META-POPULATIONS UNDER MULTIPLE STRESSOR RISKS

SIMULATION STUDIES USING A NEW PROCESS-BASED, SPATIALLY EXPLICIT MODEL

by

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‘Look deep into nature, and then you will understand everything better.’

Albert Einstein, 1951

CONTENT

Within Sections 2-4, the numbering of the subsections and the REFERENCES subsection correspond to the entries in the respective original paper.

ACKNOWLEDGEMENTS

I thank all the people who supported me during my Ph.D. time.

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LIST OF PUBLICATIONS

The present thesis is a cumulative dissertation based on the following papers, two peer-reviewed (1 & 2) and one in preparation (3):

1. HOW DOES HABITAT CONNECTIVITY INFLUENCE THE COLONIZATION SUCCESS OF A HEMIMETABOLOUS AQUATIC INSECT? - A MODELING APPROACH
2. SPACE DRIVES SYNERGISM OF LAND USE AND CLIMATIC EXTREME EVENTS IN INSECT META-POPULATIONS
3. THE SPATIOTEMPORAL PROFILE AND ADAPTATION DETERMINE THE JOINT EFFECTS AND INTERACTIONS OF MULTIPLE STRESSORS

SUMMARY

Biodiversity is declining at an accelerating rate unprecedented in human history. Globally, most ecosystems are at high risk from multiple stressors related to anthropogenic global change, including climate change and land use change. Distinct stressors often co-occur in time and space, so joint effects are not only a result of individual severity or the speed of change but also of how they interact. To estimate and address (future) risks from intensified stressor regimes, it is needed to best understand the mechanisms of stressor joint effects and interactions. However, research on the topic is not well developed yet and current knowledge is relatively low.

In the context of this thesis, the lack of (theoretical) knowledge will be reduced. Chapter 1 provides a brief introduction outlining the need for the presented research and the overall objectives of the thesis. Chapter 2 introduces a new process-based, spatially explicit meta-population model for a generic freshwater species which was applied to investigate how decreasing landscape permeability and fragmentation following global change will impact species meta-populations. It is shown that global change likely increases extinction risks by reduced habitat connectivity, however, management actions to enhance patch density can strengthen meta-populations resilience. Chapter 3 presents an extended version of the meta-population model, used to investigate how two stressors (i.e., climatic events and land use) with different spatiotemporal profiles combine over time. It was found that joint effects and interactions were mainly determined by land use, demonstrating the effectiveness of regional management to compensate for an intensified global stressor. Following on, Chapter 4 explores potential changes from more realistic scenarios, by incorporating dynamic stressor profiles (i.e., random climatic events and land use trends over time) plus adaptation into the model. It is highlighted that such complex scenarios are critical for understanding how species respond to global change, as simplified static scenarios are likely insufficient for reliable prediction of joint effects and interactions. Finally, chapter 5 briefly concludes the key findings of chapters 2-4,

discusses the limitations of the individual studies' approaches and gives a brief general outlook.

Overall, the presented thesis provides new insights into the mechanistic understanding of joint effects and interactions of multiple stressors and, thereby, contributes to extending the conceptual framework of related research.

1. INTRODUCTION AND OBJECTIVES

1.1 ANTHROPOGENIC GLOBAL CHANGE

Biodiversity loss, i.e., the extinction of species, is a natural process in Earth's history (Payne et al., 2023). Fossil records reveal most evolved species became extinct over the past 600 million years, with five major mass extinction events (i.e., a period of > 75 % species extinction) to date (McCallum, 2015; Tynan, 1986). Today, the Earth is facing the beginning of a new, sixth mass extinction (Ceballos et al., 2020; Raven and Wagner, 2021), however, unlike the previous, it is not of natural origin, rather it is driven by anthropogenic activities (Ceballos et al., 2020; Simmons et al., 2021a). Anthropogenic global change, i.e., climate change, land use change, pollution, invasive species, or resource overexploitation (Pievani, 2014; Sage, 2020), has put biodiversity and thus ecosystems worldwide under increasing pressure since the start of the Anthropocene (Brooks and Crowe, 2019). The pressure intensified continuously over the last 10,000 years, so the decline in vertebrate biodiversity since the 1500s (with a sharp increase since the 1980s) can be compared to prior mass extinctions (Ceballos et al., 2015; McCallum, 2015). Analogous trends can be observed in invertebrate species; e.g., sharp declines in insect biomass and diversity have been observed since the 1950s in Europe and the USA (Raven and Wagner, 2021).

If the current rate of biodiversity loss continues, many ecosystems will be severely damaged or disappear (Ceballos et al., 2015). Next to the general importance for Earth's life itself, ecosystems provide diverse services for human society, which are critical to mental and physical well-being, so the decline of ecosystems poses serious risks (Guerry et al., 2015; Sage, 2020). Fortunately, many drivers of anthropogenic global change that threaten Earth's biodiversity can (albeit increasingly less) likely still be moderated (Sage, 2020). Yet, optimal planning and realization of management to address future, related risks requires a clear mechanistic understanding of the drivers, to determine how related stressors impact ecosystems (Jackson et al., 2018).

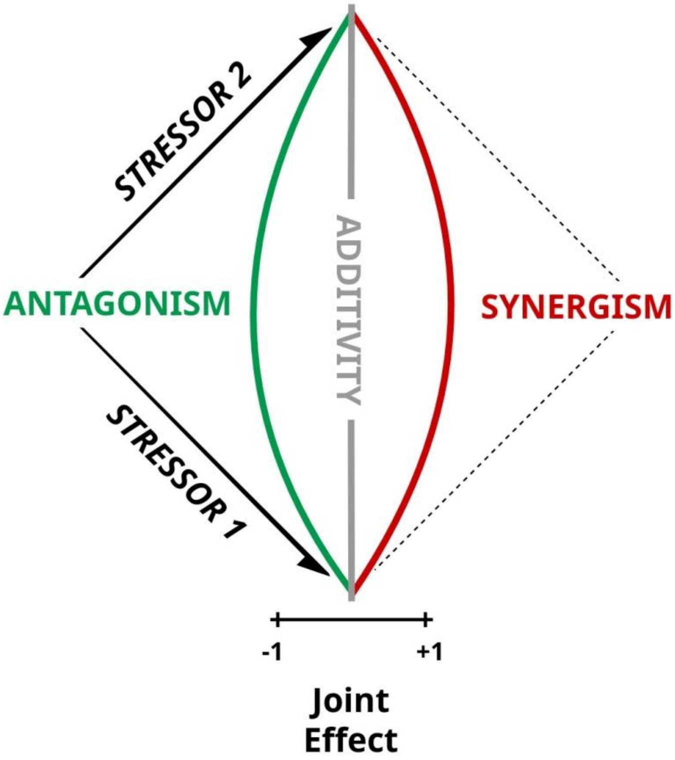

Figure 1: Schematic isobologram for interactions of a two-stressor combination. The axes represent the strength of stressors 1 and 2, respectively; the lines represent possible joint effects resulting from the combined stressors. The following interactions result: *Additivity* exists when the joint effect is equal to the sum of the individual effects of stressors 1 and 2 (grey line); when the joint effect is lower (green line), i.e., the biological response is less than the additive effect, *antagonism* emerges; and when the joint effect is higher (red line), *synergism* emerges.

Stressors frequently co-occur at different spatial and temporal scales, therefore optimizing prediction of joint effects and resulting interactions is critical to counteract ecosystem risks linked to global change (Jackson et al., 2021). Particularly, as multiple co-occurring stressors interact not only in additive effects (joint effect = sum of individual effects) but also in non-additive effects (Fig. 1), i.e., antagonisms (joint effect < sum of individual effects) or synergisms (joint effect > sum of individual effects)(Birk et al., 2020; Côté et al., 2016). Non-additive effects can result from mechanistic stressor interactions (i.e., one stressor modifies an organism’s response to another stressor), but also from other factors (e.g., nonlinear stressor-response relationships) (Hunsicker et al., 2016; Schäfer and Piggott, 2018; Turschwell et al., 2022). Synergisms resulting in rapid, disproportionate losses of biodiversity and ecosystem functions are particularly dangerous and a key problem in multiple stressor environments (Côté et al., 2016; Ratajczak et al., 2018; Turner et al., 2020). In the future, synergies are expected to occur more frequently and with higher intensity driven by anthropogenic global change (Jackson et al., 2021; Sage, 2020; Woodward et al., 2016).

1.2 MULTIPLE STRESSOR RESEARCH

Research on multiple stressors has been present in the scientific community for nearly a century and aims to understand and predict how stressors interact and the potential risks to individual organisms or populations (Orr et al., 2020). It is rapidly evolving in the face of global change and gained importance in ecology in the last two decades, and has now expanded to a wide range of stressor combinations (Bruder et al., 2019; Orr et al., 2020). Thereby, it revealed that the combined effect of two or more stressors is frequently non-additive, i.e., stronger (synergistic) or weaker (antagonistic) than predicted based on the individual effects (Piggott et al., 2015; Schäfer and Piggott, 2018); yet high variability emerged in the prevalence of antagonistic or synergistic interactions (Schäfer and Piggott, 2018). Past research in the field of multiple stressors was largely specific to either freshwater, marine, or terrestrial ecology (Orr et al., 2020) and tended toward non-interacting stressors in isolation or focused on single events of stressor co-occurrence at the local scale (Brooks and Crowe, 2019; Jackson et al., 2021; Simmons et al., 2021a). Moreover, experimental multiple stressor studies often used simplified, non-realistic stressor scenarios, resulting in distorted, if not incorrect, assessments of joint stressor effects and interactions if extrapolated on real-world situations (Catford et al., 2022; Rillig et al., 2021). Therefore, related research did not or insufficiently incorporate spatiotemporal stressor dynamics, temporally non-consistent stressor-response relationships, and/or biotic processes in ecological networks developing over space and time across ecosystems (Bruder et al., 2019; Jackson et al., 2021). It reveals that knowledge of multiple stressors to date is still relatively low (Bruder et al., 2019;

Jackson et al., 2021) and appears to be incomplete for longterm predictions at higher ecological scales, e.g., ecosystems (Brooks and Crowe, 2019).

