturbance-interval a random proportion of the population with the global parameter disturbance-intensity as upper limit dies due to environmental mortality; this submodel allows to create density fluctuations of different magnitudes. 6) Resource growth: Resource density at each patch increases by the growth rate which is either resource-density-dependent (logistic function shown by the blue, solid line) or resource-density-independent (linear function shown by the orange, dashed line).

At a certain frequency, the submodels save-lists writes output to a .csv-file located at the output-directory and the initialize-output-lists resets these output lists.

4 Design concepts

Basic principles The framework of pace-of-life syndromes suggests a covariation between a suite of physiological, behavioural and life-history traits resulting from a trade-off between early and late reproduction. Early reproduction refers to a fast pace-of-life and late reproduction represents a slower tempo. The framework by Wright et al. (2019) suggests a density-dependent selection for different paces-of-life. This model tests crucial predictions of this frame to validate the density-dependent selection framework. Thus, the model includes (1) population dynamics which are modulated by environments of varying stochasticity leading to density-fluctuations, (2) a suite of inheritable life-history / physiological and behavioural traits and (3) state variables that track behavioural expressions (e.g. movement rate) and emergent life-history traits which allow the alignment of individuals on the slow-fast continuum. In our model, the emergent property individual generation time (the average interval between reproductive events) is a measure for the pace-of-life.

Emergence Dynamics of the resource landscape and populations with heritable traits interact leading to an emergent state of patches as well as an emergent trait composition and behavioural expression in the animals' population. The animal's behaviour is imposed and not based on decision making that explicitly would take into account the predicted fitness consequences of alternative decisions.

Adaptation It is assumed that the decision to relocate implicitly reflects the adaptive behaviour to move on, once local harvesting becomes less efficient than the perceived average harvesting in the neighborhood. This mechanism relates to the Marginal Value Theorem (Charnov 1976) whereafter animals should move once the harvest rate is equal to the mean harvest rate in the habitat.

Sensing Individuals know their own energetic state and that harvest-rate at their current as well as neighbouring patches and adjust behaviour in correspondence to these states via reaction norms.

Interaction The model comprises mediated interaction via exploitation competition. The change in resource-density and, hence, harvest-rate due one animal foraging also reduces the harvest-rate for other animals.

Stochasticity The initialization of animals (location, traits) and patches (resource-density) is stochastic. During simulation, decision-making in movement and foraging, mortality, inheritance, and disturbance intensity are stochastic processes. In all these cases stochasticity represents variation that is likely to exist in reality and

Table B2.3: State variables that are saved upon birth and death of each animal.

State variable	Context	Type	Description
ticks	Observer	Integer	Current time step
who	Animal	Integer	Unique ID
BT	Animal	Float	Behavioural trait
LH	Animal	Float	Life-history trait
age	Animal	Integer	Age of animal
age-first-reproduction	Animal	Integer	Age at first reproduction
n-offspring	Animal	Integer	Number of reproductions
soma	Animal	Float	Resources in soma
count animals	Observer	Integer	Current population size
generation-time	Animal	Float	Individual generation time
times-moved	Animal	Integer	Times of inter-patch movement
r-buffer	Animal	Float	Resources in reproduction buffer
parental-who	Animal	Integer	Unique ID of parent

may have important consequences, but for which no mechanistic representation is needed or considered necessary.

Observation If the parameter `create-output` is true, file output is generated. The output consists of two files, one with the global parameter settings specific for a certain simulation run and another with state variables of animals and the observer context.

The global parameter settings exported are `n-inds`, `disturbance-interval`, `disturbance-intensity`, and `growth-type`. The settings are saved during initialization.

If, additionally, the parameter `save-landscape` is true, `harvest-rate`, `location` and `time step` are saved every 25th time step.

The submodel `initialize-output-lists` generates distinct lists for each state variable that is saved with the `save-animal-data` submodel (Table 3). `Initialize-output-lists` sets the name of the state variable as initial element of that list.

Every 10,000th time step, the submodels `save-lists` writes output to a .csv-file located at the `output-directory` and the `initialize-output-lists` resets these output lists (Table B2.3).

Rationale: Both, writing output at the end only and writing output at each step may reduce performance, hence, intermittent output generation was used. The `save-animal-data` submodel appends values to these initialized lists if an animal is created or dies.

