



Mathematisch-Naturwissenschaftliche Fakultät

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Suggested citation referring to the original publication:

Ecosphere 10 (2019) 5, Art. e02700

DOI <https://doi.org/10.1002/ecs2.2700>

ISSN (online) 2150-8925

Postprint archived at the Institutional Repository of the Potsdam University in:

Postprints der Universität Potsdam


Mathematisch-Naturwissenschaftliche Reihe ; 742

ISSN 1866-8372

<https://nbn-resolving.org/urn:nbn:de:kobv:517-opus4-435320>

DOI <https://doi.org/10.25932/publishup-43532>

Give chance a chance: from coexistence to coviability in biodiversity theory

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Citation: Jeltsch, F., V. Grimm, J. Reeg, and U. E. Schlägel. 2019. Give chance a chance: from coexistence to coviability in biodiversity theory. *Ecosphere* 10(5):e02700. 10.1002/ecs2.2700

Abstract. A large part of biodiversity theory is driven by the basic question of what allows species to coexist in spite of a confined number of niches. A substantial theoretical background to this question is provided by modern coexistence theory (MCT), which rests on mathematical approaches of invasion analysis to categorize underlying mechanisms into factors that reduce either niche overlap (stabilizing mechanisms) or the average fitness differences of species (equalizing mechanisms). While MCT has inspired biodiversity theory in the search for these underlying mechanisms, we feel that the strong focus on coexistence causes a bias toward the most abundant species and neglects the plethora of species that are less abundant and often show high local turnover. Given the more stochastic nature of their occurrence, we advocate a complementary cross-level approach that links individuals, small populations, and communities and explicitly takes into account (1) a more complete inclusion of environmental and demographic stochasticity affecting small populations, (2) intraspecific trait variation and behavioral plasticity, and (3) local heterogeneities, interactions, and feedbacks. Focusing on mechanisms that drive the temporary coviability of species rather than infinite coexistence, we suggest a new approach that could be dubbed coviability analysis (CVA). From a modeling perspective, CVA builds on the merged approaches of individual-based modeling and population viability analysis but extends them to the community level. From an empirical viewpoint, CVA calls for a stronger integration of spatiotemporal data on variability and noise, changing drivers, and interactions at the level of individuals. The resulting large volumes of data from multiple sources could be strongly supported by novel techniques tailored to the discovery of complex patterns in high-dimensional data. By complementing MCT through a stronger focus on the coviability of less common species, this approach can help make modern biodiversity theory more comprehensive, predictive, and relevant for applications.

Key words: behavioral plasticity; biodiversity; coexistence; community theory; coviability analysis; demographic noise; environmental noise; heterogeneity; individual-based modeling; intraspecific trait variation; modern coexistence theory; population viability analysis.

Received 14 August 2018; revised 27 February 2019; accepted 11 March 2019. Corresponding Editor: Scott Ferrenberg.

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INTRODUCTION

Our world views, or paradigms, determine the kinds of phenomena we perceive and the kinds of theories we formulate and test. They can make us ignore factors that are indeed essential for explaining observations. Biodiversity theory might be in this situation. Equating the maintenance of species diversity with species coexistence has made coexistence theory one of today's leading frameworks in community ecology and biodiversity theory. However, although this concept is widely accepted and used, it underrates factors that undeniably exist and that are crucial for apparent biodiversity patterns. Here, we will argue that a stronger focus on stochasticity and trait variation in small populations will be critical for understanding general biodiversity patterns and changes in the Anthropocene.

The question of "What allows interacting species to coexist?" has experienced an impressive revival against the background of an ongoing and alarming loss of biodiversity and the introduction of nonnative organisms into ecosystems worldwide. A profound theoretical background to this question is provided by what is now known as "modern coexistence theory (MCT)" (Adler et al. 2007, Mayfield and Levine 2010, HilleRisLambers et al. 2012, Letten et al. 2017, Saavedra et al. 2017), originally developed by Chesson and colleagues (Chesson and Warner 1981, Chesson 1994, 2000*a*, *b*, 2003). Modern coexistence theory is based on invasion analysis, an elegant mathematical analyses of the ability of a population on the brink of extinction to recover in a given community. Focusing on average population growth rates, two different classes of mechanisms are identified that can reduce competition and hence mediate coexistence: equalizing mechanisms that reduce the average fitness difference (recently termed competitive advantage by Barabás et al. 2018) between species and stabilizing mechanisms that reduce niche overlap.

While MCT has become one of today's leading frameworks in community ecology, the underlying formal assumptions are not always fully reflected in its verbal formulation and interpretation. This was pointed out in a recent review by Barabás et al. (2018) that provides a comprehensive overview of Chesson's coexistence theory, summarizing important methodological

assumptions and discussing terminology and possible limitations in its application. Apart from an urgently needed clarification of this influential theory, Barabás et al. (2018) precisely outline its limitations and possible misinterpretations. Limitations can on the one hand arise from the fact that the theory is founded on invasion analysis and on the other hand arise from assumptions that are needed to simplify underlying mathematical models to derive elegant and ecologically meaningful results (Box 1). In summary, Barabás et al. (2018) conclude that the theory may not apply or be useful for complex dynamics with alternative stable states, in species-rich communities, or in the presence of many limiting factors unless strong simplifying assumptions are made, such as diffuse competition (i.e., there is one common intra- and another common interspecific competition coefficient, Chesson 1994, 2000*a*, *b*, 2003). Some of the mathematical limitations of MCT have successfully been overcome by a recent approach introduced by Ellner et al. (2016, 2019). The authors use numerical simulations to partition focal population growth rates into contributions from different mechanisms (e.g., different environmental drivers) and their interactions and subsequently compare invader and resident growth rates. This approach can reveal the specific role of a broad range of potential coexistence mechanisms, including those frequently discussed in MCT. While the proposed methodology provides an important additional tool for the detailed analysis of coexistence and the applicability of MCT in specific systems, we here present a supplementary approach that addresses temporary coviability of species rather than long-term coexistence.

Biodiversity dynamics typically are complex, and most observable patterns consist of only a few abundant species that coexist for longer timespans and a much larger number of less common species that show a high level of local turnover (Siepielski and McPeck 2010, Chu and Adler 2015, Dewdney 2017; Fig. 1). To address this full diversity range, we feel that we need to supplement the objectives of MCT and identify complementing key elements that better integrate the dynamics of inferior species, which constitute the majority of species. Here, we argue that this can be achieved by a cross-level approach that links individuals, small

populations, and communities and explicitly takes into account (1) a more complete inclusion of environmental and demographic stochasticity affecting small populations, (2) intraspecific trait variation (ITV) and behavioral plasticity, and (3) local heterogeneities, interactions, and feedbacks. We will also show that powerful approaches already exist, in particular individual-based modeling and population viability analysis (PVA), which need only to be merged into a new approach that could be dubbed “coviability analysis,” which would help to complement MCT.

WANTED: NEGLECTED PRINCIPLES IN COEXISTENCE THEORY

Environmental and demographic stochasticity

Modern coexistence theory is largely based on deterministic models, though some aspects of stochasticity have been addressed in recent studies (Adler and Drake 2008, Gravel et al. 2011, Vellend et al. 2014, Ellner et al. 2016, 2019, Tredennick et al. 2017, Schreiber et al. 2018). Addressing all potential impacts of stochasticity is of particular importance in viability analyses of small populations, which are strongly affected by random variations (Melbourne and Hastings 2008, Ovaskainen and Meerson 2010). The need to accommodate small populations occurs both because in coexistence theory, invasion analysis asks whether a small population can invade and

establish in a given community and because in most communities, rank–abundance relationships show that most species have low abundances and might even be locally rare (McGill et al. 2007, Dewdney 2017). In such cases, it is not sufficient to consider the average intrinsic population growth rates of the species involved, which determine persistence of the small populations and coexistence in general, but we must also consider how small populations can persist at least temporarily despite environmental and demographic noise (Melbourne and Hastings 2008; Fig. 1). Environmental noise refers to temporal variations in population growth rates, for example, those induced by weather fluctuations, land use impacts, epidemics, or other variable environmental conditions. In contrast, demographic noise refers to fluctuations in population sizes that arise from the discrete nature of individual birth and death events (Ovaskainen and Meerson 2010, Boettiger 2018), which are affected by trait and life history differences among individuals. Due to habitat loss and fragmentation, most current populations have to cope with smaller habitats, leading to reduced population sizes that are prone to both types of stochasticity.

Clearly, environmental variability is not necessarily restricted to random fluctuations around a steady state; it may also include continuous changes or abrupt shifts such as critical transitions (van der Bolt et al. 2018). In such cases, the

Box 1.

