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Assessing biotope vulnerability to landscape changes

by

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Abstract

Largescale patterns of global land use change are very frequently accompanied by natural habitat loss. To assess the consequences of habitat loss for the remaining natural and semi-natural biotopes, inclusion of cumulative effects at the landscape level is required. The interdisciplinary concept of vulnerability constitutes an appropriate assessment framework at the landscape level, though with few examples of its application for ecological assessments. A comprehensive biotope vulnerability analysis allows identification of areas most affected by landscape change and at the same time with the lowest chances of regeneration.

To this end, a series of ecological indicators were reviewed and developed. They measured spatial attributes of individual biotopes as well as some ecological and conservation characteristics of the respective resident species community. The final vulnerability index combined seven largely independent indicators, which covered exposure, sensitivity and adaptive capacity of biotopes to landscape changes. Results for biotope vulnerability were provided at the regional level. This seems to be an appropriate extent with relevance for spatial planning and designing the distribution of nature reserves.

Using the vulnerability scores calculated for the German federal state of Brandenburg, hot spots and clusters within and across the distinguished types of biotopes were analysed. Biotope types with high dependence on water availability, as well as biotopes of the open landscape containing woody plants (e.g., orchard meadows) are particularly vulnerable to landscape changes. In contrast, the majority of forest biotopes appear to be less vulnerable. Despite the appeal of such generalised statements for some biotope types, the distribution of values suggests that conservation measures for the majority of biotopes should be designed specifically for individual sites. Taken together, size, shape and spatial context of individual biotopes often had a dominant influence on the vulnerability score.

The implementation of biotope vulnerability analysis at the regional level indicated that large biotope datasets can be evaluated with high level of detail using geoinformatics. Drawing on previous work in landscape spatial analysis, the reproducible approach relies on transparent calculations of quantitative and qualitative indicators. At the same time, it provides a synoptic overview and information on the individual biotopes. It is expected to be most useful for nature conservation in combination with an understanding of population, species, and community attributes known for specific sites. The biotope vulnerability analysis facilitates a foresighted assessment of different land uses, aiding in identifying options to slow habitat loss to sustainable levels. It can also be incorporated into planning of restoration measures, guiding efforts to remedy ecological damage. Restoration of any specific site could yield synergies with the conservation objectives of other sites, through enhancing the habitat network or buffering against future landscape change.

Biotope vulnerability analysis could be developed in line with other important ecological concepts, such as resilience and adaptability, further extending the broad thematic scope of the vulnerability concept. Vulnerability can increasingly serve as a common framework for the interdisciplinary research necessary to solve major societal challenges.

Zusammenfassung

Weltweit wurden in den vergangenen Jahrzehnten massive Veränderungen in der Landnutzung vorgenommen. Diese gingen meistens mit dem Verlust natürlicher Habitate einher. Um die Folgen auf die verbliebenen naturnahen Biotope zu bewerten, sind Analyseinstrumente notwendig, die neben einzelnen Flächen auch kumulative Effekte auf der Landschaftsebene einbeziehen. Das interdisziplinäre Konzept der Vulnerabilität kann einem solchen Analyseinstrument den Rahmen bieten. Bisher wurde es kaum für die Bewertung ökologischer Systeme herangezogen. Dabei kann eine flächendeckende Biotop-Vulnerabilitätsanalyse jene Gebiete identifizieren, die vom Landschaftswandel am stärksten betroffen sind und die gleichzeitig die geringsten Erholungsaussichten aufweisen.

Dazu wurde eine Reihe ökologischer Indikatoren gesichtet und entwickelt, um die drei Vulnerabilitätsgrößen Exposition, Sensitivität und Anpassungskapazität abzudecken. Dabei wurden die Lagebeziehungen einzelner Biotope sowie die Eigenschaften der jeweils ansässigen Artengemeinschaft ausgewertet. Der errechnete Index kombiniert sieben voneinander weitestgehend unabhängige Indikatoren und stellt eine Übersicht der Biotop-Vulnerabilität dar.

Liegt eine flächendeckende Vulnerabilitätsbewertung vor, können räumliche Häufungen von hohen Werten sowie die Verteilung der besonders hohen und besonders niedrigen Werte über die Biotoptypen hinweg analysiert werden. Dies erscheint besonders sinnvoll für Flächengrößen mit Relevanz für die Raumplanung und die Verteilung der Naturschutzflächen. Es stellte sich heraus, dass in der Planungsregion Brandenburg vor allem die Biotope mit hoher Abhängigkeit von der Wasserverfügbarkeit, sowie die Gehölze enthaltenden Offenlandbiotope (z.B. Streuobstwiesen) besonders vulnerabel gegenüber Landschaftsveränderungen sind. Im Gegensatz dazu erscheint die Mehrheit der Waldbiotope weniger verwundbar zu sein. Trotz der Möglichkeit zur Ableitung solcher verallgemeinerten Aussagen für einige Biotoptypen legt die Werteverteilung nahe, Naturschutzmaßnahmen

mehrheitlich spezifisch für einzelne Flächen zu entwerfen. Größe, Form und räumlicher Kontext einzelner Biotopflächen üben zusammengenommen häufig einen dominanten Einfluss auf die Vulnerabilität gegenüber Landschaftsveränderungen aus.

Die Demonstration der Biotop-Vulnerabilitätsanalyse auf regionaler Ebene zeigt, dass mit Methoden der Geoinformatik auch große Biotop-Datensätze detailliert ausgewertet werden können. Die damit erzielte naturschutzfachliche Analyse basiert auf transparent berechneten qualitativen und quantitativen Indikatoren und ist damit vollständig nachvollziehbar. Sie bietet gleichzeitig einen großräumigen Überblick sowie Informationen zu den einzelnen Biotopflächen. Mit der Vulnerabilitätsanalyse von Biotopen wird die vorausschauende Abwägung zwischen verschiedenen Landnutzungen erleichtert. Dies kann dazu beitragen, dass der Habitatverlust in Zukunft auf ein nachhaltigeres Maß gebremst wird. Auch kann eine solche Biotopbewertung in die Planung von Renaturierungsmaßnahmen einfließen, um ökologische Schäden zunächst dort zu beheben, wo große Synergieeffekte im Biotopverbund und mit anderen Naturschutzzielen zu erwarten sind.

Die Biotop-Vulnerabilitätsanalyse konnte im Einklang mit wichtigen ökologischen Konzepten wie Resilienz und Anpassungsfähigkeit entwickelt werden. Sie erweitert damit den ohnehin breiten thematischen Anwendungsbereich des Vulnerabilitätskonzepts. Somit kann Vulnerabilität zunehmend als Brückenkonzept dienen und der zur Lösung der großen gesellschaftlichen Herausforderungen notwendigen interdisziplinären Forschung einen gemeinsamen Rahmen geben.

Contents

1. Introduction

1.1. Background

Land is a limited resource. Globally, the competition for land has led to massive conversion of natural areas in the recent decades (Ellis and Ramankutty, 2008; Foley et al., 2005). The resulting loss, fragmentation, and degradation of habitats are the main causes of the extinction of terrestrial species (Collinge, 2001). Agriculture is the major driver of land conversion, followed by infrastructure expansion (Alkemade et al., 2009) with rates of environmental change vastly outpacing technological, policy, and social responses, leading to unsustainable development on a global level (ICSU, 2010). Recently, this has been confirmed in particular for biodiversity: more species are threatened today by global extinction than ever before (IPBES, 2019). Extinction processes following land use changes are complex and may occur with large time lags (Jackson and Sax, 2010). Thus, *ecological surprises* occur repeatedly (King, 1995) with unintended and even unpredictable impacts. The resulting damage often does not only negatively affect nature but humans as well.

Costly restoration efforts may substantially recover biodiversity and ecosystem functioning but hardly are able to restore the composition of flora and fauna prior to conversion (Barral et al., 2015). To achieve sustainable use of ecosystems, it is therefore necessary to move from remedies for negative environmental impacts towards actions informed by the precautionary principle. One useful concept to describe and anticipate the damage potential of land use change for any considered ecosystem is vulnerability. Vulnerability analysis aims to evaluate the weaknesses of a system to particular stressors through identification of potential problematic impacts that to be planned for and addressed with appropriate management (Wisner et al., 2004). It has been applied to analyse hazards, economic crisis or technological failures with potential fatal consequences for the affected human systems, and has recently emerged as a concept for the analysis of natural systems (Weißhuhn et al., 2018). In most contexts a spatially explicit approach has long been perceived as useful for vulnerability assessments (Cutter, 1996).

Given that funds for nature conservation and ecosystem management are often limited, only a selection of measures is generally feasible. Objective indicators can guide in their selection. Further, assessments that can provide management assistance *ex ante* are even more effective (Helming et al., 2011; Watts et al., 2008). Areas assessed as highly vulnerable would need the most protection from the stressor or maintenance to cope with it. The development of the vulnerability concept into a practicable ecological assessment tool would advance its integration into applied nature conservation work.

With increasing transformation of landscapes into a mosaic of semi-natural and anthropogenic formed parts, cumulative effects gain importance that cannot be derived from a single site's assessment. Furthermore, considering the rapid global decline of natural ecosystems without fragmentation or other human disturbance, semi-natural or fully managed agricultural, forest and urban ecosystems become major arenas for conservation in addition to nature reserves. A landscape ecological approach is appropriate to guide the analysis of such mosaic landscapes consisting of a complex of habitats. Therefore, vulnerability analysis should be conducted on the landscape or even higher level, requiring i) data covering large areas, ii) analytical methods allowing a proper aggregation of information, and iii) powerful data processing capabilities and suitable software environments to handle large datasets with high computational efficiency.

The source of information to describe species communities and their habitats across areas of sizes relevant for landscape planning are exhaustive biotope maps. The term *biotope* is almost synonymous with the more common term *habitat*. However, it emphasises that the biocoenosis is in the focus instead of a population. Biotope maps can be considered as inventories of nature. They are usually derived from stable correlations between spectral information acquired through remote sensing and ground truth field data from biotope cartographers. At least for terrestrial systems, the resulting biotope maps provide direct information about plant species communities, with patches of a single biotope type as the smallest spatial unit. Additional information can typically be derived indirectly with regard to core animal species groups, land use, water balance, nutrient availability, and protection status of species and habitat types.

A means for deriving aggregated quantitative information from geodata is to use landscape metrics (McGarigal, 2014), which provide abstractions of landscape elements, like frequency, heterogeneity, and connectivity (Antrop and Van Eetvelde, 2017). Beyond their individual spatial attributes, biotope patches are characterised by class attributes reflecting their biotope type, which also should be covered by an indicator set for analysing biotope vulnerability. At the level of management or policy, highly aggregated measurements are usually preferred to detailed or complex ones, accepting the inherent information loss. Summarising information by creating indexes is a common aggregation procedure. Vulnerability indexes based on quantitative geodata have been reported in various fields (e.g., Andrade and Szlafsztein, 2018; Inostroza et al., 2016; Schmidtlein et al., 2008), particularly in research on the vulnerability of natural systems (e.g., Esperon-Rodriguez and Barradas, 2015; Landguth et al., 2014; Pei et al., 2015).

To organise and process geodata requires an appropriate geospatial information system (GIS). For the thesis, *ArcGIS 10* (ESRI Inc., 2012-2019) was the principal software used. In a few cases of processing instabilities and insufficient computational efficiency, the work was supplemented by an alternative GIS software, *FME* (Safe Software, 2017). Any scientific analysis building on geodata would profit from recorded routines to keep each analytical step transparent and reproducible, i.e., the use of scripts is recommendable. A software is needed that can handle large datasets with compatible in- and output formats, can be programmed flexibly, and is well documented. In particular, the handling of raster data and vector data is fundamentally different and biotope maps often are mapped in vector format. Unfortunately, the analytical tools of *ArcGIS 10* often do not fulfil these requirements nor were they sufficient for all analytical questions arising with the biotope vulnerability analysis. Therefore, of the several freely available computer programmes, the following have been utilized to facilitate and automate the analysis of geodata in vector format: *Patch Analyst* (Rempel et al., 2012), *vLate* (Lang and Tiede, 2003), *GME* (Beyer, 2012), and *R* (R Core Team, 2018).

1.2. Overarching objective and research questions

An initial point for setting up the thesis was the idea of conceptually linking vulnerability research with ecology and ecosystem science, to potentially yield new insights and new fields of application. Working on theoretical progress from the beginning was combined with the goal of methodological improvements in vulnerability analysis. The developed methods then can be used to explore benefits for landscape planning and ecosystem management. In striving for the applicability of the concept, the thesis aims to develop an easily replicable vulnerability index, which is suitable for an analysis at the landscape level as well as at the regional level.

To examine whether the concept of biotope vulnerability can actually function as an analytical tool in science and practice, the thesis seeks to answer the following four research questions:

1. Is the interdisciplinary vulnerability concept in coherence with established ecological concepts, like resilience and adaptability? Are the three constituting vulnerability elements ‘exposure’, ‘sensitivity’, and ‘adaptive capacity’ sufficiently described to operationalize the concept for the analysis of natural systems?
2. Which established ecological indicators are suitable and which need to be newly developed to addresss biotope vulnerability to landscape change?
3. Which set of largely independent indicators is suitable to be included in a biotope vulnerability index and in which way should they be combined?
4. Which patterns appear in the vulnerability score distribution and which conservation implications at the regional level can be derived from them?

1.3. Overview of manuscripts and author contribution

The thesis combines three manuscripts, two of which have already been published in peer-reviewed journals while the third has been submitted. Both published manuscripts are open access articles distributed under the terms of the Creative Commons license (CC BY 4.0). This license permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. The third manuscript has been submitted to an open access journal and therefore, the thesis can be published open access without compromise.

The study of the vulnerability of biotopes to landscape changes started with a review of the state-of-the-art in vulnerability research. Particular focus was given to the vulnerability of natural systems, i.e., ecological systems or ecosystems (***manuscript 1***). This literature review provided the frame for developing and examining a biotope vulnerability index for a study area of landscape level. The methodological foundations for indicator selection, data processing, and analytical procedures were laid (***manuscript 2***). To cover biotope data at the regional level, the vulnerability analysis was streamlined and scaled-up. Then, the appearing vulnerability patterns were analysed (***manuscript 3***).

The **first manuscript** reviews the existing ecosystem vulnerability research and provides a summary of the ecosystem types covered and the disciplinary backgrounds of the studies. Based on the reviewed literature it aims to define ecosystem vulnerability in coherence with the ecological concepts of resilience and adaptability. Further, the systematic review was intended to raise awareness for the analysis of natural systems within the vulnerability research community. On the other hand, ecosystem vulnerability assessment should also inform nature conservation policy and ecosystem management. Thus, the Journal *Environmental Management* has been chosen for publication, as it presents academic work to researchers and practitioners. The journal focuses on the balance between use and conservation of natural resources irrespective of traditional disciplinary boundaries, which makes the interdisciplinary vulnerability concept perfectly fitting to their readership. The review article is cited as:

Weißhuhn, P; Müller, F; Wiggering, H (2018). Ecosystem Vulnerability Review: Proposal of an Interdisciplinary Ecosystem Assessment Approach. ***Environmental Management, 61*****(6), 904-915. doi: 10.1007/s00267-018-1023-8**

The **second manuscript** has the primary objective of developing and testing a set of indicators to integrate information about biotope vulnerability to landscape changes. Following the vulnerability framework, qualitative and quantitative indicators were combinded in a single index. The biosphere reserve *Schorfheide-Chorin* in the northeast of Germany served as a test case. Size and biotope characteristics of the biosphere reserve were favourable. It covered a diversity of patch arrangements in a compact shape that reduces boundary effects. Moreover, the number of biotopes was not too computationally expensive, which would hamper experimentation with different analytical and processing alternatives. As the manuscript is all about indicator selection, statistical testing of the calculated indicator values, and indexing procedures, the journal *Ecological Indicators* was very well suited. The research article is cited as:

Weißhuhn, P. (2019). Indexing the vulnerability of biotopes to landscape changes. ***Ecological Indicators, 102*****, 316-327. doi: 10.1016/j.ecolind.2019.02.052**

The **third manuscript** follows on seamlessly from the work presented in the second manuscript. The developed indicators and indexing procedures were enhanced for application to a much larger data set of all terrestrial, natural and semi-natural biotopes of the German federal state of Brandenburg. The resulting distribution of vulnerability scores was explored for spatial clusters (hot spot analysis) and thematic clusters (biotope group cluster analysis). Agglomerations of high biotope vulnerability and particularly vulnerable biotope groups could be identified, suggesting priority conservation cases. The biotope vulnerability analysis combined progress in ecologic theory with implications for conservation at the regional level. The manuscript therefore was submitted to *Global Ecology and Conservation*, which aims to publish research advancing both theory and practice from regional to global scales. It already received reviewer comments and is in preparation for resubmission to the same journal. Meanwhile, the manuscript is cited as:

Weißhuhn, P. (submitted). Regional vulnerability assessment of terrestrial biotopes regarding landscape change. ***Global Ecology and Conservation*****, x, xxx-xxx.**

The doctoral candidate is the principal author of all three manuscripts. For manuscript 1, he conducted the literature review and substantially contributed to the analysis and interpretation of results. Conception of the review and writing of the manuscript were predominantly done by him.

Manuscripts 2 and 3 were written by the doctoral candidate as the sole author, with support received gratefully and stated in the respective acknowledgment sections.

2. Manuscripts

2.1. Ecosystem vulnerability review: proposal of an interdisciplinary ecosystem assessment approach

Abstract

To safeguard the sustainable use of ecosystems and their services, early detection of potentially damaging changes in functional capabilities is needed. To support a proper ecosystem management, the analysis of an ecosystem's vulnerability provide information on its weaknesses as well as on its capacity to recover after suffering an impact. However, the application of the vulnerability concept to ecosystems is still an emerging topic. After providing background on the vulnerability concept, we summarize existing ecosystem vulnerability research on the basis of a systematic literature review with a special focus on ecosystem type, disciplinary background, and more detailed definition of the ecosystem vulnerability components. Using the Web of Science™ Core Collection, we overviewed the literature from 1991 onwards but used the 5 years from 2011 to 2015 for an in-depth analysis, including 129 articles. We found that ecosystem vulnerability analysis has been applied most notably in conservation biology, climate change research, and ecological risk assessments, pinpointing a limited spreading across the environmental sciences. It occurred primarily within marine and freshwater ecosystems. To avoid confusion, we recommend using the unambiguous term ecosystem vulnerability rather than ecological, environmental, population, or community vulnerability. Further, common ground has been identified, on which to define the ecosystem vulnerability components exposure, sensitivity, and adaptive capacity. We propose a framework for ecosystem assessments that coherently connects the concepts of vulnerability, resilience, and adaptability as different ecosystem responses. A short outlook on the possible operationalization of the concept by ecosystem vulnerability indices, and a conclusion section complete the review.

Keywords

environmental vulnerability, ecological vulnerability, ecosystem response, interdisciplinarity, resilience, adaptability

Introduction

Ecosystem services sustain and fulfill several demands of human life but rely on ecosystem processes and associated species (Daily 1997). A sustainable use of ecosystems implies a balance between protection and exploitation. Because ecosystems are defined by a close functional interconnection between their constituting abiotic and biotic elements, any use will change their conditions. Therefore, a condensed measure to assess the potential damage to ecosystems' structures and functionalities, as well as their capacities to recover, *ahead* of the change would help achieve such a balance.

A vulnerability analysis is an adequate method for understanding the weaknesses of a system and is strictly orientated towards the threat that potentially would harm the system (Wisner et al. 2004). In general, vulnerability is defined as the potential for loss (Adger 2006; Brooks 2003; Füssel 2007; IPCC 2014), but rarely has been transferred for application to ecosystems. An *ecosystem* vulnerability assessment could be used to estimate the inability of an ecosystem to tolerate stressors over time and space (Williams and Kapustka 2000). Those vulnerable ecosystems then would need a proper management to preserve their characteristics. Any kind of ecosystem management is a result of governance processes responding to ecological, socio-cultural and economic drivers (Simoncini 2011) and aims to maintain desirable levels of ecosystem function in a cost-effective and socially responsible manner (Brussard et al. 1998). It is called ecosystem-based management because it recognizes all interactions within an ecosystem, including humans (Leslie and McLeod 2007). Slocombe (1993) summarizes that ecosystem-based management is a matter of redefining management units and building on scientific knowledge on the biophysical resource use limits. Available measures for ecosystem management are to reduce local and regional stressors, designate protected areas as refuges (Okey et al. 2015), increase ecosystem resilience (e.g. Anthony et al. 2015), or involve the implementation of other conservation strategies specific to each ecoregion (cf. Watson et al. 2013).

To communicate the results of vulnerability assessments to other researchers, policy-makers, and the community at large, it is important to map vulnerability distributions (Eakin and Luers 2006), and therefore to be spatially explicit. The mapping could indicate ecosystem vulnerability hotspots that may require specific intervention of protection and maintenance (Aretano et al. 2015; Zurlini et al. 1999). So far, there are limited successful ecosystem vulnerability studies focusing on the management of natural areas or conservation (Ventura and Lana 2014), but socio-environmental studies have been undertaken longer (Villa and McLeod 2002).

Next to its application benefit for ecosystem management purposes, the concept also bears potentials for theoretical progress. To further shape the definition of ecosystem vulnerability and to investigate its relation to other theoretical concepts from ecology, will contribute to develop vulnerability towards a boundary object (cf. Collet 2012). Boundary objects could steer interdisciplinary research that seems indispensable to tackle the – typically complex – research questions related to ecosystem management or socio-ecological systems.

This review is structured according to four main objectives: i) to provide background on the vulnerability concept; ii) to summarize existing ecosystem vulnerability research with a special focus on ecosystem type, disciplinary background, and definition of the ecosystem vulnerability components; iii) to place ecosystem vulnerability in coherence with the ecological concepts of resilience and adaptability, and iv) to give a short overview on ecosystem vulnerability assessment methods ready for application.

Background: the vulnerability concept

The idea of vulnerability is based on research on natural hazards affecting human structures and communities (Janssen et al. 2006). This introduced an objectivist understanding of risk to the concept, which has been revised by the argument of risk as a matter of perception (Bürkner 2010; Weichselgartner 2001). For the analysis of social systems, the emphasis on a system's weakness is prone to criticism, as different social groups could be stigmatized, for example regarding gender, income, educational level or ethnicity (Bürkner 2010; Collet 2012). In the vulnerability of social-environmental systems, Eakin and Luers (2006) traced down the scientific roots to the three research fields of risk-hazard, political economy/political ecology, and ecological resilience. Two major antecedents for a shared definition of vulnerability are the risk-hazard and the pressure-and-release model (cf. Turner II et al. 2003). Risk-hazard models emphasize exposure and sensitivity to perturbations and stressors forming the impact of the hazard; and pressure-and-release models emphasize distinctions in risk related to different vulnerabilities of different exposure units, while both underemphasize the system's ability to cope with the disaster and learning from it (ibid.). This lead to the idea of adaptive capacity, which conceptually could link vulnerability and resilience research, and turned vulnerability assessments to the purpose of identifying feasible adaptation strategies (Engle 2011; Smit and Wandel 2006).

Interdisciplinary vulnerability concepts mainly developed with climate change research and its increasingly broad applications (e.g. IPCC 2007; IPCC 2014). Related to this, global environmental change research also has seen increased attention to the concept of vulnerability (Polsky et al. 2007; Schröter et al. 2005). A general uniform definition has been lacking for a long time (Brooks 2003) because several scientific disciplines have emphasized and advanced different scientific aspects of vulnerability research (Schluchter 2002). Nevertheless, an overarching definition would describe vulnerability as a potential for loss (Adger 2006; Brooks 2003; Füssel 2007; IPCC 2014). Further, several systematic attempts to establish an interdisciplinary methodological framework for vulnerability research outlined vulnerability as a function of exposure, sensitivity, and adaptive capacity (Frazier et al. 2014; Füssel 2007; Turner II et al. 2003). According to the state of the art, we further define vulnerability by its three constituting elements as follows:

- exposure describes the probability of a hazard (also: disturbance or stress) occurring;
- sensitivity is a measure of susceptibility to this hazard; and
- adaptive capacity characterizes the ability to cope with the hazard and its consequences.

In this context, we suggest vulnerability as a boundary object, as it enables interdisciplinary scientific exchange without abandoning a specialist's inventory of methods (Collet 2012). Typically, a vulnerability analysis integrates different methods from across several research traditions (Polsky et al. 2007).

A more recent and specific notion of vulnerability, but one consistent with the general framework, is ecosystem vulnerability. In this perspective an environmental system moves from a traditional view as a source of hazard that influences human systems to a responding system influenced by natural and anthropogenic drivers of change. Birkmann and Wisner (2006) called this a biocentric view of ecological vulnerability, in contrast to an anthropocentric view. It encompasses the analysis of the fragility and susceptibility of ecosystem components or functions themselves. A very prominent initiative for such an approach is the Environmental Vulnerability Index developed by the South Pacific Applied Geoscience Commission in cooperation with the United Nations Environment Program. This index is based on 50 indicators for estimating a general vulnerability of the environment to future shocks, calculated for each country on the globe (Kaly et al. 2004).