Meta-analyses of experimental studies with multiple stressors have yielded limited consistent findings (Côté et al., 2016; Simmons et al., 2021b). Another shortcoming of most previous research on multiple stressors is that adaptation processes of organisms, through phenotypic plasticity (Bush et al., 2016) or the evolution of life-history traits (Orr et al., 2021), have been largely ignored (Boyd et al., 2018; Orr et al., 2021; Ryo et al., 2019). Adaptation can reduce species' vulnerability to intensifying stressors so that lower effects can be expected, relative to ignoring it (Jackson et al., 2021; Patrick et al., 2021). Moreover, multiple stressors research also has been criticized for emphasizing interaction classification, thereby neglecting mechanistic understanding of joint effects (De Laender, 2018; Griffen et al., 2016).

Process-based models building on a theoretical understanding of ecological processes (transformed into mathematical formulation) provide opportunities to fill the knowledge gap (Jørgensen, 1994; Pirotta et al., 2022). Such process-based models may have the potential to provide general insights into ecological responses to novel, future environmental conditions and improve mechanistic understanding of multiple stressors across scales (Jackson et al., 2021; Turschwell et al., 2021). Unlike data-based models, which rely on much empirical information to analyze existing relationships between stressors and effects to identify and categorize interactions but have limited predictive power beyond the observed of these, process-based models have very high predictive power (Baker et al., 2018; Jager et al., 2014; Pirotta et al., 2022). Therefore, they can assist future management and optimize species conservation (Oliver and Morecroft, 2014; Patrick et al., 2021; Turschwell et al., 2022), as they can account for future risks (not yet present) from anthropogenic change beyond the range of observed stressors (Pirotta et al., 2022).

In recent decades, various types of process-based models have been used to simulate joint effects of multiple stressors mechanistically; e.g., dynamic energy budget models (DEB) to capture energy flows for specifying the level at which multiple stressors operate on an individual organism (Jager et al., 2014) or individual-based models (IBMs) to simulate how individual agents, characterized by internal state variables, interact with dynamic multiple stressors over time (Pirotta et al., 2022). In this context, also meta-population models have been developed to analyze future risks on populations by multiple stressors at the regional landscape level, taking into account population dynamics and dispersal in ecological networks (Saura et al., 2014). Yet, meta-population models are largely limited to purely terrestrial (e.g., Bocedi et al., 2014; Lakovic et al., 2017) or purely freshwater species (Anderson and Hayes, 2018; e.g., Van den Brink et al., 2007), but are scarce for species that rely on both aquatic and terrestrial habitats to complete their life cycles. Here, dispersal is not restricted to one habitat, but depends on the life stage (Tonkin et al., 2018); and meta-population structure is determined by the environmental suitability of the terrestrial habitat, but also by the spatial configuration of the aquatic habitat - specifically, for streams or rivers, its dendritic structure (Anderson and Hayes, 2018; Tonkin et al., 2018). This shortage makes it difficult to predict how multiple stressors associated with anthropogenic global change will affect such species. E.g., models are entirely lacking for freshwater hemimetabolous insects, which represent the largest group of aquatic insects (~ 2/3 of freshwater animal diversity), thus often play a central role in food webs and contribute strongly to nutrient transfer between aquatic and terrestrial habitats (Grigoropoulou et al., 2023). In addition, roughly 1/3 of freshwater hemimetabolous insect species are classified as threatened by global change, putting pressure on aquatic but also terrestrial communities (Grigoropoulou et al., 2023).

1.3 OBJECTIVES AND OUTLINE

This thesis seeks to improve our knowledge of how multiple stressors associated with anthropogenic global change operate across space and time. Thereby, it is intended to contribute to the mechanistic understanding of the effect of multiple stressors in real-world environments (with a focus on freshwater hemimetabolous insect species) by highlighting and explaining general principles. The effects of (i.) modified (multiple) stressor regimes (ii.), associated complex spatiotemporal dynamics, and (iii.) adaptation of organisms under global change were specifically investigated.

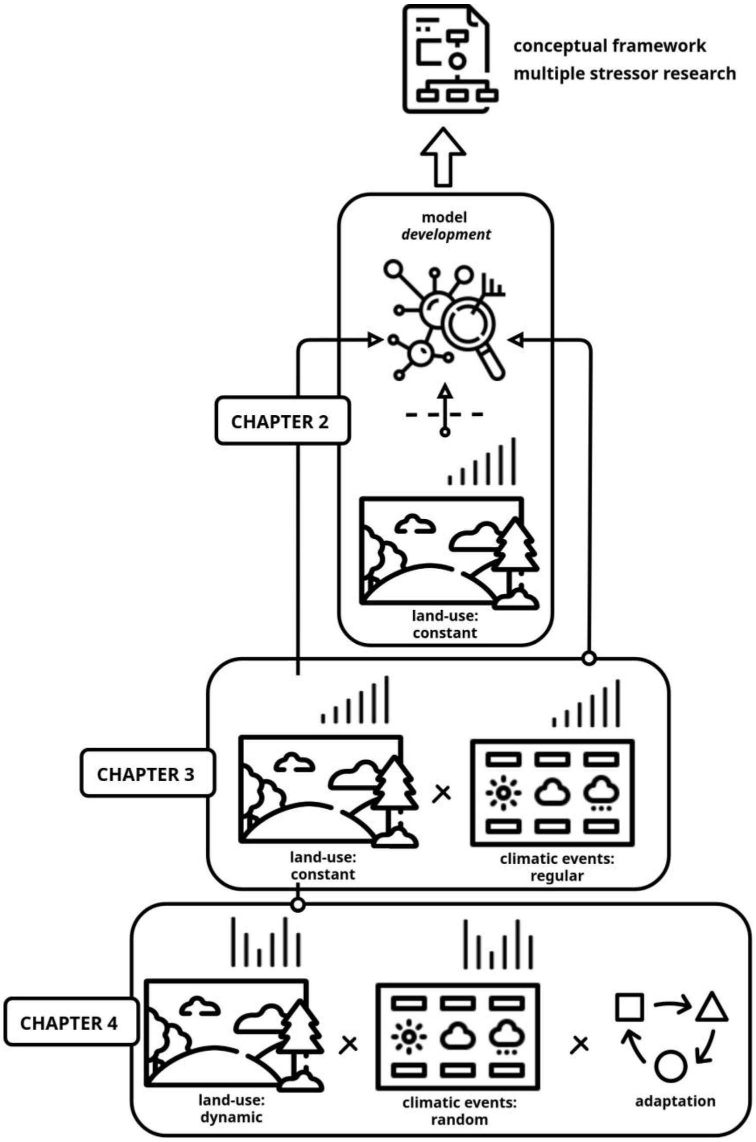

Figure 2: Conceptual overview of the structure of the research process underlying this thesis. The conceptual framework of multiple stressors research will be progressively expanded based on the work described in Chapters 2-4 by increasing the complexity and realism of the model scenarios.

A new process-based, spatially explicit meta-population model for a generic hemimetabolous freshwater insect, parameterized based on the traits of the damselfly *Coenagrion mercuriale*, was developed. As conceptually structured in Figure 2, the model was then applied to scenarios of multiple stressors that increased in complexity and realism. Chapter 2 introduces the model's underlying framework and, moreover, investigates how land use change impacts habitat connectivity and the resulting risks to species meta-populations. In this regard, the model was applied for varying stream networks and patch assemblages under different land use scenarios associated with varying landscape permeability and fragmentation. Chapter 3 presents an extended version of the meta-population model to examine how a discrete stressor and a continuous stressor with different spatiotemporal profiles combine over time. Scenarios of repetitive climatic events (the discrete stressor) with fixed frequency were added to the model, and the temporally constant land use (the continuous stressor) also determines patch qualities in a meta-population network, in addition to connectivity. In Chapter 4, a follow-up to the previous chapters is presented to further improve the mechanistic understanding of stressor interactions across scales. Redesigned scenarios reflect dynamic stressor profiles, featuring land use shifts in varying trends over time, and climatic events in random sequences, moreover, adaptation now translates into mitigation of climatic events.

We expect the present thesis to contribute to optimizing the planning and implementation of future management by expanding the conceptual framework of multiple stressor research, helping to counteract the risks of anthropogenic global change to the Earth's threatened biodiversity.