Rationale: The output listed in Tab. 3 is used to aggregate the data and analyse distributions of traits and behavioural expressions. These variables e.g. inform about the POL of an animal via the individual generation-time T_i which is calculated by:

$$T_i = \sum \frac{a_{gi}}{n_i}$$

with a_{gi} as age of individual i at reproductive event g and n_i as the number of reproductive events of individual i .

5 Initialization

Next, the submodel setup-landscape is executed. The submodel assigns a random resource-density between 8 and 10 to all patches and the respective harvest rate is calculated.

Setup-animals adds a number of animals defined by the parameter n-inds at random location to the landscape. The two traits BT and LH are drawn from a uniform distribution with a lower limit of 0 and an upper limit indicated by the parameters LH-range and BT-range. If the parameter monomorphic is set to true, all animals share the same random combination of LH and BT sampled from the uniform distribution. Gathered-resources, age, n-offspring, times-moved, generation, r-buffer are set to 0. List-age-at-reproduction is an empty list, age-first-reproduction is set to -999 to indicate no reproduction. Immigrated is set to false. Soma is set to 5, to prevent that death condition of soma < 0 is immediately fulfilled.

6 Input Data

The model does not use input data to represent time-varying environmental drivers.

7 Submodels

In each time step, submodels are performed in the order given below, but the order by which the entities (animals, patches) perform their tasks changes randomly in each time step. The submodels are described in detail in ODD section 7. The sequence starts with submodels of animals. Parameters are listed in Table B2.4.

forage-or-relocate In the submodel forage-or-relocate an animal decides between foraging and moving to another patch. The difference (Δ) between the local harvest-rate and the mean harvest-rate of neighbouring patches (perceived-current-mean-hr) forms an environmental gradient, to which an animal responds by either moving to one of the neighbouring patches or by foraging on the local patch. Δ is compared to a value k sampled from a gamma distribution. BT determines the shape para-

meter and the inverse of the rate parameter (i.e. the scale parameter) of the gamma distribution. The density function of a gamma distribution with BT defining the scale and shape parameters (equation I) is:

$$w = BT_{range} - BT$$

$$f(x) = \begin{cases} x^w * e^{-w^{-1}*x} * \frac{w^{-w}}{\int_0^{\infty} x^w * e^{-x}} & x > 0 \\ 0 & x \leq 0 \end{cases}$$

If Δ is smaller or equal k , the animal forages at the local patch, otherwise it moves to a neighbouring patch. Lower levels of BT reduce the probability of sampling lower values of k , leading to an increased likelihood of foraging at the local patch at equal Δ (Fig. B2.2).

Rationale: The probability distribution for sampling a certain value for x is modulated by BT (Fig. B2.1) leading to a continuum in responsiveness to perceived environmental cues. So, assuming a perceived difference of 1, an animal with $BT = 1.1$ will move away with about 80 % probability, an animal with a BT of 1.4 will move with a likelihood of almost 100 %. The gamma distribution, thus, allows to formulate this decision-making as reaction norm via one single parameter and without transformation of the perceived differences in harvest rates. We transformed w by subtracting BT from BT-range so that a higher value of BT corresponds to higher responsiveness.

Table B2.4: Parameters (including constant parameters) without parameters purely used for in-situ visualization.

Parameter	Type	Range	Description
n-inds	Integer	[0; 1]	Initial population density (individuals/patch)
monomorphic	Boolean	[true, false]	True: same, random initial combination of BT False: initial traits differ between animals
disturbance-interval	Float	[0; 1000]	Average length of the interval between disturbances
disturbance-intensity	Float	[0; 100]	Upper percentage of population removed at disturbance event