Methods

This review analyzes the emerging concept of ecosystem vulnerability and is based on a literature search in the *Web of Science™ Core Collection* (enabling the following databases: SCI-EXPANDED, SSCI, CPCI-S, CPCI-SSH, BKCI-S, and BKCI-SSH). First, a title search provided descriptive overview on the development of the different terms connected with the vulnerability of natural systems (this section).

Second, the main search covered the title, abstract, author keywords and keywords plus® and provided the literature sample for the structured review (sections 3.2 and 3.3).

To support a conceptual analysis, the literature search was designed to focus on scientific articles that explicitly refer to the vulnerability concept, recognizing this would exclude literature on “resilience”, “risk”, “damage”, “degradation”, or “change” that may be related to the discussion on ecosystem vulnerability. To cover the broad disciplinary roots of a vulnerability analysis of natural systems, the search included the terms “ecosystem vulnerability”, “ecological vulnerability” and “environmental vulnerability”. We aimed to cover vulnerability research on several ecological scales and therefore considered the vulnerability of populations, communities and habitats. Unfortunately, the term “community vulnerability” turned out to be unsuitable, as very few related to ecological communities, with the others relating to human communities. Therefore, we only added “population vulnerability” and “habitat vulnerability” to the query, which connected the exact terms with OR and was last updated on June 22nd, 2016.

For overviewing the usage of the vulnerability concept applied to ecosystems research, we started to search the publication title over 25 years, from the beginning of 1991 to the end of 2015, and itemized the different terms (see figure 1). Note that articles including socio-ecological vulnerability were also covered, but these comprised only 5% of the results returned due to the term “ecological vulnerability”.

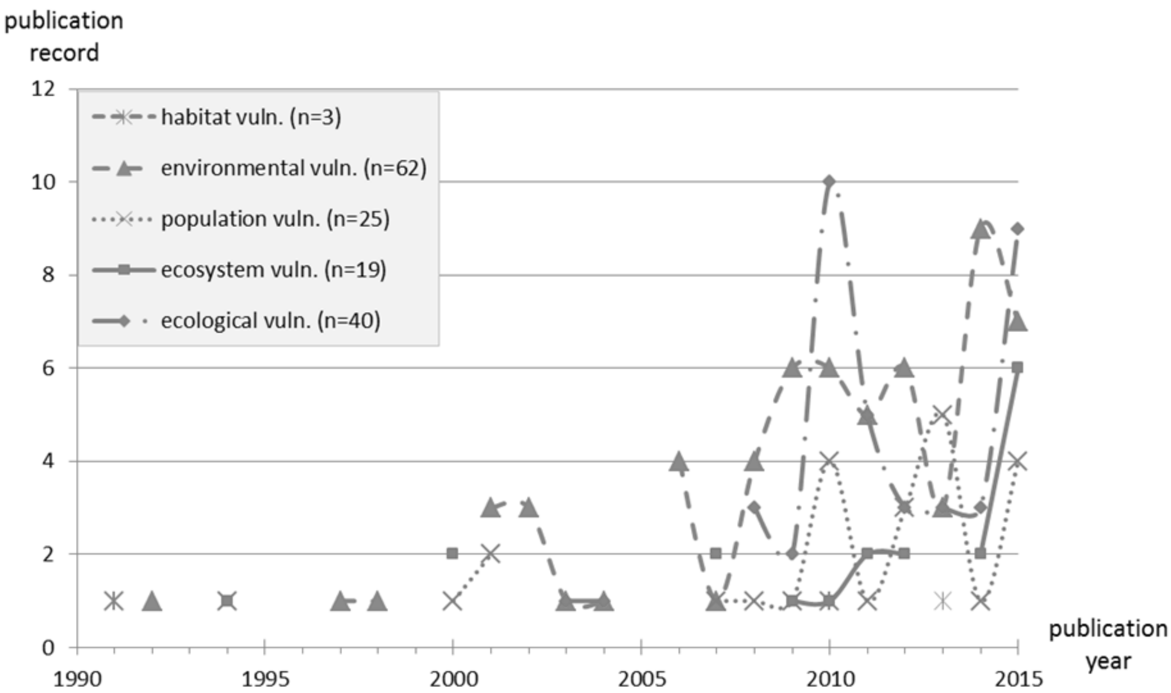

Figure 1: A temporal overview of the use of different vulnerability terms in the publication title (n=149). All terms conceptualize natural systems as more or less vulnerable.

In our sample of 149 papers ranging from 1991 to 2015, the term habitat vulnerability occurred earliest, but with only 3 articles; it appears to be rather un-established. In the nineties, the terms environmental and ecosystem vulnerability arose. While environmental vulnerability gained remarkable attention from 2009 onwards and exhibited the most applications over the entire period, the use of the term ecosystem vulnerability only caught on very recently. In our sample, the term ecological vulnerability occurred late, first in 2003, but its use increased sharply in 2010, reaching a total maximum of 10 articles in a year. The term population vulnerability varied between 5 and only 1 title mention per year; therefore, this term seems to not play a major role in this research field, yet.

For the main search, the same five vulnerability terms were applied to TOPIC. To cover the period of increased interest in the concept from 2010 onwards (indicated by the annual number of publications constantly exceeding 10, see Figure 1) and to reach an adequate number of articles for in-depth analysis, we limited our literature to the five years from 2011 to end of 2015 while excluding all document types other than articles and reviews in English. The resulting 238 articles we filtered by abstract reading to sort out any artifact items and articles not related to the vulnerability of natural systems (e.g., public health vulnerability). During this process, we found the term "population vulnerability" repeatedly used to refer to human populations instead of natural populations (species or species assemblages) and "environmental vulnerability" used, to a minor extent, to refer to psychological phenomena. Furthermore, we identified some articles using "environmental vulnerability" as a combination of both biophysical and socioeconomic factors that affect a human-natural system. Because such an understanding of environmental vulnerability does not focus on ecosystems as the responding system (cf. section 2), these were also omitted. Overall, **129** articles were reviewed. Additionally, for the sections 5, 6, and 7 other thematic leading publications (e.g., published before 2011 or not in the Core Collection) were considered to give a comprehensive picture.

For the analysis of the investigated ecosystem type and disciplinary roots (cf. section 3.2), we decided to cite references exemplarily if the number of articles belonging to one group was too high to cite all of them. To safeguard reproducibility, we cited the top three articles ranked by the SJR index (SCImago 2007) from their publishing journal in the publication year of the article, and as a secondary criteria, we selected the most recent article. To give a diverse picture, we did not choose two articles from the same journal.

Vulnerability of different ecosystems and in different disciplines

To reach a profound understanding of the concept of ecosystem vulnerability, which is necessary to provide a so far lacking comprehensive and in-depth definition, the disciplinary roots may reveal characteristic orientations. A too narrow scope in the major application areas (in the sense of the natural systems under investigation) could have biased the conceptual development or identify gaps in ecosystem vulnerability research. Therefore, we also paid attention to the type of ecosystem that has been assessed.

More than half of the 129 reviewed ecosystem vulnerability studies apply to a certain type of ecosystem (for an overview, see table 1). These 72 articles exhibited a major focus on water-related ecosystems: marine and coastal ecosystems (including mangroves) accounted for 30 papers (e.g. Anthony et al. 2015; Guizien et al. 2014; Ifrim et al. 2011) and freshwater ecosystems (including rivers, lakes, and wetlands), accounted for 22 papers (e.g. Alric et al. 2013; Landguth et al. 2014; Macary et al. 2014). Another focus was also given to forest ecosystems (e.g. Hwang et al. 2014; McWethy et al. 2013; Zolkos et al. 2015). Only three articles dealt with grassland ecosystems (Lopez-Poma et al. 2014; Qiao et al. 2013; Ursino 2014), and only one was concerned with agricultural ecosystems (Couto et al. 2015). Additional two articles were concerned with desert ecosystems (Cruz-Elizalde et al. 2014; Munson et al. 2015) and one with an oasis (Pei et al. 2015). The other 57 articles involved vulnerability analysis at a different kind of spatial scale, for example, administrative regions, river-basins, or climatic zones.

Table 1: Focus ecosystems of the reviewed vulnerability studies (n=129)

Focus ecosystem	**Number of articles**
Marine and coastal ecosystems	30
Freshwater ecosystems	22
Forest ecosystems	13
Grassland and agricultural	4
Desert and oasis ecosystems	3
No particular ecosystem mentioned	*57*

Observing the (explicitly stated) disciplinary origin of the articles was the task to identify the main scientific communities that promote the concept of ecosystem vulnerability. Note that each article potentially belonged to more than one research field.

A total of 54 of the reviewed articles were strongly linked to **conservation ecology** (≈42%). Of these, 29 articles addressed a wide range of particular species: ten articles focused on aquatic species (e.g. Ateweberhan et al. 2011; Guizien et al. 2014;

Landguth et al. 2014), nine on plant species (e.g. Arianoutsou et al. 2013; Gonzalez-Moreno et al. 2013; Kalusova et al. 2013), five on bird or bat species (e.g. Erickson et al. 2015; Furness et al. 2012; Tranquilla et al. 2013) and five on other animal species (e.g. Drever et al. 2012; Dufresnes and Perrin 2015; Lacasella et al. 2015). Furthermore, 15 addressed whole habitats (e.g. Gauthier et al. 2013; Giakoumi et al. 2015; Kalusova et al. 2013), and four focused on the vulnerability of the protected area itself (e.g. Aretano et al. 2015; Cruz-Elizalde et al. 2015; Tomczyk 2011). Eight of the 54 articles related to conservation ecology investigated the vulnerability to invasive species (e.g. Hulme 2012; Kalusova et al. 2013; Olden et al. 2011). Further, from an ecological and evolutionary perspective, Diaz et al. (2013) framed response functions opposed to specific effect functions of certain species for vulnerability analysis of ecosystem services.

Ecosystems and geographic regions were classified as vulnerable to **climate change** in the latest IPCC Assessment Report (IPCC 2014). A reference to the vulnerability of ecological systems to climate change could be found in 30 studies (≈23%); of these, 8 were in connection with nature conservation. Beyond our literature sample, we found that ecosystem vulnerability to climate change is commonly analyzed by using ecological response models (NWF 2011) and climate adaptation of ecosystems is implemented via the so-called MARISCO approach (Ibisch and Hobson 2014), for example.

An ecosystem-related concept of vulnerability was also discussed in **ecotoxicology** (De Lange et al. 2010), particularly in the context of ecological risk assessment (ERA), which is conceptually close to ecosystem vulnerability (Chen et al. 2013). In our literature sample, we found 21 articles attributable to ERA (≈16%). An additional paper dealt with contamination in a *regional* risk assessment (Zabeo et al. 2011). The ERAs were applied to aquatic ecosystems (e.g. Agatz et al. 2012; Gergs et al. 2013; Kulkarni et al. 2014), and fewer addressed contamination of the soil (e.g. Couto et al. 2015; Pinedo et al. 2014; van Gestel 2012) or groundwater (Caniani et al. 2015).

To a minor extent, landscape ecology was present (12 articles), often in connection with fire regimes. The remaining articles, which have not been assigned to any of the aforementioned disciplinary groups (≈25%), rather occasionally shared a common research area. They often addressed ecosystem vulnerability to multiple environmental changes and included a strong integrated management orientation (e.g. oil pollution management). Other related research fields expected to be found explicitly, like restoration ecology (5 articles), environmental impact assessment (3 articles), ecosystem-based management (1 article), and natural resource management (no article), so far seemed not to have substantially adopted the concept of ecosystem vulnerability.

Defining ecosystem exposure, sensitivity, and adaptive capacity

The application of the vulnerability concept generally has been approached through its three components: exposure, sensitivity, and adaptive capacity. Nevertheless, our review identified rather diverse or incomplete definitions of ecosystem exposure, ecosystem sensitivity, and ecosystem adaptive capacity. Understandably, the formative influences, from several research traditions (cf. section 2), coined different meanings of ecosystem vulnerability. Therefore, we furthered the application of the concept by delivering a clear and general description of the meanings of ecosystem exposure, ecosystem sensitivity and ecosystem adaptive capacity. We paid heed to a common understanding of the three elements of ecosystem vulnerability, which were often – but not always – mentioned implicitly only.

Exposure of ecosystems

The exposure of an ecosystem expresses the degree of change that it is projected to experience (e.g. Cabral et al. 2015; Zolkos et al. 2015). According to the abruptness of the change, the terms disturbance (abrupt) and stress (continuous) can be distinguished. A disturbance or shock could have consequences of similar severity for an ecosystem as an enduring or increasing stress perceived as nearing a threshold or tipping point (Redman 2014). Examples in our literature sample of these exposures were effects of climate change (e.g. Moe et al. 2013; Okey et al. 2015), land use changes like deforestation or urbanization (e.g. Ventura and Lana 2014) , invasive species (e.g. Arianoutsou et al. 2013; Olden et al. 2011), and effects from pesticides (van Gestel 2012), oil spill (Cai et al. 2015) or other toxicants (e.g. Vigneron et al. 2015) . According to Ippolito et al. (2010), the different stressors should be addressed by single and separate vulnerability assessments as long as the combining effects and interrelations are not yet fully understood. Nevertheless, un-assessed stressors are present and could influence the investigated vulnerability and combining effects may show most relevance to ecosystem management. For example, Agatz et al. (2012) investigated the combined effects of different chemicals on Daphnia magna populations, and Alric et al. (2013) combined climate warming with changes in nutrient inputs and fisheries management practices for lake ecosystems.

With regard to the term “disturbance”, we adhere to the absolute definition (in contrast to relative disturbance). According to this definition, disturbances can be determined as directly measurable changes in an ecosystem and are independent of statistical distribution, a recurrence period or predictability that would define a relative disturbance. White and Jentsch (2001) described the properties of disturbances, of which those deriving from exogenous factors were assigned as features of exposure. These are, on the one hand, the expansion and spatial distribution of disturbance (in relation to ecosystem size or ecosystem heterogeneity) and, on the other hand, the duration and frequency of the disturbance (in relation to ecosystem lifespan or recovery time). To assess the exposure of an ecosystem, the probability of a disturbance or spatial proximity to a disturbance source could guide the analysis (Frazier et al. 2014). Another option is to analyze the amount of (spatially located) system elements that are affected by a given disturbance. For example, this could mean determining the area of the ecosystem under threat (Dong et al. 2015).

Sensitivity of ecosystems

Given a certain disturbance or stress, sensitivity describes the susceptibility of the ecosystem. It expresses the degree to which a system is likely to be affected by or be responsive to the change (cf. Zolkos et al. 2015) and could tell us about the expected severity of the impact. A long-term exposure to one stress may lead to the development of increased tolerance (or decrease in sensitivity), but potentially increases the vulnerability to other environmental changes. This could mean, for example, that according to micro-evolutionary processes the resulting population, which successfully survived a first stress from a toxicant, is less competitive for foraging and likely to be more affected to another stress like a nourishment-poor period (Vigneron et al. 2015). The sensitivity could be determined by specific indicators according to the ecosystem and exposure under investigation. Illustrative factors from our literature sample were, for instance, the elevation of coastal wetlands exposed to sea level rise (Chu-Agor et al. 2011), for river ecosystems under climate change the amount of flow (Abbasov and Smakhtin 2012) or resistance of water temperature to air temperature increase (Trumbo et al. 2014), the chemical susceptibility of freshwater ecosystems to toxicants (Ippolito et al. 2012), and abundance of habitat loss-sensitive fish species (compared to more generalist species) for a coral ecosystem exposed to bleaching (Cinner et al. 2013).

In contrast to exogenous disturbance factors, intensity and specificity are endogenous disturbance factors and are defined by the inherent properties of the ecosystem. However, these properties are hardly measured by holistic ecosystem indicators so far. Therefore, many aspects of ecosystem sensitivity are derived from the inherent characteristics of species (NWF 2011). For example, differences in sensitivity to environmental influences between functionally similar species stabilize ecosystem processes and related services. In contrast, if these differences exist predominantly between functionally differing species, an ecosystem tends to be more vulnerable to changes (Chapin et al. 1997). In conservation ecology this is referred to as species redundancy within functional groups (Rosenfeld 2002; Walker 1992).

In the context of human dependency on ecosystems and the consequences of a potentially dramatic decline in ecosystem services, it seems conceivable to view particular important ecosystems as high-reliability systems. The importance of an ecosystem could be derived from its relevance for water supply (local importance), food provision (e.g. regional importance), carbon sequestration (global importance), or any other ecosystem service that is hard to do without in a specific context. This borrowing from sociological technology studies implies that efficiency and profit maximization should be subordinate to the reliability of the system (Kaufmann and Blum 2013). The concept of ecosystem reliability (Naeem 1998) addresses sensitivity (or resistance) properties, not vulnerability as a whole. Substantial fluctuations in service provision (as would be accepted within the concept of resilient systems) should be prevented.

Adaptive capacity of ecosystems

Adaptive capacity describes a system's ability to cope with the impact of a disturbance. In contrast to planned adaptation measures of a society or community, for natural systems the term autonomous adaptation appears (Metzger et al. 2006), emphasizing spontaneous ecological changes within the affected ecosystem. Therefore, the adaptation is self-organized by the ecosystem as a sum of responses of its biophysical entities. Although accounting for adaptive capacity is key in determining vulnerability, its characterization regarding natural systems is scarce (Okey et al. 2015).

The reviewed literature was scarce in descriptions of how to measure the adaptive capacity of a natural system. A few equaled it with a potential to recover, e.g. with a quick reproduction (number of seedlings produced per adult, number of juveniles per number of dead adults) from a mangrove forest (Ventura and Lana 2014), or with repopulation of a coral ecosystem with original species instead of leaving the field to competitors (Cinner et al. 2013). Others used the term resilience in a very similar meaning and tried to estimate it, for example, by the connectivity between ecosystems of the same type (Peng et al. 2015), the natural succession rate after a tsunami (Romer et al. 2012), the local vegetation cover (Zhang et al. 2015) or the local biodiversity in general (Song et al. 2015). Overall it seems that the adaptive capacity of ecosystems originates dominantly from the biological entities rather from the abiotic ecosystem components, but is hard to measure specifically. Therefore, the analysis of ecosystem adaptive capacity may be approached from the community of organisms and their interrelations. This would also include the ecological levels below a community of species: the adaptive capacity of single species, of single populations of these species, and even the capacity of individuals to adapt to a certain impact. Observations on the level of single plants indicate the existence of an ecological memory after drought, frost or heat stress, as their responses to such types of disturbances improved due to the stressors experienced. This supports the broader theory of ecological memory that refers to whole ecosystems and involves more than pure acclimatization or repopulation opportunities (Walter et al. 2013). On the species level, a high genetic differentiation within and between populations promotes adaptive capacity, which could differ between locations and along geographic distances (NWF 2011). Species respond according to their ability to maintain or enhance population quantity or to invade the disturbed environment afresh (Diaz et al. 2013). On the community level, this translates to a response diversity within a functional group of species (Elmqvist et al. 2003). A high adaptive capacity of plant communities would be governed in particular by species with a long-lived seed bank, ruderal strategy and high regenerative and dispersion capacities (Van Looy et al. 2016). Similarly, the dispersal abilities of animal species (e.g. by migration) should be integrated to such a community assessment to better estimate the adaptive capacity of ecosystems. .

Coherent concepts for ecosystem assessment

The idea of vulnerability as a system's characteristic is interrelated to other applied concepts of global change science, like exposure, sensitivity, resilience, adaptive capacity, and adaptation (Smit and Wandel 2006). As exposure, sensitivity, and adaptive capacity are directly included in vulnerability according to our definition, two main concepts remain for comparison regarding theoretical coherence for ecosystem assessment. Regarding socio-ecological systems Adger (2006) stated common terminological and methodological ground for the three concepts of vulnerability, resilience, and adaptation. Building on this, we suggest that the ecosystem response to a stress or a disturbance ultimately can be described being either: i) vulnerable, ii) resilient, or iii) adaptive (see figure 2). Still, this framework leaves the question of how to define the reference state of regular variation ahead of the disturbance/ stress (or the original basin of attraction). A high or low undisturbed variability would clearly influence the interpretation of the system response. The boundary between a vulnerable and a resilient response would be based on the lower level of regular variation, measured by a threshold value of the investigated state variable. The same is for the boundary between a resilient and an adaptive response regarding the upper level of regular variation.

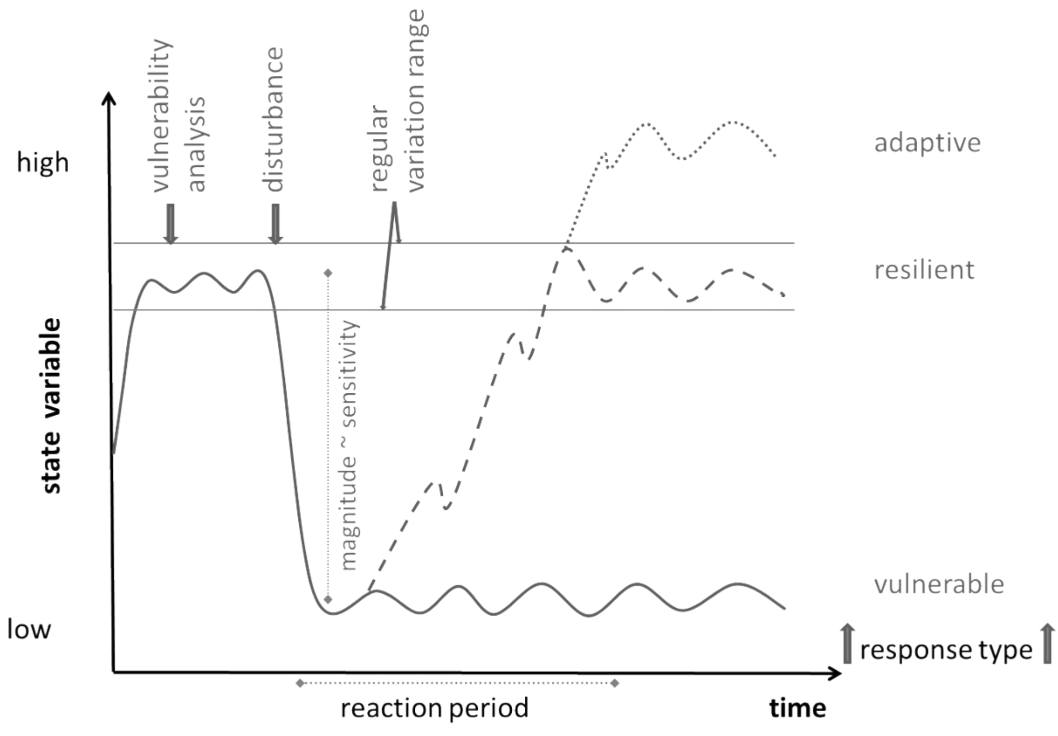

Figure 2: Ecosystem response framework for coherently placing vulnerability analysis next to the concepts of resilience and adaptability, based on White and Jentsch (2001).

When expanding the concept of vulnerability to ecosystems, the question arises of whether vulnerability is in coherence with other measures of assessing an ecosystem's response to a disturbance. Therefore, we sum up the specific relationship of vulnerability with the two closely related, established concepts of resilience and adaptability.

Vulnerability and resilience

In the context of vulnerability, resilience arises as a general antithesis to vulnerability (Eakin and Luers 2006; Frazier et al. 2014; Kaufmann and Blum 2013). Vulnerability viewed as the opposite of resilience, is limited to the idea of coping and could profit from the natural science–driven perspective of resilience by understanding the responses to stressors (Renaud et al. 2010). Both vulnerability and resilience can be viewed as specific to a system and to a perturbation (Aretano et al. 2015).

Similar to ecosystem vulnerability, resilience is a dynamic indicator of ecosystem behavior following the occurrence of a disturbance. However, the concept of resilience was shaped in different schools of thought and the diversity of definitions leads to concurring or diverging meanings (Brand and Jax 2007; Fisichelli et al. 2016). Following the initial meaning of the word resilience (latin: resilire = rebound, spring back), we would consider the concept in no conflict with ecosystem vulnerability (see Figure 2). This meaning was preserved when ecological resilience was introduced that describes the ability of a system to return to a former attractor state after a disturbance has occurred (Gunderson and Holling 2002; Müller et al. 2010). In comparison, vulnerable ecosystems would experience a regime shift to a new, in anthropogenic view often unfavorable attractor state. This builds on the original idea introduced by Holling (1973) of using resilience to explain the persistence of species that show high population variance, which was understood to be detrimental to survival. The duration of the recovery phase is used as an indicator of the resilience of a system (engineering resilience, according to Pimm 1984). In other approaches (Walker et al. 2006; Walker et al. 2004), disturbance intensities reveal the load frame within which a system can react resiliently. For ecological resilience, Redman (2014) identified a tendency to judge outcomes that maintain the conditions of the pre-existing system as a positive result, although a resilient system could be in an undesirable state and may be improved by change. Members of the Resilience-Alliance (2014) forged an overarching meaning of resilience of socio-ecological systems that subsumes a self-organizing capacity, a resistance to disturbances or stresses and an evolutionary adaptation and learning process (Carpenter et al. 2001; Folke et al. 2003). Nevertheless, these added components actually reflect non-resilient processes (Fisichelli et al. 2016; Müller et al. 2016) and we suggest to stay with the more strict definition explained above.