2. HOW DOES HABITAT CONNECTIVITY INFLUENCE THE COLONIZATION SUCCESS OF A HEMIMETABOLOUS AQUATIC INSECT? - A MODELING APPROACH

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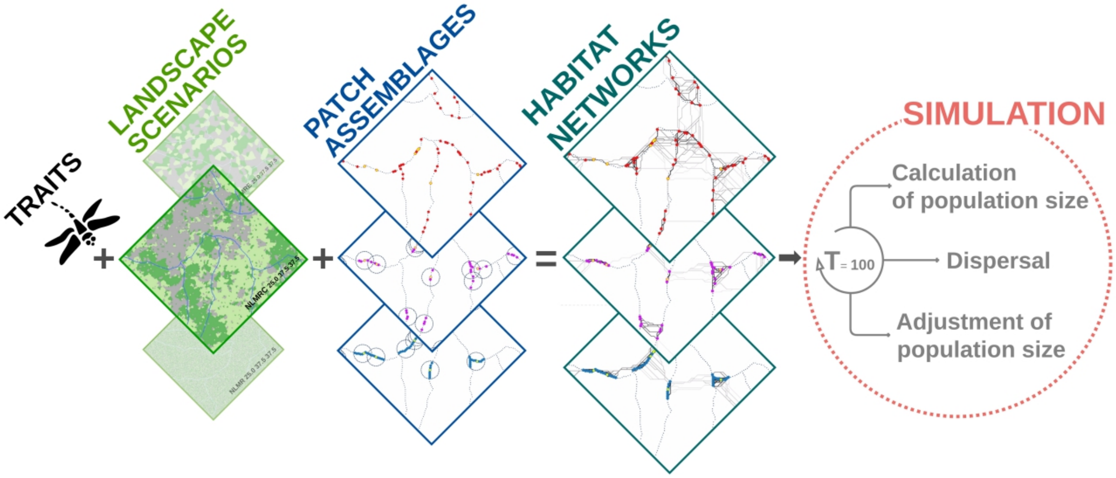
GRAPHICAL ABSTRACT



HIGHLIGHTS

- Process-based meta-population model for hemimetabolous freshwater insects
- Analysis of how habitat connectivity affects patch colonization
- ANOVA of key habitat parameters
- Patch colonization success strongly influenced by habitat connectivity
- Habitat patch number most important, followed by landscape permeability

ABSTRACT

Climate and land-use change constitute major threats to biodiversity. Beside pure habitat loss, changing environmental conditions are likely to result in decreasing landscape permeability and increasing landscape fragmentation. This compromises habitat connectivity and, thereby increases threats to meta-population persistence. Comprehensive theoretical knowledge and general understanding of key parameters affecting habitat connectivity are therefore mandatory to assess risks of environmental change. However, related studies are scarce for hemimetabolous freshwater insects, which depend on both aquatic and terrestrial sites to complete their life cycle.

We developed a process-based, spatially explicit meta-population model for a hemimetabolous freshwater insect, parameterized based on the traits of a damselfly, and analyzed the influence of varying landscape permeability on patch colonization for differently structured coextensive habitat networks. The in total 675,000 networks were set up by varying (1) landscape scenarios, representing different levels of permeability, (2) stream networks and (3) derived habitat patch assemblages, using least-cost path analysis.

We found that habitat connectivity in general strongly determined the proportion of colonized habitat patches (Spearman’s ρ = 0.64). Moreover, a multi-factorial ANOVA of the parameters used for habitat network set up showed that the number of habitat patches had the largest effects on the colonization success

(18.6 % explained variance) followed by varying proportions of three landscape types incurring increasing dispersal costs (13.1 %) and the spatial arrangement of habitat patches (7.1 %).

The introduced model generated theoretical knowledge how changing environmental conditions (e.g. landscape permeability) can influence the habitat connectivity of hemimetabolous freshwater species and, thus, has the potential to support conservation through habitat management within changing landscapes. Its design facilitates future adaptation to real hemimetabolous species and real-world habitats.

KEYWORDS

Dispersal · Environmental change · Habitat network · Landscape permeability · Meta-population · Spatial ecology

1. INTRODUCTION

Climate and land-use change constitute major threats to biodiversity resulting in pure habitat loss and in decreasing landscape permeability (Lechner et al., 2017; Titeux et al., 2016; Vos et al., 2006) and, in turn, in increasing landscape fragmentation (Hanski, 2011; Opdam and Wascher, 2004; Wilson et al., 2016). This situation jeopardizes the persistence of meta-populations because these rely on the capability of individuals to disperse between subpopulations and to recolonize extincted patches (Bocedi et al., 2014; Moilanen and Nieminen, 2002). Extinction risks of local subpopulations or whole meta-populations, therefore, increase if subpopulations become unconnected and extirpated patches inaccessible (Chisholm et al., 2011; Heino et al., 2017; Wilson et al., 2016). Knowledge of spatial conditions affecting habitat connectivity (Didham et al., 2012; Purse et al., 2003; Saura et al., 2014) consequently is fundamental for habitat management of species affected by environmental change (Laita et al., 2011; Wilson et al., 2016).

Process-based models building on theoretical understanding of ecological processes (transformed into mathematical formulation) can provide general insights into ecological responses to novel, future environmental conditions (Cuddington et al., 2013; Evans et al., 2012; Petchey et al., 2015). One advantage of such models, as compared to statistical or rule-based, explanatory models based on past empirical data is the ability to forecast the effects of changing environments (Cuddington et al., 2013; Evans, 2012; Gustafson, 2013; Urban et al., 2016). Given that process-based models rely on causal relations based on ecological theory rather than on correlations within past data sets, they can facilitate general understanding of ecological processes, especially under novel environmental conditions (Evans, 2012; Marquet et al., 2014).

Accordingly, process-based, spatially explicit meta-population models are useful tools to study species dispersal (Hanski, 1989; Saura et al., 2014). They can be used to quantify the theoretical importance of habitat parameters on the capacity of species to disperse between suitable habitat patches (Hanski, 1989; Urban, 2005) and, in turn, to analyze potential risks to meta-population persistence under changing environmental conditions. The key habitat parameters in the context of connectivity have been identified as (1) landscape permeability, (2) the spatial arrangement of habitat patches and (3) habitat patch number, since those determine, in combination with species-specific dispersal traits, the overall habitat connectivity (Fahrig and Merriam, 1994; Luque et al., 2012). Nevertheless, the relative importance of those parameters and their interactions on meta-population persistence is uncertain and under discussion (Doerr et al., 2011; Hodgson et al., 2011; Villard and Metzger, 2014).

Over the last decades, multiple meta-population models have been developed. However, these are often site-specific and largely restricted to fully terrestrial (Bocedi et al., 2014; e.g. Heino and Hanski, 2001; Lakovic et al., 2017) or fully freshwater species (Anderson and Hayes, 2018; e.g. Van den Brink et al., 2007), i.e. species that complete their life cycle entirely in one ecosystem. Freshwater and terrestrial species differ strongly in terms of the factors that determine their dispersal and the spatial structure of their meta-populations. For instance, the dispersal of freshwater species without terrestrial life stage is restricted to the stream network and influenced by its permeability (Tonkin et al., 2018b). The number of habitat patches and their arrangement is determined, besides the general environmental suitability, by the dendritic stream structure (Anderson and Hayes, 2018; Eros and Campbell Grant, 2015; Tonkin et al., 2018a). By contrast, the dispersal of most fully terrestrial species as well as the number and arrangement of their habitat patches is generally less restricted by specific spatial structures. The dispersal depends mainly on the landscape permeability (Eros and Campbell Grant, 2015; Lechner et al., 2017, 2015), whereas, the number and arrangement of habitat patches is mainly determined by the environmental suitability of a landscape (Hodgson et al., 2011; Purse et al., 2003).

Insects are among the organisms that have suffered a strong decline in biomass in the last decades (Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019; Simmons et al., 2019). However, spatially explicit meta-population models for hemimetabolous freshwater insects, which constitute the largest group of aquatic insects, are lacking. This impedes our capacity to forecast how changing environmental conditions will impact these species, which rely on suitable aquatic stream sites for larval development but primarily disperse and mate in the terrestrial system.

We developed a hypothetical process-based, spatially explicit meta-population model for a hemimetabolous freshwater insect, parameterized based on data of the European damselfly *Coenagrion mercuriale*.

We simulated population dynamics and dispersal processes within multiple generic habitat networks, starting with an initial configuration of fully colonized habitat patches. The habitat networks were set up by varying the key habitat parameters determining habitat connectivity: (1) Levels of landscape permeability were simulated using artificial landscapes with different proportions and spatial configurations of four landscape types combined with (2) different arrangements and quantities of habitat patches along multiple stream network structures. Finally, we used the habitat patch occupancy after a simulation run as an indicator of the colonization success.

Consistent with meta-population theory (Hanski, 1999; Leibold et al., 2004; e.g. Moilanen and Nieminen, 2002) we expected that the colonization success in our model would be strongly related to habitat connectivity. Furthermore, we investigated the relative importance of the parameters (1) proportion and (2) configuration of landscape types determining landscape permeability as well as the (3) stream network structure, the (4) habitat patch proportion and (5) arrangement on the colonization success of a hemimetabolous freshwater insect.

To our knowledge, this is the first study combining a high number of landscape and habitat scenarios, and examining their influence on population persistence, in particular for hemimetabolous freshwater insects.

2. MATERIAL & METHODS

The core parts of the presented process-based, spatially explicit meta-population model are: the derivation of habitat networks (see Figure 1 - A) and the simulation of population dynamics and dispersal (see Figure 1 - B).