BT-range	Float	2 (const.)	Upper boundary of the behavioural trait
LH-range	Float	2 (const.)	Upper boundary of the life-history trait (1 if breeding-type “income-breeding”)
stochasticity-BT	Float	[0; 1]	Standard deviation of behavioural trait heritability
stochasticity-LH	Float	[0; 1]	Standard deviation of life-history trait heritability
breeding-type	String	[cb, ib]	Whether individuals always invest a relative amount (trait) of their soma to reproduction, or if individuals invest all resources that exceed a certain threshold
maintenance-cost	Float	[0.01; 0.25]	Maintenance costs as resources per time step
reproduction-threshold	Float	[30; 100]	Number of resources required for reproduction
growth-type	String	[linear, logistic]	Relationship between growth-rate and resource-density
resource-growth-rate-logistic	Float	[0.01; 10]	Growth rate of logistic growth
resource-growth-beta-logistic	Float	[0.01; 2]	Modifier of density dependence of logistic growth
resource-growth-rate-linear	Float	[0.01; 0.3]	Growth rate with linear growth
resource-growth-limit	Float	[5; 20]	Maximum resources per patch with linear growth
encounter-rate	Float	[0; 1]	Rate at which animals encounter resources
handling-time	Float	[0; 1]	Time needed for animals to process resources
max-pxcor	Integer	50 (const.)	Number of patches in x-direction
max-pycor	Integer	50 (const.)	Number of patches in y-direction
create-output	Boolean	true / false	Whether to export any simulation data
output-directory	String	“/path/to/dir”	Output path ^b
save-landscape	Boolean	true / false	Whether to save harvest rate of patches

restart?

Boolean true / false

Whether to restart the simulation if population went extinct

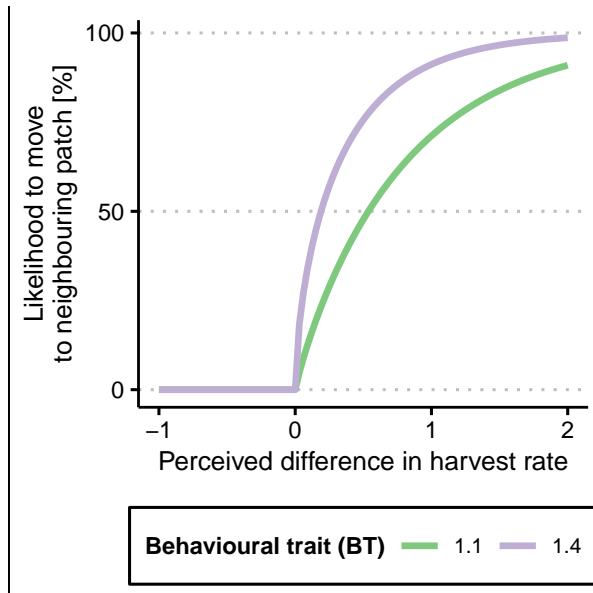


Figure B2.2: Behavioural trait. Likelihood of moving to a neighbouring patch at a certain perceived difference in harvest rate between local and neighbouring patches. Higher BT values correspond to higher responsiveness to increasing differences in harvest rates. At negative differences, animals do not move to other patches. Differences in harvest rates beyond 2 are unlikely.

forage If the animal decides not to move: The subsubmodel forage reduces the resource-density of the patch the animal is located at and increases the soma of the animal by the harvest-rate of the patch. The state variable gathered-resources is incremented by the same amount. As the resource-density changed, the harvest-rate is calculated for the new level (details explained in the grow-resources submodel).

relocate If the animal decides to move: relocate moves the animal from the current patch to the neighbouring patch with the highest harvest-rate and increments its times-moved by one.

allocate-resources In the allocate-resources submodel animals allocate resources from soma first to maintenance and then to r-buffer. The maintenance costs are determined by the parameter maintenance-cost.

Rationale: The maintenance cost were set to a level that is equal or higher than the point at which harvest-rate equals growth rate, i.e. maintenance costs make staying at only one patch an non-sufficient strategy to meet energetic demands and prevent starvation.

The amount of resources allocated from soma to r-buffer is determined by the status of soma after foraging ($soma_{t+\frac{1}{2}}$) and LH.

$$r.buffer_{t+1} = r.buffer_t + LH^3 * soma_{[t + \frac{1}{2}]} \quad (.8)$$

$$r.buffer_{t+1} = \begin{cases} r.buffer_t + soma_{t+\frac{1}{2}} - LH^{10} & \log_{10}(soma_{t+\frac{1}{2}}) > LH \\ r.buffer_t & \log_{10}(soma_{t+\frac{1}{2}}) \leq LH \end{cases} \quad (.9)$$

After allocating resources to reproduction, soma is reduced by the amount allocated to r-buffer ($soma_{t+1}$).