Limitations of modern coexistence theory (derived from Barabás et al. 2018)

Key limitations with regard to less abundant species with high turnover

Chesson's theory is largely based on the assumption of a single limiting factor. This makes the theory considerably less convenient for analyzing more realistic communities with multiple limiting factors

Deriving the theory from a mathematical invasion analysis assumes that the invaders' environment is stationary, that is, that the resident community, in the absence of any invading species, eventually settles to some stationary state. If the species' stationary state does not exist for all species as invaders, then invasion analysis fails

Only one species at a time is considered to be invasive. There is no framework for multiple species being in the invader state, that is, at low density

While temporal and spatial variability play important roles in the theory, their statistical properties have to be constant in time

Invading species at low densities do not feedback to their surroundings

Communities are typically assumed to be closed in the sense that the net effect of immigration and emigration is zero

Species' interactions are typically described based on the assumption of diffuse competition. Such a simple interaction structure is particularly needed for the evaluation of multispecies stationary states. Indirect and intransitive effects as part of an entire web of interactions are not taken into account

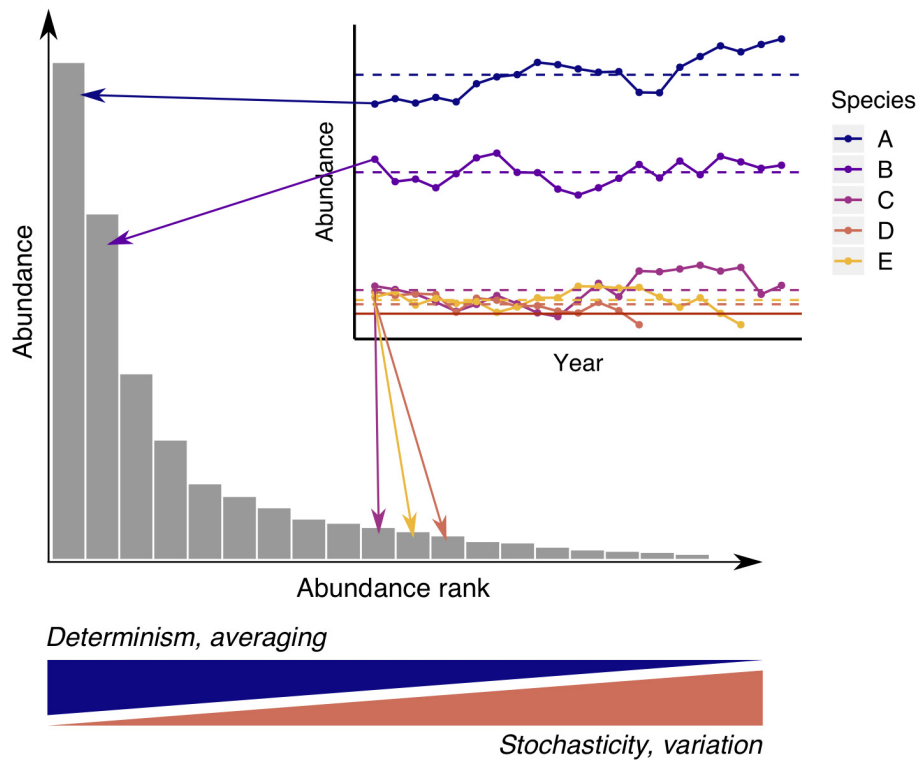


Fig. 1. Most communities comprise two groups of species: those that are so abundant (A, B) that stochasticity can be ignored and considering average population growth rates is sufficient (i.e., existence is not at risk) and those many species (e.g., C, D, E) that have such low abundances that stochasticity and hence trait variation and local heterogeneity matter (i.e., existence and hence viability are at risk; e.g., D and E are crossing critical, e.g., extinction, thresholds [solid red line in time series diagram]).

observed co-occurrence of species can be more influenced by extinction debts (i.e., the delayed process of species extinction after habitat destruction, Chen and Peng 2017) than by current stabilizing or equalizing mechanisms. Other aspects of environmental noise that are important for population survival but are rarely considered in MCT are the degree and type of its correlation, that is, its color (Ripa and Lundberg 1996, van der Bolt et al. 2018). For example, red-dened noise, that is, positively correlated stochastic fluctuations, can either increase or decrease extinction risks depending on the probability of extreme events and the sensitivity of the population (Schwager et al. 2006). In either case, to deal with extinction risks of small populations, one has to consider threshold dynamics (e.g., those caused by Allee effects) and nonlinear dynamics (Ovaskainen and Meerson 2010).

Overall, while some of these aspects of environmental and demographic stochasticity have been addressed in the literature on modern coexistence, a complete integration of stochastic extinction dynamics of small populations is still missing. At least some of the missing aspects can probably be integrated into MCT through individual-based simulations following the numerical approach outlined by Ellner et al. (2019, see *Introduction*). However, we argue that shifting the focus from long-term coexistence to also include shorter-term coviability of species will require or at least strongly benefit from additional tools that are already provided by PVAs.

Intraspecific trait variation and behavioral plasticity

Unstructured mathematical population and community models ignore ITV by considering

average individuals. However, differences in age, size, and other morphological, physiological, or behavioral traits have been shown to matter in large numbers of both structured (Ozgul et al. 2010) and individual-based population models (Fischer et al. 2016) and empirical studies (Siefert et al. 2015). Intraspecific trait variation can arise through genetic variability or phenotypic plasticity, and the relative contribution of either to observed individual variation is still unknown (Siefert et al. 2015). However, both sources of variation can have similar and possibly multifaceted effects at the community level (Bolnick et al. 2011, Violle et al. 2012). Individual variation in important traits such as resource-use efficiency or the timing of life history events, for example, not only affects individual fitness per se but also may mediate the outcome of individual interactions, and hence competition, or the effect of disturbance on populations and communities (Lavorel and Garnier 2002). Particularly fit individuals may be less affected by disturbance and thereby buffer populations against extinction, in spite of their low numbers (Grimm et al. 2005). Although no general theory has yet emerged on the importance of ITV, structured ITV, which is related to inheritance or other forms of spatial or temporal correlation, is likely to have stronger effects on coexistence than unstructured, or random, ITV.

While in plants ITV is related to morphological or physiological traits, animals can additionally express variation in behavioral traits or even entire behavioral syndromes. When variation exists between individuals but behavior within the same individuals is consistent across time and through contexts, behavioral types are also referred to as personalities. Our understanding of the role of animal personalities in biodiversity is even less advanced than that of the role of ITV in general; however, pioneering studies suggest that, at least temporarily, the fate of communities is affected. For example, personalities of founder species in spider communities lead to divergent communities, although these eventually converge and finally collapse (Pruitt et al. 2016). Additionally, personality-dependent space use can influence spatial population structure (Spiegel et al. 2017) as well as trophic interactions and community structure in food webs (Start and Gilbert 2017). In addition to consistent behavioral differences between individuals, individuals make

adaptive decisions, for example, to maximize growth or survival, that depend on their internal states and their individually experienced biotic and abiotic environments. Habitat selection of brown trout, for example, depends not only on size and age but also on the presence of conspecifics, predators, and the features of a river's morphology and flow regime (Railsback and Harvey 2013). Likewise, animals invest different proportions of ingested energy into maintenance, growth, and reproduction depending on their size, their maturity, and resource availability (Sibly et al. 2013, Galic et al. 2018). These and other kinds of behavioral plasticity reflect important evolutionary principles and have consequences for species survival and hence coexistence (Jeltsch et al. 2013a).

Local heterogeneities, interactions, and feedbacks

For small aquatic organisms living in small and well-mixed habitats, for example, those in the laboratory, it makes sense to assume a well-mixed community with typically high individual numbers (Martin et al. 2013). This corresponds well to the implicit mathematical assumption made in models ignoring spatial relationships that all individuals of one species can interact with all individuals of other species in the same community (Yitbarek and Vandermeer 2017). The picture changes if we assume terrestrial organisms and in particular sessile ones, which only experience local neighborhoods consisting of a few individuals, for example, trees in forests (Fischer et al. 2016). How this local neighborhood is composed can differ significantly depending on relative abundances but also on any process that leads to spatial pattern formation, including species interactions (Pringle and Tarnita 2017) as well as small-scale resource, disturbance, and habitat heterogeneities (Bergholz et al. 2017) and founder (van Gestel et al. 2014) or simply chance effects (Yitbarek and Vandermeer 2017). In particular, when populations are small, such local neighborhoods can be decisive for population extinction or survival. On the negative side, spatially isolated individuals, that is, individuals in neighborhoods that otherwise only consist of heterospecifics, may have problems finding a mate or, in case of plants, being pollinated (Lachmuth et al. 2018). Such Allee effects are well explored in both coexistence theory and extinction theory (Courchamp et al. 2008, Kramer et al. 2018). However, spatial isolation may also reduce

the chance of being found by a predator or herbivore or of being infected by a species-specific disease (Comita et al. 2014).