Vulnerability and adaptability

The concept of adaptability was introduced to demonstrate that ecosystems follow certain optimization processes under undisturbed framework conditions in the succession process (Müller 1998), during which the values of selected variables (orientors, cf. Müller and Leupelt 1998) increase. In general, a natural entity maintains a dynamic response towards thermodynamic balance (Arreguin-Sanchez and Ruiz-Barreiro 2014). If a system responds to a disturbance by recovering, the initial values of the state variables (e.g., biodiversity) can be exceeded, showing an adaptive response (see Figure 2). This has similarities to the concept of ecological memory that leads to an improved response after several disturbances of the same type (cf. Walter et al. 2013).

Adaptability (or the ability for adaptation) has a similar meaning as or is closely related to adaptive capacity (Smit and Wandel 2006), and therefore seems to be compatible with the concept of vulnerability. Further, adaptive capacity in turn has been identified as a common thread linking vulnerability and resilience (Engle 2011).

Operationalization of ecosystem vulnerability assessments

Decision-makers often have to prioritise options for action on the ground and can only use theoretical concepts of vulnerability to a limited extent (Luers 2005). Therefore, this review offers a straightforward assessment procedure as an – by no means exhaustive – outlook for application.

A site-specific ("place-based") reference to vulnerability seems indispensable (Cutter 1996; Turner II et al. 2003). In contrast to supra-regional considerations, place-specific studies map the individual specifics of vulnerability characteristics more effectively. This is particularly the case in the context of analysing ecosystem functions and regulatory processes in connection with biodiversity and nature protection (Metzger et al. 2006). Moreover, proximity relationships and cumulative ecological degradation effects could be taken into account due to spatial referencing (Jackson et al. 2004).

Therefore, a common approach to assessing a system's vulnerability is the overlap of spatial characteristics relating to a specific change or disturbance and summing them up in a vulnerability index (Frazier et al. 2014). Involving relatively little effort, index-based mapping enables a relatively wide range of factors to be considered compared to modelling. Vulnerability indices can be understood as systematically documented and transparent hypothesis frameworks that can be based on empirical data and expert opinions (Blatt et al. 2010). They can be applied as solution-oriented tools, evaluating scenarios and identifying trade-offs, rather than only assessing and monitoring existing conditions (Vollmer et al. 2016).

An index of ecosystem vulnerability should not be substantiated with general but stressor-specific environmental indicators that include information on exposure, sensitivity and the adaptive capacity of an ecosystem (Villa and McLeod 2002). Still, this entails difficult choices about the selection, standardisation, weighting, and aggregation of indicators (Barnett et al. 2008). Possibly, the application of an analytical hierarchy process (AHP) helps to create a weighted set of indicators in the GIS overlay procedure (e.g. Cai et al. 2015; Wang et al. 2015).

Conclusions

Applying the vulnerability analysis to natural systems creates new opportunities for efficient ecosystem assessment. It reveals the damage potential on the basis of a current constellation of factors and could function as an early warning system. We conclude that this ecosystem-oriented approach is still pioneering work compared to the overall vulnerability research and suggest using the term *ecosystem* vulnerability instead of environmental vulnerability (in parts interpreted as vulnerability to environmental factors) or ecological vulnerability (confused with research of socio-ecological systems that often investigate a coupled human-environment system suffering from a disturbance and responding to it). The terms population and community vulnerability would only be of comparable meaning in a strict ecological context. To not compromise the interdisciplinary application of the concept, in both cases we recommend strengthening the term ecosystem vulnerability, subsuming populations and communities of species under ecosystems.

Ecosystem vulnerability has been adopted most notably in conservation biology, climate change research and ecological risk assessments. Up to date, it has not significantly shaped the plenty of other research fields dealing with environmental impacts or ecosystem management. Marine and freshwater ecosystems are of major concern, followed by forest ecosystems, whereas agricultural or grassland ecosystems have rarely been considered so far.

The constituting elements ecosystem exposure, ecosystem sensitivity and ecosystem adaptive capacity can be defined consistently. Their more detailed description, deduced from the reviewed literature, underpins the theoretic basis of the ecosystem vulnerability concept.

A key advantage of the vulnerability concept is the coherence with resilience and adaptability as different kinds of ecosystem responses in combination with its function as a boundary object that potentially enables interdisciplinary exchange to better tackle complex problems, such as climate change and biodiversity loss. The creation of vulnerability indices is a straightforward option to efficiently implement the concept for ecosystem assessment and management.

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2.2. Indexing the vulnerability of biotopes to landscape changes

Abstract

Biodiversity loss is one of the great challenges of our times, and it is primarily driven by losses of natural and semi-natural areas. To avoid further biodiversity losses, landscape planning and ecosystem management could benefit from a condensed measure that tracks regional and cumulative ecological degradation from past and ongoing landscape changes. The affected species communities can be described spatially explicit by biotopes. A vulnerability map of biotopes will identify areas with a high potential to be adversely affected and a low capacity to recover. These vulnerability hot spots may require specific protection and maintenance interventions to be sustained. Following the interdisciplinary vulnerability concept, an indicator set related to landscape change was developed for the biotopes of the biosphere reserve Schorfheide-Chorin (Germany), which have been mapped as vector data according to the Brandenburg mapping key. The indicator set was structured into indicators of biotope exposure, sensitivity, and adaptive capacity. It covered patch metrics, like the size, the fractal dimension, and the amount of similar patches in the surrounding of each patch, as well as class metrics, like the mesh size, the state of endangerment and the average dispersal range of each biotope type. The resulting vulnerability index covered a biotope area of around 130,000 ha, and the study area could be extended readily. European biotopes are already mapped and monitored across large areas, primarily for nature conservation purposes. The biotope vulnerability index developed within this study is intended for application at large spatial scales and has the potential for a straightforward transfer to biotope maps from other German federal states and European regions.

Keywords

landscape metrics; habitat loss; fragmentation; nature conservation; vulnerability mapping

Introduction

Background

The world is facing an ongoing, anthropogenic loss of biodiversity, and most international strategies to halt this process are far from being successful (CBD, 2014). In terrestrial ecosystems, habitat loss and fragmentation due to landscape change are generally considered to be the main drivers for the extinction of terrestrial species (Collinge, 2001). Although Tscharntke et al. (2012) presented convincing arguments that fragmentation *per se* has been overestimated as a biodiversity threat, several generalizable consequences of fragmentation can be distinguished from more idiosyncratic, system-specific responses (Haddad et al., 2015). Valid metrics to judge the state of affected natural and semi-natural habitats and the species communities living within them, would need to include both the amount and configuration of remaining habitat as well as fragmentation-mediated effects. To address the ecological consequences of habitat loss and fragmentation, an analysis of biotopes regarding their vulnerability to landscape change, is a measure of interest. Nature conservation managers could benefit from an objective prioritization of vulnerable areas, which have the most need for protection or maintenance. The database for such an assessment seems to be available in biotope maps. For example, the European conservation directives linked to the Natura-2000-network have been responsible for a considerable amount of survey work, which has led to the development of increasingly standardized inventories of habitats and species that can be used in other projects (Evans, 2006). As a result, throughout the European Union, large areas of biotopes have been mapped with a high level of detail (e.g., Alexandridis et al., 2009; Bell et al., 2015; Frélichová et al., 2014; Viciani et al., 2016).

State-of-the-art knowledge

The understanding of vulnerability as a potential for loss caused by external impacts applies to several different topics (Adger, 2006; Füssel, 2007). Assessing the vulnerability of natural systems has emerged from several research fields, and the terms ecological, environmental, or ecosystem vulnerability are used interchangeably

(Weißhuhn et al., 2018). A major goal of species protection is to safeguard minimum viable populations over the long run (Shaffer, 1981; Soulé, 1987). Therefore, the vulnerability of natural populations to different stressors (e.g. heat, eutrophication, climate change, habitat change) has been analysed, for example, regarding plants (D'Amato et al., 2013; Kilkenny, 2015), insects (Bonelli et al., 2011), different vertebrate species (Drever et al., 2012; Dufresnes and Perrin, 2015), and several aquatic species (Landguth et al., 2014; Vigneron et al., 2015). It is well known that nature conservation is more effective when the arenas of biological activity are conserved than when the temporary occupants of those arenas are conserved (Beier and Brost, 2010). Instead of focusing only on single species or even single populations, ecosystem vulnerability analysis would be more suited to guide conservation efforts by including species assemblages and their habitats (De Lange et al., 2010; Ippolito et al., 2010), which for terrestrial systems can be spatially delimited in the units of the local scale, i.e., biotope patches.

Knowledge gaps

To inform a pattern-oriented management strategy that is complementary to the traditional species-oriented conservation (Fischer and Lindenmayer, 2007), spatially explicit vulnerability scores on a scale relevant for management are necessary. However, the various indicators available to measure the consequences of habitat loss and fragmentation on biotopes have not been connected to the vulnerability concept yet, in contrast to substantial research efforts on multiple vulnerabilities of aquatic ecosystems or regarding the consequences of climate change (Weißhuhn et al., 2018). Furthermore, biotopes are commonly mapped as vector data, i.e., as point, line, or polygon elements. However, geospatial analytical tools for vector data seem to be limited compared to those available for raster data, perhaps because mathematical modelling is easier and computationally faster with raster data (e.g. Zaragozí et al., 2012). In particular, the use of distance-related and neighbourhood metrics is scarce, and therefore, a promising ArcGIS extension (*vLate*) that addresses this gap has been developed (Lang and Tiede, 2003). Nevertheless, the processing time for proximity analysis grows rapidly with patch number and virtually precludes application when considering a large number of patches and larger buffer distances that could cover a wider landscape context. The alternative, which is to elaborately converge the vector data into raster format, is associated with undesirable cartographic generalization, and this process alters the boundaries and shapes of patches, as well as their spatial relationships with other patches (Corry and Nassauer, 2005). Apart from the spatial configuration of the biotope patches, also other ecological attributes of the biotopes with relevance to their vulnerability regarding landscape change may be considered. Biotopes are characterised by their specific community of plant and animal species, which share some distinctive ecological attributes, like a typical nutrient balance, water availability, dispersal behaviour, or rarity.

Objectives

First, the overall applicability of the vulnerability concept to biotopes was to be demonstrated by the use of established and customized landscape metrics to analyse biotope maps. A small and easily replicable set of largely uncorrelated indicators should fit demands of potential application well and has to reflect biotope exposure, sensitivity and adaptive capacity to landscape change. The indicator set was then developed into a biotope vulnerability index, which should be calculated for a case-study area at a minimum of a landscape scale. Covering such a large spatial extent demanded highly aggregated measures while avoiding compromising valuable spatial information. A deeper analysis of the resulting vulnerability patterns was not the aim of this study, while the limitations and opportunities of the calculated biotope vulnerability scores were in the focus.

Methods

Case-study area and geodata

To test the vulnerability indicators to be developed, I searched for open access, spatially gapless geodata of an area large enough to cover a diversity of patch arrangements; however, I aimed to reduce the boundary inaccuracy effects that stem from the surrounding areas that are not included in the analysis. At the same time, the data should consist of a limited number of elements to ensure the analysis is not too computationally heavy, as this condition would hinder experimentation with different analytical steps and processing alternatives. The Schorfheide-Chorin, located north of Berlin in Germany (Figure 1), fulfilled these requirements, as its area of approximately 130,000 ha is fairly compact and is made up of 46,249 patches, of which 35,330 patches remained after deleting the borders within adjacent patches of the same biotope type (i.e., dissolved according to "Biotyp_8st"). Furthermore, the case-study area shows – in a German context – a high proportion of diverse natural and semi-natural biotopes and therefore is assumed to exhibit ecosystem processes and flows dominated by self-organization to a large extent, rather than being mainly controlled by humans. Nevertheless, the Schorfheide-Chorin is a substantially transformed, fragmented landscape; therefore, certain ecological concepts, such as meta-population theory, should be considered.

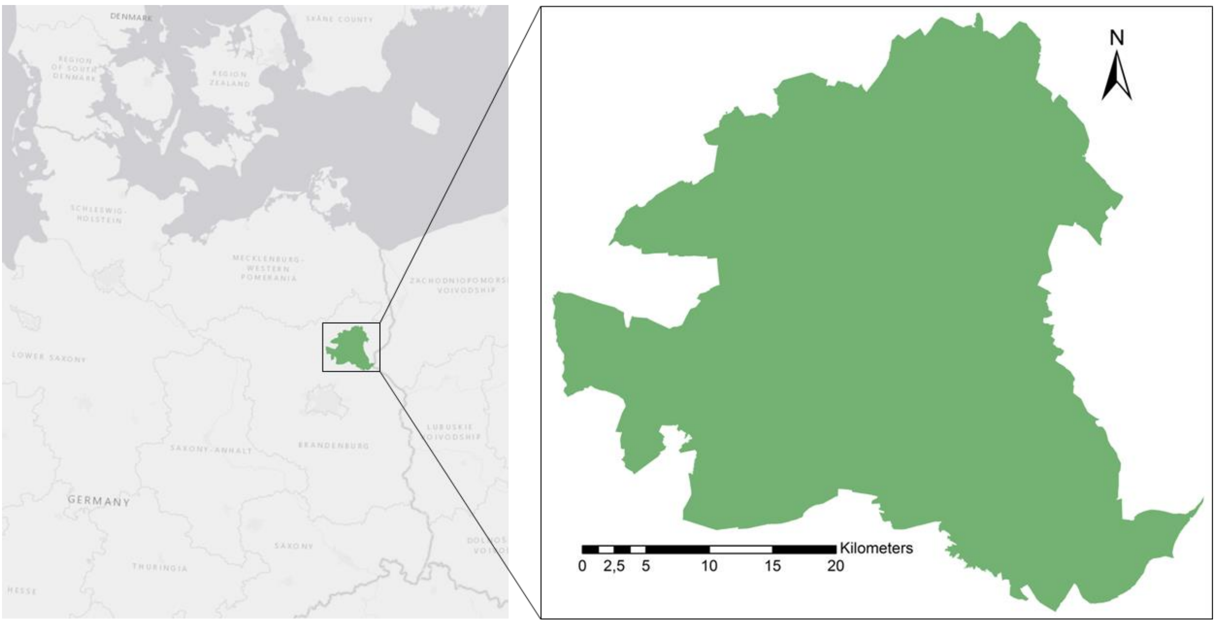

Figure 1: Situated in Northeast Germany, Central Europe, the Biosphere Reserve Schorfheide-Chorin is part of a postglacial landscape. The shape of the reserve (right) originates from the Landesamt für Umwelt Brandenburg (2013b) and the background map (left) from ESRIs 'World Light Gray Canvas Base' with copyright from OpenStreetMap contributors and the GIS user community.

The analysed biotope map of the Schorfheide-Chorin is polygon data in vector format and was clipped from a complete mapping effort by the federal state of Brandenburg in 2009 (Landesamt für Umwelt Brandenburg, 2013a) and projected with the coordinate system ETRS_1989_UTM_Zone_33N. The boundary of the case-study area, i.e., the clipping feature, was delineated by the shape of the Biosphere Reserve “Schorfheide-Chorin” (Landesamt für Umwelt Brandenburg, 2013b).

The biotope mapping code, which was originally developed for terrestrial recording, has been adjusted for remote sensing data (Luftbild Umwelt Planung GmbH, 2013), while it stayed specific to the biotopes of the state and does not apply to the national or broader scales. The Brandenburg biotope map has a high spatial resolution of 0.5 meters regarding the spectral information (colour infrared) and a thematic resolution of approximately 2500 biotope types, which are delimited with respect to the plant species community and land use. The biotope types allow statements on water balance, nutrient availability, common animal species, and several conservational aspects, and thus provide much more differentiated information than that derived from, for example, a typical land cover or land use map. The biotope type is coded as an 8-digit number, of which the first two digits give the biotope class, the next two digits give the biotope group, and the remaining digits define the specific forms of the biotope and some characteristics of the main plant species. For example, the number “05103210“ encodes wet meadows and pastures (“10”), which belong to the class of grasses and forb stands (“05”). The fifth digit (“3“) shows a nutritious site, and the sixth (“2”) defines the meadow as a species-poor type. The seventh digit (“1“) explains that the share of wooden plants is below 10%. The last digit, the zero, has no information value in this case.

Processing

For the indicator calculation, several GIS tools were used. The central software used to organize, display and edit the biotope data was ArcGIS (version 10.2.2). Because the vulnerability analysis was largely executed at the patch level (cf. next section), the field calculator was of particular use to calculate the values for each row, i.e. for each biotope patch. However, regarding vector data, the ArcGIS tools are rather limited compared to the tools that are available for raster data, especially regarding the analysis of neighbourhoods. Therefore, the add-in Patch Analyst (5.2.0.16) was utilized, which includes a separate set of tools designed for vector data (Rempel et al., 2012) and can easily produce a number of popular landscape metrics. This freeware is more convenient to apply and document sophisticated attribute modelling or other reclassification procedures than is the respective ArcGIS tool. So-called "query sets" can be edited in a simple text editor following visual basic syntax and imported for application in Patch Analyst. For transparency and further use, the four applied query sets are documented in the Supplementary Material (S1). To complement the tools regarding subdivision analysis and proximity, the freely available ArcGIS (10.x) extension vLate (2.0 beta) was utilized (Tiede, 2012). For automatization and flexibility reasons, the vulnerability analysis of such a large number of patches was supported by a type of GIS software called the Geospatial Modelling Environment (GME). The GME is an open source, stand-alone software, but it is compatible with ArcGIS in terms of modelling input and output. The GME is the successor of Hawth's Tools, both of which were established and programmed by Hawthorne Beyer. The GME provides small 'building blocks' that can be used to flexibly construct sophisticated work flows, but it also has completely self-contained analysis tools. It uses the powerful open source software R as the statistical engine to drive some of the analysis tools (Beyer, 2012). Again, for transparency and further use, the documented GME functions are available in the Supplementary Material (S2).

In addition to spatial processing, thematic processing is also necessary to achieve a useful scale for the interpretation of the analytical results. This processing involves thematic aggregation and translation from German to English. However, there seems to be a lack of systematically documented proper translation of terms from plant sociology and vegetation science. Finally, at the aggregated level of biotope types, convincing common names have been identified to refer to the same group of biotopes. Additionally, selecting an appropriate thematic resolution, i.e., defining the number of classes, is a critical choice because it influences the landscape classification and landscape metrics (Buyantuyev and Wu, 2007). When making this choice, there is always a compromise between the amount of detail and the degree of abstraction. Obviously, the differentiation of more than 1,000 biotope types would be difficult to clearly interpret. On the other hand, resulting in only a handful of biotope types would entail information losses due to too much aggregation. Although arbitrarily set, the number of classes was bound to lie between ten to less than 100 classes to be meaningful. Furthermore, as the biotype classification becomes more distinguished, the closer the classification approaches the species level. Biotope vulnerability analysis is considered a complementary tool to traditional nature conservation approaches that are usually organized around species protection and thus should not deviate from the species community approach. For this study, the most appropriate scale was the biotope group. Therefore, the mapping code was cut after the fourth digit. In the case of urban areas, two digits were sufficient because further differentiation was not ecologically meaningful, and biotope maps are generally limited for this land cover type. In a few exceptional cases, the fifth digit holds valuable information on nutrient balance or water availability, which can have strong ecologic influences on the particular species community; in these cases, this value was included. Overall, this led to 58 different aggregated biotope types with an adequate equivalent in the English language, and these results are documented in the Supplementary Material (S3). All interior borders of adjacent patches of the same class were then dissolved. After deleting 311 clipping artefacts (fragments <100 m^2 on the edge of the case-study area), there were 29,712 patches remaining for the vulnerability analysis.

Biotope vulnerability analysis

To assess the state of biotopes in the face of historical and current landscape changes, this analysis follows the vulnerability concept. It has been widely agreed that vulnerability is a function of the system's exposure, sensitivity, and adaptive capacity (Füssel, 2007; Turner et al., 2003). Ecosystem vulnerability considers the natural system as the responding unit to a certain stressor or disturbance (Weißhuhn et al., 2018; Williams and Kapustka, 2000). Therefore, biotope vulnerability should describe the potential for loss in the species community. Biotope exposure is defined by the change in biotope configuration in the landscape, and biotope sensitivity to this change describes the likelihood of a species community being affected and could provide information about the expected severity of the impact. Finally, biotope adaptive capacity would entail the ability of the affected species community to respond and persist (Weißhuhn et al., 2018).

This biotope vulnerability analysis is based on landscape ecological theory, i.e., spatial patterns are related to ecological processes. This relationship has been demonstrated at multiple scales for many taxa by a rich, consolidated set of landscape metrics (Turner, 2005). These landscape metrics quantify the spatial characteristics of patches, classes of patches, or entire landscape mosaics (McGarigal, 2014). They result in an abstraction of the landscape and allow to describe certain meta-properties, such as heterogeneity, diversity, information content and connectivity (Antrop and Van Eetvelde, 2017). The vast array of landscape metrics subdivides into categories of measures that are correlated with each other, and a relatively small set should be selected based on the analytical question (Lausch and Herzog, 2002; Riitters et al., 1995). This has been implemented by judging promising biotope vulnerability indicators based on their pairwise correlation. The correlation matrices were calculated after scaling and centring, which makes the indicators comparable, using the 'scale'-function and the 'cor'-function of *R* (R Core Team, 2018). As most variables failed to show a bivariate normal distribution, the nonparametric measure Kendall's tau (τ) was preferred to the (also calculated) Pearson's correlation coefficient, which generally is considered first for more statistical efficiency. Furthermore, Kendall's tau was preferred to the also suitable robust Spearman's rank correlation coefficient because it shows lower gross-error sensitivities and lower variability (Croux and Dehon, 2010; Hryniewicz and

Karpiński, 2014). Kendall's tau ranges from 0 (no correlation at all) to 1 / -1 (perfect correlation). Two thresholds set *a priori* (but arbitrarily) were used as criterion to assess the correlation strength, i.e. to judge on negligible or serious correlation. Correlation coefficients of $-0.3 > \tau > 0.3$ are considered undesirable, and correlations with $-0.5 > \tau > 0.5$ are unacceptable (see the Results section). In cases of remarkable pairwise correlation, the choice for either of the suitable indicators for the vulnerability index was guided by a search for the highest possible explanatory power of the compared indicators. This explanatory power was indicated by the *variance weights* (for details, see the Index calculation section).

The highly aggregated metrics at the landscape scale are usually no longer spatially explicit and often difficult to interpret. In contrast, patch metrics more directly inform about local properties. To keep the meta-information spatially explicit, the indicators, as well as their related vulnerability scores, were calculated per patch. In the final vulnerability map, each polygon could be traced back to its individual indicator values.

For analysing biotope vulnerability, eleven indicators were considered in the landscape ecological literature. They cover the properties of individual patches and the patch configuration in its surroundings, as well as the properties of the patch class, i.e., the biotope type (see Table 1). While several indicators could be conceived for the sensitivity and adaptive capacity of the system, only one exposure indicator was chosen. This approach is similar to those used in other vulnerability case studies (e.g. Inostroza et al., 2016; Mamauag et al., 2013) and keeps the vulnerability analysis stressor-specific (Ippolito et al., 2010). Further, including multiple indicators to measure the loss or fragmentation of biotopes would inevitably introduce multicollinearity, i.e. the indicators are correlated as they describe a state of the same landscape process. For biotope sensitivity, six promising indicators were identified, while four indicators were examined for the adaptive capacity of the biotopes. The final indicator set (see Results section) should avoid multicollinearity and cover sensitivity and adaptive capacity in a balanced way, while each indicator measures biotope exposure, sensitivity, or adaptive capacity.

Table 1: Short description and calculation of the indicators considered for biotope vulnerability to landscape change; these are based on the patch traits, surrounding patch configuration, and class characteristics of the biotope types.