Rationale: We assume that an increase from a threshold of 5 to 10 is more significant than an increase from 50 to 55, hence, it is necessary to resolve lower levels of thresholds / relative investment with a finer resolution. We chose the decadic logarithm of soma, to resolve lower thresholds with a finer resolution (in case of capital breeding) and the power of 3 in case of income breeding.

check-mortality Next, the check-mortality submodel checks whether animals die due to a soma below 0.

check-reproduction The check-reproduction submodel checks whether an animal's r-buffer is above the threshold for reproduction (determined by the reproduction-threshold parameter). In this case, one animal is created at a random location with BT and LH inherited from the reproducing animal. The parental traits are the mean of a normal distribution with a standard deviation respectively defined by the parameters stochasticity-BT and stochasticity-LH. The inherited traits are sampled from this distribution. If an inherited trait is outside the range given by BT-range or LH-range respectively, the trait is sampled again leading to a truncated distribution. The state variable generation is incremented by one compared to the parental generation. The state variables age, r-buffer, n-offspring of the offspring are set to zero. The age-first-reproduction of the offspring is set to -999 and the list-age-at-reproduction of the offspring is empty. The state variables age-first-reproduction, n-offspring and, list-age-at-reproduction of reproducing animals are updated accordingly and the threshold for reproduction is subtracted from r-buffer. At the end of the animal-specific submodels, animals age by one time unit.

disturb At a probability given by the parameter disturbance-interval, the submodel disturb lets a proportion of animals die. The proportion is sampled from a uniform distribution with 0 as the lower limit and the upper limit given by the parameter disturbance-intensity.

Rationale: If disturbance-interval is set to 200 and disturbance-intensity is set to 50,

with a probability of 0.5 % (1/200) a disturbance occurs and between 0 and 50 % of the population dies.

grow-resources Next, the submodel grow-resources increases the resource-density (N) by growth-rate which depends on the parameters growth-type as well as the current resource-density of a patch. For the growth-type linear the resource-density (N_t) increases by a fixed amount defined by the parameter resource-growth-rate-linear until the capacity given by the parameter resource-growth-limit is reached:

$$N_{t+1} = N_t + \text{resource.growth.rate.linear} \quad (.10)$$

For growth-type logistic, N_{t+1} is calculated following Richards's logistic growth equation (Fig. B2.3; Richards 1959; Tsoularis and Wallace 2002):