Local neighborhoods create temporary, small-scale niches that change with the specific composition and possible local feedbacks. Such feedbacks include facilitation processes for plants (Lin et al. 2012, Bulleri et al. 2016) but, for example, also the benefits low-numbered prey may experience as a result of group building or herd building with other prey species (Schmitt et al. 2016) or because, in the case of tree seedlings, they become less affected by herbivores (Janzen-Connell hypothesis; e.g., Petermann et al. 2008). Additionally, temporary behavioral adaptations of neighboring individuals of different species may lead to temporary local niche separations (Nakano et al. 1999, Connors et al. 2015, Jennings et al. 2016). All these local and temporary mechanisms can impact reproductive success and mortality risks at the individual level. For populations that are down to a few individuals, these mechanisms may decide whether extinction or (co)existence occurs. It is important to note that local neighborhoods and other heterogeneities go well beyond the spatial structure of a limited number of connected (sub)populations that form a metacommunity. While important coexistence mechanisms have been identified at the metacommunity level within MCT (Shoemaker and Melbourne 2016, Leibold and Chase 2017), underlying mechanisms still focus on populations rather than on the specific local conditions an individual experiences.

THE WAY FORWARD

To provide a more complete picture of biodiversity dynamics, we so far identified the need to complement MCT with an individual-based perspective and a more complete inclusion of noise and heterogeneity affecting small populations. Interestingly, for both aspects, there is a rich body of methods, concepts, and tools that have not yet been sufficiently integrated into theory of biodiversity dynamics, that is, individual-based models (IBMs) and PVAs.

Individual-based modeling

Individual-based modeling, also referred to as agent-based modeling, lends itself particularly to

research questions when one or more of the following aspects are considered essential: ITV, spatial heterogeneity, local interactions, and adaptive behavior (Grimm et al. 2006). In addition, by explicitly representing individuals, taking into account demographic and environmental stochasticity is straightforward. Individual-based models are thus ideal tools to address the key gaps in current biodiversity research identified above. However, the question remains whether IBMs also have the potential to advance more general biodiversity theory.

Progress in individual-based modeling toward unifying theories has been slower than anticipated by its early advocates (Huston et al. 1988, DeAngelis and Grimm 2014) both because of methodological challenges regarding optimal model design, communication, parameterization, and validation and because of a strong demographic legacy where, as in more aggregated mathematical models, demographic rates and behavior are imposed via observed empirical relationships. In only the last decade or so, IBMs started letting demography and behavior emerge from submodels representing adaptive decision making (Railsback and Harvey 2013). Only if the response of individuals to changing conditions is fully captured can the responses of higher levels also be understood and predicted (Railsback and Harvey 2002, Stillman et al. 2014, Schibalski et al. 2018). Also, specific software (e.g., NetLogo, Wilensky 1999), documentation protocols (ODD, Grimm et al. 2006, 2010; TRACE, Schmolke et al. 2010, Grimm et al. 2014), and design and validation guidelines (pattern-oriented modeling; Grimm and Railsback 2012) emerged, which led to an overall maturation of individual-based modeling in ecology.

To date, IBMs have been used mostly for populations, not communities. Since IBMs are, by their nature, more complex than mathematical models and often tailored to specific species, modeling entire communities by representing interacting individuals seems like a daunting task. However, sufficient know-how has accumulated over the last two decades to make this possible, and in some fields, in particular forest ecology, community IBMs have already been widely used for more than 20 yr (Fischer et al. 2016).

To limit the complexity of community IBMs, we need generic descriptions of species, individuals, and their interactions where differences can be specified by parameter values. Forest IBMs are a good example: Individual trees are typically described by only one state variable, diameter at breast height. All other structural features of a tree are derived by allometric relationships (Botkin et al. 1972) which have the same functions, but different species-specific parameters. Interaction is represented via vertical competition for light: The trees standing on a certain plot define the vertical profile of leaf layers from which the light actually available for photosynthesis in each layer can be calculated. Similarly, in fish community models, all fish species are characterized by the same set of variables (age, developmental stage, irreversible mass representing tissue that can grow or stay, fat reserves, and gonad mass), and species are only distinguished via different trait values (e.g., potential growth rate, maximum irreversible mass, or egg size). Consequently, trophic interactions are solely based on size differences, not species identities (Giacomini et al. 2013).

Examples of generic models of individuals are energy budget models (Martin et al. 2013, Sibby et al. 2013), fitness-seeking habitat selection (Railsback and Harvey 2013), or growth models derived from metabolic scaling theory (Lin et al. 2014). Generic models of species interactions include zone-of-influence models of competition among animals (Berger et al. 2008) or plants (Lin et al. 2014), or allometrically scaled home-range models (Buchmann et al. 2011, Buchmann et al. 2012, Prevedello et al. 2016, Teckentrup et al. 2018).

A further means for limiting complexity is by modeling functional types, defined by characteristic trait combinations, instead of species. Such types can be defined from the outset, as in some forest models (Fischer et al. 2016), or they can emerge during community assembly. May et al. (2009), for example, used all possible trait combinations (81 plant functional types) in a trait-based grassland model to initialize the model world. Similar to real community assembly, only a small subset of these types was able to coexist. Interestingly, as pointed out above, only two or three functional types became dominant, while most of the other 5–8 types, which were able to persist for a decade or more, had low densities

and were prone to extinction. This model, IBC-grass, was later augmented with clonal species and parameterized with data from grassland monitoring plots and then correctly predicted observed patterns in species richness (Weiss et al. 2014). The model was also used to explore the effects of root herbivory (Körner et al. 2014) and herbicides (Reeg et al. 2017), and is used below to demonstrate how a coviability analysis (CVA) can be implemented with an existing, well-tested community IBM. For further examples of community IBMs that would allow for a CVA, see Grimm et al. (2017) and references therein.

The amount of data produced by IBMs can be immense. Model analysis therefore is challenging. Systematic model simplification, dubbed robustness analysis (Grimm and Berger 2016), can help in identifying essential mechanisms and thereby reducing complexity. Moreover, sophisticated methods for global sensitivity analysis exist (Cariboni et al. 2007) and are implemented in ready-to-use R-packages (Thiele et al. 2014).

Furthermore, approaches to studying IBMs analytically and interpolating between IBMs and more rigorous mathematical models can pave the way for theory refinement embracing the level of individuals (Black and McKane 2012). Individual-based models are also increasingly merged with mathematical models, leading to hybrid models that combine the advantages of both model types (Vincenot et al. 2016). The overall agenda and the specific instruments for implementing a modern cross-level, stochastic theory of biodiversity dynamics thus exist and are ready to be used.

Population viability analysis

Given the current rate and intensity of environmental change, the described relevance of stochasticity, and the high local turnover of inferior species, the assumption of steady states as a basis for coexistence analyses falls short when we seek to get a more complete picture of biodiversity dynamics. The term coexistence usually is interpreted as referring to long-term stable (eternal) coexistence. While this is relevant for the more abundant and dominant species, a large part of biodiversity dynamics is more ephemeral. Addressing these more transient dynamics requires exploring factors that prolong temporary coviability of species, explicitly including

species with low abundances. For example, most specific models and theories involving small populations show a clear effect of habitat size on species viability, for example, in the island theory of biogeography (Patiño et al. 2017), or the mid-domain effect, which is one possible explanation of the latitudinal gradient in species richness (Colwell et al. 2004). An exclusive focus on existence in absolute terms may neglect key mechanisms underlying observed biodiversity patterns.

For single species, extensive research led to a well-developed theory of viability (or persistence) in the form of PVA (Table 1; Boyce 1992, Henle et al. 2004, Ovaskainen and Meerson 2010, Singer and Frank 2016), and model-based PVAs have become standard tools to support conservation (Pe'er et al. 2013, Singer and Frank 2016). With a focus on viability and extinction risks, both demographic noise and environmental noise are at the core of PVA. Overall, PVA provides a large body of examples and concepts, for example, the intrinsic mean time to extinction (Grimm and Wissel 2004), that could make

valuable contributions to biodiversity theory (Table 1, Fig. 2).

However, to be useful in a community context, PVAs would have to go beyond the focus on single species and more fully integrate species interaction. We therefore argue for CVA. While the inclusion of species interactions in PVAs has already been argued for by Boyce (1992), it has rarely been implemented due to the additional complexity and uncertainty it involves (but see Stephan and Wissel 1999).