Indicator	Description	Calculation
Mesh size *[exposure]*	Class metric; in mosaic landscapes, it reflects the degree of splitting	$mesh = \frac{1}{A_t} \sum_{i=1}^{n} A_i^2$, calculated with vLate[a] A_t = total area of case study; n = number of patches in the class; A_i = area of patch i
Patch size *[sensitivity]*	Patch metric; classification into four groups of patch size	Reclassification of patch area to four groups, stratified by threshold values <1 ha, 1-10 ha, 10-50 ha, >50 ha
Core area *[sensitivity]*	Patch metric; just the interior of a patch	Calculated with PA[b], buffer distance: 100 m
Fractal dimension *[sensitivity]*	Patch metric; measures shape complexity	Fractal dimension= $\frac{2*\ln P}{\ln A}$ P = patch perimeter; A = patch area
Class patches & class area *[sensitivity]*	Class metric; number and area of patches for each biotope type	Calculated with PA[b]
Endangerment *[sensitivity]*	Class metric; represented by the conservation priority of each aggregated biotope type according to German and European law	Binary value [0,1]: substantial parts of the aggregated biotope type are either protected by §30 of the German Federal Act for the Protection of Nature or equal a priority habitat type of the European Habitats Directive (Annex I)
Surrounding patches *[adaptive capacity]*	Patch metric; number of surrounding patches of the same aggregated biotope class, which potentially support migration from and to the	Counting the centroids from class patches within a circular buffer of 10 km; GME[c] functions: *buffer, splitdataset* (centroids), *countpntsinpolys,*

	species community of the analysed patch	ArcGIS[d] functions: *feature to points* (centroids), *merge* (buffer), *join field*
Surrounding sources *[adaptive capacity]*	Patch metric; number of surrounding source patches of the same class, which potentially support the periodic immigration to the species community of the analysed patch	See the calculation of **surrounding patches**, with number of centroids from patches designated as source patches (defined by patch size >10 ha)
Near natural area *[adaptive capacity]*	Patch metric; natural or semi-natural area in the close surrounding that is assumed to support migration compared to altered patches	Total area [ha] of (semi-)natural patches within a typical maximum edge distance of 125 m; naturalness [0,1] is defined according to aggregated biotope type descriptions; GME[c] functions: *buffer, isectpolypoly* ArcGIS[d] functions: *merge* (buffer), *Join field*
Dispersal range *[adaptive capacity]*	Class metric; classification according to a mean dispersal ability of the least mobile animal species group that is characteristic, i.e., essential, to the biotope type	Reclassification with PA[b], analysing the biotope type descriptions and attributing three dispersal range classes with increasing species mobility [1,2,3]

[a] Vector-based Landscape Analysis Tools; [b] Patch Analyst; [c] Geospatial Modelling Environment; [d] ArcGIS Desktop

Index calculation

The biotope vulnerability index consists of three sub-indexes for the three vulnerability elements: exposure, sensitivity and adaptive capacity. The calculation of the final vulnerability score is not yet standardized but is widely considered to be an averaging procedure based on the linear dependency of vulnerability from its constituting elements. Studies that explicitly integrate across all three vulnerability elements numerically suggest either a summation (e.g. Frazier et al., 2014) or a multiplication (e.g. Dong et al., 2015) of exposure, sensitivity, and adaptive capacity (the latter with reversed sign or reciprocal, respectively). Although in both ways the sub-indexes contribute equally, a summation would imply that the importance of a sub-index would decrease with decreasing scores. In contrast, a multiplication implies that any sub-index could bring vulnerability to zero, regardless of the two other values. This approach seems to be in line with the concept, as a biotope would be considered to be not vulnerable if either its sensitivity to the stressor is negligible or its exposure is obsolete. For adaptive capacity, the index generation should reflect that it only takes effect as a response to the impact, which is formed by exposure and sensitivity (Mamauag et al., 2013). Because adaptive capacity could mitigate the impact on a biotope patch only at a longer timescale, this parameter should indeed decrease the vulnerability proportionally but never bring the vulnerability scores to zero (cf. Ippolito et al., 2010). Therefore, in Equation 1, exposure and sensitivity are combined in the numerator, while adaptive capacity is delineated in the denominator to halve vulnerability, given that all sub-index scores range from 0 to 1.

$$V_i = \frac{E_i \times S_i}{(1+A_i)} \qquad (1)$$

where V_i is the vulnerability, E_i is the exposure, S_i is the sensitivity, and A_i is the adaptive capacity of patch i.

The sub-indexes E_i, S_i, and A_i are calculated from the associated indicator values, which are normalized to scores from 0 to 1 using Equation 2.

$$\beta_i = \frac{x_i - x_{min}}{x_{max} - x_{min}} \qquad (2)$$

where β_i is the normalized indicator score of patch i, x_i is the actual indicator value of patch i, and x_{min} and x_{max} are the corresponding minimum and maximum values of the indicator across all patches in the study area, respectively.

Both of biotope sensitivity and biotope adaptive capacity need an aggregation procedure to feed their respective input indicators into one score each. Directly averaging the normalized indicator values would tacitly treat them as having equal importance, which is not known. Therefore, variance weights were applied that reflect the explanatory power of each indicator. Similar to the method used by Frazier et al. (2014), these variance weights are based on a principal component (PC) analysis and the corresponding PC loadings from the indicators. The PCs were calculated using the 'prcomp'-function of *R* (R Core Team, 2018), which performs a singular value decomposition of the centred and scaled data matrix from the eleven indicators that were initially considered. Because each successive PC contributes progressively less to the explained variation, it seems reasonable for reducing complexity to consider the first components of most importance only (Schmidtlein et al., 2008). The first four PCs, accounting for 69 % of the total variance were considered for the calculation of the variance weights. The proportion of explained variance from the PCs 1 to 4 has been multiplied by the absolute values of the PC loadings from each indicator. Then, these four products were summed for each indicator to produce its final variance weight (see Equation 3).

$$y_j = \sum_{j,k=1}^{4} v_{PC_k} \times l_{j,PC_k} \qquad (3)$$

where y_j is the weighting quantifier of indicator j, v_{PC_k} is the proportion of the explained variance from principal component k, and l_{j,PC_k} is the loading from indicator j on each of the first four principal components k. As only one indicator was used for biotope exposure, no weighting was applied here.

The vulnerability sub-indexes of sensitivity and adaptive capacity were tested for the remaining correlation strength, i.e., measuring the common variance inherent in each indicator, by applying the Kaiser-Meyer-Olkin (KMO) criterion, which was calculated using the 'psych'-package for R (Revelle, 2018). Originally intended to test the applicability of factor analysis, a KMO criterion (also called measuring sampling adequacy, MSA) above 0.8 or even 0.9 is recommended, while values less than 0.5 would suggest that a factor analysis is entirely unsuitable (Kaiser, 1970), and therefore, the tested indicators should not be linked by some hidden common factor. Alternatively, the condition number of a matrix can be used as a diagnostic tool for multicollinearity. In comparison to bivariate correlation analysis, this method is a multivariate test. The condition number of the scaled indicator matrices was estimated using the 'kappa'-function of *R* (R Core Team, 2018). A condition number lower than 30 is, by rule of thumb, a signal that relevant multicollinearity is not expected (Belsley et al., 2005).

For display purposes, the patch-wise scores from the vulnerability index and its sub-indexes are aggregated by reclassification into five classes (values from 0 to 1), which are stratified according to their statistical distribution (quintiles).

Results

Indicator set

To avoid multicollinearity, of two indicators that were highly correlated pairwise, at least one was excluded from the final indicator set (see highlighted correlation coefficients in Table 2). Due to the large sample size, all correlation coefficients not close to zero, i.e., $-0.05 > \tau > 0.05$, were highly significant, as indicated by p-values below 0.001. According to the variance weights (Table 3), three indicators for both biotope sensitivity and biotope adaptive capacity were retained, while only one indicator was planned *a priori* for biotope exposure (cf. the Methods section). Therefore, the four indicators of *core area*, *class patches*, *class area*, and *surrounding sources* were not used. An undesirable slight correlation remained between *mesh size* and *patch size* ($\tau = 0.34$) as well as between *mesh size* and *dispersal range* ($\tau = -0.34$). The KMO criterion for the three retained sensitivity indicators was 0.53 and, similarly, 0.50 for the three retained adaptive capacity indicators, which indicated these indicators were largely independent from each other. This result is supported by the very low condition numbers (< 2) of the respective scaled indicator matrices for both indicator groups.

Table 2: Lower triangle of correlation matrix of the scaled indicators considered for biotope vulnerability analysis. The pairwise correlation coefficients are calculated according to Kendall's tau, using the 'cor'-function of *R (R Core Team, 2018)*. Unacceptable strong correlations for using both indicators in the same index are highlighted, and undesirable partial correlations are slightly highlighted. The rows of indicators that were sorted out to reduce multicollinearity are displayed in grey.

	Mesh size	Patch size	Core area	Class patches	Class area	Fractal dimension	Surrounding patches	Surrounding sources	Endangerment	Dispersal range
Patch size	0.34***									
Core area	0.23***	0.43***								
Class patches	0.23***	0.00	-0.01*							
Class area	0.71***	0.31***	0.22***	0.43***						
Fractal dimension	-0.22***	-0.30***	-0.22***	0.00	-0.21***					
Surrounding patches	0.15***	0.01	0.00	0.63***	0.34***	0.00				
Surrounding sources	0.69***	0.34***	0.23***	0.34***	0.75***	-0.22***	0.36***			
Endangerment	-0.24***	-0.16***	-0.09***	-0.20***	-0.25***	0.10***	-0.09***	-0.25***		
Dispersal range	-0.34***	-0.22***	-0.09***	-0.08***	-0.30***	0.14***	-0.06***	-0.27***	0.26***	
Near natural area	0.02**	0.18***	0.16***	0.00	0.01*	0.11***	0.01	0.02**	0.14***	0.09***

* **correlation significant at 0.05 level**

** **correlation significant at 0.01 level**

*** **correlation significant at 0.001 level**

Table 3: Principal component loadings from all eleven indicators on the first four principal components (PC 1-4), which accounted for 69% of the total variance in the data matrix. The exact proportion of variance of the first four PCs is given in brackets. The variance weights are calculated from the sum of the absolute values from the PC loadings multiplied by the proportion of variance of the respective PC (cf. Equation 3). The weights are used to select indicators in cases of remarkable correlation and later for weighting the indicators in the indexing process.

	PC1 (0.3051)	**PC2 (0.1735)**	**PC3 (0.1157)**	**PC4 (0.0913)**	**Variance weights**
Mesh size	0.2639	-0.1583	0.4641	-0.5193	0.2113
Patch size	0.3432	-0.3734	-0.2149	0.1852	0.2091
Core area	0.2774	-0.3700	-0.2932	0.1416	0.2053
Class patches	0.2740	0.5344	-0.2185	0.0218	0.2036
Class area	0.4684	-0.0359	0.2035	-0.3171	0.2016
Fractal dimension	-0.2249	0.1571	-0.1446	-0.2103	0.1957
Surrounding patches	0.2618	0.5201	-0.2903	-0.0171	0.1785
Surrounding sources	0.4637	0.1215	-0.0348	-0.1304	0.1629
Endangerment	-0.2258	-0.1156	-0.2795	-0.4182	0.1595
Dispersal range	-0.2038	0.0225	-0.2897	-0.5672	0.1514
Near natural area	0.1205	-0.2964	-0.5431	-0.1298	0.1318

Vulnerability maps

The seven chosen indicators and their transformation into index scores were applied to the case-study area of the Schorfheide-Chorin biosphere reserve. To emphasize, the computed vulnerability indexes do not provide an absolute meaning, and the scores must be interpreted relative to the case-study area. The patch-wise scores were normalized to range between 0 and 1 and are displayed in a categorical scale of 5 levels (i.e., low, slightly low, intermediate, slightly high, and high) according to the statistical distribution (quintiles) of the scores, which underlines the relative meaning. Although the overall biotope vulnerability was targeted, separate quantifications of each exposure, sensitivity and adaptive capacity index were given. This approach allows for the determination of variations in the vulnerability levels as combinations of the sub-indexes, which is more transparent for scientific discussion than are bulk vulnerability quantifications (Inostroza et al., 2016). Therefore, Figure 2 shows the vulnerability index for the whole case-study area, while Figure 3 shows a better visualization of an exemplary section in the southeast for comparison of biotope vulnerability with biotope exposure, sensitivity, and adaptive capacity. This zoomed-in portion of the whole map shows the large detail that a patch-wise analysis provides (especially compared to the common landscape metrics).

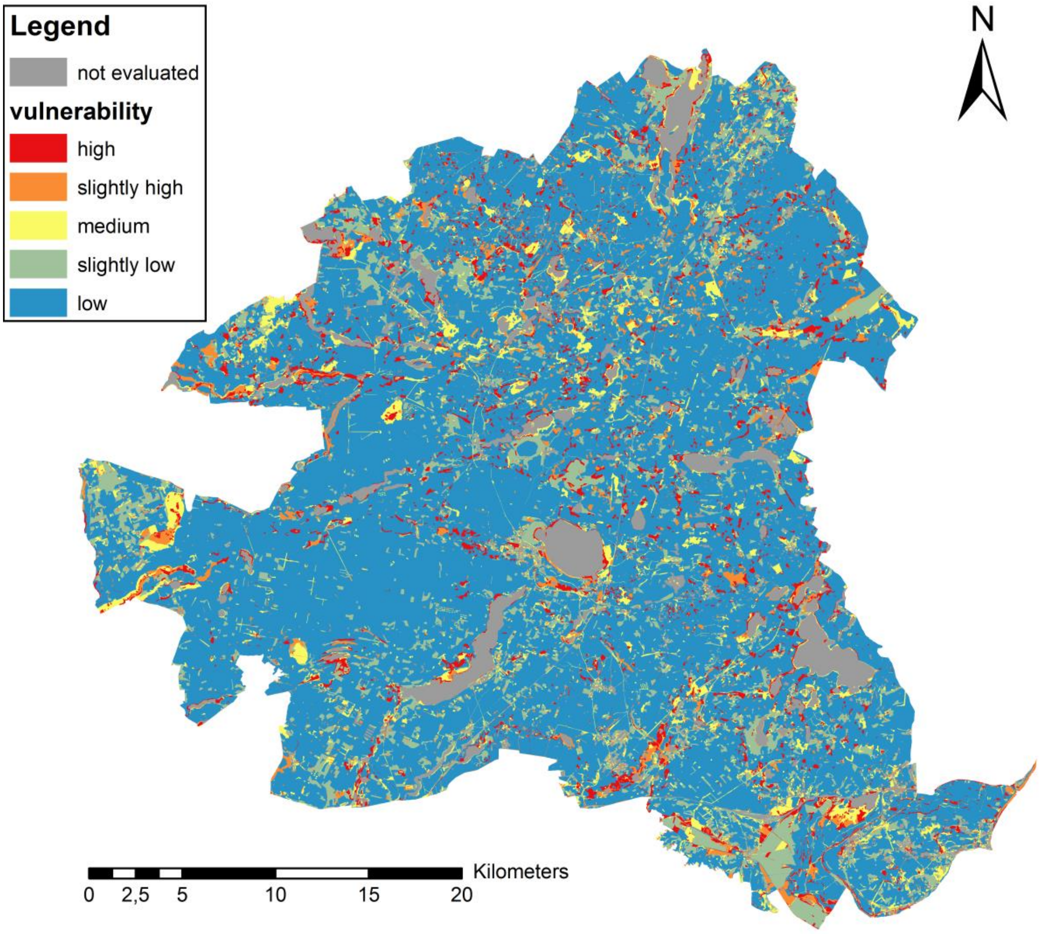

Figure 2: Biotope vulnerability map of the *Schorfheide-Chorin*, showing a five-scaled index from low to highly vulnerable patches compared to all patches in the map. All waters and built-up areas were excluded from the index due to inappropriate information content in the biotope data.

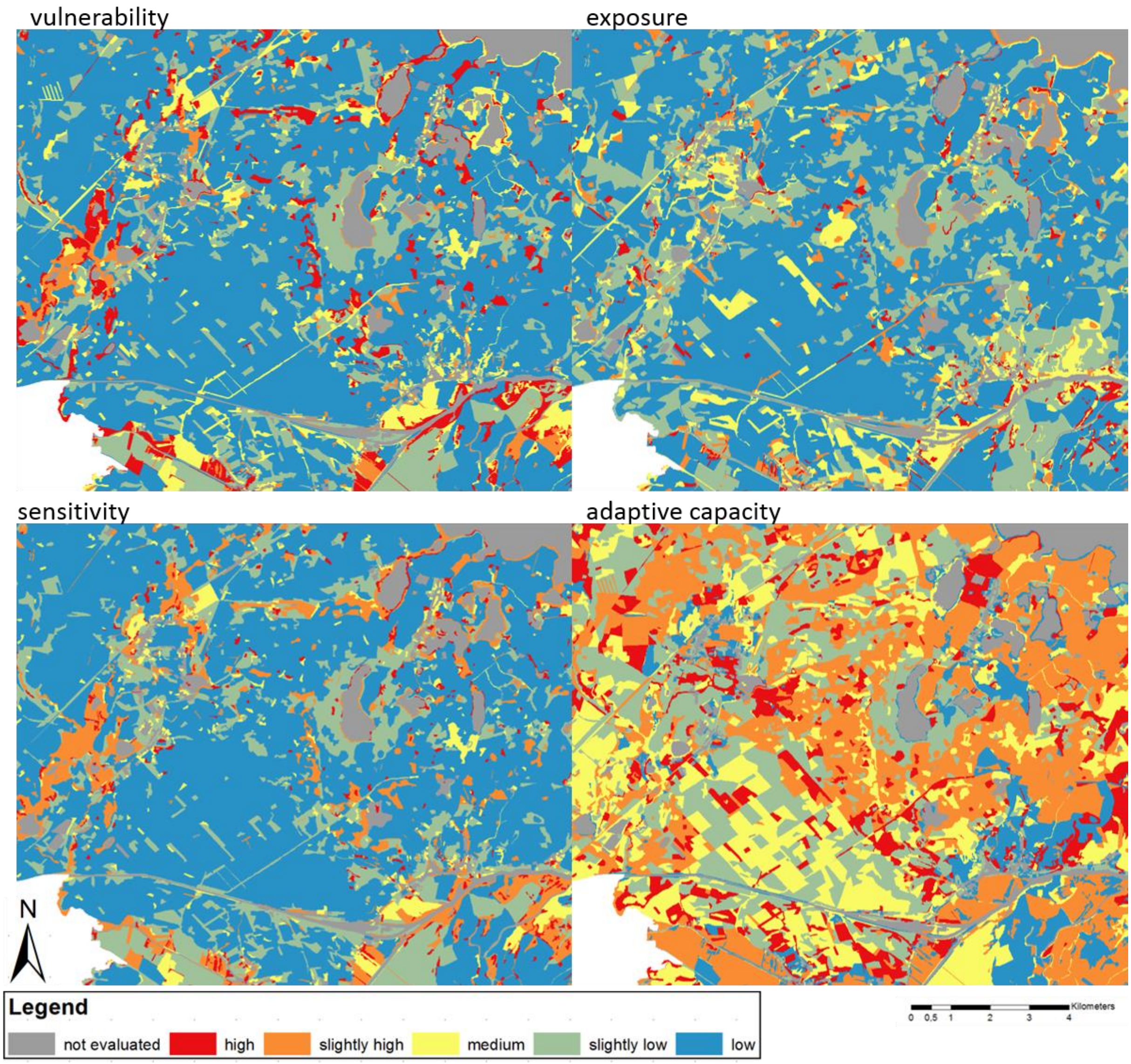

Figure 3: Comparison of the biotope vulnerability index with its sub-indexes exposure, sensitivity, and adaptive capacity in an exemplary part of the *Schorfheide-Chorin* case-study area. All indexes are pictured with five gradations referring to the quintiles of the score distribution in the whole case-study area, ranging from low to high. All waters and built-up areas were excluded from the indexes due to inappropriate information content in the biotope data.

The biotope vulnerability map shows patches of low vulnerability across a large spatial extent. This result is due to the patch size effect, as large patches tend to have lower vulnerability. However, the overall number of patches with low biotope vulnerability is equal to the number of patches with high scores (i.e., one quintile of all patches per gradation). Furthermore, all patches close to the edge of the case-study area exhibit a bias towards lower values for all indicators, including neighbourhoods, i.e., surrounding natural area (125 m from the edge) and surrounding patches of the same biotope type (10 km from the edge). Hence, these areas close to the edge are biased towards lower adaptive capacity, and in return higher vulnerability.

Discussion

Conceptual limitations

Analysing biotope vulnerability is about predicting the cumulative consequences of certain stressors or disturbances to the biotope system. Doubtless, as stated by Parkes et al. (2003), attempting to develop an assessment approach that works for all types of vegetation in patches of all shapes and sizes is an ambitious task. Still, the theoretically driven index provides an overview on vulnerable or rather robust biotope patches regarding habitat loss and fragmentation on a scale large enough to be useful for landscape planning. Still, a conceivably conservation management plan for either a cluster of vulnerable patches of different biotope types or a particular vulnerable biotope type in several locations can build on the index as the scores are calculated for each biotope explicitly. The suggested score provides a substantial reduction in complexity, which should facilitate practical application and communication of results. It could complement practised biotope evaluation methods that are usually applied to assess necessary compensation for environmental impacts from, for example, construction projects or land use changes. This topic is commonly handled under the term biodiversity offset, for which I refer to two comprehensive overviewing publications for further reading (Gardner et al., 2013; Wende et al., 2018). These practised biotope evaluation points to issue that scientific justification is too limited to support decision-making alone. The ecosystem management decision to offset, maintain, protect or restore a biotope would heavily rely on societal values and their legislative implementation. The degree of vulnerability could provide just one line of argumentation, as a biotope that is not considered valuable or worthy of protection can be vulnerable and vice versa. Further, decision-makers who are viewing aggregate vulnerability maps may like to rapidly turn to the original indicators to understand and interpret the aggregate vulnerability indexes (Abson et al., 2012). The biotope vulnerability index could return similar scores for two locations where different drivers are at work. Furthermore, for nature conservation purposes, the presented biotope vulnerability does not account for species with more complex habitat and resource requirements. These species may need larger habitat fragments (Rösch et al., 2013) or may require more movement among distinct habitats during their lifetime to survive (Tscharntke et al., 2012). This biotope vulnerability analysis was focused on the loss of natural habitat and biodiversity loss, which is likely the planetary boundary mankind is exceeding most (Rockström et al., 2009). For the future, Pimm (2008) judges that, next to landscape change, increasingly climate change will drive species extinction.

Considering vulnerability as a system property resulting from the exposure, the sensitivity and the adaptive capacity allow for potentially holistic analyses (Frazier et al., 2014). Nonetheless, exposure has recently been described as the mere spatial location of the system under consideration in an area that is probable to be adversely affected (Dong et al., 2015). Thus, vulnerability encompasses only the sensitivity to harm and a lack of capacity to cope with this harm (IPCC, 2014). As long as the driver of vulnerability is properly addressed, both conceptions should fulfil the purpose of obtaining an overview of the vulnerable system elements. However, for the sake of the vulnerability concept as a boundary object, conceptual clarity and unity seem preferable.

Central for the choice of indicators was the concept of meta-communities (cf. Leibold et al., 2004) across similar biotope types, which is based on meta-population theory (cf. Hanski, 1999; Ouborg, 1993). Considered as a population of populations, meta-populations entail fragmented populations, which are sufficiently connected to overcome inevitable local extinction by demographic and environmental stochasticity. Analogously, for this analysis all patches of the same biotope type within a connectivity threshold are considered to form a meta-community. An essential assumption is the distinction between source and sink populations that inhabit different, spatially distinct biotopes (Kristan, 2003; Pulliam, 1988). The propagating source populations spill over individuals to neighbouring habitats and, therefore, provide immigration to sink populations or even re-colonization of habitats after local extinction. However, a source population could also go extinct after more extreme disturbances. Then, normally sink populations provide re-colonization (Foppen et al., 2000). Following from the theory of habitat islands (cf. MacArthur and Wilson, 1967), less-isolated biotopes are generally more species rich due to more frequent immigration and increased probability of re-colonization by successfully crossing a rather hostile human-influenced landscape. Assuming the functional roles of species according to the redundancy hypothesis (Walker, 1992), these diverse species communities should be more adaptive because some species can compensate for the functions provided by species that go extinct in the community. Aggregating across individual species (i.e., considering species communities) and ecological processes (i.e., considering only a few indicators for each element of vulnerability) surely under-appreciates the complexity of ecological processes and the differences between individual species (Fischer and Lindenmayer, 2007). Nevertheless, it seems rather impossible to analyse the vulnerability of every single species in a given landscape.

One major limitation of the developed biotope vulnerability index is its static approach, which is based on a current snapshot of the landscape. Although the current distribution of the biotopes is a result of past landscape development, the method did not account for the processes of landscape changes, neither past nor present, or for the effect of future landscape configuration. Time lags regarding extinction debt or immigration credit of species communities (Jackson and Sax, 2010; Kolk et al., 2017) were not included. Metapopulation dynamics play out over several generations. For long-living species, these processes would take centuries.

To create any index, indicator selection, aggregating and weighting procedures must be considered. For this study, the final indicators should not show multicollinearity or rely on artificial subjective factors derived from expert interviews. Therefore, the reapplied ecosystem vulnerability indexing method of analytical hierarchy processing (e.g. Chang and Chao, 2012; Qiao et al., 2013; Zhang et al., 2015) was not considered. Principal component analysis or factor analysis has successfully been used in other vulnerability analyses to objectively select and weight the important variables, especially when the number of potential indicators is large (Abson et al., 2012; Inostroza et al., 2016).

Of course, the biotope maps introduce uncertainty to the vulnerability analysis. On the one hand, the interpretation of the spectral information is not free of error. On the other hand, the vector data consist of sharply delineated surfaces and discrete patches. Lausch et al. (2015) summarized the discrepancy between patch-based land-cover maps and the real landscape. The interpretation of a landscape consisting of a mosaic of patches is conceptually simple and appeals to human intuition. However, patches subsume all internal heterogeneity, although most ecological attributes are inherently continuous in their spatial variation. Alternatively, the use of surface metrics (McGarigal et al., 2009) or the implementation of transition zones (Schmidt et al., 2017) could be considered to better represent internal patch heterogeneity.