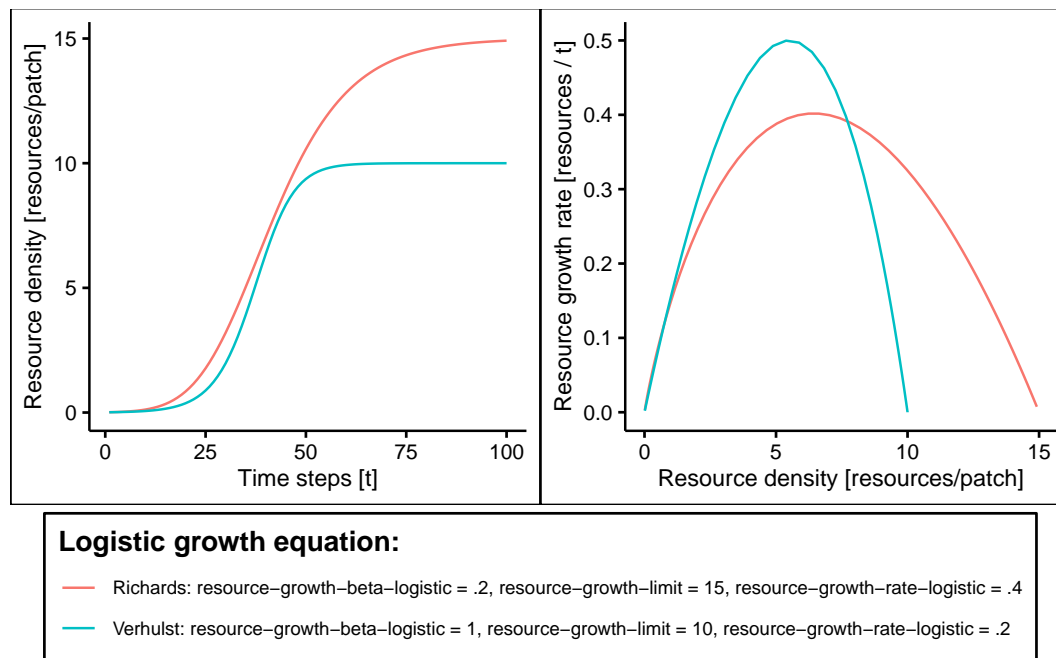


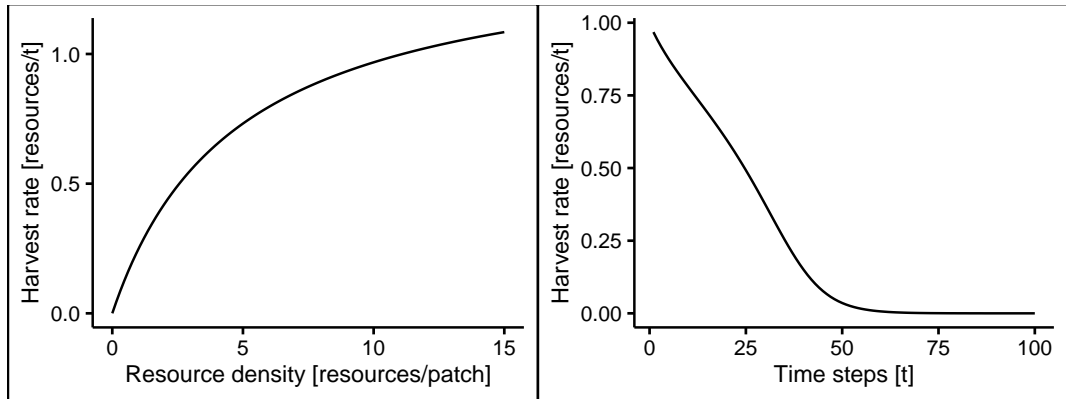
Figure B2.3: Exemplary logistic growth curves. Richards' growth equation reduces to Verhulst's growth equation if resource-growth-beta-logistic is set to 1. Parameters were chosen so that the population density was limited to levels below 1. The initial resource density was 0.01.

$$k = \left(\frac{N_t}{\text{resource.growth.limit}} \right)^{\text{resource.growth.beta.logistic}}$$

$$N_{t+1} = N_t + \text{resource.growth.rate.logistic} * N_t [1 - k] \quad (.11)$$

Harvest-rate follows a type II function. As this is a function of resource-density it is updated if resources are grown or harvested, respectively:

$$\text{harvest.rate} = \frac{\text{encounter.rate} * N}{1 + \text{encounter.rate} * \text{handling.time} * N} \quad (.12)$$



Harvest function – parameters: — handling-time = 0.7, encounter-rate = 0.3

Figure B2.4: Harvest rate function. Left: Harvest rate function with default parameters Right: Change in harvest rate over time if one animal stays on a patch with an initial resource density of 10 and resource growth following a Verhulst's growth curve as specified in Fig. B2.3.

Further submodels plot-LH-dist, plot-BT-dist, plot-BT-LH, plot-count-animals and color-landscape visualize state variables of animals and patches and the parameters plot-update-frequency, plot-animals and plot-landscape allow disabling of the visualization and the frequency at which the visualization is updated. As these submodels are neither part of the simulation or the output, they are not further described in this protocol.

B3 Additional tables

Table B3.1: Parameter settings used for the results in Figures 3.3, 3.4, 3.5 and 3.6.

PARAMETER	VALUE	DESCRIPTION
create-output	true	Generates any output as .csv
disturbance-interval	100, 125, 150, 200, 300, 500	Average interval between disturbances
disturbance-intensity	50, 80	Maximum percentage of population removed after disturbance
resource-growth-beta-logistic	-	Density dependence at logistic growth
resource-growth-rate-logistic	-	Growth rate at logistic growth
resource-growth-limit	15	Maximum resource-density at logistic and linear growth
resource-growth-rate-linear	0.15	Resource growth rate at linear growth
growth-type	“linear”	Defines if linear or logistic resource growth
handling-time	0.7	Time to handle a resource unit
encounter-rate	0.3	Rate at which resources are encountered
maintenance-cost	0.15	Fixed amount of resources spent per time step
n-inds	0.1	Initial population density (0.1 = 250 individuals)
output-directory	“simulations/ experiment/ ISO-date/”	Path to the output folder
plot-animals	false	Plot traits and density in the interface
plot-landscape	false	Plot resource density in the interface
plot-update-frequency	999999	Frequency of updating landscape and animals in the interface
monomorphic	false	Defines whether all individuals in initial population have the same trait combination
reproduction-threshold	50	Accumulated amount of resources required to produce one offspring
breeding-type	“capital”	Defines if life-history trait resembles capital or income breeder
save-landscape	false	Create harvest rate as additional output

stochasticity-BT	0.75	Standard deviation of inherited traits with the parental trait as the mean
stochasticity-LH	0.75	Standard deviation of inherited traits with the parental trait as the mean
restart?	true	Restart population in case populations goes extinct