Earlier approaches, termed community viability analysis, analyzed secondary extinctions following the loss of important species (e.g., keystone species, Ebenman and Jonsson 2005; for secondary extinction, see also Berg et al. 2015). In contrast to our approach, the term community viability analysis in these earlier studies was restricted to cases where the loss of one species triggered a cascade of secondary extinctions with potentially dramatic effects on the functioning and stability of the community. Additionally, species interactions have recently been

Table 1. Key concepts from population viability analysis (PVA).

Concept	Definition
Viability	The ability to persist despite the strong influence of random variations
PVA	Model-based analysis of the viability of small populations, that is, their ability to persist over certain time horizons. Extinction is inevitable for small populations, which is in contrast to the assumption of existence in coexistence theory. The task of PVA is to rank management options regarding their potential to reduce extinction risk
Intrinsic mean time to extinction (T_m)	Metric of viability, determined from a large number of runs of population models. This conservation currency is an intrinsic property of the modeled population that allows different assessments of viability to be compared between alternative scenarios (e.g., alternative management measures). Mathematical approaches devised from general Markov models of stochastic population dynamics can be used to evaluate any simulation model concerned with extinction. In this approach, T_m can be directly linked to the probability of extinction for a given timeframe $P_0(t)$ (Grimm and Wissel 2004); see Fig. 2B
Probability of extinction ($P_0(t)$)	Another metric of viability, determined by the proportion of simulation runs of a model where the population goes extinct within the time horizon t . For small probabilities of extinction, $P_0(t) \approx t/T_m$
Extinction threshold	Once abundance is below a certain threshold, extinction risk tends to increase abruptly. Extinction thresholds can be determined from a large number of simulations, plotting $P_0(t)$ for all observed population sizes as a starting point (Hildenbrandt et al. 2006). Note: Instead of the extinction underlying the previous measures, specific population thresholds of quasi-extinction can be used as an alternative (e.g., $P_{15}(t)$ with a quasi-extinction threshold of 15 individuals, or implementing T_m as the intrinsic mean time to quasi-extinction)
Extinction vortex	The cascade of negative growth rates leading to small population sizes, where even if growth rates are no longer negative, environmental noise reduces populations below the extinction threshold, where demographic noise gives the coup de grâce to the population
Minimum viable population (MVP)	Originally defined as the initial population size (of a simulation) that allows for a previously defined viability. For calculations, often an arbitrary extinction risk $P_0(100) = 0.01$ is defined, which corresponds to a T_m of 10,000 yr. Note, however, that this MVP is not independent of the minimum carrying capacity of the habitat. A complete MVP assessment thus specifies both the minimum carrying capacity needed for the required viability and the minimum initial population size required to actually exploit, in terms of viability, the given minimum carrying capacity (Grimm and Storch 2000)

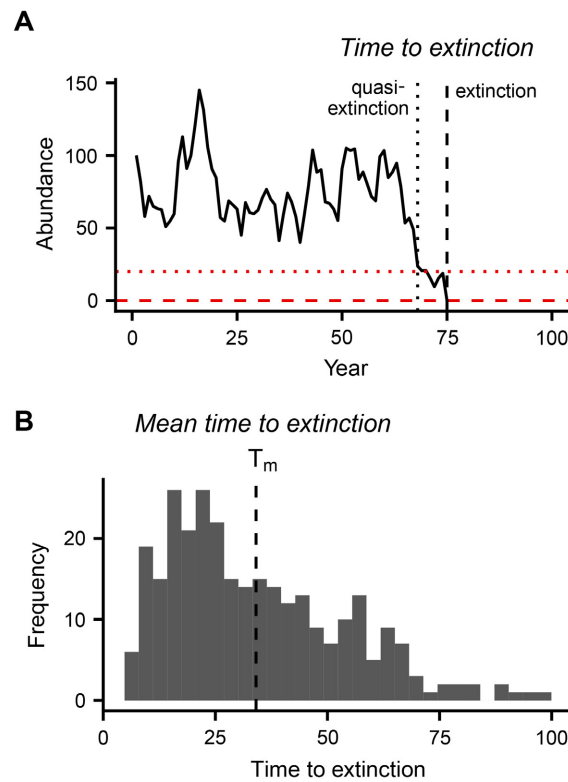


Fig. 2. Examples of important concepts from population viability analysis. For purely demonstrative purposes, data were generated with a stochastic version of a simple phenomenological population growth model. (A) Trend of abundance of a population that goes extinct in year 75 (time to extinction, vertical dashed line). An alternative to extinction (zero abundance), quasi-extinction is the event where abundance falls below a certain threshold (e.g., 20 individuals, horizontal dotted line). (B) Frequency distribution of times to extinction for multiple runs of the model. The vertical dashed line indicates the mean time to extinction T_m .

considered to analyze population viability of fluctuating species, adding a community aspect to classical single-species PVAs (Singer and Frank 2016). However, what is still missing and needed in this context are community-based PVAs that take into account dynamic changes caused by nonstationary environments and interactions between individuals of different species.

Coviability analysis

From a modeling perspective, scaling up from the individual to the community level while taking into account nonstationary conditions and all types of noise can be realized by a combination of cross-level, stochastic community models, for which IBMs are particularly suited, and an updated toolbox originally developed for PVAs. We advocate that such a combination will enable

a CVA that complements current coexistence theory approaches.

Cross-level, stochastic community models bridge specific aspects of individuals (e.g., ITV and behavioral plasticity, see above) and community dynamics. For a CVA, only those aspects at the individual level that can be expected to change the extinction risk of at least one of the species need to be considered. For example, in a metacommunity or a range-shift context, mainly the dispersal success between the different habitat patches will be influenced by individual trait differences, whereas local population and community dynamics may be sufficiently described by more generalized population models (Jeltsch et al. 2011, Lurgi et al. 2015). In other cases, interactions between individuals also determine local community dynamics and biodiversity

(Buchmann et al. 2013, Weiss et al. 2014, Schibalski et al. 2018, Teckentrup et al. 2018); thus, individual trait variations and trade-offs must be considered at that level.

Using PVA tools in a CVA context means applying established measures for focal single species (e.g., mean time to extinction) but also establishing analogous or related measures at the multispecies level. Such measures should, for example, indicate typical (“mean”) time periods until a community’s diversity falls below a previously defined threshold. We used the individual-based grassland

model, IBC-grass (May et al. 2009, Weiss et al. 2014, Reeg et al. 2017), to demonstrate the general procedure of performing a CVA with a community of grassland plant species that are typically found at mid-European field margins (Fig. 3). Such a community has two key features that make CVA a better tool for studying its diversity than MCT.

1. These systems typically include a few dominant species and many more species at low-to-medium abundance (Weiss et al. 2014).

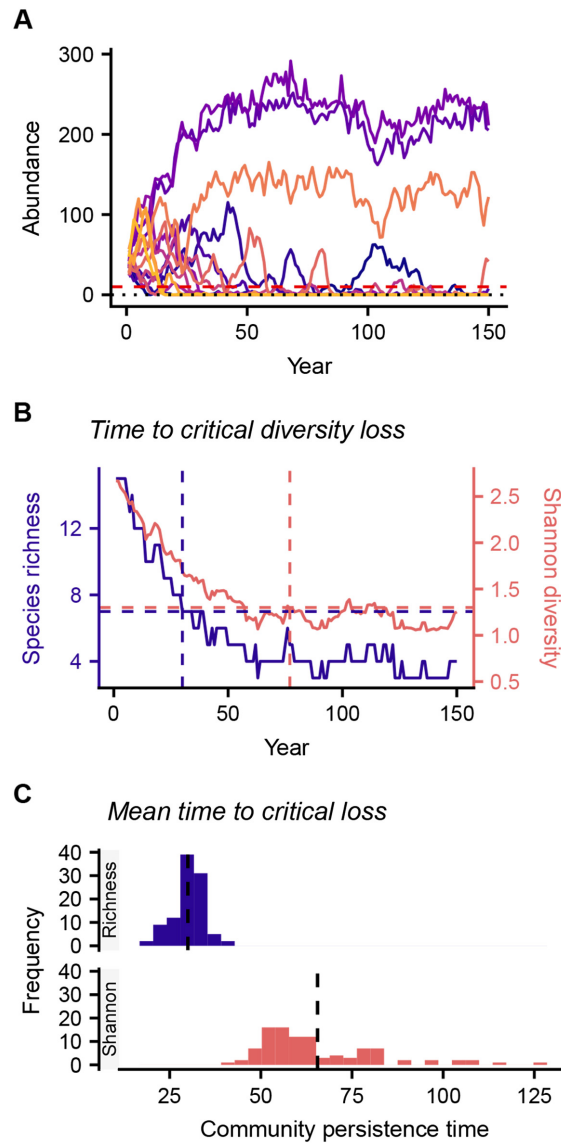


Fig. 3. Example of how key measures from population viability analysis (PVA) can be extended to the