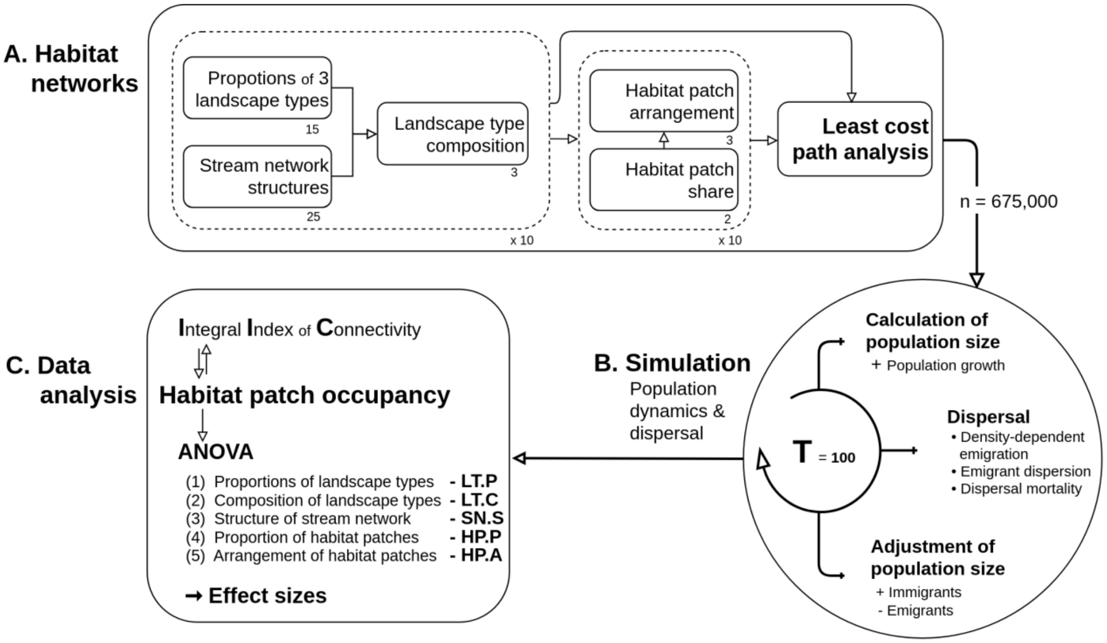


Figure 1: Flow chart of the meta-population model (**A** & **B**) and the data analysis approach (**C**). **A**: derivation of the habitat networks (**n** = 675,000) using a least-cost path analysis - each parameter is labeled below according to its number of levels. Dotted boxes represent the intermediate steps 'Landscape scenarios' (see Section 2.1.1) and 'Habitat scenarios' (see Section 2.1.2) and are labeled below according to the number of implemented replications per step. **B**: three steps composing the simulation of 'Population dynamics & dispersal' (see Section 2.2). **C**: final habitat patch occupancy (1) compared to the ecological network connectivity measure 'Integral Index of Connectivity' (see Section 2.3.1) and (2) used to investigate the relative importance of the habitat parameters on the results (ANOVA; see Section 2.3.2).

2.1 Habitat Networks

We created multiple habitat scenarios that were set up by the following habitat parameters: (1) landscape type proportions (*LT.P*), and their (2) spatial configuration (*LT.C*), determining landscape permeability, (3) stream network structure (*SN.S*), (4) proportion (*HP.P*) and (5) spatial arrangement (*HP.A*) of suitable aquatic habitat patches. Using least-cost path analysis (Adriaensen et al., 2003) these habitat scenarios were converted into habitat networks. The habitat networks (in total 675,000) served as input for the simulation of population dynamics and dispersal (see Section 2.2; see Figure 1 - B).

2.1.1 Landscape scenarios: Proportions and configurations of landscape types

We used neutral landscape model (NLM) algorithms (Etherington et al., 2015) to create multiple artificial landscapes with different levels of landscape permeability. Each of the produced landscape rasters had an extent of 50 km x 50 km and an initial resolution of 25 m x 25 m per pixel.

The artificial landscapes were set up with varying (1) proportions and (2) configurations of three initial landscape types (LT) incurring increasing dispersal costs (LT 1 = 50, LT 2 = 75, LT 3 = 100; see Section 2.4.1). LT 1 represents 'open agricultural land', LT 2 'forestry' and LT 3 'urban area'. To investigate the effect of increasing costs on dispersal we varied the proportion of each landscape type from 0 to 100 % in steps of 25 % - the remaining proportion was accordingly distributed equally between the other two landscape types. Furthermore, to determine the effect of the landscape configuration on dispersal the differing landscape type proportions were spatially distributed in three forms using the NLM algorithms 'random', 'random element nearest-neighbour' and 'random cluster nearest-neighbour'. The NLM algorithm 'random' created landscape rasters without spatial auto-correlation, each pixel was independently assigned a landscape type (see Figure 2). The algorithm 'random cluster nearest-neighbour' created landscape rasters with unevenly sized and highly fragmented landscape type clusters (Etherington et al., 2015; Saura and Martínez-Millán, 2000). Landscape rasters produced by the algorithm 'random element nearest-neighbor' consisted of irregularly shaped but evenly sized and highly aggregated landscape type clusters (Etherington et al., 2015).

To furthermore include a realistic stream network structure into the artificial landscapes we used a section of a stream network from South-West Germany (GeoPortal.rlp2017). Each raster-pixel intersecting a stream segment was classified as LT 4 'aquatic' and assigned with the lowest dispersal cost value of 25 reflecting the tendency of many freshwater insects to disperse along the stream corridor (Hallmann et al., 2017; Masters et al., 2007; Milko et al., 2012; Tonkin et al., 2018a).

However, these interim artificial landscapes (see Figure 2 A. - C.) would be characterized by sharp edges and omit edge effects in the transition zone between different landscape types, with potentially reciprocal influence of the types on each other, e.g. modification of micro-climate, resource availability (Fahrig (2017); Fischer and Lindenmayer (2007)). We conceptualized that adverse and beneficial edge effects (resulting in in- and decreased environmental stress) to reduce and extend the capacity to disperse in affected areas, respectively.

To account for edge effects in the model, we resampled all rasters to a new pixel-size of 100 m x 100 m (see Figure 2 D. - F.) using the resampling algorithm ‘gdalwarp’ of the Python package ‘GDAL 3.0.2’ with the method ‘average’ (GDAL/OGR, 2018). Thereby, each pixel of a resampled raster is assigned with the average cost of the (25 m x 25 m) pixels of the underlying interim ‘non-resampled’ raster it covers.

Finally, we split each artificial landscape raster in 25 tiles of 10 km x 10 km to represent a wide range of stream network structures SN.S in terms of stream segments with varying densities and configurations. The resulting rasters are hereafter defined as landscape scenarios.

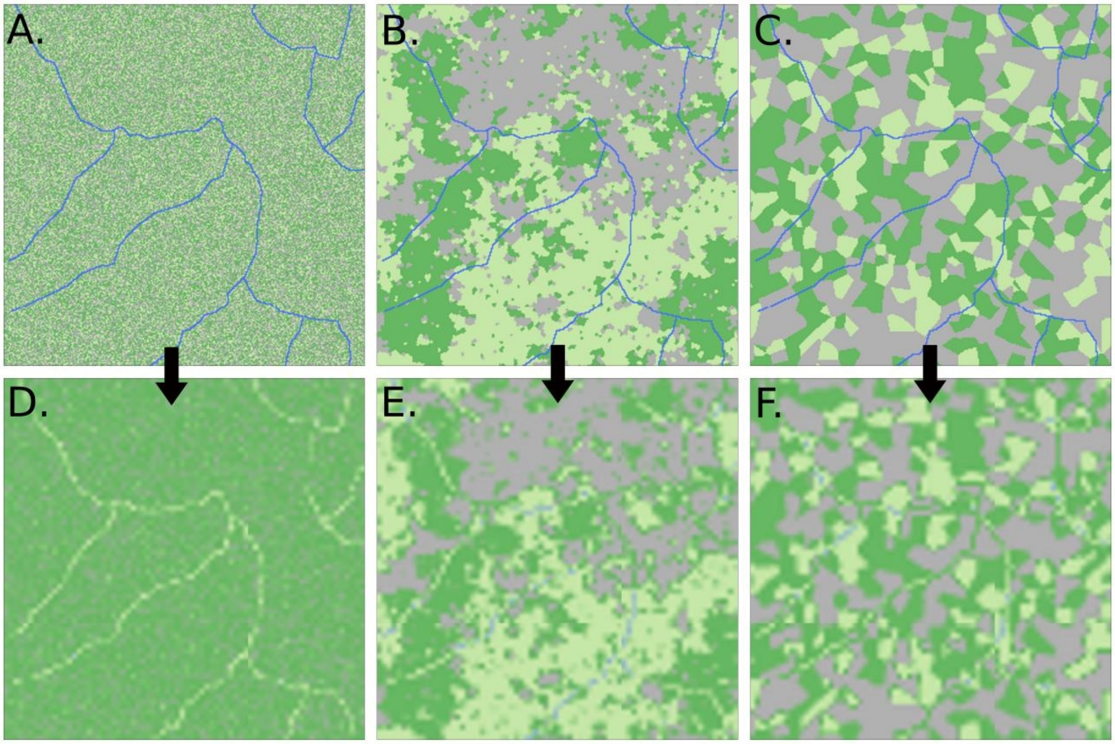


Figure 2: Examples of landscape scenarios created by the neutral landscape model algorithms ‘random’ (A. & D.), ‘random cluster nearest-neighbour’ (B. & E.) and ‘random element nearest-neighbour’ (C. & F.) for a proportion of 25 % of landscape type 1 and a proportion of 37.5% of landscape type 2 and 3 each. A. - C.: Interim ‘non-resampled’ rasters with a pixel-size of 25 m x 25 m. Light-green pixels represent landscape type 1 ‘open agricultural land’ (50 cost units), dark-green pixels landscape type 2 ‘forestry’ (75 cost units), gray pixels landscape type 3 ‘urban area’ (100 cost units) and blue pixels represent landscape type 4 ‘aquatic’ (25 cost units). D. - F.: Resulting ‘resampled’ rasters with a pixel-size of 100 m x 100 m. Pixel values correspond to the average dispersal costs resulting from resampling the underlying interim ‘non-resampled’ raster. Pixels are visualized by a continuous color scheme from dark-blue (25.0 cost units) over light-green (50.0 cost units) and dark-green (75.0 cost units) to gray (100.0 cost units).