Table B3.2: Parameter sets used for one-at-a-time sensitivity analysis (including variable parameters only, see Tab 3 for constants, resource-growth-rate-logistic and resource-growth-beta-logistic are not included as they do not affect the simulation with linear growth)

n-inds	maintenance-cost	reproduction-threshold	resource-growth-rate-linear	resource-growth-limit	handling-time	encounter-rate	stochasticity-BT	stochasticity-LH	disturbance-interval
0.55	0.15	50	0.15	15	0.7	0.3	0.5	0.5	100
0.055	0.15	50	0.15	15	0.7	0.3	0.5	0.5	100
0.1	0.2	50	0.15	15	0.7	0.3	0.5	0.5	100
0.1	0.08	50	0.15	15	0.7	0.3	0.5	0.5	100
0.1	0.15	75	0.15	15	0.7	0.3	0.5	0.5	100
0.1	0.15	40	0.15	15	0.7	0.3	0.5	0.5	100
0.1	0.15	50	0.15	15	0.7	0.3	0.5	0.5	100
0.1	0.15	50	0.15	15	0.7	0.3	0.5	0.5	100
0.1	0.15	50	0.225	15	0.7	0.3	0.5	0.5	100
0.1	0.15	50	0.08	15	0.7	0.3	0.5	0.5	100
0.1	0.15	50	0.15	17.5	0.7	0.3	0.5	0.5	100
0.1	0.15	50	0.15	10	0.7	0.3	0.5	0.5	100
0.1	0.15	50	0.15	15	0.85	0.3	0.5	0.5	100
0.1	0.15	50	0.15	15	0.35	0.3	0.5	0.5	100
0.1	0.15	50	0.15	15	0.7	0.65	0.5	0.5	100
0.1	0.15	50	0.15	15	0.7	0.15	0.5	0.5	100
0.1	0.15	50	0.15	15	0.7	0.3	0.75	0.5	100
0.1	0.15	50	0.15	15	0.7	0.3	0.25	0.5	100
0.1	0.15	50	0.15	15	0.7	0.3	0.5	0.75	100
0.1	0.15	50	0.15	15	0.7	0.3	0.5	0.25	100
0.55	0.15	50	0.15	15	0.7	0.3	0.5	0.5	500
0.055	0.15	50	0.15	15	0.7	0.3	0.5	0.5	500
0.1	0.2	50	0.15	15	0.7	0.3	0.5	0.5	500
0.1	0.08	50	0.15	15	0.7	0.3	0.5	0.5	500
0.1	0.15	75	0.15	15	0.7	0.3	0.5	0.5	500
0.1	0.15	40	0.15	15	0.7	0.3	0.5	0.5	500
0.1	0.15	50	0.15	15	0.7	0.3	0.5	0.5	500
0.1	0.15	50	0.15	15	0.7	0.3	0.5	0.5	500
0.1	0.15	50	0.225	15	0.7	0.3	0.5	0.5	500
0.1	0.15	50	0.08	15	0.7	0.3	0.5	0.5	500
0.1	0.15	50	0.15	17.5	0.7	0.3	0.5	0.5	500
0.1	0.15	50	0.15	10	0.7	0.3	0.5	0.5	500
0.1	0.15	50	0.15	15	0.85	0.3	0.5	0.5	500
0.1	0.15	50	0.15	15	0.35	0.3	0.5	0.5	500
0.1	0.15	50	0.15	15	0.7	0.65	0.5	0.5	500
0.1	0.15	50	0.15	15	0.7	0.15	0.5	0.5	500
0.1	0.15	50	0.15	15	0.7	0.3	0.75	0.5	500
0.1	0.15	50	0.15	15	0.7	0.3	0.25	0.5	500
0.1	0.15	50	0.15	15	0.7	0.3	0.5	0.75	500

Table B3.3: Constant parameters of the one-at-a-time sensitivity analysis.

disturbance-intensity	create-output	save-landscape	Plot-update-frequency	plot-animals	plot-landscape	growth-type	breeding-type	mono-morphic	restart
50	true	false	9999999	false	false	“linear”	capital-breeding	false	false

**C Supplementary material to: Model of interaction
between hyphal movement and micro-structured
environments**

C1 Additional table

Table C1.1: Entities and variables of the model. For variables, the entity context is specified.