(Fig. 3. *Continued*)

community level for coviability analysis. We used the individual-based grassland model, IBC-grass (May et al. 2009, Weiss et al. 2014, Reeg et al. 2017), to simulate a community of 15 plant functional types typically found at mid-European field margins (Reeg et al. 2017). The model is based on a two-layer zone-of-influence approach of above- and belowground competition (May et al. 2009) and includes important ecological processes such as dynamic resource allocation to shoots and roots, clonal growth, grazing, trampling, and seed input from the (implicitly modeled) metacommunity, as well as the effect of human actions such as mowing (Weiss et al. 2014, Reeg et al. 2017). A detailed description of the model version used here can be found in Reeg et al. (2017). Starting from a realistic scenario with empirically validated parameter values (Weiss et al. 2014, Reeg et al. 2017), we simulated a eutrophication scenario, in which belowground resources increased incrementally every ten years over the course of 150 yr. This led to quasi-extinction of most species, where we defined quasi-extinction to occur when a species' yearly average abundance fell below 10 individuals. We simulated 100 replicates. (A) Sample population trends of 15 competing plant functional types (one replicate). Most populations died out by year 150. (B) Example of an analog to time to quasi-extinction in PVA (Fig. 2A): trend of two diversity measures (species richness, blue line; Shannon diversity, red line) of the community in panel A. Horizontal dashed lines indicate defined thresholds, below which the community is deemed to have experienced critical diversity loss (here, as an example, set at 50% of the initial diversity value prior to the start of our eutrophication scenario). Vertical dashed lines indicate the time until the community crossed the respective thresholds for at least 20 yr (time to critical diversity loss). Note that due to seed input from the metacommunity, species rebounded occasionally and species richness did not decrease monotonically. (C) Example of an analog to mean time to quasi-extinction from PVA (Fig. 2B): distribution of times to critical diversity loss for selected diversity measures, namely, species richness (blue, upper histogram) and Shannon diversity (red, lower histogram). Vertical dashed lines indicate the mean of the distribution (mean time to critical diversity loss).

For these rare species, risk of extinction due to demographic noise is high. In addition, individuals of the rare species experience variable local competitive environments, depending on which other species are in their direct vicinities, which they can only evade through dispersal.

2. Field margins are often prone to eutrophication, because croplands are heavily fertilized and fertilizer displacement techniques are often not precise enough to prevent spreading into non-target areas. Over time, nutrients build up, leading to gradually changing abiotic environmental conditions for grassland species in the field margins.

In our simulated eutrophication scenario, most populations quickly declined below a quasi-extinction threshold and finally died out (Fig. 3). Analogous to time to quasi-extinction and its mean as measures in PVA, we here used the decline in species richness and Shannon diversity as CVA measures to quantify critical diversity losses. In CVA, critical loss has to be specifically defined, for example, by a lower bound on species richness or a range of another diversity dimension that is deemed deficient.

Similar to PVAs, this analysis could be combined with an evaluation of alternative management actions that influence community processes and allow a community to evade critical loss. In our example, we used varying mowing frequency and external seed input as alternative management measures impacting critical coviability (Fig. 4).

The example shows that CVA will allow defining and quantifying coviability of species in a community context and integrating complex interaction webs without assumptions of stationary conditions while also simultaneously providing an established framework for analyzing noise effects. This provides an alternative aim and approach as compared to MCT.

As shown in our example (Figs. 3, 4), CVA can further bridge basic research and conservation: On the one hand, it will help derive novel insights into the co-occurrence of species and the dynamics of communities; on the other hand, it will lead to quantitative predictions of biodiversity changes that are urgently needed in conservation.

CVA and biodiversity theory

While CVA per se clearly is not a theory, it enables identification of mechanisms and general

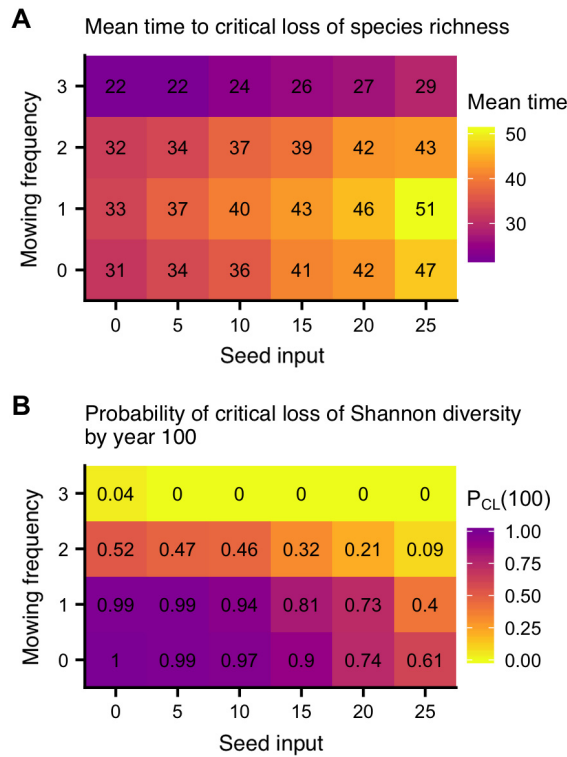


Fig. 4. Example of a coviability analysis, using the same individual-based grassland model, IBC-grass (May et al. 2009, Weiss et al. 2014, Reeg et al. 2017), as in Fig. 3. We evaluated the effect of alternative management actions (varying mowing frequency and seed input) on critical coviability measures such as those defined in Fig. 3. The baseline seed input in the validated scenario (Fig. 3) was 10 seeds per PFT per year, and all other scenarios represent either additional seed input or exclusion through human intervention. A community was considered to have experienced critical loss when the diversity measure fell below a threshold of 50% of the initial value. Note that colored tiles are annotated with the values of the coviability measure as per color legend (i.e., mean time to critical diversity loss, and probability of critical loss by year 100, respectively) for easier readability. (A) Effect of management actions on the mean time to critical diversity loss (CL; Fig. 3C) for species richness as diversity measure. The mean time to critical loss was longest for the scenario with one mowing event per year for any level of seed input. Additional seed input could help to further prolong the expected time to critical loss. (B) Effect of management actions on the probability of critical loss by year 100 ($P_{CL}(100)$ as an analog to $P_0(100)$ in population viability analysis; Table 1), for Shannon diversity as a diversity measure. The probability of critical loss could be severely reduced by high mowing frequency (up to three times per year). The contrast between the effects of mowing frequency on species richness (A) and Shannon diversity (B) was due to evenness: High mowing frequency assured that the dominant plant functional types that withstood the extended eutrophication were fairly even in abundance, keeping the Shannon diversity high despite a loss of many species.

principles that can help explain spatiotemporal biodiversity patterns in a changing world. These principles will both enrich biodiversity theory and allow for testable predictions. For example, CVA can help to detect mechanisms that work at fine scales at the level of interacting individuals in spatially and temporally variable environments. This includes complex mechanisms

related to movement of individual animals in response to variable environmental conditions. Actual movement paths and thus interactions with con- and heterospecifics depend not only on the motion and navigation capacity of the moving organisms but also on individual's personalities, their current internal state, and individually experienced external factors (as described in the

emerging field of movement ecology; Nathan et al. 2008, Jeltsch et al. 2013a, Spiegel et al. 2017). The individual-based approach in CVA makes it particularly useful for identifying possible consequences of such individual features at the higher level of populations, communities, and thus biodiversity dynamics. The same holds for the role of ITV (see section *Intraspecific trait variation and behavioral plasticity*): In a recent study based on the IBC-grass model that we also used for our example in Figs. 3, 4; Crawford et al. (2019) show that ITV can increase species diversity in a simulated grassland. Findings in this study suggest that ITV actively maintains diversity by helping species on the margins of persistence, but mostly in habitats of relatively low alpha and beta diversity. Interestingly, the positive effects of ITV in these spatially explicit, individual-based simulations are in contrast to earlier studies based on mathematical models embedded in the framework of MCT (Barabás and D'Andrea 2016, Hart et al. 2016). This contrast is of particular interest since it hints at additional coviability- or coexistence-enhancing mechanisms revealed by the differing approach.

On a cautionary note, it is not a priori clear if factors such as animal personality or intraspecific trait variation average out at higher organizational levels or indeed have an effect at the community level. Few empirical studies so far address this topic but several recent results indicate that individual variability can affect spatial niches, temporary coviability, or even long-term coexistence (Pruitt and Modlmeier 2015, Canestrelli et al. 2016, Pruitt et al. 2016, Cote et al. 2017, Schirmer et al. 2019). In either case, we argue that the approach of CVA will enable the exploration of conditions under which these factors impact species interactions and to which degree this scales up to influence coviability or even coexistence.