For a meaningful analysis of the more than 2000 different biotope types in the raw biotope data, an appropriate aggregation was applied. The aggregation influences the size of the biotope class and even the size and shape of individual patches. Using the first four digits of the biotope mapping code turned out to be a good compromise between the necessary aggregation and the required level of detail. For the targeted extension of the vulnerability analysis to the whole Brandenburg habitat map, which displays even more biotope types than the case-study area, the classification of aggregated biotope types should follow this compromise more rigorous to avoid potentially confusing exceptions.

One goal of the biotope vulnerability index was to develop a largely automated analysis that was applicable to very different locations and extents of biotope data. The use of multiple processing tools yielded valuable indicators but was a constraint for automatization because they could only be integrated manually. The workflow had to be adapted to the tools rather than the opposite. One solution could be the use of scalable software to extend the available formulas, increase the assessable formats, and avoid dealing with any specific software, as proposed by Zaragozí et al. (2012). Furthermore, for very large data sets, computationally intensive buffers may turn into a disadvantage. However, proximity metrics or neighbourhood analysis do not seem to work without buffers if vector data are being used.

The choice of indicators

Providing a vulnerability index of biotopes exemplifies another application area of the interdisciplinary vulnerability concept. The quality of the index predominantly relies on the quality of its constituting indicators. In general, the indicator set was satisfying regarding the coverage of biotope spatial traits, number of indicators, independence of indicators and balance of patch and class metrics. Alone, the exposure indicator *mesh size* introduces some multicollinearity with two other indicators and does not reflect individual patch exposure to landscape change. In the following paragraphs, all eleven indicators considered for biotope vulnerability will be discussed regarding their benefits and limitations.

Mesh size measures the average size of the patches as if the landscape would consist of patches with equal size only but would exhibit the same overall degree of division (e.g. McGarigal and Marks, 1995). This metric was considered to be adequate for the description of biotope exposure because it applied to all phases of fragmentation, showed low sensitivity to very small patches, was independent of the overall landscape size (i.e., the size of the case-study area), and was mathematically simple (Jaeger, 2000). However, due to multicollinearity and missing patch-specific information (see above), alternative indicators must be conceived and tested, for example, the prevalence of anthropogenic edges (Fischer and Lindenmayer, 2007).

Patch size is the most fundamental spatial property of a biotope. Its great ecological meaning is demonstrated, for example, by the strong correlation to occurrence and abundance of certain species and the fact that most species have minimum area requirements (McGarigal and Marks, 1995). Small patches are assumed to harbour smaller populations with lower chances of local survival. Spreading the same amount of biotope area across a larger extent would not seem wise, as it would result in smaller patches. Still, this approach lowers the risk of simultaneous eradication by either anthropogenic change or environmental stochasticity (Bonn et al., 2014). Within an appropriate extent regarding the exposure, five different locations are ideal in terms of lowering this risk, while beyond, no significant increase is proven (Vreugdenhil et al., 2003). To better interpret patch size, four size classes were formed, combining the work from Parkes et al. (2003) with metapopulation theory. Two classes of sink biotopes (<1 ha and 1-10 ha) were distinguished from two classes of source biotopes (10-50 ha and >50 ha). Although soil micro- and mesofauna often persist in very small patches, most walking animals, such as forest spiders, small mammals and larger macrofauna, require biotopes larger than ten hectares to establish viable populations (Jedicke, 1994); additionally, Foppen et al. (2000) suggested considering only patches larger than ten hectares as source patches for a bird metapopulation of reed warblers. Therefore, patches >10ha are assumed to harbour mainly source populations of the multiple species that were characteristic to the species communities of each biotope type. Other factors being equal, a larger patch should encompass more species and larger populations. However, the total population carrying capacity of a biotope (or a network of biotopes) reaches a plateau, after which increasing the biotope area will no longer have a significant effect on the population size (Bonn et al., 2014). Therefore, no class was introduced for very large-scale ecosystems (e.g., 10,000 ha), which provide viability to the vast majority of its animal populations (Vreugdenhil et al., 2003). Furthermore, such biotope sizes are rare in fragmented landscapes.

The **core area** is the interior of a biotope and describes the remote influence of human interventions that reach into the unaltered or natural biotope. Small patches are assumed to exhibit comparatively larger edge effects. Assuming edge effects can reach up to 100 m into a patch, which is a rough estimation applied across several biotic and abiotic factors (cf. Schmidt et al., 2017), the presence (or absence) of a core area was calculated, resulting in a binary indicator. However, this value was too correlated with patch size.

Class patches and class area, i.e., the number of patches of an aggregated biotope type or its cumulated area, may represent the rarity of a biotope type within the study area. Rare biotope types should be more sensitive to further losses of biotopes or increasing fragmentation than more common biotope types. Both could be considered in relation to the maximum patch number or maximum area across all classes.

The fractal dimension measures the shape complexity. Much of the presumed importance of the spatial pattern is related to edge effects (McGarigal and Marks, 1995), and therefore, from the large group of patch metrics, one metric describing the shape of the patch should be included. The fractal dimension has the advantage over other shape metrics in that it does not vary with patch size and it already provides normalized values, as it approaches one for shapes with simple perimeters and two when shapes are more complex (LaGro, 1991). A biotope with a complex shape is associated with a higher sensitivity due to increased edge effects and less compactness. Nevertheless, the shape is also connected to adaptive capacity, as relatively stretched patches would facilitate connectivity to other patches of the same class.

Endangerment of a biotope type is related to the rarity of the associated species community. Further loss of biotope area should have worsened effects on endangered biotope types compared to a biotope type that is not threatened at all. The European Union Habitats Directive (Annex I) provides a legal protection status for a choice of endangered habitat types, which could be translated to biotope types. Furthermore, in Germany, biotopes could be given a national conservation status by §30 of the German Federal Act for the Protection of Nature (*Bundesnaturschutzgesetz)*. The sensitivity indicator of this work simply distinguishes biotope types with conservation status by either of the legal nature protection systems from others that have no protection status. This status is usually granted to very specific biotope types. To implement this information to the aggregated classes of biotope types, essential parts of the class were required to have a conservation status to define the overall endangerment to the aggregated class. Specifically, this means it should consist of a majority of protected sub-types or contain at least one priority habitat type, knowing that such a generalization over protection status may conflict with application in practical nature conservation.

Surrounding patches of the same aggregated biotope type reflect migration opportunities for the associated species community. The role of migration is central in the debate as to whether a successful conservation strategy should focus on a single large refuge or on several small conservation refuges (cf. Simberloff and Abele, 1982). An intermediate number of habitat patches seems to maximize the time to extinction, because it best supports a habitat network (Ovaskainen, 2002). To be computationally more effective and independent of patch shape, which is already covered by the patch fractal dimension, the centroids of the relevant patches were counted.

Typically, the connectivity of biotopes is analysed considering a nearest neighbour proximity only. However, a more extensive proximity analysis that entails all patches within a defined search radius would be more realistic to represent interactions between biotopes (Tiede, 2012), such as seed dispersal or mating. Nevertheless, relevant population interactions beyond a certain distance are very unlikely. According to Foppen et al. (2000), the proximity threshold was set to 10 km, but other distances may also be plausible, as many species interactions would require a much smaller distance. Certainly, instead of distance, the species-specific barrier effects of the surroundings would be more meaningful. However, even more complex indicators that integrate dispersal barriers, population genetic data or spatio-temporal variation in local abundance would still miss the factors that act within patches, which can also produce variation in dispersal traits among individuals and populations (Lowe and McPeek, 2014). Consequently, no insights into eco-evolutionary causes and consequences of dispersal at the community level should be expected. Furthermore, species assemblages traversing fragmented landscapes may be exposed to a spatial filtering process, which would drive long-term changes in the community composition (Saura et al., 2014). This change could even change the biotype type as a whole, which is not depictable without multi-temporal biotope analysis.

Additionally, connecting habitats should be focused on in terms of connecting populations for genetic exchange, which prevents inbreeding depression and increases abundance above critical levels. However, enhancing connectivity at the species level may lead to a loss of diversity at the community and genetic levels (Bonn et al., 2014). Landscape-scale genetic variability maintained by local adaptation may provide insurance against changing environmental conditions (Hughes and Stachowicz, 2004), but a high connectedness can lead to the dilution of these unique population genotypes and to the reduction of genetic diversity at larger scales (Ovaskainen, 2012). Too much gene flow among local populations may even impede the process of local adaptation (North et al., 2011). The optimal level of connectivity is likely to differ among species and may be difficult or even impossible to ascertain (Tscharntke et al., 2012).

The **surrounding source patches** of the same biotope type alone should be an interesting indicator to predict the adaptive capacity of biotopes. This value also reflects migration opportunities, though the focus is taken from emigration (e.g., to escape from stressors or disturbances or to disperse) to immigration. For example, after a severe impact on the species community in a particular patch, immigration from source patches of the same biotope type would provide a rescue effect from local extinction.

The **near natural area** reflects the biotope adaptive capacity by the amount of neighbouring native vegetation, which is assumed to support migration more than modified, human-influenced areas. Regardless of ecological similarity, the overall amount of native vegetation cover on a landscape is essential to evaluate landscape connectivity (Fischer and Lindenmayer, 2007). The edge between two different biotopes influences the ability of individuals from both species communities to successfully cross the boundary of their home patch. Because the concept of sharp edges between patches is challenged by the concept of transition zones, the search radius (i.e., buffer distance) was set to 125 m, which is the typical maximum extent of a transition zone in fragmented landscapes (Schmidt et al., 2017).

The **dispersal range** of the species community complemented the purely distance-related indicators of biotope adaptive capacity. Based on the assumption that dispersal is critical to maintaining target populations and biodiversity (Baldwin et al., 2012), it should be included when analysing biotope adaptive capacity. This indicator entails a simplification of community dispersal ranges, which requires the assumption that dispersers are random with respect to individual- and population-level traits and that geographic variables are the primary predictors of interpatch dispersal rates. In general, dispersal refers to movements of individuals or propagules from a source location (e.g., birth or breeding site) to another location, where establishment and reproduction may occur, influencing the gene flow between the separated populations (Nathan and Shohami, 2013). Although the terms 'dispersal' and 'migration' are used interchangeably in some disciplines, here, animal dispersal range is distinguished from animal migration range in the context of round-trip seasonal movement (e.g., migratory birds).

Body size primarily drives variation in the maximum distance that species are capable of bridging through its effects on metabolism and the cost of locomotion (Hein et al., 2012). Some species need corridors of sheltered dispersal, as non-habitat area or area with inappropriate vegetation is perceived as a dispersal boundary (Hansson, 1991). Nevertheless, particular low mobility does not doom species to complete isolation in fragmented landscapes, as colonization is also realized by passive dispersal in many different forms (Dörge et al., 1999). Detailed data on dispersal and habitat requirements are available for only a small proportion of taxa, and the incorporation of specific needs of many species can become highly complex and uncertain (Beier and Brost, 2010). Therefore, a probable dispersal range of a core species group of each biotope type was chosen as a rule of thumb to contribute to the adaptive capacity of biotopes. Patches of the same biotope type within a distance lower than the range of its dispersal class are more likely to be genetically connected and potentially form a meta-community. Building on habitat network distances proposed by Jedicke (1994), three dispersal classes based on a major species group can be distinguished.

Dispersal class I has the lowest mobility of less than 0.5 km and would include biotopes characteristically populated with epigeic arthropods or gastropods. For example, the arthropod Australian treecreeper species disperse between 0.19 and 0.55 km on average (Doerr and Doerr, 2005). For gastropods, the mobility of snails is representative and is restricted well below 0.1 km (Dörge et al., 1999).

Dispersal class II has an intermediate mobility below 3 km and should cover species communities characterized by amphibians. For example, juvenile salamanders dispersed up to 670 m, and a wood frog over 1000 m (Preisser et al., 2000).

Dispersal class III has a mobility of approximately 3 km and includes species communities characterized by flying insects or reptiles. For example, several butterfly species show a probability of approximately 0.5% crossing 3 km (Konvicka et al., 2012), which may suffice for species survival. The species groups of walking mammals and terrestrial birds were excluded because they are usually able to cross much larger dispersal distances and would not be the limiting factor for estimating the connectivity of biotopes. According to body size, the maximum natal dispersal distance differs strongly between species. For example, a very small mammal, e.g., the prairie vole with 0.03 kg, would probably cross only 0.14 km, while the lynx (approximately 10 kg) disperses beyond 900 km. Similarly, very small birds cross 1.3 km, while larger (and non-residential) birds disperse beyond 1000 km (Sutherland et al., 2000).

If several of these species groups were essential to a biotope type, the dispersal range of the least mobile species group was considered; otherwise, the species community of a biotope patch was assumed to not have the potential to be fully connected. Eventually, the survival of species could not be assessed on dispersal ability or regional resource distribution alone, but the match between both is informative (Konvicka et al., 2012).

Conclusion

Originally designed to locate protected areas and to fulfil nature conservation reporting obligations, biotope maps can be exploited for vulnerability analysis to support conservation managers and landscape planning. The biotopes could be characterized by certain spatial and community-specific properties (i.e., sensitivity and adaptive capacity) and landscape changes that alter the biotope composition (i.e., exposure). For the Schorfheide-Chorin case-study area, it was shown that the rich information content of biotope vector data could be exploited in a systematic and transparent way, resulting in a condensed, easily displayable index. The aggregated information at the landscape scale does not preclude a detailed zoom-in, either spatially down to each individual patch or thematically to the underlying indicators of biotope exposure, sensitivity, and adaptive capacity. The set of seven indicators proved to be synoptic, largely uncorrelated and in line with the interdisciplinary concept of vulnerability.

A partly automated analysis makes the biotope vulnerability index relatively easily available for larger datasets. Adjusted to the Brandenburg mapping key, a comprehensive analysis of the whole federal state is within range, and with a few adjustments, the method may be transferred to other biotope maps and could therefore inform conservation or planning agencies in more regions.

Generally, such aggregated vulnerability maps are intended to support managers of the respective system. For ecosystem managers, a biotope vulnerability analysis provides an overview and information on areas where a closer look seems fruitful to identify causes of vulnerability hot spots and develop mitigation measures. Including the spatial context of vulnerable biotopes may help to reverse past negative effects of landscape change by means of spatial planning.

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2.3. Regional assessment of the vulnerability of biotopes to landscape change

Abstract

To halt habitat loss, landscape planning and conservation management could benefit from a regional analysis of the cumulative impacts on biotopes caused by landscape changes. A vulnerability map of biotopes will determine those with a high potential to be adversely affected and a low capacity to recover. The identification of vulnerability hot spots will provide guidance for potential protection and maintenance interventions. Following the interdisciplinary vulnerability concept, the analysis at the regional level (≈ 30,000 km²) was structured into biotope exposure, biotope sensitivity, and biotope adaptive capacity. It involved patch and group metrics to describe the vulnerability of terrestrial, (semi-) natural biotopes to landscape change. For the 32 biotope groups that were distinguished within this study, a relative ranking of vulnerability level is provided. At the level of biotope patches, spatial clusters and thematic clusters were identified. The biotopes dependent on high water availability, such as wet meadow, riparian habitat, and peatland were found to be particularly vulnerable. Moreover, herbaceous perennials, shrubland, groves, orchard meadows, and several pristine forest types also scored high, while the majority of forest biotope patches were less vulnerable to landscape change. The biotope vulnerability index applied at the regional level provided a sound overview for conservation planning. Only a few biotope groups showed a homogenous vulnerability level across their associated patches, suggesting that management based on local contexts is needed for the majority of biotopes.

Keywords

landscape metrics; habitat loss; fragmentation; nature conservation; vulnerability index

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Introduction

The planetary boundary of biosphere integrity has clearly been exceeded (Rockström et al., 2009; Steffen et al., 2015), and most international strategies to halt biodiversity losses have been far from successful (CBD, 2014). In terrestrial ecosystems, habitat loss and fragmentation due to landscape change are generally considered to be the main drivers of the extinction of terrestrial species (Collinge, 2001), although fragmentation *per se* has been overestimated as a biodiversity threat (Tscharntke et al., 2012). Primarily in already highly transformed landscapes, nature conservation managers seek to judge past and current threats to the remaining natural and semi-natural habitats and could benefit from an objective prioritization of vulnerable areas. A vulnerability analysis of the biotopes for which they are responsible would tell them which habitats and corresponding species communities have the most need for protection or maintenance.

Assessment of the vulnerability of natural systems has emerged from several research fields – mainly conservation biology, climate change research, and ecological risk assessment – and the terms ecological, environmental, or ecosystem vulnerability are used interchangeably (Weißhuhn et al., 2018). Derived from the general understanding of vulnerability across very different topics and disciplines as a potential for loss caused by external impacts (Adger, 2006; Füssel, 2007), biotope vulnerability should describe the potential for loss in the species community within its respective habitat. It has been widely agreed upon that vulnerability is a function of a system's exposure, sensitivity, and adaptive capacity (Füssel, 2007; Turner et al., 2003). Correspondingly, biotope exposure is defined by the (driver of) change in biotope configuration, biotope sensitivity describes the likelihood of a species community being harmed by this change, and biotope adaptive capacity entails the ability of the affected species community to respond and persist (Weißhuhn et al., 2018).

A major goal of species protection is to safeguard populations that are capable of evolving (e.g., Agatz et al., 2012; Veith and Seitz, 1995). However, conservation efforts are more effective when the arenas of biological activity are conserved rather than single species or even single populations (Beier and Brost, 2010). If a vulnerability analysis is to inform a pattern-oriented management strategy that is complementary to traditional species-oriented conservation (Fischer and Lindenmayer, 2007), it should include species assemblages and their habitats (De Lange et al., 2010; Ippolito et al., 2010) and provide spatially explicit scores. Therefore, analysing the vulnerability of biotopes appears to be an interesting solution.

The database for such an assessment seems to be available in biotope maps. For example, in Germany, all the state environmental authorities have developed biotope maps, and some of them are already comprehensive (e.g. Altena et al., 2018). Throughout the European Union, large areas of biotopes have been mapped with a high level of detail (e.g., Alexandridis et al., 2009; Bell et al., 2015; Frélichová et al., 2014; Viciani et al., 2016). These biotope maps provide information on water balance, nutrient availability, common animal species, and several conservational aspects and thus report more biological detail than, for example, a typical land cover or land use map.

Biotopes are commonly mapped as vector data, which limits the available geospatial analytical tools. In particular, the use of distance-related and neighbourhood metrics is scarce, and processing time grows rapidly with patch number and buffer size (Lang and Tiede, 2003). However, to cover a wider landscape context for each biotope and to analyse biotope maps on an extent that is useful for conservation management, a large number of patches and large buffers are to be analysed. This calls for measures on a high level of abstraction to feed into a biotope vulnerability index. Such a set of computationally effective, largely uncorrelated indicators has been suggested recently (Weißhuhn, 2019) to calculate spatially explicit vulnerability scores for biotopes on a landscape scale.

Based on this work, the objective of the current study is to apply a biotope vulnerability analysis at the regional scale using the federal state of Brandenburg (Germany) as an example. This involves i) calculating a number of patch and group metrics customized to analyse biotope maps, ii) transforming those metrics into a vulnerability map, which will then be analysed in terms of its vulnerability patterns, and iii) discussing the implications of detected vulnerability hot spots and the analytical limitations of the vulnerability index.

Methods

Study area and geodata processing

The application of the biotope vulnerability analysis on a regional level, covering almost 30,000 km² of the federal state Brandenburg (Figure 1), was based on open-access, spatially gapless geodata from the Landesamt für Umwelt Brandenburg (2013). The biotopes were mapped in 2009 with a spatial resolution of 0.5 metres for the spectral information (colour infrared) and a thematic resolution of approximately 2500 biotope types, which are delimited with respect to the plant species community and land use. Each biotope type was coded as an 8-digit number, of which the first two digits give the biotope class, the next two digits give the biotope group, and the remaining digits define the specific forms of the biotope and some characteristics of the main plant species. For example, the number "05103210" encodes wet meadows and pastures ("10"), which belong to the class of grasses and forb stands ("05"). The fifth digit ("3") indicates that the site is nutrient rich, and the sixth digit ("2") defines the meadow as a species-poor type. The seventh digit ("1") indicates that the percentage of woody plants is below 10 %. The last digit, the zero, has no informative value in this case.

The biotope mapping code, which was originally developed for terrestrial recording, has been adjusted for remote sensing data (Luftbild Umwelt Planung GmbH, 2013), while it stayed specific to the biotopes of the state and does not apply to the national or broader scales.

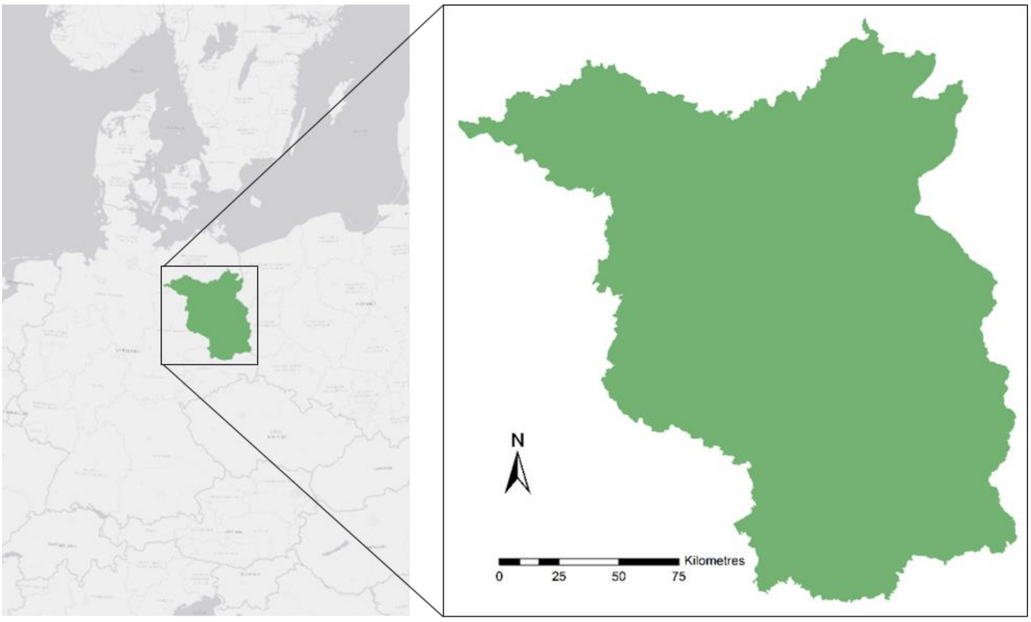

Figure 1: Perimeter of the federal state Brandenburg (the area of the city of Berlin within it is not clipped out here). The Brandenburg biotopes belong to a postglacial landscape situated in northeast Germany, Central Europe. The background map (left) was obtained from ESRIs "World Light Gray Canvas Base" with copyright from OpenStreetMap contributors and the GIS user community.

The main software used to organize, display and edit the biotope data was *ArcGIS Desktop 10.6*, supplemented by the freeware add-ins *Patch Analyst* (Rempel et al., 2012) and *V-LATE* (Tiede, 2012). Furthermore, to run intersection analyses on large tables faster and in a more stable manner than in *ArcGIS*, two alternative tools in *FME Desktop* (Safe Software, 2017) were used, namely, "PointOnAreaOverlayer" and "AreaOnAreaOverlayer". The polygon data in vector format were projected with the coordinate system ETRS_1989_UTM_Zone_33N.

In addition to spatial processing, thematic processing is also necessary to achieve a useful scale for the interpretation of the analytical results. This processing involves thematic aggregation and translation from German to English, leading to 38 different biotope groups (see Table 1). All interior borders of adjacent patches within the same biotope group were then dissolved, reducing the number of patches to 486,690, of which 74 % belonged to terrestrial, (semi-) natural patches. According to the spatial extent of the analysis, the most appropriate aggregation level was the biotope group (Weißhuhn, 2019). In a few cases, very similar biotope groups were merged to attain a similar degree of ecological differentiation across all groups. Furthermore, a few biotope types were regrouped to emphasize the abiotic factors, such as water balance or nutrient supply, rather than strictly following plant sociological aspects[1]. Such a different assignment approach was also considered reasonable in the introduction to the biotope mapping manual (LUA, 2007). For example, forest mires and peatlands with woods were originally considered as a part of the forest biotope class, although they are often adjacent to other biotopes of the peatland class and more similar to those in terms of water level, pH value, nutrients, etc. In the case of urban areas, special biotopes, and all water biotopes, the biotope class was considered as the aggregation level. For these biotope groups and for arable lands, the information extractable from biotope maps is generally limited. Although urban areas can provide high-quality habitat features for some species (Freeman et al., 2011; Matthies et al., 2017), the species communities in those biotopes are heavily subjected to anthropogenic influence. In the case of aquatic habitats, the species community is largely difficult to map via remote sensing. Biotope vulnerability analysis related to landscape changes seems to not apply here or would otherwise need very different indicators and different data on species occurrence. These biotopes were only used for neighbourhood analysis, and no vulnerability index scores are reported.