2.1.2 Habitat scenarios: Patch arrangement and initial source patches

We assumed that only a fraction of the stream network provides suitable conditions for the modeled species. Suitable habitat patches within the landscape scenarios were selected based on a given proportion of 10 or 20 % pixels of the landscape scenarios intersecting the corresponding SN.S using three approaches (‘random’, ‘random around centers’ and ‘contiguous around centers’; see Figure 3).

The approach ‘random’ randomly assigned the relevant percentage of all eligible pixels as habitat patches. The approach ‘random around centers’ selected 5 % of all eligible pixels as centers and then arranged the remaining pixels randomly within a radius of 500 m around each of these centers along the stream network. The same principle was used for the approach ‘contiguous around centers’ except that only 2.5 % of all eligible pixels are selected as centers resulting in a more contiguous arrangement of the remaining habitat patches.

To provide comparable results among the different approaches, we defined identical initial (fully colonized) source habitat patches for habitat scenarios based on equal landscape scenarios and patch shares (Figure 3). To decrease the variability and given our focus on landscape connectivity and related landscape variables, we further assigned a constant habitat quality (HQ = 0.625) to all habitat patches, though habitat quality likely varies in heterogeneous landscapes (Brink et al., 2013; Ye et al., 2013) and along streams.

2.1.3 Least-cost path analysis

Dispersal of the hemimetabolous freshwater insect in our model is not restricted to the stream network, it predominantly occurs overland by aerial movement (Tonkin et al., 2018a).

To set up the final habitat networks for each habitat scenario we first determined all possible connections of a habitat patch x with all other patches y (where $x \neq y$) that exhibit an euclidean distance less or equal to the maximum dispersal distance Γ_{Dmax} of 2500 m through open agricultural land (see Table 1; see Section 2.4.1).

Second, all possibly connected patches within a habitat scenario in combination with the corresponding landscape scenario served as input for the least-cost path analysis (Galpern et al., 2011; Lechner et al., 2017). The analysis identified the connection exhibiting the minimal dispersal cost between two connected habitat patches (see Figure 3). Thereby, the euclidean distance per connection is converted into a 'cost distance' that also takes species-specific dispersal costs per landscape scenario into account (Adriaensen et al., 2003; Lechner et al., 2017; Tonkin et al., 2018a). The resulting least-cost paths indicate one likely dispersal route between two habitat patches (Avon and Bergès, 2016) and, therefore, were used for the dispersal simulation (see Section 2.2.2). To calculate the least-cost paths we applied the algorithm 'route_through_array' from the 'skimage.graph' package (Walt et al., 2014) for Python (Python Core Team, 2021).

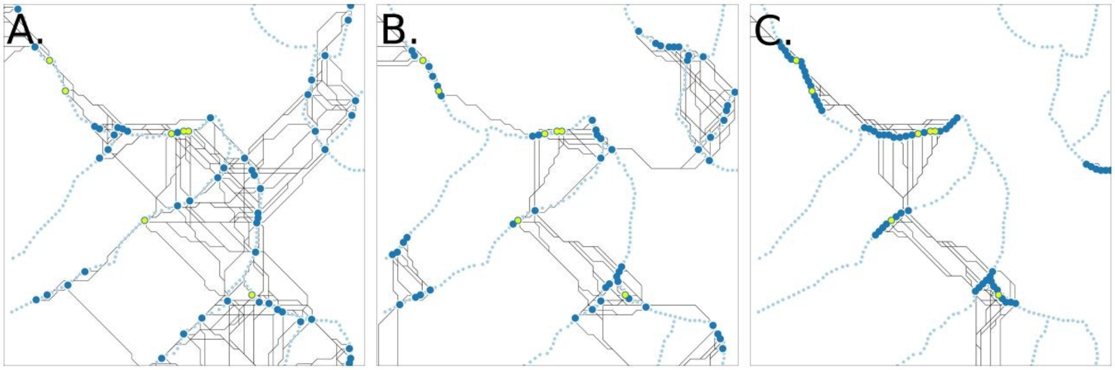


Figure 3: Examples of habitat networks resulting from three habitat patch arrangements (A. = random, B. = random around centers and C. = contiguous around centers) for a habitat patch proportion of 20 % based on the same landscape scenario. Small light-blue points represent 'aquatic' pixels. Dark-blue points represent habitat patches; initial source habitat patches are highlighted in yellow. Black lines represent connections between habitat patches below the maximum connectivity costs.

Only connections below the maximum connectivity cost threshold Γ_{Cmax} of 1250 cost units (see Table 1) were considered. Γ_{Cmax} translates the maximum dispersal distance Γ_{Dmax} of 2500 m through open agricultural land to cost units:

$$\Gamma_{Cmax} = \frac{\Gamma_{Dmax}}{P_{width}} \cdot CV \qquad (1)$$

where P_{width} is the pixel width of the landscape scenarios (see Section 2.1.3) and *CV* corresponds to the dispersal costs for pixels assigned to LT 1 (see Section 2.1.1).

2.2 Simulation of population dynamics & dispersal

At the start of each simulation run, the initially fully colonized habitat patches were sources for the colonization of non-colonized, connected habitat patches over the simulated timespan *T* (see Section 2.1.2). The colonization process is initiated by density-dependent dispersal due to simulated population growth in colonized habitat patches (Corbet, 1963; Córdoba-Aguilar, 2008), a mode of dispersal likely caused by strong intra-specific competition (Murdoch and Oaten, 1975). We assumed that patches connected to a source with low dispersal costs are preferably colonized (Nouhuys and Hanski, 2002) and thus receive a higher proportion of individuals. Moreover, we expected that the colonization success for habitat patches is directly related to the dispersal costs for a connection (Baguette and Van Dyck, 2007; Purse et al., 2003).

2.2.1 Population growth

For each simulated time step *t* the current population size N_t is determined for all colonized habitat patches using a logistic growth function. We use the classic Verhulst model (e.g Tsoularis and Wallace, 2002) to calculate $N_t(x)$ per habitat patch *x* for the present *t*:

$$N_t(x) = \frac{N_{ad,t-1}(x) \cdot K(x)}{N_{ad,t-1}(x) + (K(x) - N_{ad,t-1}(x)) \cdot e^{-r \cdot 1}} \qquad (2)$$

where r is the intrinsic growth rate, $N_{ad,t-1}(x)$ the population size adjusted by changes due to dispersal processes (see Section 2.2.3) at the previous time step (t - 1) and $K(x)$ the carrying capacity of the habitat patches.

Given that in general demography and population-level fitness are strongly dependent on habitat quality HQ (Sutherland and Norris, 2002; Ye et al., 2013) we defined the carrying capacity $K(x)$ per patch according to its specific $HQ(x)$:

$$K(x) = HQ(x) \cdot Ab_{max} \quad (3)$$

where Ab_{max} is the maximal abundance of individuals per habitat patch and HQ corresponds to the HQ value of habitat patch x.

2.2.2 Dispersal

Emigration potential

We assumed positive density-dependent dispersal (Corbet, 1963; Córdoba-Aguilar, 2008) which can be expected for insect species (Matthysen, 2005; Purse et al., 2003; Travis et al., 1999). Therefore, the number of emigrating individuals per source habitat patch increases with abundance due e.g. to intra-specific competition (Amarasekare, 2004; Bowler and Benton, 2005; Heino, 2013). The specific number of emigrating individuals $N_{em,t}$ per habitat patch x is calculated as follows:

$$N_{em,t}(x) = R_{dis}(x) \cdot N_t(x) \quad (4)$$

where $N_t(x)$ is the current population size and $R_{dis}(x)$ is the density-dependent dispersal rate:

$$R_{dis}(x) = \beta \cdot (\frac{N_t(x)}{K(x)})^{s+1} \quad (5)$$

where s quantifies the propensity to disperse due to density and $ß$ is the per capita emigration rate scaled by the intrinsic growth rate of the population (Amarasekare, 2004). In case $s > 0$ the simulated emigration rate increases with population density at an accelerating rate towards $ß$ (Amarasekare, 2004).

Dispersion of emigrants

Next, the emigrating individuals $N_{em,t}$ per habitat patch x disperse to all directly connected patches y that are currently not fully colonized (i.e. $N_t(y) < K(y)$). Following Nouhuys and Hanski (2002) as well as Purse et al. (2003), habitat patches cost-effective connected to a colonized patch x are more likely to be colonized. Hence, those receive a higher fraction $F_t(x,y)$ of $N_{em,t}(x)$ per t (for technical details see Appendix A.1).

Dispersal mortality

The colonization success between two habitat patches x and y is directly related to the dispersal costs $C(x,y)$ of the specific connection, as mortality risks of dispersing individuals (for damselflies e.g. caused by predation or traffic (Rouquette, 2005)) or energetic reserve exhaustion increase with dispersal costs (Baguette and Van Dyck, 2007; Córdoba-Aguilar, 2008; Rankin and Burchsted, 1992).