An important question for future studies is the identification of spatial scales at which mechanisms that enhance local coviability are also relevant at regional scales and if these mechanisms can then be described by MCT. This clearly also relates to mechanisms explaining regional biodiversity dynamics summarized in metacommunity theory (Holyoak et al. 2005, Logue et al. 2011). While at a first glance CVA is more suited to address local biodiversity dynamics, recent

findings indicate that mechanisms emphasized by CVA can also be relevant at larger scales. For example, individual differences in key personality traits seem to be important for dispersal and resulting large-scale biodiversity patterns (Canestrelli et al. 2016, Cote et al. 2017) and individual variation across and within coexisting species has the potential to affect not only species coexistence at local communities, but also regional diversity patterns (Costa-Pereira et al. 2018). Vice versa, regional-scale coexistence or coviability mechanisms are likely important in maintaining a regional species pool from which locally transiently coexisting species in our CVA framework may be recruited. These mechanisms may stem from spatial MCT, such as the spatial storage effect and fitness–density covariance, but may also be related to coviability mechanisms as outlined above, which remains to be investigated.

Future studies combining CVA and more analytical approaches are needed to disentangle the transitions and boundaries between mechanisms that merely enhance shorter-term and more local coviability and those that contribute to long-term coexistence at regional scales.

Overall, CVA has the potential to reveal coviability-enhancing mechanisms that are not yet covered by coexistence studies (Ellner et al. 2019). Its quantifying measures (e.g., mean time to critical biodiversity loss; Fig. 3) even allow for an evaluation of the relative strength of these mechanisms under different assumptions and alternative scenarios (Fig. 4). Future research will probably show that at least some of these mechanisms can also be categorized as equalizing or stabilizing according to MCT. Thus, CVA will also contribute to MCT by providing candidate mechanisms for longer-term coexistence that could then be studied with more analytical tools of MCT. As such, the advocated approach of CVA is not in contrast to MCT but supplements it to embrace conditions under which the basic assumptions of this theory are not met or conditions which are not yet covered by current approaches of MCT. Neither approach is exclusive, but they complement each other as they have different realms (Fig. 1).

CVA and empirical research

From an empirical perspective, CVA entails an explicit inclusion of the majority of less abundant

species rather than focusing on abundant species, for which coexistence can likely be explained by MCT (Chu and Adler 2015). Thus, CVA goes beyond niche differences and average fitness differences of the most common, co-occurring species at each site. Clearly, there is a general trade-off in applying stochastic, individual-based simulation models that are underlying the CVA approach: On the one hand, they are more difficult to interpret than mathematical models and they do not easily provide the generality and qualitative insights that can come from analytic formulas for coexistence mechanisms. On the other hand, these models lend themselves especially well to studying fine-scale mechanisms that are not covered by more classical approaches (Crawford et al. 2019). This general modeling dilemma between generality vs. realism or precision (Levins 1966, Barabás et al. 2018) is also reflected in the data needed for model parameterization and evaluation. Stochastic simulation models underlying CVA are probably more realistic but require data on and analyses of environmental and demographic noise, changing environmental drivers, and trait variation and their effects on demographic processes and interactions. Since interactions between individuals always have an important spatial component, data generally need to be spatially explicit and site-specific rather than averaged. This list calls for strategies to reduce the complexity and thus also the data need of IBMs that typically underlie the CVA approach (such strategies are discussed above in *Individual-based modeling*). Clearly, which specific data are needed for model construction and parametrization also depends on the specific study system, the questions asked, and the hypotheses that are tested. For more theoretical investigations, missing data can be replaced by scenarios and assumptions that are varied systematically to provide principle insights into possible coviability-enhancing mechanisms. In case of our example (Figs. 3, 4), the model was parameterized to represent a specific grassland community, but to evaluate the role of different management measures for critical biodiversity loss, we systematically varied theoretical scenarios of seed input and mowing frequency (compare Crawford et al. 2019 for theoretical studies on the role of ITV for coexistence). Insights from such theoretical CVA

studies can then inspire new empirical research and experiments. In either case, CVA calls for a close interaction of empirical studies, experiments, and models (Jeltsch et al. 2013b).

The resulting large volumes of data from multiple sources call for novel techniques tailored to the discovery of complex patterns in high-dimensional data (Kelling et al. 2009), including statistically reinforced machine learning approaches (Ryo and Rillig 2017). This would also allow for identifying nonlinear dynamics and thresholds, for example, those related to Allee effects or the disruption of spatial dynamics such as source-sink or metapopulation and metacommunity dynamics.

CONCLUSIONS

The Anthropocene, as a period of unprecedented change and in particular habitat loss and fragmentation, calls for biodiversity concepts and theory that go beyond the idea of long-term coexistence. We here introduce CVA as a complementing approach focusing on the plethora of species that are less abundant and often show high local turnover. Through a cross-level approach that links individuals, small populations, and communities, the focus is shifted toward the temporary local (co)viability of species in a community context under nonstationary conditions. This approach requires not only a stronger investment in stochastic cross-level community models that consider relevant variability at the individual level but also an enhanced effort to integrate multidimensional, spatiotemporal data from multiple sources with novel data analysis techniques.

While CVA has the potential to enhance biodiversity theory by revealing coviability-enhancing mechanisms that are not yet covered by coexistence studies, it also can be more directly linked to specific and clearly defined scenarios, applications, and management. Therefore, this approach can help make modern biodiversity theory more predictive and relevant for applications.

ACKNOWLEDGMENTS

This work was supported by the Deutsche Forschungsgemeinschaft in the framework of the BioMove Research Training Group (DFG-GRK 2118/1). We

thank Uta Berger, Stephanie Kramer-Schadt, and Viktoriia Radchuk for helpful comments. We are further grateful for the comments of two anonymous reviewers, which greatly helped to improve the manuscript.

LITERATURE CITED

- Adler, P. B., and J. M. Drake. 2008. Environmental variation, stochastic extinction, and competitive coexistence. *American Naturalist* 172:E186–E195.
- Adler, P. B., J. Hillerislambers, and J. M. Levine. 2007. A niche for neutrality. *Ecology Letters* 10:95–104.
- Barabás, G., and R. D’Andrea. 2016. The effect of intraspecific variation and heritability on community pattern and robustness. *Ecology Letters* 19:977–986.
- Barabás, G., R. D’Andrea, and S. M. Stump. 2018. Chesson’s coexistence theory. *Ecological Monographs* 88:277–303.
- Berg, S., A. Pimenov, C. Palmer, M. Emmerson, and T. Jonsson. 2015. Ecological communities are vulnerable to realistic extinction sequences. *Oikos* 124:486–496.
- Berger, U., C. Piou, K. Schiffers, and V. Grimm. 2008. Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. *Perspectives in Plant Ecology, Evolution and Systematics* 9:121–135.
- Bergholz, K., F. May, I. Giladi, M. Ristow, Y. Ziv, and F. Jeltsch. 2017. Environmental heterogeneity drives fine-scale species assembly and functional diversity of annual plants in a semi-arid environment. *Perspectives in Plant Ecology, Evolution and Systematics* 24:138–146.
- Black, A. J., and A. J. McKane. 2012. Stochastic formulation of ecological models and their applications. *Trends in Ecology and Evolution* 27:337–345.
- Boettiger, C. 2018. From noise to knowledge: How randomness generates novel phenomena and reveals information. *Ecology Letters* 21:1255–1267.
- Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, and M. Novak. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* 26:183–192.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* 60:849–872.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481–506.
- Buchmann, C. M., F. M. Schurr, R. Nathan, and F. Jeltsch. 2011. An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. *Oikos* 120:106–118.
- Buchmann, C. M., F. M. Schurr, R. Nathan, and F. Jeltsch. 2012. Movement upscaled – the importance of individual foraging movement for community response to habitat loss. *Ecography* 35:436–445.
- Buchmann, C. M., F. M. Schurr, R. Nathan, and F. Jeltsch. 2013. Habitat loss and fragmentation affecting mammal and bird communities – the role of interspecific competition and individual space use. *Ecological Informatics* 14:90–98.
- Bulleri, F., J. F. Bruno, B. R. Silliman, and J. J. Stachowicz. 2016. Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology* 30:70–78.
- Canestrelli, D., R. Bisconti, and C. Carere. 2016. Bolder takes all? The behavioral dimension of biogeography. *Trends in Ecology and Evolution* 31:35–43.
- Cariboni, J., D. Gatelli, R. Liska, and A. Saltelli. 2007. The role of sensitivity analysis in ecological modelling. *Ecological Modelling* 203:167–182.
- Chen, Y., and S. Peng. 2017. Evidence and mapping of extinction debts for global forest-dwelling reptiles, amphibians and mammals. *Scientific Reports* 7:44305.
- Chesson, P. 1994. Multispecies competition in variable environments. *Theoretical Population Biology* 45:227–276.
- Chesson, P. 2000a. General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology* 58:211–237.
- Chesson, P. 2000b. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Chesson, P. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. *Theoretical Population Biology* 64:345–357.
- Chesson, P., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117:923–943.
- Chu, C., and P. B. Adler. 2015. Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecological Monographs* 85:373–392.
- Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: What have we learned so far? *American Naturalist* 163:E1–E23.
- Comita, L. S., S. A. Queenborough, S. J. Murphy, J. L. Eck, K. Xu, M. Krishnadas, N. Beckmann, and Y. Zhu. 2014. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental

- evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology* 102:845–856.
- Connors, M. G., E. L. Hazen, D. P. Costa, and S. A. Shaffer. 2015. Shadowed by scale: subtle behavioral niche partitioning in two sympatric, tropical breeding albatross species. *Movement Ecology* 3:28.
- Costa-Pereira, R., V. H. Rudolf, F. L. Souza, and M. S. Araújo. 2018. Drivers of individual niche variation in coexisting species. *Journal of Animal Ecology* 87:1452–1464.
- Cote, J., T. Brodin, S. Fogarty, and A. Sih. 2017. Non-random dispersal mediates invader impacts on the invertebrate community. *Journal of Animal Ecology* 86:1298–1307.
- Courchamp, F., L. Berec, and J. Gascoigne. 2008. *Allee effects in ecology and conservation*. Oxford University Press, Oxford, UK.
- Crawford, M., F. Jeltsch, F. May, V. Grimm, and U. E. Schlägel. 2019. Intraspecific trait variation increases species diversity in a trait-based grassland model. *Oikos* 128:441–455.
- DeAngelis, D. L., and V. Grimm. 2014. Individual-based models in ecology after four decades. *F1000Prime Reports* 6:39.
- Dewdney, A. J. 2017. *Stochastic communities: a mathematical theory of biodiversity*. CRC Press, Boca Raton, Florida, USA.
- Ebenman, B., and T. Jonsson. 2005. Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology and Evolution* 10:568–575.
- Ellner, S. P., R. E. Snyder, and P. B. Adler. 2016. How to quantify the temporal storage effect using simulations instead of math. *Ecology Letters* 19:1333–1342.
- Ellner, S. P., R. E. Snyder, P. B. Adler, and G. Hooker. 2019. An expanded modern coexistence theory for empirical applications. *Ecology Letters* 22:3–18.
- Fischer, R., et al. 2016. Lessons learned from applying a forest gap model to understand ecosystem and carbon dynamics of complex tropical forests. *Ecological Modelling* 326:124–133.
- Galic, N., L. L. Sullivan, V. Grimm, and V. E. Forbes. 2018. When things don't add up: quantifying impacts of multiple stressors from individual metabolism to ecosystem processing. *Ecology Letters* 21:568–577.
- Giacomini, H. C., D. L. DeAngelis, J. C. Trexler, and M. Petrer Jr. 2013. Trait contributions to fish community assembly emerge from trophic interactions in an individual-based model. *Ecological Modelling* 251:32–43.
- Gravel, D., F. Guichard, and M. E. Hochberg. 2011. Species coexistence in a variable world. *Ecology Letters* 14:828–839.
- Grimm, V., D. Ayllón, and S. F. Railsback. 2017. Next-generation individual-based models integrate biodiversity and ecosystems: Yes we can, and yes we must. *Ecosystems* 20:229–236.
- Grimm, V., and U. Berger. 2016. Structural realism, emergence, and predictions in next-generation ecological modelling: synthesis from a special issue. *Ecological Modelling* 326:177–187.
- Grimm, V., U. Berger, D. L. DeAngelis, J. G. Polhill, J. Giske, and S. F. Railsback. 2010. The ODD protocol: a review and first update. *Ecological Modelling* 221:2760–2768.
- Grimm, V., and S. F. Railsback. 2012. Pattern-oriented modelling: a 'multi-scope' for predictive systems ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:298–310.
- Grimm, V., E. Revilla, J. Groenvelde, S. Kramer-Schadt, M. Schwager, J. Tews, M. C. Wichmann, and F. Jeltsch. 2005. Importance of buffer mechanisms for population viability analysis. *Conservation Biology* 19:578–580.
- Grimm, V., and I. Storch. 2000. Minimum viable population size of capercaillie *Tetrao urogallus*: results from a stochastic model. *Wildlife Biology* 6:219–225.
- Grimm, V., and C. Wissel. 2004. The intrinsic mean time to extinction: a unifying approach to analysing persistence and viability of populations. *Oikos* 105:501–511.
- Grimm, V., et al. 2006. A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* 198:115–126.
- Grimm, V., et al. 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecological Modelling* 280:129–139.
- Hart, S. P., S. J. Schreiber, and J. M. Levine. 2016. How variation between individuals affects species coexistence. *Ecology Letters* 19:825–838.
- Henle, K., S. Sarre, and K. Wiegand. 2004. The role of density regulation in extinction processes and population viability analysis. *Biodiversity and Conservation* 13:9–52.
- Hildenbrandt, H., M. S. Müller, and V. Grimm. 2006. How to detect and visualize extinction thresholds for structured PVA models. *Ecological Modelling* 191:545–550.
- HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* 43:227–248.

- Holyoak, M., M. A. Leibold, and R. D. Holt, editors. 2005. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. *BioScience* 38:682–691.
- Jeltsch, F., K. A. Moloney, M. Schwager, K. Körner, and N. Blaum. 2011. Consequences of correlations between habitat modifications and negative impact of climate change for regional species survival. *Agriculture, Ecosystems and Environment* 145:49–58.
- Jeltsch, F., et al. 2013a. Integrating movement ecology with biodiversity research – exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology* 1:6.
- Jeltsch, F., et al. 2013b. How can we bring together empiricists and modellers in functional biodiversity research? *Basic and Applied Ecology* 14:93–101.
- Jennings, D. E., J. J. Krupa, and J. R. Rohr. 2016. Foraging modality and plasticity in foraging traits determine the strength of competitive interactions among carnivorous plants, spiders and toads. *Journal of Animal Ecology* 85:973–981.
- Kelling, S., W. M. Hochachka, D. Fink, M. Riedewald, R. Caruana, G. Ballard, and G. Hooker. 2009. Data-intensive science: a new paradigm for biodiversity studies. *BioScience* 59:613–620.
- Körner, K., H. Pfestorf, F. May, and F. Jeltsch. 2014. Modelling the effect of belowground herbivory on grassland diversity. *Ecological Modelling* 273:79–85.
- Kramer, A. M., L. Berec, and J. M. Drake. 2018. Allee effects in ecology and evolution. *Journal of Animal Ecology* 87:7–10.
- Lachmuth, S., C. Henrichmann, J. Horn, J. Pagel, and F. M. Schurr. 2018. Neighbourhood effects on plant reproduction: an experimental-analytical framework and its application to the invasive *Senecio inaequidens*. *Journal of Ecology* 106:761–773.
- Lavorel, S., and É. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16:545–556.
- Leibold, M. A., and J. M. Chase. 2017. *Metacommunity ecology*. Volume 59. Princeton University Press, Princeton, New Jersey, USA.
- Letten, A. D., P. J. Ke, and T. Fukami. 2017. Linking modern coexistence theory and contemporary niche theory. *Ecological Monographs* 87:161–177.
- Levins, R. 1966. The strategy of model building in population ecology. *American Scientist* 54:421–431.
- Lin, Y., U. Berger, V. Grimm, and Q. R. Ji. 2012. Differences between symmetric and asymmetric facilitation matter: exploring the interplay between modes of positive and negative plant interactions. *Journal of Ecology* 100:1482–1491.
- Lin, Y., F. Huth, U. Berger, and V. Grimm. 2014. The role of belowground competition and plastic biomass allocation in altering plant mass–density relationships. *Oikos* 123:248–256.
- Logue, J. B., N. Mouquet, H. Peter, H. Hillebrand, and Metacommunity Working Group. 2011. Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology and Evolution* 26:482–491.
- Lurgi, M., B. W. Brook, F. Saltre, and D. A. Fordham. 2015. Modelling range dynamics under global change: Which framework and why? *Methods in Ecology and Evolution* 6:247–256.
- Martin, B. T., T. Jager, R. M. Nisbet, T. G. Preuss, and V. Grimm. 2013. Predicting population dynamics from the properties of individuals: a cross-level test of Dynamic Energy Budget theory. *American Naturalist* 181:506–519.
- May, F., V. Grimm, and F. Jeltsch. 2009. Reversed effects of grazing on plant diversity: the role of below-ground competition and size symmetry. *Oikos* 118:1830–1843.
- Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13:1085–1093.
- McGill, B. J., et al. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10:995–1015.
- Melbourne, B. A., and A. Hastings. 2008. Extinction risk depends strongly on factors contributing to stochasticity. *Nature* 454:100–103.
- Nakano, S., K. D. Fausch, and S. Kitano. 1999. Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charts. *Journal of Animal Ecology* 68:1079–1092.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences USA* 105:19052–19059.
- Ovaskainen, O., and B. Meerson. 2010. Stochastic models of population extinction. *Trends in Ecology and Evolution* 25:643–652.
- Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, and T. Coulson. 2010. Coupled dynamics of body mass and population