VARIABLES & ENTITIES	ENTITY CONTEXT	TYPE OF VARIABLE
anastomosis-heading Pertains only to the procedure autotropism. It informs about the side on which the detected hypha is located, and the value in degrees by which the hyphal tip is deflected from this side in case of negative autotropism.	hyphal-tip	continuous
anastomosis-nodes Pertains only to the procedure anastomose. Number of agents (ends) connected by the link with which the hyphal tip is about to anastomose. Under the condition that the number of these agents equals 2 (end1 and end2 of this link), the anastomosis procedure will proceed. It is implemented to ensure that the hyphal tip does not anastomose with its own immediate hypha.	hyphal-tip	integer
anastomosis-probability Set by user, probability that the hyphal tip will actually anastomose, if the opportunity for that is detected (i.e. a hypha is ahead). When set to 1, hyphal tips always anastomose with the hypha that intersect their path.	hyphal-tip	continuous
anastomosis-status Result of the procedure get-anastomosis-status. List remains empty, if no hypha is detected on the "collision course". In case of positive result of the get-anastomosis-status procedure, the list contains two items: Item "is", and item "potential-IS-link". Item "is" is the intersection (anastomosis) point and contains two variables, the x and y coordinate of the intersection (anastomosis) point. Item "potential-IS-link" is an agent, an intersection link. That is, the link with whom the hyphal tip is about to anastomose.	hyphal-tip	list
autotropism-cone-angle Value in degrees, set by user. Defines the extend of perimeter ahead of the hyphal tip, which the given hyphal tip is to scan for presence of other hyphae.	hyphal-tip	continuous
autotropism-strength Defines the intensity by which the hyphal tip will change its current heading towards or away from another hypha ahead of it. If the value is negative, the hyphal tip will deflect its growth from the detected hypha (i.e. negative autotropism). If the value is positive, it will lean its growth towards the detected hypha (i.e. positive autotropism).	hyphal-tip	continuous

collision-angle	hyphal-tip	continuous	The angle between the heading of the hyphal tip and the surface with which it is about to collide.
collision-branching-threshold	hyphal-tip	continuous	A value in degrees set by the user. It is compared to collision-angle. If collision-angle is smaller than collision-branching-threshold
collision-status	hyphal-tip	list	Result of the procedure get-collision-status. List remains empty, if no particle surface is detected on the "collision course". In case of positive result of the get-collision-status procedure, the list contains three items: x and y coordinates of the point at which hyphal tip will collide with the surface, and the heading of the trajectory of the hyphal tip (angle of the intersecting probe link).
dir1 , dir2	hyphal-tip	continuous	Values dir1 and dir2 are given in degrees and indicate two alternative, opposite directions for sliding alongside the particle surface.
distance-list	hyphal-tip	list	Collects the distances to all hyphae in perimeter of autotropism. The collected values are compared, and the lowest value is used to assign the value of min-dists.
dist-travelled	hyphal-tip	continuous	Updated every time step, maintains information about the distance which hyphal tip passed since its creation. Used to trigger the lateral branching event once the dist-travelled is larger than lateral-branching-interval.
is	hyphal-tip	list	List that contains two variables: x and y coordinate of the intersection point between the trajectory of the hyphal tip and the hyphal link this tip is to anastomose with.
last-node	N/A	agent	The node to which the hyphal tip is immediately connected by the link, i.e. the node hyphal tip hatched as the last.
lateral-branching-angle	hyphal-tip	continuous	Set by user, the angle at which the lateral branches grow from their parental hypha. Set as a mean value and its standard deviation.
maximum-grain-diameter	helper	continuous	Set by user, the diameter of largest particles in the environment.
memory?	hyphal-tip	Boolean	