[1] In particular, the following assignments were additionallly applied to the biotope mapping key: 0121 → 045; 0123 → 022; 0124 → 022; 0221 → 045; 0334 → 045; 0456 → 047; 0719 → 022; 0810 → 047

Table 4: List of all 38 biotope groups and their percent coverage in the study area. The English names and the truncated biotope codes are based on the original mapping code and the German descriptions from the Brandenburg biotope map (Landesamt für Umwelt Brandenburg, 2013). The six biotope groups that were not evaluated in terms of vulnerability are displayed in grey, as they do not refer to terrestrial, (semi-) natural biotopes. Altogether, the evaluated biotope groups accounted for 74 % of all patches and cover 58 % of the study area.

Biotope code	Translated name	Coverage [%]
01	stream	0.44
02	standing water	2.32
022	riparian vegetation	<0.01
031	bare soil	0.22
032	ruderal vegetation	2.10
045	reeds	0.24
046	peatland	0.41
047	peatland forest	1.01
0510	wet meadow	2.59
0511	fresh meadow	4.07
0512	dry grassland	0.38
0513	fallow grassland	1.78
0514	herbaceous perennials	0.11
0515	intensive grassland	6.01
0516	lawn	0.15
06	heather	0.45
0710	shrubland	0.16
0711	grove	0.34
0712	forest edge	0.01
0713	hedges, avenue and individual trees	<0.01
0717	orchard meadow	0.08
0720	orchard	0.12
0811	pristine alder-ash forest	0.21
0812	pristine alluvial forest	0.06
0815	pristine maple-ash forest	<0.01
0825	pristine coniferous forest	0.15
0826	cleared woodland	0.57
0828	pioneer forest	0.47
0829	pristine deciduous forest	0.28
083	deciduous forest	4.00
084	coniferous forest	20.01
085	deciduous-coniferous mixed forest	2.74
086	coniferous-deciduous mixed forest	7.59
0913	arable land	32.22
0914	fallow, game forage field	2.02
10	urban green	1.42
11	special biotope	0.29
12	built-up area	4.99

Vulnerability index generation

For this study, the indicator set suggested in Weißhuhn (2019) for analysing biotope vulnerability was used. It proved to be both synoptic and to avoid multicollinearity by being constrained to a small selection of indicators, as recommended by Riitters et al. (1995) and Lausch and Herzog (2002). The seven indicators cover all three vulnerability elements, with one indicator for biotope exposure and three indicators each for biotope sensitivity and biotope adaptive capacity. Biotope exposure to landscape change was measured by the *mesh size* of each biotope group, whereby small values indicate a high level of fragmentation (Jaeger, 2000), and highly fragmented landscapes often have experienced significant losses of natural habitat, and the two variables are inevitably correlated to some degree (Smith et al., 2009). The size and shape of a patch (referred as patch size & fractal dimension, cf. McGarigal and Marks, 1995) and the conservation priority of the biotope group to which the patch belongs (*endangerment*) can be used to estimate biotope sensitivity. Small patches with complex shapes assigned legal protection status would be assessed as the most sensitive to (further) habitat losses. The adaptive capacity of a patch is reflected by the number of surrounding patches belonging to the same biotope group, the amount of pristine or near-natural area in its neighbourhood, and its assignment to one of three dispersal classes as defined by its biotope group. Species communities with high average dispersal ability within biotope patches in a pristine neighbourhood with plenty of migratory options from and to similar patches would obtain a high score.

These indicators measure the properties of an individual patch, the patch configuration in its surroundings, or the properties of the patch's biotope group (see Table 2). All indicators, as well as their related vulnerability scores, are spatially explicit and were calculated for each patch. In its application to a much larger dataset, the suggested indicator set was tested in terms of whether it continued to show low levels of pairwise correlation and whether the indicators exhibit a relevant amount of common variance. To this end, a correlation matrix was calculated after scaling and centring using the "scale" function and the "cor" function in *R* (R Core Team, 2018). The nonparametric measure Kendall's tau (τ) was preferred to Pearson's correlation coefficient because most variables failed to show a bivariate normal distribution and was also preferred to Spearman's rank correlation coefficient because it shows lower gross-error sensitivities (Croux and Dehon, 2010). Correlation coefficients of $\tau > 0.3$ are considered undesirable, and correlations of $\tau > 0.5$ are unacceptable to fulfil the aim of using largely independent indicators only. Furthermore, using the "psych" package in *R* (Revelle, 2018), the Kaiser-Meyer-Olkin (KMO) criterion was applied to assess the common variance inherent in the indicators. Originally intended to test the applicability of factor analysis, a KMO criterion above 0.8 or even 0.9 is recommended, while values less than 0.5 would suggest that factor analysis is entirely unsuitable (Kaiser, 1970) and therefore that the tested indicators are not linked by some hidden common factor.

Table 5: Short description and calculation method of the exposure, sensitivity, and adaptive capacity indicators considered for biotope vulnerability to landscape change (adapted from Weißhuhn, 2019). The indicators cover patch traits, the configuration of surrounding patches, as well as biotope group characteristics.

Indicator	Description	Calculation
Mesh size *[exposure]*	Group metric; in mosaic landscapes, it reflects the degree of splitting	$mesh = \frac{1}{A_t} \sum_{i=1}^{n} A_i^2$, calculated with *V-LATE* A_t = total area; n = number of patches in the class; A_i = area of patch i
Patch size *[sensitivity]*	Patch metric; classification into four groups of patch size	Attribute modelling with *Patch Analyst*, four groups, stratified by threshold values <1 ha, 1-10 ha, 10-50 ha, >50 ha
Fractal dimension *[sensitivity]*	Patch metric; measures shape complexity	Fractal dimension= $\frac{2*\ln P}{\ln A}$ P = patch perimeter; A = patch area
Endangerment *[sensitivity]*	Group metric; represent the conservation priority of each aggregated biotope group according to German and European law	Attribute modelling with *Patch Analyst*, defined according to the biotope type descriptions, endangerment [0,1] implies that substantial parts of the class are either protected by §32 Bundesnaturschutzgesetz or equal a priority habitat type of the European Habitats Directive (Annex I)
Surrounding patches *[adaptive capacity]*	Patch metric; number of surrounding patches of the same aggregated biotope group, which potentially support migration from and to the species community of the analysed patch	Counting the centroids from class patches within a circular buffer of 10 km; *ArcGIS* tools: buffer, feature to points, join field *FME* tools: PointOnAreaOverlayer
Near natural area *[adaptive capacity]*	Patch metric; natural or semi-natural area in the close surrounding that is assumed to support migration compared to altered patches	Total area [ha] of (semi-) natural patches (defined according to biotope type descriptions) within a distance of 125 m; *ArcGIS* tools: buffer (outside only), join field *FME* tools: AreaOnAreaOverlayer
Dispersal range *[adaptive capacity]*	Group metric; classification according to a mean dispersal ability of the least mobile animal species group that is characteristic, i.e., essential, to the aggregated biotope group	Attribute modelling with *Patch Analyst*, defined according to the biotope type descriptions, attributing three dispersal range classes with increasing species mobility [1,2,3]

The biotope vulnerability index consists of three sub-indexes for the three vulnerability elements: exposure, sensitivity and adaptive capacity. The final vulnerability score is calculated as delineated in Equation 1, following the argumentation in Weißhuhn (2019).

$$V_i = \frac{E_i \times S_i}{(1 + A_i)} \tag{1}$$

where V_i is the vulnerability, E_i is the exposure, S_i is the sensitivity, and A_i is the adaptive capacity of patch i. The sub-indexes E_i, S_i, and A_i were each calculated as a weighted average from the associated normalized indicator values and range between 0 and 1. The weights reflect the explanatory power of the seven contributing indicators. These variance weights are based on a principal component (PC) analysis and the corresponding PC loadings from the indicators (e.g. Frazier et al., 2014). The PCs were calculated using the "prcomp" function in *R* (R Core Team, 2018). The first five PCs were considered, each contributing more than 10 % of the variance and accounting for 85 % of the total variance. The proportion of explained variance for PCs 1 to 5 was multiplied by the absolute values of the PC loadings for each indicator. Then, these five products were summed for each indicator to provide its variance weight (see Equation 2).

$$y_j = \sum_{j,k=1}^{5} v_{PC_k} \times l_{j,PC_k} \tag{2}$$

where y_j is the weighting quantifier of indicator j, v_{PC_k} is the proportion of the explained variance from principal component k, and l_{j,PC_k} is the loading as an absolute value from indicator j on each of the first five principal components, k. These variance weights were further scaled in a way in which the highest weight equalled 1 while keeping the difference between weights the same. Although this step is not mathematically necessary because the final index has no absolute interpretation but a relative meaning, it keeps the vulnerability scores and the sub-index values easy to interpret by sheer number on a range from 0 to 1.

For display purposes, the patch-wise scores from the vulnerability index and its sub-indexes are aggregated by reclassification into five classes (values from 0 to 1), which are stratified according to their statistical distribution (quintiles).

Vulnerability pattern analysis

To detect distinct groups within the spatial distribution of vulnerability scores, a hot spot analysis was conducted. A hot spot is an area where patches with a high vulnerability level are surrounded by patches that also have high vulnerability scores, while a cold spot is represented by a number of patches of particularly low vulnerability scores within an area of largely low vulnerabilities. The *ArcGIS* tool "OptimizedHotSpotAnalysis" was used, with a number of outlier locations of 6,202 (1.7 % of the total number of patches), a fixed distance band of 811 metres (rounded) based on the average distance to 30 nearest neighbours, and a result of 94,531 statistically significant output features based on a false discovery rate correction (cf. Caldas de Castro and Singer, 2006).

Apart from spatial patterns, other patterns can also be searched for in the distribution of scores within the biotope groups or across them. This explorative task can be supported by cluster analysis. Clustering involves partitioning data into groups (clusters) such that the observations within one cluster are more similar to one another than those in different clusters. Any detected (*a priori* unknown) patterns may be interpreted as identifying specified clusters based on the similarity to the clusters' features (Halkidi et al., 2001). For example, pristine alluvial forest (biotope group "0812") is expected to exhibit a particular range and variance of vulnerability scores that either resemble those of other forest biotope groups or are perhaps more similar to those of other pristine biotope groups instead. To be aware of the influence of the applied cluster algorithm, a partitional and a hierarchical analysis were performed, and the resulting clusters were compared. Every clustering task requires the analysis of a certain assumption regarding the dissimilarity between the cases. As the biotope vulnerability dataset consisted of a numeric variable (vulnerability score) and a categorical variable (biotope group), the dissimilarity was calculated according to the *gower* method (Gower, 1971) using the *R* package "cluster" (Maechler et al., 2018). The hierarchical clustering involved a simple agglomerative process, i.e., each patch at the beginning was assigned to its own cluster, and then, at each stage, the two most similar clusters were joined iteratively based on the unweighted pair group method with arithmetic mean (UPGMA). The calculation was implemented using *R* and the *R* package "fpc" (Hennig, 2018). In contrast to the hierarchical analysis, the data were also clustered with the *k-means* method, i.e., the patches were partitioned to a number of groups with the aim to minimize the overall distance between the centre of the group and its group members. Again, the mix of numerical and categorical variables is problematic. One solution is k-prototyping, i.e., the computation of cluster prototypes consisting of cluster means for numeric variables (as in k-means) and cluster modes for categorical variables (Huang, 1998). This calculation was implemented using the *R* package "clustMixType" (Szepannek, 2018).

The crucial point in both approaches is that the number of clusters must be set *a priori*. Therefore, the algorithms should be run for different numbers of clusters to find meaningful clustering. In the past, very different criteria have been used to judge the appropriate number of clusters. This clustering built on four different internal criteria to attain more confidence. The *elbow method* is a very basic but robust criterion because it directly measures the sum of the within-cluster dissimilarities. A bend in the curve of decreasing within-cluster dissimilarity with increasing number of clusters suggests the appropriate number. The silhouette coefficient compares the average distance to elements in its assigned cluster with the average distance to elements in other clusters (Rousseeuw, 1987). The Dunn criterion helps to identify dense and well-separated clusters. It is the ratio of the minimum separation distance between two clusters to the maximum diameter found in the clusters (Dunn, 1974). As the Dunn criterion is based on two edge values and is potentially skewed by outliers, the Dunn2 criterion was also applied, which uses a minimum average value of separation and a maximum average cluster diameter (Hennig, 2018).

Unfortunately, especially for the distance matrix but also for the random initializations associated with k-prototyping, computational effort increases substantially with the size of the input dataset. Therefore, a sample for the cluster analysis was drawn utilizing the *R* package “splitstackshape” (Mahto, 2018). The sample size was chosen as a compromise between data representation and computational effort. At a minimum, the correlations between the indicators should be mimicked precisely, and the distribution of patch numbers across the biotope groups should be reflected. Further, omitting a group entirely would compromise the meaning of the results. As correlations roughly stabilize around n=250, while n>1000 is necessary for accuracy and confidence (Schönbrodt and Perugini, 2013), correlograms were calculated for repeated samples of 500, 5000, and 50,000 patches. The correlations already seemed accurately portrayed at n=500, but the significance of the weak correlations as shown in the full dataset was reached at n=5,000. Then, a sample of 0.015 % of the patches from all biotope groups was drawn, plus one patch from each group to cover the rare biotope groups with at least one patch. This resulted in a total number of patches of 5,464 for the cluster analysis. Data visualization was conducted in *R* with the *R* packages “ggplot2” (Wickham, 2016) and “factoextra” (Kassambara and Mundt, 2017).

Results and discussion

Indicator correlations and weights

To check for multicollinearity, the pairwise correlations of the seven indicators were calculated using Kendall’s τ, visualized in Figure 2, which was produced using the *R* package “ggcorrplot” (Kassambara, 2018). For all correlations, p-values were virtually zero (i.e., $p \ll 0.001$), and therefore, due to the large sample size, weak correlations were also found to be significant. Undesirable slight correlations occurred between *fractal dimension* and *patch size* ($\tau = 0.31$) and *endangerment* and *dispersal range* ($\tau = 0.34$). There was also a slight negative correlation between *mesh size* and *dispersal range* ($\tau = -0.31$) and *endangerment* and the number of *surrounding patches* ($\tau = -0.39$). Overall, the correlations were quite low. Additionally, a KMO of

0.56 suggests that the dataset is not meaningfully influenced by a hidden factor, i.e., the collinearity seems neglectable. For a further discussion of the particular indicators and their ecological suitability, see Weißhuhn (2019).

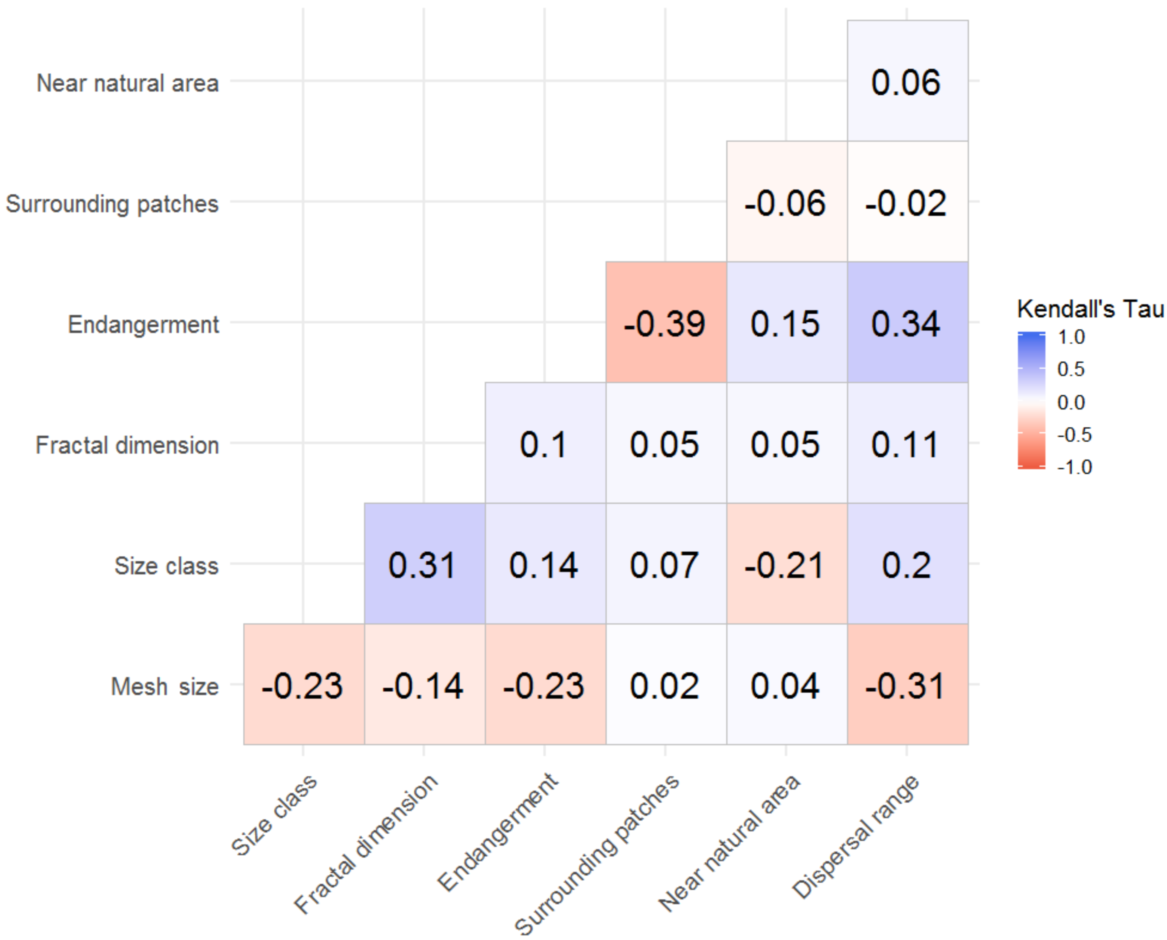

Figure 2: Visualization of the lower triangle of the correlation matrix for the seven indicators for biotope vulnerability (axis labels). Colour intensity indicates correlation strength, and blue colouration highlights positive correlation, while red colouration represents negative correlation.

An advantage of this vulnerability index is that it does not rely on artificial subjective weighting factors, which are necessary, for example, in the repeatedly applied analytical hierarchy process (e.g., Chang and Chao, 2012; Hou et al., 2015). The variance weights slightly favoured the sensitivity indicators over the adaptive capacity indicators, while the exposure indicator *mesh size* ranked in between. The differences in the variance contributions of the indicators did not differ much, which generally limits the influence of the weights. The weight for the lowest contribution to variance of *near natural area* amounted to 79 % of the variance weight calculated for *fractal dimension*, which provided the largest contribution to variance (cf. Table 3). Comparing the final biotope vulnerability index values to the same index values calculated without index weights reveals slightly reduced numbers, as expected by the weights, which ranged from 0.938 to 1. The largest difference amounts to a reduction below 2.5 % in cases of very high vulnerability scores. However, in very few cases, the index score was even slightly increased (always less than 1.2 %) by the index weights in cases of high adaptive capacity and relatively small contributions of the sensitivity or exposure indicators.

Table 6: Indicator loadings on the first five principal components (PC 1-5), which accounted for 85 % of the total variance in the dataset. The exact proportions of variance of the first five PCs are given in parentheses. The variance weights for each indicator were calculated by summing the absolute values of the indicator loadings on each PC multiplied by the proportion of variance of the respective PC (cf. Equation 2). The final index weights express the variance weights but scaled to have the maximum weight of exactly 1 (no change in score), with all other weights accordingly lower. All numbers are rounded to three decimal places for display.

Indicator	**PC1 (0.271)**	**PC2 (0.202)**	**PC3 (0.152)**	**PC4 (0.123)**	**PC5 (0.101)**	**variance weights**	**index weights**
Mesh size	0.470	0.107	0.129	0.330	0.784	0.290	0.995
Size class	0.447	0.401	0.191	0.203	0.344	0.292	0.997
Fractal dimension	0.364	0.300	0.317	0.633	0.062	0.295	1.000
Endangerment	0.441	0.501	0.026	0.111	0.142	0.253	0.958
Surrounding patches	0.156	0.640	0.298	0.342	0.165	0.277	0.982
Near natural area	0.121	0.257	0.856	0.083	0.083	0.234	0.938
Dispersal range	0.462	0.106	0.153	0.559	0.456	0.288	0.993

Vulnerability index

Based on the seven indicators and their transformation into index scores, a biotope vulnerability index was calculated for the study area at a regional scale (≈30,000 km²). Among all the biotope patches in Brandenburg, those *not* referring to terrestrial, (semi-) natural biotope groups were excluded from the index calculation (cf. Methods section). This also excluded all major dissolving artefacts, i.e., patches of extreme shape or size that would skew the value distribution to a large degree. For example, a built-up area patch that runs along the route of highways and stretches across large parts of the study area would have an absurdly high number of neighbours. The normalization and indexing procedure was therefore based on 362,217 patches (74 % of the total patch number and covering 58 % of the study area).

The patch-wise scores ranged between 0 and 1 and are displayed on a categorical scale of 5 levels (i.e., low, slightly low, medium, slightly high, and high) according to the statistical distribution (quintiles) of the scores, which underlines their relative meaning (see Figure 3). This means that each of the five vulnerability levels accounts for the same number of patches, although a first glance at the vulnerability map may suggest otherwise, as the blue area dominates, indicating the patches with low vulnerability. This is due to the size effect, as larger biotope patches, generally speaking, have been less exposed to fragmentation, are less sensitive to landscape changes and, to a lesser extent, have a higher chance to have similar neighbouring biotopes for population exchange. A reduced exposure and sensitivity score, as well as an increased adaptive capacity score, would in turn result in a lower vulnerability score. The detailed inspection of the map revealed that red- and orange-coloured patches often follow the river courses and borders of lakes, indicating the special susceptibility of the underlying biotopes. In contrast, streets are repeatedly bordered by blue patches, which represent rows of avenue trees or other edge strip vegetation. In those parts of the study region with large areas of arable land or built-up area, which together make up 88 % of the grey (not evaluated) parts of the map, biotope patches with low vulnerability are rare.

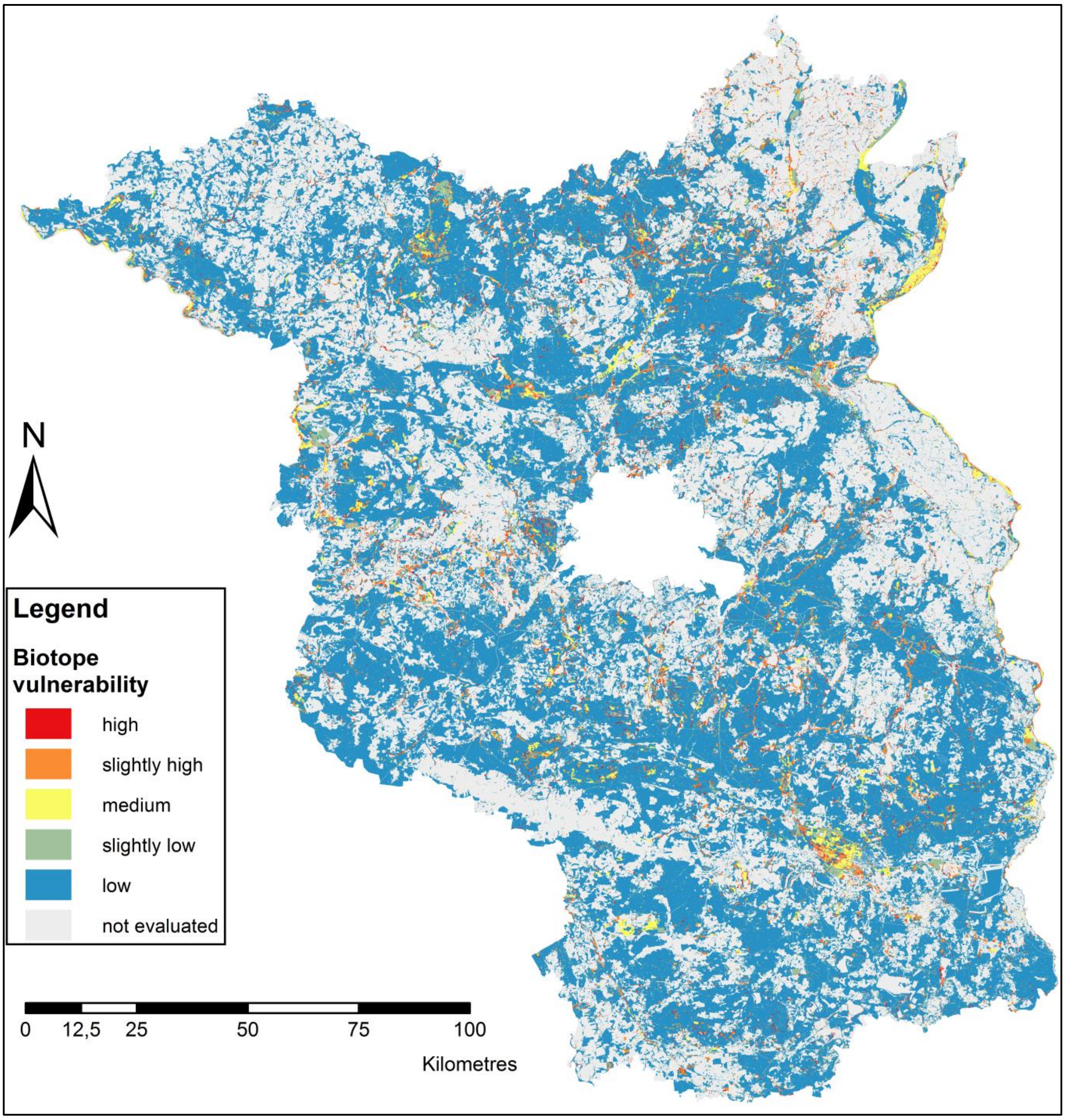

Figure 3: Biotope vulnerability map of Brandenburg (Germany) showing a five-scaled index indicating patches with low to high vulnerability. The relative score is given for all terrestrial, (semi-) natural biotope patches. Non-evaluated patches included built-up areas, arable land and all aquatic biotopes.