- growth in response to environmental change. *Nature* 466:482.
- Patiño, J., R. J. Whittaker, P. A. Borges, J. M. Fernández-Palacios, C. Ah-Peng, M. B. Araújo, and L. de Nascimento. 2017. A roadmap for island biology: 50 fundamental questions after 50 years of The Theory of Island Biogeography. *Journal of Biogeography* 44:963–983.
- Pe'er, G., Y. G. Matsinos, K. Johst, K. W. Franz, C. Turlure, V. Radchuk, and K. Henle. 2013. A protocol for better design, application, and communication of population viability analyses. *Conservation Biology* 27:644–656.
- Petermann, J. S., A. J. Fergus, L. A. Turnbull, and B. Schmid. 2008. Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology* 89:2399–2406.
- Prevedello, J. A., N. J. Gotelli, and J. P. Metzger. 2016. A stochastic model for landscape patterns of biodiversity. *Ecological Monographs* 86:462–479.
- Pringle, R. M., and C. E. Tarnita. 2017. Spatial self-organization of ecosystems: integrating multiple mechanisms of regular-pattern formation. *Annual Review of Entomology* 62:359–377.
- Pruitt, J. N., D. I. Bolnick, A. Sih, N. DiRienzo, and N. Pinter-Wollman. 2016. Behavioural hypervolumes of spider communities predict community performance and disbandment. *Proceedings of the Royal Society of London B: Biological Sciences* 283: 20161409.
- Pruitt, J. N., and A. P. Modlmeier. 2015. Animal personality in a foundation species drives community divergence and collapse in the wild. *Journal of Animal Ecology* 84:1461–1468.
- Railsback, S. F., and B. C. Harvey. 2002. Analysis of habitat-selection rules using an individual-based model. *Ecology* 83:1817–1830.
- Railsback, S. F., and B. C. Harvey. 2013. Trait-mediated trophic interactions: Is foraging theory keeping up? *Trends in Ecology and Evolution* 28:119–125.
- Reeg, J., T. Schad, T. G. Preuss, A. Solga, K. Körner, C. Mihan, and F. Jeltsch. 2017. Modelling direct and indirect effects of herbicides on non-target grassland communities. *Ecological Modelling* 348:44–55.
- Ripa, J., and P. Lundberg. 1996. Noise colour and the risk of population extinctions. *Proceedings of the Royal Society of London B: Biological Sciences* 263:1751–1753.
- Ryo, M., and M. C. Rillig. 2017. Statistically reinforced machine learning for nonlinear patterns and variable interactions. *Ecosphere* 8:e01976.
- Saavedra, S., R. P. Rohr, J. Bascompte, O. Godoy, N. J. Kraft, and J. M. Levine. 2017. A structural approach for understanding multispecies coexistence. *Ecological Monographs* 87:1–17.
- Schibalski, A., K. Körner, M. Maier, F. Jeltsch, and B. Schröder. 2018. Novel model coupling approach for resilience analysis of coastal plant communities. *Ecological Applications* 28:1640–1654.
- Schirmer, A., A. Herde, J. A. Eccard, and M. Dammhahn. 2019. Individuals in space: Personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization. *Oecologia*. <https://doi.org/10.1007/s00442-019-04365-5>
- Schmitt, M. H., K. Stears, and A. M. Shrader. 2016. Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe. *Behavioral Ecology* 27:1073–1077.
- Schmolke, A., P. Thorbek, D. L. DeAngelis, and V. Grimm. 2010. Ecological models supporting environmental decision making: a strategy for the future. *Trends in Ecology and Evolution* 25:479–486.
- Schreiber, S., J. M. Levine, O. Godoy, N. Kraft, and S. Hart. 2018. Does deterministic coexistence theory matter in a finite world? Insights from serpentine annual plants bioRxiv. <https://doi.org/10.1101/290882>
- Schwager, M., K. Johst, and F. Jeltsch. 2006. Does red noise increase or decrease extinction risk? Single extreme events versus series of unfavorable conditions. *American Naturalist* 167:879–888.
- Shoemaker, L. G., and B. A. Melbourne. 2016. Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology* 97:2436–2446.
- Sibly, R. M., V. Grimm, B. T. Martin, A. S. Johnston, K. Kułakowska, C. J. Topping, and D. L. DeAngelis. 2013. Representing the acquisition and use of energy by individuals in agent-based models of animal populations. *Methods in Ecology and Evolution* 4:151–161.
- Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, and V. L. Dantas. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* 18:1406–1419.
- Siepielski, A. M., and M. A. McPeck. 2010. On the evidence for species coexistence: a critique of the coexistence program. *Ecology* 91:3153–3164.
- Singer, A., and K. Frank. 2016. Viability of cyclic populations. *Ecology* 97:3143–3153.
- Spiegel, O., S. T. Leu, C. M. Bull, and A. Sih. 2017. What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters* 20:3–18.
- Start, D., and B. Gilbert. 2017. Predator personality structures prey communities and trophic cascades. *Ecology Letters* 20:366–374.
- Stephan, T., and C. Wissel. 1999. The extinction risk of a population exploiting a resource. *Ecological Modelling* 115:217–225.

- Stillman, R. A., S. F. Railsback, J. Giske, U. T. A. Berger, and V. Grimm. 2014. Making predictions in a changing world: the benefits of individual-based ecology. *BioScience* 65:140–150.
- Teckentrup, L., V. Grimm, S. Kramer-Schadt, and F. Jeltsch. 2018. Community consequences of foraging under fear. *Ecological Modelling* 383:80–90.
- Thiele, J. C., W. Kurth, and V. Grimm. 2014. Facilitating parameter estimation and sensitivity analysis of agent-based models: a cookbook using NetLogo and R. *Journal of Artificial Societies and Social Simulation* 17:11.
- Tredennick, A. T., P. B. Adler, and F. R. Adler. 2017. The relationship between species richness and ecosystem variability is shaped by the mechanism of coexistence. *Ecology Letters* 20:58–968.
- van der Bolt, B., E. H. van Nes, S. Bathiany, M. E. Vollebregt, and M. Scheffer. 2018. Climate reddening increases the chance of critical transitions. *Nature Climate Change* 8:478–484.
- van Gestel, J., F. J. Weissing, O. P. Kuipers, and A. T. Kovács. 2014. Density of founder cells affects spatial pattern formation and cooperation in *Bacillus subtilis* biofilms. *ISME Journal* 8:2069–2079.
- Vellend, M., D. S. Srivastava, K. M. Anderson, C. D. Brown, J. E. Jankowski, E. J. Kleynhans, and I. H. Myers-Smith. 2014. Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos* 123:1420–1430.
- Vincenot, C. E., S. Mazzoleni, and L. Parrott. 2016. Hybrid solutions for the modeling of complex environmental systems. *Frontiers in Environmental Science* 4:53.
- Violle, C., B. J. Enquist, B. J. McGill, L. I. N. Jiang, C. H. Albert, C. Hulshof, and J. Messier. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* 27:244–252.
- Weiss, L., H. Pfestorf, F. May, K. Körner, S. Boch, M. Fischer, J. Müller, D. Prati, S. A. Socher, and F. Jeltsch. 2014. Grazing response patterns indicate isolation of semi-natural European grasslands. *Oikos* 123:599–612.
- Wilensky, U. 1999. NetLogo. Center for Connected Learning and Computer-Based Modeling. Northwestern University, Evanston, Illinois, USA. <http://ccl.northwestern.edu/netlogo/>
- Yitbarek, S., and J. H. Vandermeer. 2017. Reduction of species coexistence through mixing in a spatial competition model. *Theoretical Ecology* 10:443–450.