Set by the user. Informs the hyphal tip about its behavior after the sliding period, when the edge of the surface is reached. At this point, hyphal tip either resumes the original heading before sliding (memory? ON), or maintains the new heading equal to the direction of sliding (memory? OFF).

min-dists	hyphal-tip	continuous
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Informs the hyphal tip about the nearest hypha ahead of it and within the autotropism perimeter. Enables to select this hypha to be acted upon.

momentum	hyphal-tip	continuous
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It is the fraction of the distance the hyphal tip can still move in given time step, which is transported between procedures. At the beginning of each time step, it equals the distance of propagation-speed (set by the user). If for instance only half of this distance is "used" before encountering the sliding surface, other half is transported to the procedure slide as momentum.

move-towards-surface	hyphal-tip	continuous
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Because of the technical reasons inherent to NetLogo language, hyphal tips colliding with the particle surface do not touch this surface. Instead, they approximate their position to its very close vicinity, maintaining a margin M. Move-towards-surface is the real distance between the hyphal tip and the surface, minus the value M.

my-hyphal-nodes	patch	agent set
------------------------	-------	-----------

The nodes which lie on the surface of the given patch, and of all patches in its neighborhood (in-radius 2). It is used to save computational requirements of the procedure get-anastomosis-status. The probes and probing links will be only hatched in case the value of my-hyphal-nodes is larger than zero.

my-surfaces	patch	agent set
--------------------	-------	-----------

In procedure get-collision-status, the function of this variable is analogical to the function of my-hyphal-nodes in procedure get-anastomosis-status. Only if the value is positive, the procedure will hatch probes and probing links. If there are no surfaces, this step will be skipped to save computational requirements.

node	N/A	agent
-------------	-----	-------

Each time step, or after predefined (by user) number of time steps, the hyphal tip hatches a node. These agents are interconnected by hyphal links, and together with them they create the hyphal. Their additional functions are described in particular procedures.

node-frequency	hyphal-tip	integer
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Set by the user, frequency of time steps at which the node is hatched by the hyphal tip. Hatching the node every time step increases the resolution, but also the computational requirements.

parental-momentum	hyphal-tip	continuous
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Residual momentum (see variable: momentum) specific to the branches created by the collision induced branches.

perception-range	hyphal-tip	continuous
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Distance at which a hyphal tip may perceive other hyphae in the context of autotropism. Set by the user.

potential-IS-links	patch	agent set
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Hyphal links in vicinity of the hyphal-tip that is scanning environment for potential anastomosis.

probe	N/A	agent
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Probe hatched by the hyphal tips in procedures get-anastomosis-status, get-collision-status, autotropism. The probe moves to the position where hyphal tip is about to move and creates a link back to its parental hyphal tip.

probe-link	N/A	agent
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The link between the probe and its parental hyphal tip. In case this link intersects with another one (surface link, or hyphal tip), their intersection coordinates are used to update the results of the given procedures.

propagation-speed	hyphal-tip	continuous
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Set by the user, distance hyphal tip passes during each time step.

random-propagation-angle	hyphal-tip	continuous
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Set by the user, the degree of hyphal wiggling, or to what degree the trajectory of hyphal tip deviates from a straight line. The hyphae grow as straight lines, in case the variable random-propagation-angle is set to zero.

retention-time	hyphal-tip	continuous
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After the lateral branch is hatched in form of a hyphal tip, it does not start growing immediately (which would make it an apical branch). It waits for a value of time steps defined by retention-time.

roundness	particles	continuous
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Set by the user, defines the degree to which the particle surface is smooth (round), or not (sharper angles).

sliding-count	hyphal-tip	integer
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Formally it is an integer, increases every time step the hyphal tip finds itself in the sliding status. For the purposes of procedures, it behaves as a Boolean: When equal zero, it informs the procedure the hyphal tip is not sliding. When larger than zero, it is sliding.

surface-link	N/A	agent
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Links that form the surface of particles.

the-hyphae-start patch agent set

The nodes in vicinity of the hyphal tip. The agent set includes my-hyphal-nodes, but excludes the last-node of the given hyphal-tip. The function of distinguishing between these two agent sets (the-hyphae-start vs. my-hyphal-nodes) is to prevent the identification of hyphal-tip's own link as a link to anastomose with or to react upon through autotropism.