Hence, the number of individuals $N_{im,t}(x,y)$ immigrating from x into y is calculated by reducing the fraction $F_t(x,y)$ of the total number of emigrants $N_{em,t}(x)$ depending on the ratio of the connectivity costs of the specific connection $C(x,y)$ and the maximum connectivity costs Γ_{Cmax}:

$$N_{im,t}(x, y) = (1 - \frac{C(x,y)}{\Gamma_{Cmax}})^{2} \cdot F_{t}(x, y) \cdot N_{em,t}(x) \qquad (6)$$

2.2.3 Adjustment of the population size

Finally, the population size for each habitat patch was adjusted for dispersal. At the end of each time step, the sum of immigrating individuals from all directly connected source habitat patches (*y* in S_{inter}) was added to the population size $N_t(x)$. In the case of a source habitat patch, the number of emigrated individuals $N_{em,t}(x)$ was subtracted:

$$N_{ad,t}(x) = N_{t}(x) + \sum\nolimits_{y \epsilon S_{inter}} N_{im,t}\,(y, x) - N_{em,t}(x) \qquad (7)$$

Furthermore, colonized habitat patches become source habitat patches in the next time step as soon as their population exceeds a predefined threshold Γ_{sHP}.

2.3 Model application

We created 10 artificial landscapes for each of the 15 landscape type proportions (*LT.P*) and the three spatial compositions of the landscape types (*LT.C*) to minimize bias from a specific realization (in total 450; see Section 2.1.1). Moreover, any artificial landscape was split in 25 even landscape scenarios (in total 11,250; see Section 2.1.1), which represent varying densities and configurations of stream network structures (*SN.S*).

We further used three approaches to create varying habitat patch arrangements (*HP.A*) along the stream-network within the landscape scenarios (see Section 2.1.2). Again to minimize bias from individual realizations, each arrangement was applied 10 times with two habitat patch proportions (*HP.P*) of 10 % or 20 % of all 'aquatic' pixels selected as habitat patches (see Section 2.1.2).

Overall, this resulted in a total of 675,000 different habitat networks (10 x (15 *LT.P* x 3 *LT.C* x 25 *SN.S*) x 10 x (3 *HP.A* × 2 *HP.P*).

Population dynamics and dispersal were simulated for each habitat network over a timespan *T* of 100 reproductive periods based on varying configurations of initial (fully colonized) source habitat patches. Therefore, 10 times per network a proportion of 10 % of the patches was selected as initial source habitat patches (see Section 2.1.2). To provide comparable results among the different *HP.A* approaches, we defined identical initial source habitat patches for habitat scenarios based on equal landscape scenarios and patch proportions (see Figure 3).

2.4 Model Parameterization

Although the presented model is in general hypothetical, several model parameters were parameterized relative to traits of the European damselfly *Coenagrion mercuriale* (see Table 1).

2.4.1 Parameterization: Habitat networks

Based on a literature review we identified a maximum dispersal distance and four main landscape types LT affecting the dispersal of *Coenagrion mercuriale*. Consequently, we assigned different relative levels of permeability to the landscape types 'aquatic', 'open agricultural land', 'forestry' and 'urban area'. The type-specific level was assessed based on previous studies and, subsequently, transformed to relative, numeric dispersal cost values.

Streams are identified as the most important dispersal corridors and dispersal along a watercourse is more likely than dispersal via terrestrial landscape types, hence leading to a high connectivity of patches allocated along the same stream

(Hepenstrick et al., 2014; Kastner et al., 2015; Keller et al., 2013). Therefore, the landscape permeability for LT 4 'aquatic' was assumed highest and its dispersal cost was set to the lowest value of 25. Frequent dispersal between populations of *Coenagrion mercuriale* connected solely via continuous open agricultural land was found by several studies (Keller et al., 2012; Keller and Holderegger, 2013). Hence, we assumed the second highest permeability for the LT 1 'open agricultural land' and set its dispersal cost to 50. In contrast, forest patches as well as urban areas have been identified as potential barriers and may impede dispersal of *Coenagrion mercuriale* (Kastner et al., 2015; Keller et al., 2012; Watts et al., 2004), in particular, urban areas have been described as impermeable (Watts et al., 2004). Consequently, we set the dispersal cost as 75 for LT 2 'forestry' and as 100 for LT 3 'urban areas'.

The maximum dispersal distance Γ_{Dmax} for *Coenagrion mercuriale* implemented in the model refers specifically to dispersal through open agricultural land, i.e. LT 1. Keller et al. (2012) and Keller and Holderegger (2013) found a good connectivity of meta-populations within a radius of 1.5 - 2 km linked via continuous open agricultural land. In addition, they found evidence for overland dispersal over larger distances in rare cases. Accordingly, we set Γ_{Dmax} to 2500 m. To generalize the LT 1 specific maximum dispersal distance Γ_{Dmax} to a parameter valid for all four landscape types we converted it into the unspecific maximum connectivity cost threshold Γ_{Cmax} (see Section 2.1.3).

2.4.2 Parameterization: Simulation

The maximum abundance per habitat patch Ab_{max} was set to 100 as empirical values for abundances of *Coenagrion mercuriale* ranged from 68.3 (Hepenstrick et al., 2012) to 211.5 individuals (Kastner et al., 2015) per 100 m transect. Salcher and Schiel (2015) reported abundances up to 100 individuals per 100 m transect in the region around Tübingen, Germany. The parameter intrinsic growth rate *r* was set to 2, as K.-J. Contze (personal communication, June 16, 2017) stated it can be expected that habitat patches are fully colonized by European damselflies 2 - 3 years after an initial colonization. In the absence of literature data, we set the per capita emigration rate *ß* as well as the parameter governing density-dependent dispersal *s*: *ß* to 0.2 and *s* to a moderate positive value of 0.5.

Table 1: Parameter values used for setting up the habitat networks and the simulation of population dynamics and dispersal.

Parameter	Symbol	Value	Unit	Reference	Comment
habitat quality	*HQ*	0.625			
max. dispersal distance	Γ_{Dmax}	2500	m	Keller et al. (2012) & Hepenstrick et al. (2014)	For *Coenagrion mercuriale* through open agricultural land
max. connectivity costs	Γ_{Cmax}	1250	costs	derived from Keller et al. (2012) & Hepenstrick et al. (2014)	2.1.3
timespan	*T*	100	reproduction periods		
maximal abundance	Ab_{max}	100		Hepenstrick et al. (2012) & Kastner et al. (2015)	For *Coenagrion mercuriale* per 100 m transect: 68.3 - 211.5
intrinsic growth rate	*r*	2		K.-J. Contze (personal communication, June 16, 2017)	Habitat patches expected to be fully colonized by damselflies 2 - 3 years after initial colonization
emigration rate	*ß*	20	%	Amarasekare (2004)	
propensity to disperse	*s*	0.5		Amarasekare (2004)	
threshold source	Γ_{sHP}	20	individuals		

habitat patch

2.5 Data analysis

We used the final patch occupancy per habitat network as an indicator for the colonization success (see Figure 1 - C). To determine how habitat connectivity is related to the colonization success, we compared the results to the ecological network connectivity measure ‘integral index of connectivity’ (IIC).

Although there is a big variety of graph-theoretic connectivity measures (Laita et al., 2011), we selected the IIC as it is based on shortest paths and provides reliable information on the degree of connectivity between patches (Laita et al., 2011; Pascual-Hortal and Saura, 2006). It is a graph-based index measuring habitat connectivity in terms of the probability that two randomly selected habitat patches *x* and *y* are directly or indirectly connected (Lechner et al., 2017). The IIC is calculated as follows:

$$IIC = \frac{\sum_{x=1}^{n}\sum_{y=1}^{n}\frac{A_{HP}(x)A_{HP}(y)}{1+nl_{xy}}}{A_L^2} \qquad (8)$$

where A_{HP} is the area of each habitat patch (here: one raster pixel, 0.01 km²) and nl_{xy} is the number of links per connection (topological distance) between connected patches *x* and *y*. A_L is the total landscape area. In the context of the present study, we define A_L as the total area of sustainable aquatic habitat patches or rather raster pixels per landscape scenario intersecting a habitat patch (see Section 2.1.2). The IIC ranges from 0 to 1 and increases with improved connectivity; for details see Pascual-Hortal and Saura (2006).

To investigate the relative importance of the habitat parameters (1) landscape type proportions (*LT.P*), (2) landscape type configuration (*LT.C*), (3) stream network structure (*SN.S*), (4) habitat patch proportion (*HP.P*) and (5) habitat patch arrangements (*HP.A*) as well as their two-way interactions, we used eta squared (η^2) (Lakens, 2013) as a measure of effect size derived from analysis of variance (ANOVA) with *F*-test. The calculations of the ANOVA and the η^2 were done in R version 3.5.1 (R Core Team, 2018) using the package 'sjstats' for η^2 (Lüdecke, 2018).

3. RESULTS & DISCUSSION

3.1 Habitat connectivity

Our analysis based on the IIC values indicated that colonization success of the modeled species is strongly influenced by habitat connectivity: the percentage of colonized suitable habitat patches increased with decreasing IIC values (see Figure 4).