One purpose of large-scale assessments of biotopes is to facilitate the conservation planning of individual sites with reference to their wider ecological context, which many conservation organizations often lack (Freeman et al., 2011). Compared to species-specific or local conservation management, the regional assessment of biotope vulnerability allows cumulative ecological degradation to be taken into account (Jackson et al., 2004). A regional conservation management plan would need a stronger level of spatial and thematic abstraction, which the vulnerability index provides. However, this aggregate index comes at a price. The biotope vulnerability index could give the same score for two locations where different drivers are at work. Thus, it may be beneficial to either provide quantifications of each biotope exposure, sensitivity and adaptive capacity score for the determination of variation in vulnerability levels (Inostroza et al., 2016) or to use the original indicators to underpin ecological planning and management decisions (Abson et al., 2012). Even the seven underlying metrics do not account for the more complex habitat and resource requirements that many species have. Particular species may need larger habitat fragments (Rösch et al., 2013) or may require more movement among distinct habitats during their lifetime to survive (Tscharntke et al., 2012). Moreover, the interpretation of a landscape consisting of a mosaic of patches is conceptually simple and intuitive but subsumes all internal heterogeneity, although most ecological attributes are inherently continuous in their spatial variation (McGarigal et al., 2009). For a meaningful analysis, 38 biotope groups were aggregated from the more than 2000 different biotope types in the raw biotope dataset. This thematic aggregation influences the size of the biotope group and, in many cases, the size and shape of the biotope patches. Using the first four digits of the biotope mapping code turned out to be a good compromise between the necessary aggregation and the required level of detail. The applied aggregation across species and space, i.e., considering species communities within homogenous patches of habitat, surely underestimates the complexity of ecological processes and the differences among individual species. Nevertheless, it seems rather impossible to analyse every single species within a given landscape (Fischer and Lindenmayer, 2007).

Another limitation of the developed biotope vulnerability index is its static approach, which is based on a current snapshot of the landscape. Although the current distribution of biotopes is a result of past landscape development, the method did not account for the processes of landscape change, either past or present, or for the effect of future landscape configuration. Time lags regarding extinction debts or immigration credits of species communities (Jackson and Sax, 2010; Kolk et al., 2017) were not included.

An artefact in the vulnerability distribution was expected, as all patches close to the border of the study area exhibit a bias towards lower values for all indicators based on neighbourhoods, i.e., surrounding natural area (125 m range) and surrounding patches of the same biotope group (10 km range). Hence, these areas close to the border, especially in corners, should exhibit falsely lower scores for adaptive capacity and in turn higher scores for vulnerability. However, this effect was not observed. This results seems to have occurred because many patches in the interior of the study area are so isolated (in the sense of habitat islands according to MacArthur and Wilson, 1967) that they did not differ significantly in terms of the metrics on neighbourhood. The remaining weak difference may be overridden by the other indicators.

Spatial vulnerability patterns

The particular vulnerability of water-related biotopes was confirmed by hot spot analysis. Additionally, large cold spots and a high density of cold spots potentially point to areas of low concern (cf. Figure 4). To depict what kind of biotope group commonly underlies the spatial clusters with high or low vulnerability scores, an arbitrary but illustrative zoom-in is provided. In Figure 5, three hot spots and two cold spots have been marked on both a hot spot map and a map of aggregated biotope groups. Cluster A shows a typical arrangement of highly vulnerable patches around a village. It is a small hot spot consisting of meadow, shrubland and grove surrounded by arable land and separated by settlement. Clusters B_1 and B_2 are hot spots of vulnerable meadows, reeds and peatland surrounded by intensive grassland and other meadows. Cluster C is a cold spot of forested area that encloses patches of heather, ruderal vegetation, and settlement. Cluster D is a cold spot of a forest-meadow mosaic surrounded by arable land and other meadows and forests of insignificant vulnerability clustering.

The search for vulnerability hot spots aimed at sharpening the vulnerability map with regard to its guiding function for prioritizing conservation efforts. The hot spots reflected all major areas of high vulnerability evident in the vulnerability map and further emphasized agglomerations of small vulnerable patches within areas of otherwise low vulnerability. Overall, it did not reveal many new insights, but this may be different in other regions or when the spatial grouping of scores differs due to other underlying indicators. On the other hand, the analysis of cold spots may provide guidance towards principles of robustness or resilience. With additional information on the habitat requirements of the different species communities, this can be translated into management principles regarding the biotope group-specific minimum area and biotope group-specific optimal spatial arrangement of patches. At this point, the concepts of green infrastructure and biotope networks must be mentioned, which are inherent in the European conservation sites under the label of NATURA 2000 and especially elaborated in the German nature conservation community (e.g. Altena et al., 2018; Jedicke, 1994).

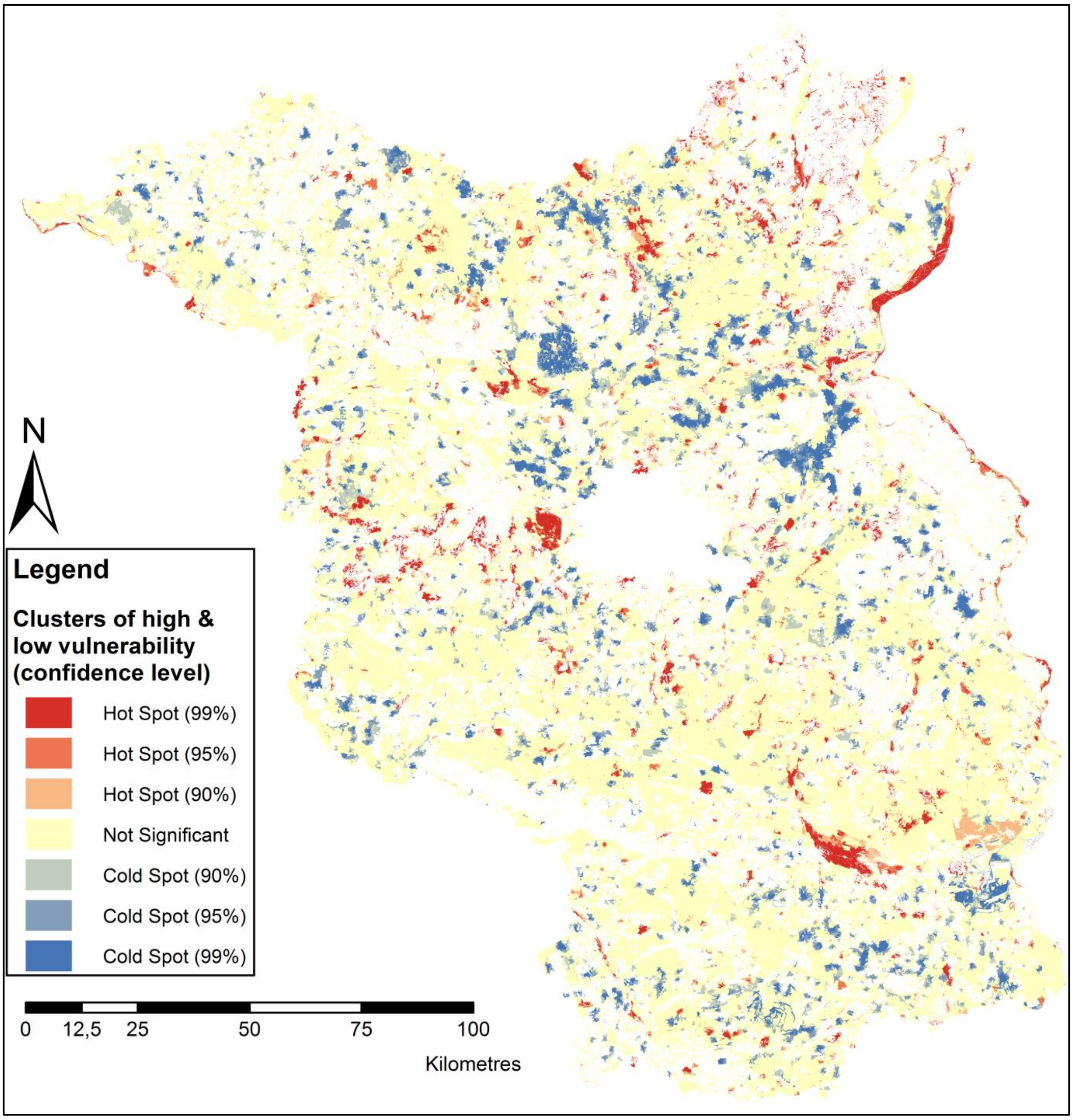

Figure 4: Map of vulnerability hot spots in Brandenburg (Germany). Red areas indicate of patches with high vulnerability scores in the neighbourhood of other patches with high scores, while blue areas indicate patches with low vulnerability scores in the neighbourhood of other low-scoring patches. The colour intensity increases with the likelihood of not detecting a grouping as a result of randomness.

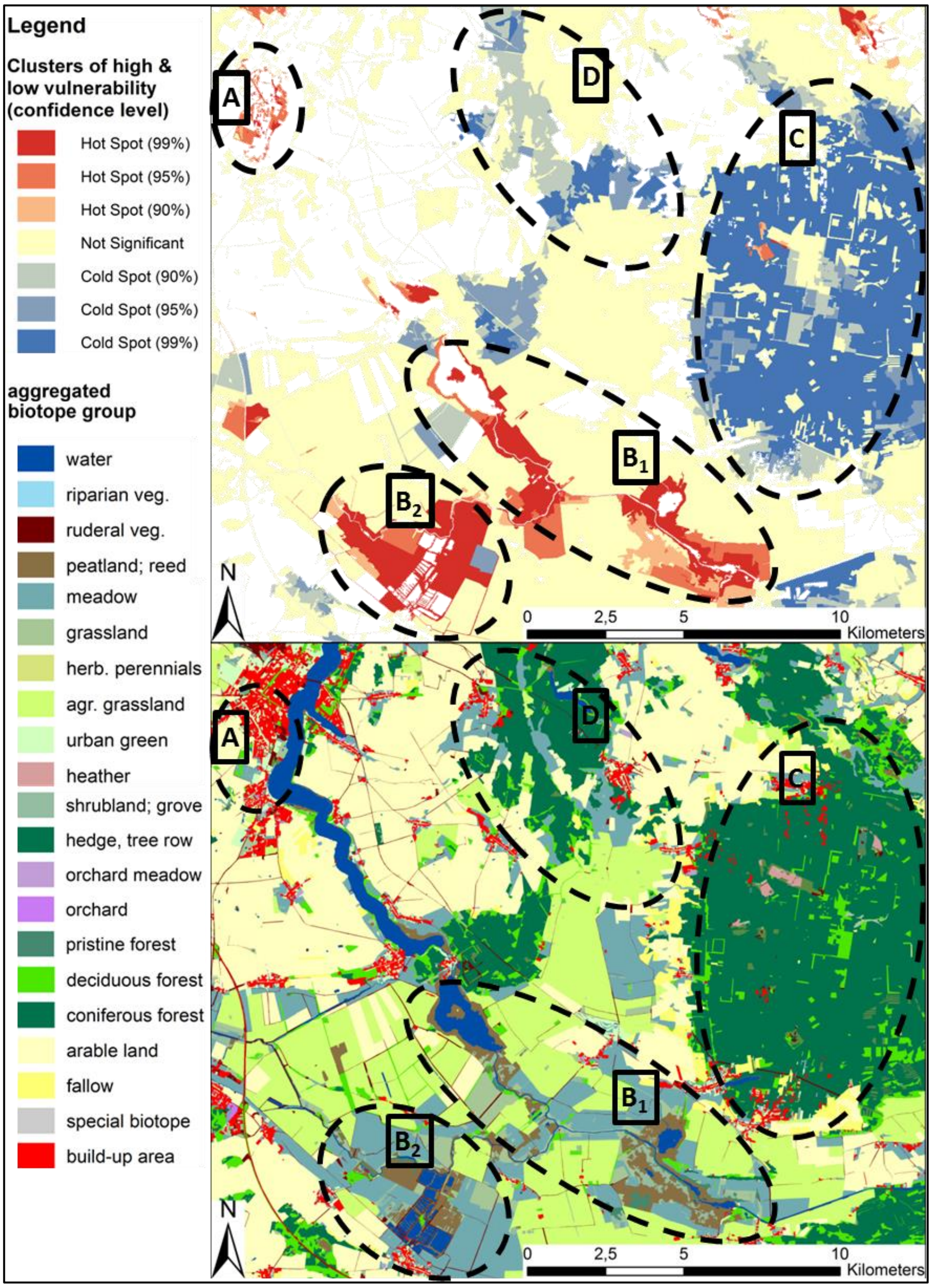

Figure 5: Spatial clusters of biotope vulnerability hot spots (A, B_1, B_2) and cold spots (C, D) in an illustrative subarea (≈50 km²) of the study region. The upper map shows the confidence level of the patches as vulnerability hot spots or cold spots, while the lower map shows the underlying biotope groups.

Biotope group vulnerability patterns

In addition to the spatial prioritization of conservation efforts, biotope groups that repeatedly obtained high vulnerability scores were also of interest. Furthermore, the identification of similarities in the vulnerability distributions of biotope groups potentially yields a reduction in necessary management options.

According to each biotope group, the vulnerability distribution is depicted in Figure 6. The boxplots show, as usual, the median as a black line, the boxes represent 50 % of the input data for each group, while the whiskers represent data points beyond the lower and upper quartiles up to 1.5 times the range of the box (interquartile range). If data points lie beyond the whiskers, they are displayed as dots and often considered outliers. Additionally, the width of the box was drawn to be proportional to the square root of the number of observations in the groups, i.e., wider boxes in the diagram indicate a more frequent occurrence of the biotype group.

The maximum range within a biotope group was limited to 0.55 (compared to the overall range of 0.89), and the interquartile range was below 0.13, with one exception of 0.17 in one of the two very rare biotope groups ("0815", n=10). Therefore, an important part of the variance seemed to derive from the different types of biotope groups.

The herbaceous perennials ("0514") were the biotope group with the highest vulnerability level, followed by several ecologically very different biotope groups with mean scores (and mostly also the lower quartile, i.e., the lower end of the box) above 0.5. These further biotope groups of major concern for conservation management, according to this study, included riparian vegetation ("022"), all three groups of peatland and reeds ("045", "046", "047"), shrubland ("0710"), groves ("0711"), orchard meadows ("0717"), all the pristine deciduous forest with particular main tree species ("0811", "0812", "0815"), pristine coniferous forests ("0825"), and pioneer forests ("0828"). The interpretation of the group of patches labelled with pioneer forest needs to be considered with particular care regarding the vulnerability scores. They show a high botanical diversity and potentially are more similar to their belonging successional forest type than to each other. Perhaps it would be ecologically sound to split these patches and allocate them to their most similar forest biotope type. Remarkably, the pristine deciduous forest with a diversity of native main tree species ("0829") scored lower than all the other pristine forest biotope groups but still considerably higher than the commercial forest biotope groups. Another interesting observation was that rarity did not automatically render biotope groups highly vulnerable. Neither a small overall number of patches nor a low overall amount of area reliably predicted high vulnerability scores. However, of the top ten biotope groups according to patch number, 8 scored low, and among the top ten biotope groups according to area, 9 scored relatively low. Indeed, a remarkable negative correlation with vulnerability scores was observed. The correlation coefficient (Kendall's tau) was -0.35 for a pairing with the number of patches per biotope group and -0.51 for a pairing with the occupied area per biotope group (both p-values were numerically equal to zero).

The most striking distribution of vulnerability scores was that for the biotope group of coniferous forests ("084"). All patches that were evaluated to have zero vulnerability (in relation to all patches that were assessed) occurred in this group, and the group exhibited zero scores only. This sharp distinction from the other biotope groups also reappeared in the cluster analysis (cf. Figure 7-9). This result can be explained by the far greatest share of area (20.01 %) that this biotope group covers in Brandenburg. Its exposure and sensitivity is low, while its adaptive capacity is high. Other biotope groups with homogenous scores, i.e., ranging below 0.2., with outliers excluded, were riparian vegetation ("022"), herbaceous perennials ("0514"), lawn ("0516"), and the biotope groups of non-forest woods, such as shrubs, hedges, and orchards ("0710", "0711", "0712", "0713", "0717", "0720"). The individual patch traits seemed to be of minor importance for those biotope groups, which would suggest the existence of a generalizable interpretation for each of their vulnerability scores. Furthermore, these biotope groups with a particularly small range of scores were often represented by only a small number of patches (i.e., compact boxplots tend to have slim boxes, cf. Figure 6). All the other biotope groups showed a rather large range of vulnerability scores, suggesting more differentiation among the patches.

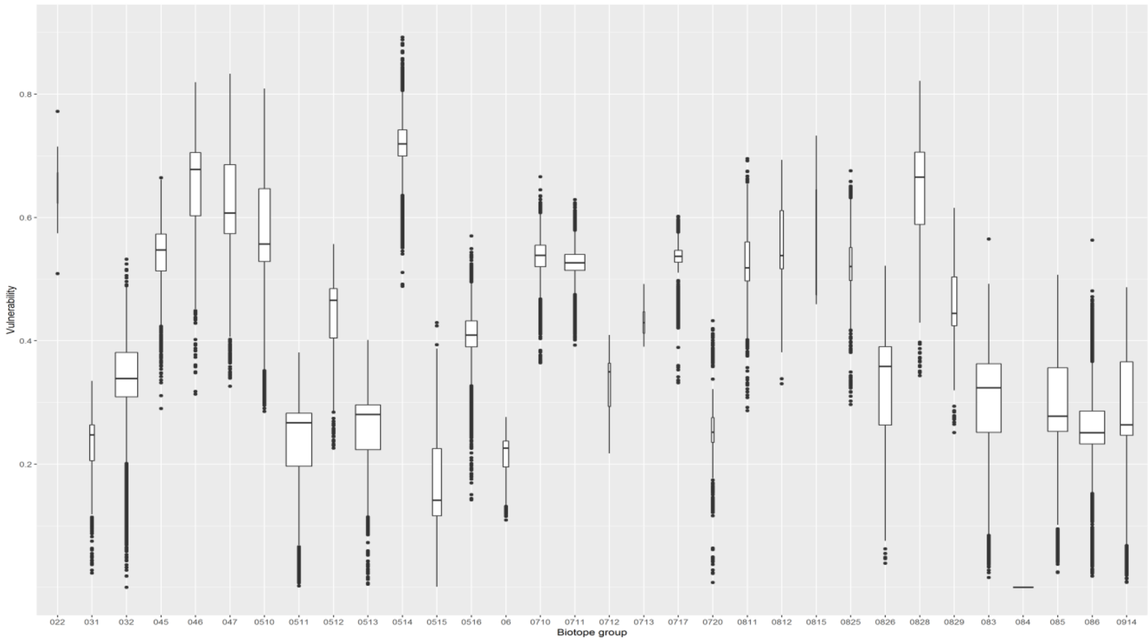

Figure 6: Vulnerability distribution of each of the 32 evaluated biotope groups displayed as boxplots with box width representing the number of underlying observations (patches). The overall number of patches was 362,217, and the overall vulnerability scores ranged from 0 to 0.89.

For the cluster analysis, a sample from the full dataset was used (cf. Methods section). The vulnerability distribution per biotope group of the sample for the cluster analysis (n=5464) largely resembled the distribution of the whole dataset (n=362,217). As expected, the full range of scores for each biotope group and the number of outliers were lower. The two rarest biotope groups were represented by only one patch (“022” and “0815”) and would therefore skew visualization. Nevertheless, overall, the boxes have almost the same position and size as their counterparts in the whole dataset, and the sample can therefore be considered to be sufficiently representative.

The hierarchical clustering identified 3 different clusters, while the partitional clustering identified 4 different clusters. The four applied criteria to decide on the appropriate number of clusters (cf. Methods section) were largely concordant for the hierarchical clustering, while the decision for the k-prototyping was a compromise between the contradicting criteria.

The cluster dendrogram derived from hierarchical clustering (Figure 7) shows that one cluster (blue) was formed right at the beginning and then separated from the rest throughout the whole iterative process. Patches from the other biotope groups were stepwise merged into two further clusters (yellow, red). A large jump in merged cluster dissimilarity occurred at a number of 32 clusters (1 blue, 13 green, 18 red). Apparently, these clusters reflect the 32 biotope groups. It turned out that the early-formed cluster (blue) consisted of all and only patches of the biotope group of coniferous forest (“084”). Furthermore, the algorithm distributed all patches of one biotope group homogenously into one of the clusters, i.e., no biotope group was spread across several clusters. Thus, the categorical variable seemed to dominate the process. The allocation to the clusters is depicted in Figure 8. The biotype groups in the three clusters were classified as “high vulnerability” (red), “low vulnerability” (green), and “not vulnerable” (blue).

The partitional clustering with k-prototypes showed more differentiated patch allocation to four different clusters (cf. Figure 9). Of the 32 biotope groups, 13 had patches allocated to two clusters, and ten had patches distributed to three clusters. While the groups belonging to two clusters partly showed priority to one of them, the biotope groups belonging to three clusters did not show priority to one of them, which makes the assessment of their vulnerability difficult and would demand differentiated management. Every cluster included at least one biotope group entirely. The cluster of highly vulnerable biotope patches (red) had three groups fully allocated to it (“022”, “0514”, “0828”), and another two were almost fully allocated to it (“046”, “047”). The cluster of biotope patches with slightly high vulnerability (orange) made up all patches in three groups, of which two were very small (“0711”, “0713”, “0815”), and dominated in another two (“0512”, “0829”). The patch cluster of slightly low vulnerability (green) only had one small biotope group entirely allocated to it (“0720”) and dominated in three other groups (“031”, “0511”, “0513”). Similar to the results from hierarchical clustering, the biotope group of coniferous forests (“084”) was entirely allocated to the cluster of low vulnerability (blue), but now patches from ten other biotope groups were also included. Nevertheless, this cluster reached no dominance in these other groups. Thus, more biotope groups could be clearly evaluated to have high vulnerability (many concerns) than low vulnerability (few concerns). Moreover, many biotope groups occur to some extent in rather robust patches if they are otherwise vulnerable and the other way around.

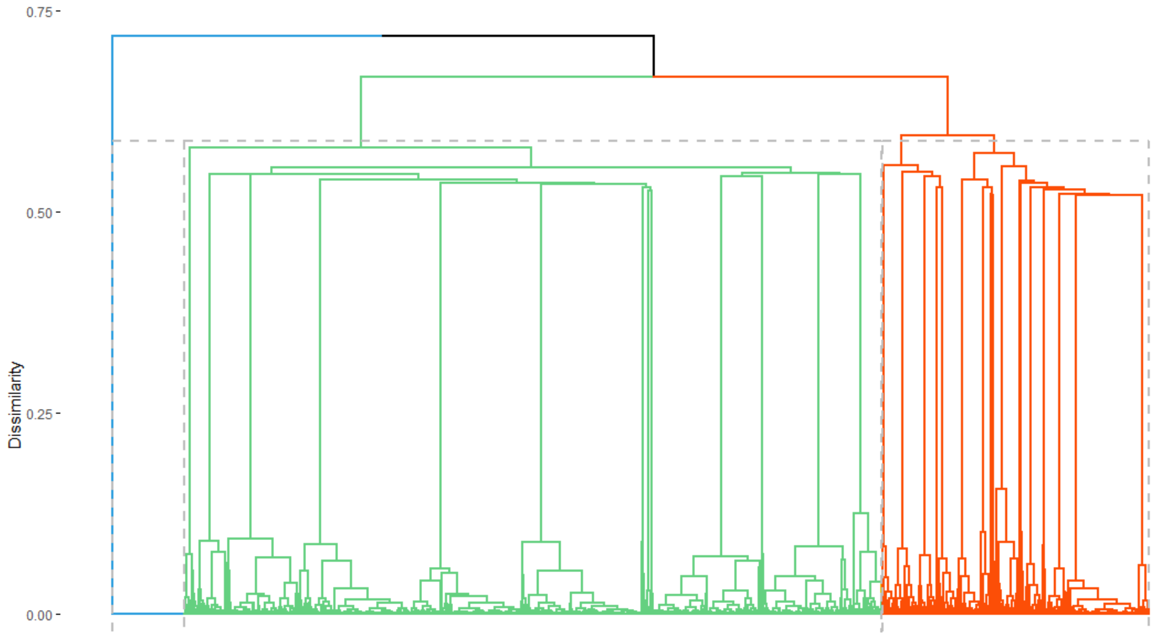

Figure 7: Cluster dendrogram illustrating the results of the hierarchical clustering with three clusters represented by the blue, green, and red branches, respectively. The dissimilarity was based on the variables *vulnerability score* (numerical) and *biotope group* (categorical).