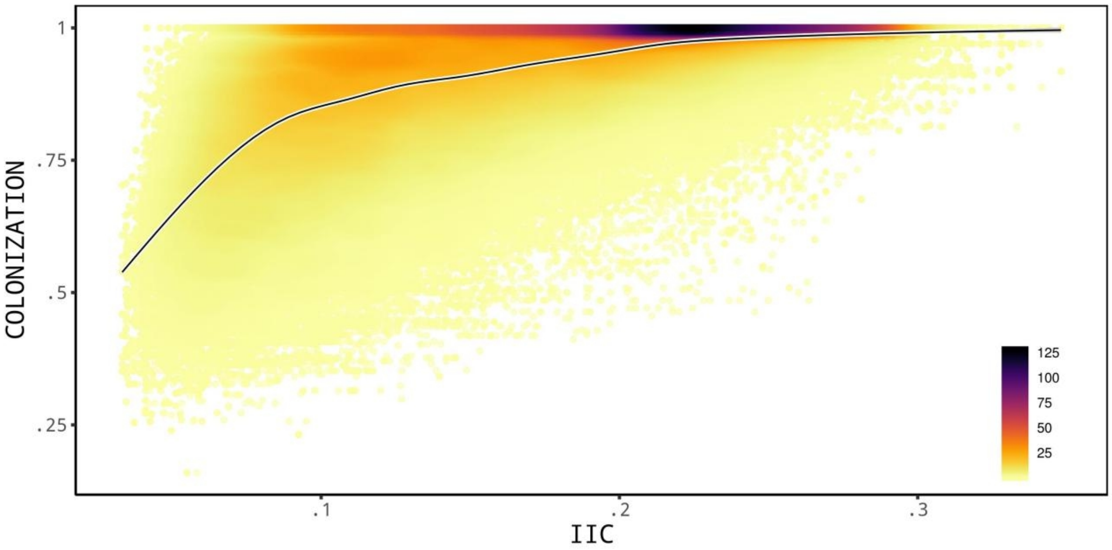


Figure 4: *Relation between the integral index of connectivity IIC (x-axis) and the proportion of colonized suitable habitat patches (y-axis) per habitat network. Overlapping points are colored by density using the 2D kernel density estimation function from the R package 'MASS' (Ripley et al., 2019). The black line represents a smoothing curve (generalized additive model). Due to the high number of habitat networks, a random subset of 10 % (675.000) of the total results is shown.*

The positive relationship (Spearman's $\rho = 0.64$, $p < 0.001$) between the IIC and the proportion of colonized habitat patches matches our expectation (see Figure 4). In addition, the result is in agreement with ecological theory (Baguette and Van Dyck, 2007; Chisholm et al., 2011; Matisziw and Murray, 2009; e.g. Moilanen and Nieminen, 2002), which states that habitat connectivity generally determines colonization probability.

The relatively high variability in the results (see Figure 4) may be explained by the high number of habitat networks produced resulting in different arrangements of habitat patches and source habitat patches for similar overall dispersal costs per habitat scenario the least-cost path analysis was based on. Habitat networks with low IIC values typically consisted of multiple non-connected clusters of habitat patches. In case each cluster contained an initial source habitat patch, the colonization rate was likely high, although no dispersal between these clusters occurred. Conversely, the majority of habitat patches could be highly connected in one to very few clusters, containing all initial source patches. Therefore, the remaining patches were not connected to a source patch, resulting in comparably low colonization rates.

Furthermore, the IIC ignores the dispersal costs per connection (Laita et al., 2011). Thus, a high connectivity of habitat patch clusters may not correspond to a high colonization rate over T due to high dispersal costs and related mortality in the case of an unsuitable distribution of source habitat patches. This effect conforms to the known limitation of the IIC due to the oversimplified binary representation of connections (Laita et al., 2011; Saura and Pascual-Hortal, 2007).

3.2 Importance of parameters

The evaluation of individual effects and the two-way interactions of the habitat parameters (see Table 2) showed that the proportion of habitat patches (*HP.P*) had the strongest effect on the colonization success, followed by landscape type proportions (*LT.P*), habitat patch arrangement (*HP.A*) and stream segment structure (*SN.S*). The landscape type configuration (*LT.C*) explained only a negligible proportion of the variance. Furthermore, the explanatory power of the two-way interaction effects was low.

3.2.1 Landscape permeability

The results indicated that decreasing average dispersal costs per habitat scenario led to increasing colonization success (see Figure 5). The *LT.P*, one of two habitat parameters determining landscape permeability, explained the second highest proportion (13.1 %) of the variance in the colonization success. This suggests that the varying landscape permeability of the artificial landscape scenarios, resulting from different proportions of the four landscape types (see Section 2.1.1), strongly affects the dispersal of hemimetabolous freshwater species.

The general relevance of landscape permeability for animal dispersal and population dynamics has been widely recognized in terrestrial ecology (Pinto and Keitt, 2009; Zeller et al., 2012). With decreasing landscape permeability mortality rates during dispersal between habitat patches increase (Strien and Grêt-Regamey, 2016). In the worst case, connections disappear (Baguette and Van Dyck, 2007; King and With, 2002) resulting in lower habitat connectivity and, in turn, lower colonization success. Comparable effects of landscape permeability on dispersal can be expected for aquatic species, which primarily disperse overland (Smith et al., 2009; Tonkin et al., 2018a).

However, even though previous studies showed that species rather disperse through homogeneous areas with low costs than through heterogeneous areas with variable costs (King and With, 2002; Ricketts, 2001) the explanatory power of *LT.C*, the other parameter determining landscape permeability, was low (0.2 %). Although the graphical analysis (see Figure 5) showed minor differences between the three *NLM* algorithms used.

Table 2: Multi-factorial ANOVA for main and two-way interactive effects of landscape type proportions (**LT.P**), landscape configuration (**LT.C**), habitat patch proportion (**HP.P**), habitat patch arrangement (**HP.A**) and stream segment (**SN.S**) on the colonization success. The **p**-values of all parameters were below 0.001.

Term	Degrees of freedom	Sum of squares	F value	Eta squared
HP.P	1	17410	17410	0.186
LT.P	14	12262	135663	0.131
HP.A	2	6654	515376	0.071
SN.S	24	5749	37102	0.061
HP.P : LT.P	14	3308	36595	0.035
HP.P : SN.S	24	1812	11693	0.019
HP.P : HP.A	2	813	62969	0.009
HP.A : SN.S	48	768	2477	0.008
HP.A : LT.P	28	549	3038	0.006
LT.P : SN.S	336	367	170	0.004
LT.C	2	217	16771	0.002
LT.C : HP.P	2	56	4337	0.001
LT.C : LT.P	28	91	503	0.001
LT.C : HP.A	4	10	385	0
LT.C : SN.S	48	9	30	0
Residuals	6749422	43574		

3.2.2 Stream network

In our study, the stream network structure *SN.S* explained 6.1 % of the variance. The number of pixels per 10 km x 10 km landscape tile intersecting a *SN.S* correlated positively with the percentage of colonized habitat patches (see Figure 5). Higher habitat patch densities generally produced better connected habitat networks and we expect that the resultant enhanced connectivity of habitat networks explained a significant proportion of the variance explained by the *SN.S*. However, the influence of the *SN.S* on the connectivity certainly depends on further parameters, such as the geometry of the network (e.g. number and spatial arrangement of branches).

In general, stream networks exhibit a dendritic spatial structure and the dispersal of hemimetabolous species is necessarily influenced by the individual network structure (Brown et al., 2011; Tonkin et al., 2018a, 2018b). Furthermore, the strength of the influence of the spatial network structure on the habitat connectivity depends on dispersal potential (Keitt et al., 1997; Tonkin et al., 2018a), where strong aerial dispersers are less influenced than poor dispersers (Tonkin et al., 2018a). Future studies should therefore further examine the influence of the *SN.S* to precisely analyze how e.g. dispersal traits and network structure, but also habitat quality and the potential variability of streams (e.g. due to droughts), influence the colonization. Particularly since spatial stream network structures but also the stability of stream habitats can vary widely in time and between different geological and climatic regions (Frissell et al., 1986).

3.2.3 Habitat patches: proportion & arrangement

The results further showed that doubling the *HP.P* per stream network had the strongest effect on the colonization success, accounting for 18.6 % of the variance. Since we run only two levels (10 and 20 %) of *HP.P*, no conclusion regarding the general relationship between *HP.P* and the habitat connectivity as well as the resulting colonization success can be drawn.

However, generally an increase of patches within a habitat leading to higher patch density results in enhanced connectivity of habitat networks (Hanski, 1999; Villard and Metzger, 2014). Due to generally shorter distances between patches, first, dense networks possess more pairwise direct connections per patch and, thus, more indirect connections between habitat patches, via intermediate patches (Laita et al., 2011; Minor and Urban, 2008). Second, within dense networks the costs per connection are generally lower. Consequently, decreasing landscape permeability less likely results in the loss of direct connections and, moreover, the loss of direct connections can be compensated (over time) by indirect connections.

The habitat patch arrangement *HP.A* accounted for 7.1 % of the variance. The graphical analysis furthermore showed that the *HP.A* approach 'random' resulted in clearly higher colonization success compared to the two other approaches (see Figure 5), which both led to more clustered *HP.A*.