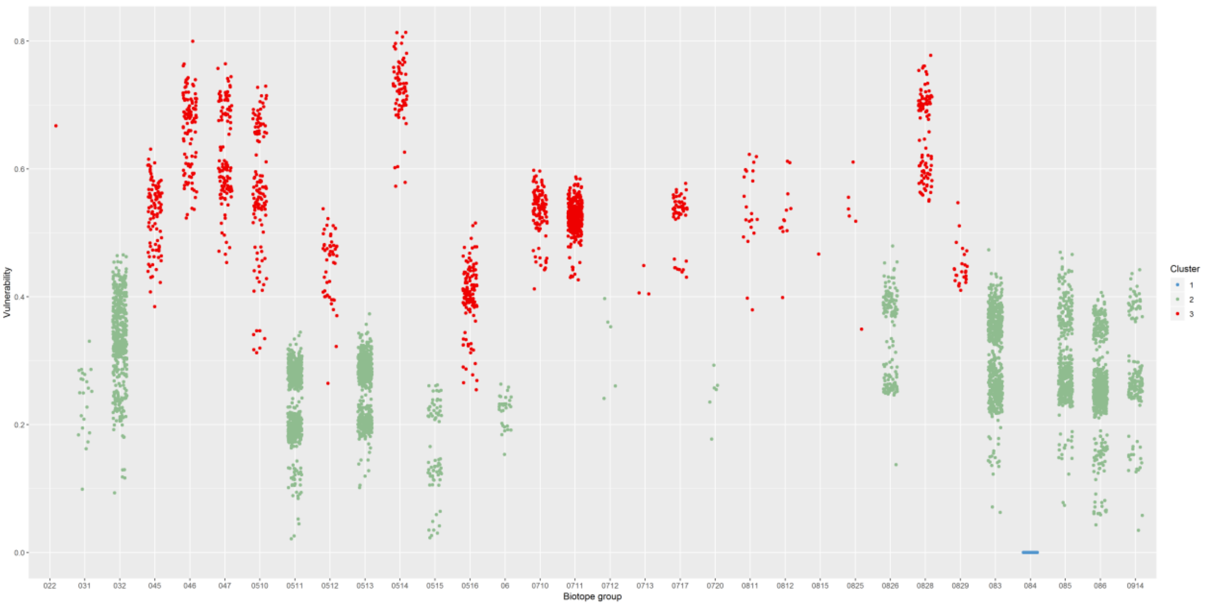

Figure 8: Distribution of the patches from each of the biotope groups (x-axis) in terms of their vulnerability score (y-axis) and their allocation to one of three clusters (different colours) derived from hierarchical clustering.

Figure 9: Distribution of the patches from each of the biotope groups (x-axis) in terms of their vulnerability score (y-axis) and their allocation to one of four clusters (different colours) derived from k-prototyping.

The clusters found by k-prototyping better handled the categorical variable, as expected. Nevertheless, k-prototyping mainly builds upon the k-means algorithm and is therefore prone to noise and outliers and cannot detect the non-convex shapes of clusters (Halkidi et al., 2001). Furthermore, the decision to use four clusters was less confident than the decision to use three clusters for the hierarchical clustering. In general, the definition of the number of clusters *a priori* remains a constraint in both approaches but could be amended by the use of different internal evaluation criteria. A strict external validation criterion, i.e., a test of whether the vulnerability level was correctly assigned to a biotope patch was not applicable, as a true vulnerability level is not available. Nevertheless, the vulnerability clusters do not seriously contradict the vulnerability map or the analysis of spatial clusters.

Conclusion

Finally, with consideration of the discussed limitations, the prioritization of conservation effort for the study region can be inferred from the results. The vulnerability score distribution and the analysis of the different spatial and thematic clusters suggest the following:

i) A handful of ecologically very different biotope groups are likely to be highly vulnerable to further landscape change and have no refuge patches of low vulnerability. They would need the most attention of conservation management.

ii) With the exception of a few patches, the biotopes dependent upon wet conditions, such as the wet meadow, riparian, or peatland biotopes, are generally in a vulnerable condition.

iii) The majority of forest biotope patches are less vulnerable to landscape change, but a larger share of the pristine forest patches is concerned.

iv) For more than half of the biotope groups, the vulnerability of their patches differs considerably, and a general level of concern cannot be substantiated.

These statements provide an overview of biotopes for which a closer look seems fruitful to identify the causes of severe vulnerability and develop mitigation measures not only at the level of habitat or species community but also at the population, species, or ecosystem level. Any implementation of results into conservation interventions should be substantiated by more specific information on the concerned species and on the local context. A conservation strategy could be oriented to the major source of a biotope's vulnerability, which is either the exposure to landscape change, the sensitivity to the consequences of change, or the lack of adaptive capacity to cope with that change. Accordingly, the aims of conservation management interventions may address the drivers of habitat loss in one case, while in another area, the biotope networks need to be restored to reconnect populations. The important point is that interventions in a particular protected piece of land are not necessarily the most useful to safeguard its biodiversity in the long run, but its neighbourhood and other patches of a similar biotope type in the same landscape should also be considered. With a few adjustments, the partly automated method may be transferred to other biotope maps and could therefore inform conservation or planning agencies in other regions as well.

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3. Overarching discussion

The three manuscripts presented above were all devoted to deploy the vulnerability concept on biotopes and to answer the four research questions. The overall work of the thesis consists of a theory-driven part and an application-oriented part and therefore, the discussion is structured accordingly.

Research question 1 was fully addressed within the first manuscript. The reviewed literature provided evidence on sufficient conceptual flexibility of vulnerability research to add natural systems as analytical objects. It could be shown that ecosystem vulnerability can be defined without invoking fundamental contradictions to established ecological concepts. However, the review also found a lack in comprehensive definitions of the vulnerability elements. Such definitions were then compiled to further the operationalization of the concept. The conclusions of the review feed into the first part of the discussion on advancing theory.

To answer **research question 2** also required a strong backing in ecological theory. Then, however, in developing the biotope vulnerability indicators, the work presented in the second manuscript subsequently took off to operationalize the concept. Based on biotope data, which provided a spatially explicit, species community-based representation of the natural system, applicability of the concept at the landscape level was demonstrated. Although not conclusive, eleven potential indicators were selected or developed to cover biotope exposure, biotope sensitivity, and biotope adaptive capacity to landscape change. This included six metrics measuring spatial attributes of each biotope site (*patch size*, *core area*, *fractal dimension*, *surrounding patches*, *surrounding source patches*, *near natural area*) and five metrics measuring spatial and community-specific attributes of the biotope groups (*mesh size*, *class patches*, *class area*, *endangerment*, *dispersal range*).

Research question 3 was also addressed within the second manuscript. To combine the potential biotope vulnerability indicators within a single index, multicollinearity between them was to avoid. Seven indicators remained, which were weighted according to their variance contribution in the following. The indicator set included *mesh size*, *patch size*, *fractal dimension*, *surrounding patches*, *near natural area*, *endangerment*, and *dispersal range*. The weighted scores of each indicator were included in the calculation of three sub-indexes on exposure, sensitivity, and adaptive capacity, respectively. Finally, the vulnerability index was calculated from the sub-indexes.

Research question 4 builds on the preceding research questions. It asks for an analysis of the distribution of vulnerability scores as well as for practical conclusions for conservation at the regional level. For this purpose, the third manuscript extended and streamlined the developed methodology from the second manuscript. Additionally, methods to identify vulnerability hot spots were developed. As result, distinctive vulnerability patterns were determined on the regional level. Highly vulnerable areas and particular vulnerable biotope groups could be identified. Finally, these results can provide guidance in conservation planning. Although the conclusions from manuscripts 3 were appropriate to answer research question 4, it was not possible to comprehensively capture the overall advantages or limitations for conservation practice within the research article. Therefore, the wider implications for nature conservation will be addressed in the second, application-oriented part of the discussion.

3.1. Advancing theory: conceptual coherence and interdisciplinarity

The general notion of vulnerability as a potential for loss has allowed its development and implementation across several very different research disciplines and also in interdisciplinary research (Eakin and Luers, 2006; Füssel, 2007). However, the framework of vulnerability assessment and related terms have been variously interpreted, creating challenges for researchers as well as practitioners to apply them (Martin et al., 2017). Vulnerability statements partly have been based on popular views and everyday theory without making all normative content of its terms and categories explicit (Bürkner, 2010). Further, even central institutions of core vulnerability research fields, like climate change, do not adhere to the same notion of vulnerability over time. For example, the Intergovernmental Panel on Climate Change (IPCC) provided different vulnerability definitions in its fourth and fifth assessment report (IPCC, 2007, 2014). The first definition has been adopted widely within the conservation community, but not the renewed (Foden et al., 2019).

Thus, the question arises, which definition serves interdisciplinary vulnerability research best, in order to tackle complex problems in particular with regard to ecosystems.

Coherent terms across multiple disciplines

The literature review for the first manuscript of the thesis revealed that an overarching and interdisciplinary conception of vulnerability actually has been outlined (Füssel, 2007; Turner et al., 2003), though not yet accepted or implemented widespread. In particular, it rarely has been applied to natural systems and the vulnerability concept seems not yet well-known in ecosystem science. The few reported statements on the vulnerability of natural systems have so far remained rather intangible and merely assessed vulnerabilities of single species.

Given that vulnerability is used as a conceptual framework in very heterogeneous research contexts, the overlap between the definitions is remarkable (Bürkner, 2010). Vulnerability research already spans over a broad range of disciplines, like hazard science, psychology, anthropology, sociology, geography, history, military science, or political economy, among others. With ecological resilience and conservation biology the concept of vulnerability also gained a foothold in the analysis of natural systems, and thereby further was widening its scope.

It turned out that the definition of vulnerability as a function of exposure, sensitivity, and adaptive capacity (in conformity with IPCC, 2007) proved to be in coherence with established ecological concepts. The typification as one of three possible system responses to a certain stress or disturbance, i.e., a vulnerable, resilient, or adaptive response, is new and applicable from individuals up to ecosystems. If an ecologic entity responds vulnerable (Weißhuhn et al., 2018), the organism, population, species, or species community is not able to recover to pre-disturbance levels (White and Jentsch, 2001) nor to respond adapted due to previously experienced stresses (Walter et al., 2013).

However, no single theoretical perspective is sufficient to analyse all possible situations. While allowing competing theoretical perspectives, any interdisciplinary conceptual framework must strive for a common language, which cannot be totally free of cognitive preconceptions and inherent limitations (McGinnis and Ostrom, 2014). The match of the deployed definition in particular disciplines and their topics must be judged by experts in the respective fields. Still, for ecology and likely for other ecosystem-related subjects, coherence with the existing overarching conception of vulnerability can be maintained.

Interdisciplinarity and sustainable land use

There is no doubt that respecting the ecological boundaries of planet earth is a prerequisite for sustainable development, re-formulated as international policy mission in the Sustainable Development Goals (SDG). Still, a successful implementation of every single SDG needs science to be involved and a valuable contribution from science would need cross-sectoral thinking (Rhyner, 2016). As no individual can be an expert in all fields relevant for any of the SDGs, this implies a necessity for teamwork across disciplines. However, advancing division of labour and accompanying more efficient production of research results have, since the beginning of modern science, increasingly divided research into new disciplines (Kuhn, 1973; Politi, 2019). Therefore, communication between cooperating researchers and agreement on common paradigms or concepts is hampered by unfamiliar terms and different notions of the same terms. Integrative research is widely acknowledged and proclaimed. Still, it is far from becoming mainstream due to obstacles in practical collaboration and barriers in the scientific reward system (Buizer et al., 2015). At this point, the vulnerability framework could function as a bridging concept, which enables interdisciplinary scientific exchange without abandoning an experts inventory of methods (Collet, 2012). This way, it may steer research collaborations across disciplines and beyond academia, which is requested by the goal of science policy to turn thoughts and resources to the *Grand Challenges* (e.g., ICSU, 2010; Swedish Presidency of the European Union, 2009). To fully exploit vulnerability as a bridging concept, it also should fit within the ecological sciences, to which this thesis contributed substantially.

To inform decision-making about risks resulting from impacts of global change, not only the consideration of expertise from multiple disciplines, but also the consideration of multiple interacting stressors is demanded (Schröter et al., 2005). Further, the ultimate goal of conservationists would be to assess an ecosystem's vulnerability to all stressors at work that eventually would lead to collapse. However, this may render vulnerability analysis inextricable complex. As long as the number and kind of stressors as well as the multiple interrelations between them are unclear, stressor-specific assessments are less uncertain. The integration of the results of different ecosystem vulnerabilities so far remains an open research issue. This endeavour may learn from sustainability impact assessments of policies, which offer a bundle of methods for the objective aggregation and synthesis of synergies and trade-offs between multiple policy options (Jacob et al., 2012; Miedzinski et al., 2013).

3.2. Advancing application: guiding nature conservation

Land use policies usually have to deal with trade-offs between competing land use options. Regulations apply for specific socio-ecological contexts and can only receive limited guidance from theoretical results of vulnerability research (Luers, 2005). To be useful, the level of complexity of the analysis and the communication of results need to be tailored for the audience of the vulnerability assessment report (Foden et al., 2019). Thus, the results of a biotope vulnerability assessment should provide site-specific scores without neglecting an overall interpretation (Frazier et al., 2014). The suggested biotope vulnerability index at the regional level is spatially explicit for every biotope patch. This involves a much larger computation effort compared to classical landscape metrics or vulnerability indexes on large spatial scales, which provide single numbers or scores for the whole study area. However, the increasing availability in processing power and partly automation in the analysis make the effort affordable for potential users of the biotope vulnerability indicator set. Once the vulnerability index has been calculated, a detailed analysis for certain biotope groups or a specific part of the map is relatively easy. Eventually, enabling large areas to be assessed resource-efficiently will play an essential role for usability, because detailed ecological assessments that are considered too expensive, are rarely used in conservation management (Henle et al., 1999).

The use of a spatially explicit index and the reliance on biotope data require a more territorial conservation perspective. However, this is neither the sole conservation approach nor endorsed by everyone, for good reasons. For example, only establishing nature reserves is potentially insufficient to safeguard particularly valued species and perhaps overly restricts other land use options.

From species protection to the conservation of biotopes

The denotation of a vulnerable species is well-known from the *Red List of Threatened Species* that has been published for more than 50 years by the International Union for Conservation of Nature. Historically, in nature protection great emphasis was given to the issue of species extinction, though the closely related problem of the extinction of local populations seems to be of similar importance (Ehrlich and Daily, 1993). Extinction risks of particular populations within a specific time frame are less uncertain than predictions of species extinction (Mace and Lande, 1991). The number of species going extinct should not distract from other indicators signalling biodiversity loss: dwindling population sizes and range shrinkages constitute a serious anthropogenic erosion of biodiversity. Indeed, this is documented for virtually all vertebrate species worldwide (Ceballos et al., 2017), and recently not only for certain invertebrate species groups (e.g., Conrad et al., 2006; Thomas et al.,

2004) but also generally across all flying insects (Hallmann et al., 2017). Hence, before going extinct, species usually become rare, i.e., decrease in abundance and shrink in range. Very rare species then are most vulnerable to extinction by laws of population dynamics. Very small population sizes are prone to inbreeding depression, stochastic (catastrophic) events, and where applicable insufficient interactions of individuals, like mating or cooperation. Further, rare species include those that may be locally abundant but are geographically highly restricted (Foden et al., 2013) and species rare locally but may be relatively common regionally (Margules and Usher, 1981). Thus, safeguarding any species' survival mandates to avoid them becoming overly rare and focussing on the persistence of its populations (Quammen, 1996).

However, such an endeavour relies on available habitat, especially in a time of increasing land use competition. This includes the ongoing spreading of anthropogenic impacts, like deforestation in the tropics (Hansen et al., 2013) or infrastructure expansion globally (Laurance et al., 2014), as well as the amplification of negative environmental impacts, for example, from agricultural intensification (Tilman et al., 2002). If habitat conservation is so essential to safeguard the earth's biodiversity, the main question is how to find the best sites or regions to establish protected area. Should it be the most vulnerable regions, reacting to occurring pressures; the most irreplaceable regions, following traditional conservation approaches; or even the lowly vulnerable regions, to render conservation proactive (Brooks et al., 2006)? A straightforward idea to prioritise conservation efforts was to focus on biodiversity hot spots, as 44 % of all species of vascular plants and 35 % of all species in four vertebrate groups are confined to only 1.4 % of land surface (Myers et al., 2000). This seems very efficient. Indeed, almost all schemes for evaluation of habitat and wildlife potential consider diversity to be of fundamental importance, though there are complications with the maximum local diversity approach. Emphasis on the sheer number of species is questionable when applied simplistically and irrespective of regional ecology, particularly in human-shaped areas (Noss, 1983). Splitting up habitat area or designing reserves of extremely heterogeneous habitat patches may boost diversity indexes but potentially erode the viability of ecosystems.

Another conservation claim, to set aside around 10 % of land globally, has been discussed to be sufficient to safeguard the world's terrestrial biodiversity (McNeely et al., 1994). Conservation efforts up to the beginning of the 21st century have led to as much as 11.5 % of protected area. Still, as the coverage varies widely geographically, the global protected-area system is far from complete (Brooks et al., 2004). So setting protected-area targets to 20 %? Or even to fanciful 50 %? A preoccupation with assigning half of earth to protected area still might achieve little for biodiversity conservation, as the remote, cold, arid, unproductive, and in particular also relatively species poor areas probably would be preferred (Pimm et al., 2018). Habitat protection then must be progressed despite uncertainty regarding priority areas, unless high rates of extinction are considered unacceptable (Martin et al., 2017).

The idea of setting aside tidy museum areas of nature for conservation purposes slowly gave way to the management of biodiversity on a larger spatial scale (Noss, 1995). This emphasizes the necessity to scale-up from methodological explorative research on small study areas to the regional level for application purposes.

It can be argued that the analysis of biotope vulnerability is complementary to the traditional conservation system based on species protection, as it turns from exploring population and species viability to the analysis of species assemblages and their habitats (De Lange et al., 2010; Ippolito et al., 2010). This pattern-oriented approach enhances the knowledge base on conservation issues derived from species-oriented approaches, especially in human-shaped landscapes (Fischer and Lindenmayer, 2007). The research on landscape patterns originates from island biogeography (MacArthur and Wilson, 1967) and the descendent conception of a mosaic landscape, which consists of demarcated habitat patches located within a 'background' matrix and potentially connected to other patches by corridors. Conservationist become increasingly aware, that precisely this matrix is not a hostile, appropriated piece of land but still habitat to plenty of species, ranging from often unknown protozoa and invertebrates in the soil to well-known vertebrates of cultural and urban lands. On the contrary, turning this often very large inter-biotope area into uninhabitable land for most animals probably is a major cause for the exacerbating decline in the abundance of many former common, rather generalist vertebrate and invertebrate species in the recent decades (e.g., Inger et al., 2015; Sánchez-Bayo and Wyckhuys, 2019). For many species, high intensity modern agriculture and forestry leads to a land of low forage value, unsuitable for breeding and with periodic lethal treatment, like mowing or pesticide application (Streitberger et al., 2018).

Due to the high temporal dynamic of biota and suppression of several natural dynamics, agricultural area often cannot be appropriately described by biotope mapping, with the exception of long-term (extensive) grasslands and meadows. It seems challenging to predict the ecology of landscape mosaics when those mosaics are constantly changing (Noss, 1995). A stable plant community – excluding repeating seasonal dynamics – seems to be a precondition to define biotopes (LUA, 2007), which then provide valuable information on biocoenosis and main abiotic conditions in addition to spatial distributions. Thus, the biotope vulnerability index excluded these patches from the evaluation. The indicators would have to be adapted in order to assess the vulnerability of arable land and intensive grassland. Perhaps those land use types need a fundamentally different ecological backing, as is the case for the aquatic ecosystems and highly regulated urban biotopes. Future research is needed to use the biotope vulnerability concept to guide management interventions also in these areas.

Nevertheless, even presuming a perfect, objectively derived, thematically fitting vulnerability map, any decision on a particular ecosystem management intervention will still depend on social and political values.

Ecological interventions and values

The biotope vulnerability analysis was developed to provide objective guidance to ecological interventions at the regional scale. In general, ecological interventions pursue two mutually exclusive goals: either conservation or restoration of nature. While nature conservation aims to preserve biodiversity and to stabilise ecosystem functions, ecological restoration intends to recover biodiversity and to revitalize ecosystem functions. In addition, the likelihood of success of different interventions and their associated costs are also important.

Given enough resources and effort, anything other than stark abiotic changes may theoretically be reversible. Still, restoration efforts on profoundly altered ecosystems are less effective and less efficient compared to slightly changed or semi-natural ecosystems (Hobbs et al., 2014). Thus, regardless of the theoretic and practical improvements in ecological restoration over the past decades (Jones, 2017), the conservation of undisturbed nature is central to successfully halt biodiversity loss. Moreover, the potential to repair should not ease ecosystem degradation by using restoration as argument to justify access to resources in undisturbed environments (Hilderbrand et al., 2005). Whether the lossless regeneration of something of equal value to the original ecosystem is possible at all, is a philosophical question (Elliot, 1982). However, where conservation has failed to sustain ecosystem functioning and to prevent major extinctions, restoration should be considered (Palmer et al., 2004). In doing so, ecologically-designed restoration is preferable, as technological fixes to maintain ecosystem processes, like water purification or hand pollination, being an expensive and often ineffective alternative (Palmer et al., 2016).

Whether restoration or conservation of nature, both should not only adress threatened species, but also impaired ecosystem functions. But preserving nature in a desired state is in contrast with dynamic conservation focused on keeping natural processes working. The ideal of cultural landscapes stands opposite to the idea of wilderness. Obviously, different conservation narratives compete with each other. On the other hand, they are also used jointly as justification for nature conservation action (Hertog and Turnhout, 2018). So how much intervention is permissible or even indispensable?

The answer depends on the definition of the target state of the ecosystem that seems worth of protection or goal of recovery. The problem amounts to the question of reference conditions. Admittedly, the literature is remarkably inconsistent on this topic. Selecting the reference condition is a multifaceted problem relying either on historical records, paleoecological data, quantitative models, best professional judgment, or extant reference sites (Rohr et al., 2018). The disagreement on reference conditions reflects the roots of restoration ecology in different ethical reasoning. However, restoration ecology increasingly follows a utilitarian approach requiring restoration for multiple uses (Paschke et al.), similar to the concept of multifunctionality in any kind of land use (Huang et al., 2015; Pasari et al., 2013; Wiggering et al., 2003). It could be considered an advantage of the biotope vulnerability concept that it is not at all dependent on reference conditions, but uses the conservation status and spatial configuration of the biotopes at the time of assessment.

It seems that the justification of intervention level cannot be resolved on a purely scientific basis. It depends on the varying valuation of different aspects of nature. Considering the pristine state of nature the ultimate goal, with all pristine biotopes of equal importance to conservation, would emphasise the existence value of each and every species. On the contrary, considering the use value of nature as guiding principle emphasises cultivated ecosystems. The present non-native species and the substantial benefits obtained from them perhaps are valued more than native species (Brussard et al., 1998). The concept of ecosystem services has been developed on the central idea, that people obtain benefits from ecosystems (MEA, 2005). In this environmental economics' perspective, investments in both, conservation and restoration are viewed to generate substantial ecological, social and economic benefits at once (de Groot et al., 2010). In other cases, invasive species may be fought hard due to their negative impact on native and often endemic species of high conservation value (e.g., Misso and West, 2014) or on intended land use (e.g., Hulme, 2012).

In fact, different species are differently valued by people, adding direct and indirect use values to intrinsic values of species existence (Pascual et al., 2010). Conservation practice embraces concepts like flagship or umbrella species, indicating a hierarchy of bestowed attention, protection laws, and financial resources.

Overall, the degree of vulnerability could be of secondary importance if a biotope is not considered valuable or worthy of protection. Vice versa, a biotope may receive much conservation resources regardless if it is actually vulnerable or not.

4. Conclusion

Sustainable land use systems need science-based information on the natural and semi-natural parts of a landscape to estimate to which degree a certain land use endangers ecosystem persistence. The biotope vulnerability assessment was developed to provide advice for landscape planning and conservation management regarding priority areas in face of habitat loss and fragmentation. It supports the application of the precautionary principle to avoid unintended environmental impacts after land use changes, including cumulative degradation effects.

The biotope vulnerability index was established on the basis of the vulnerability framework, which is applicable in various research topics and disciplines. However, its large potential to function as a boundary object across research disciplines has so far been limited in the ecological sciences. A major advancement of the thesis is to conceptually embedding the notion of ecosystem vulnerability in the fields of ecology, especially landscape ecology and ecosystem science.

A spatial and thematic cluster analysis of the biotope vulnerability index applied at the regional level finally provided ecological and conservation implications of the so far rather intangible concept of ecosystem vulnerability.

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Author’s declaration

I prepared this dissertation myself and without any illegal assistance. The work is original except where indicated by references in the text and no part of the dissertation has been submitted for any other degree.

This dissertation has not been presented to any other university for examination, neither in Germany nor in any other country.

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