The arrangement of patches generally determines (under otherwise identical conditions) the connectivity of habitats (Chisholm et al., 2011; Laita et al., 2011; Villard and Metzger, 2014). Randomly or rather variously arranged habitat patches create more indirect connections within a network (Anderson and Hayes, 2018; Baguette and Van Dyck, 2007), whereas clustered habitat patch arrangements lead to more cost-effective connections within the clusters, but the clusters often remain unconnected (Anderson and Hayes, 2018; Hodgson et al., 2011). The presented results indicate that those generally positive effects of variously arranged patches on the colonization also apply to variously (randomly) arranged patches along streams; although (given the dendritic stream structure) the patch arrangement is much more predetermined in any instance.

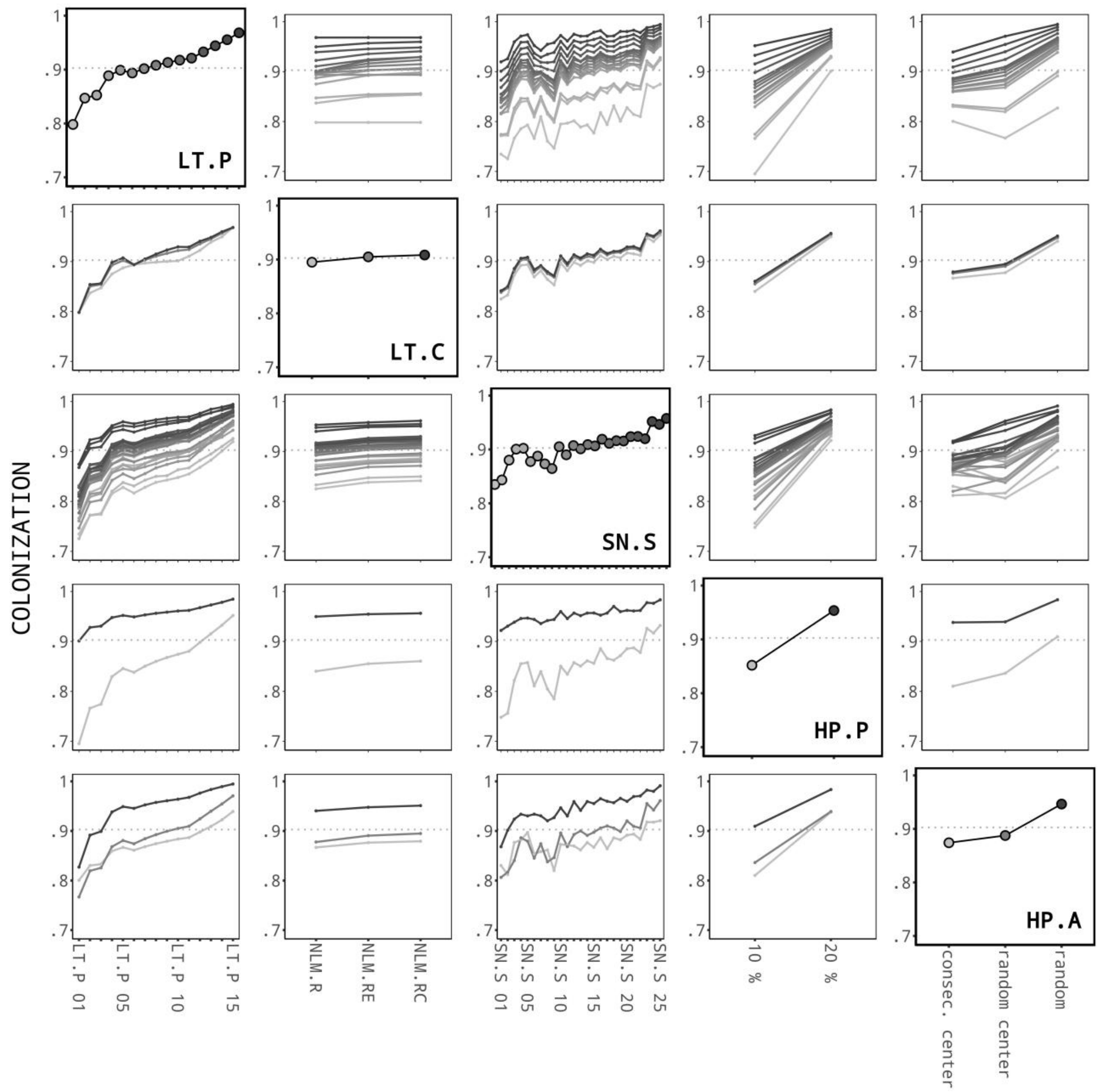


Figure 5: Interaction plot for the main and two-way interaction effects on the rate of colonized habitat patches (y-axis) per habitat parameter (x-axis). The main effects are arranged diagonally and labeled in the lower right: **LT.P** - landscape type proportions, **LT.C** - landscape type configuration, **HP.A** - habitat patch arrangement, **HP.P** - habitat patch proportion and **SN.S** - stream network structure. The parameter **LT.P** is sorted by the mean dispersal costs of the resulting specific habitat scenarios in descending order. The parameter **SN.S** is sorted ascending by the number of pixels per 10 km x 10 km landscape tile intersecting the stream network. The specifications of the parameter **LT.C** results from three varying spatial distributions of the different landscape type proportions using the neutral landscape model (NLM) algorithms (1) random (NLM.R), (2) random element nearest-neighbour (NLM.RE) and (3) random cluster nearest-neighbour (NLM.RC); see Section 2.1.1 for details. The specifications of the parameter **HP.A** result from three habitat patch arrangement approaches 'random', 'random around centers'

and ‘contiguous around centers’; see Section 2.1.2 for details. The two-way interaction effects are arranged as follows: the interactions are colored according to the gray scale of the factor in the corresponding horizontal sub-plot of the main effect; the number of factors corresponds to those of the main effect in vertical direction. The dotted line per sub-plot represents the average colonization of all simulations.

3.2.4 Two-way interactions

The explanatory power of all two-way interaction effects was low (equal or less than 3.5 %; Table 2). The three strongest interaction effects all involved *HP.P*: *HP.P* and *LT.P* (3.5 %), *HP.P* and *SN.S* (1.9 %), *HP.P* as well as *HP.A* (0.9 %).

The effect of decreasing landscape permeability, primarily caused by the *LT.P*, on the colonization success was less pronounced for habitat networks with a high potential connectivity resulting from comparably dense networks with a high *HP.P*. We assume losses of direct connections because of exceeding the maximal connectivity costs, can often be compensated by indirect connections. Accordingly, the *HP.P* and the *SN.S* interacted comparably strongly, as the patch number per habitat scenario was directly related to stream network density. Furthermore, networks with a random *HP.A* were less affected by decreasing landscape permeability compared to the other arrangements. This can be explained by randomly arranged patches resulting in more indirect connections making networks less sensitive against the loss of direct connections. Colonization success was differently affected by the other arrangements ‘random around centers’ and ‘contiguous around centers’ depending on the respective *SN.S*.

3.2.5 Unexplained variance

The five habitat parameters including their two-way interactions explained 53.4 % of the variance in the colonization success. The remaining variance can largely be explained by the stochastic variability of the habitat networks. The random distribution of initial source habitat patches within the networks as well as the 10 random habitat networks set up for each patch arrangement approach and patch proportion per habitat scenario likely were responsible for a relevant proportion of the unexplained variance. Moreover, higher level interactions may explain additional, albeit likely a low proportion, of the remaining variance.

3.3 Model parameters and omission of processes

The development of process-based, spatially explicit meta-population models is complicated by factors such as the degree of abstraction and the relatively complex analyses and interpretation required. The necessity to control the complexity of the model structure and to approximate parameter values based on literature references lead to simulation results that are difficult to verify for specific real-world species (Forbes et al., 2008; Hanski, 1994; Saura et al., 2014).

In this context, several parameters used in setting up the habitat networks and the simulation represented estimates (e.g. cost values of landscape types) in the absence of precise values which affects the results (see Section 2.4). Moreover, we did not consider the potential effects of (1) isolation such as reduction of genetic variability (Hanski, 1989; Watts et al., 2006) and (2) deferred costs of dispersal, both of which can compromise meta-population viability (Baguette and Van Dyck, 2007; Burgess et al., 2012). We further omitted potential negative impacts of high connectivity on population viability such as the effects of diseases that may spread rapidly in highly connected habitats (Minor and Urban, 2008). However, such aspects could relatively easily be incorporated into the current process-based model and parameter estimates could be updated in the light of new knowledge or to reflect the traits of a different model species (Cuddington et al., 2013).

We conclude that the presented model has the potential to generate (at a minimum) theoretical knowledge and general understanding how changing environmental conditions influence the habitat connectivity of hemimetabolous freshwater species under varying scenarios.

4. CONCLUSION

The results indicate that habitat connectivity for hemimetabolous freshwater species is strongly determined by similar parameters affecting terrestrial habitat connectivity. Comparable with terrestrial species the number and arrangement of habitat patches as well as the permeability of the surrounding landscape largely determine the colonization success (Hanski, 1989; Hodgson et al., 2011; Lechner et al., 2017). Here, it is especially noteworthy that high potential network connectivity, primarily resulting from a high number of patches, had a relevant positive effect on the resilience of habitat networks to decreasing landscape permeability. Nevertheless, the modeled colonization is considerably regulated by the spatial structuring of the stream network.

The persistence of species threatened by environmental change will strongly depend on the preservation of habitat connectivity and, therefore, on habitat management on landscape-scales (Hanski, 1989; Hodgson et al., 2011; Lechner et al., 2017; Watts et al., 2006). To preserve or improve habitat connectivity, management for hemimetabolous freshwater species must, in addition to the protection and improvement of the single patches, focus on the habitat as a whole (Hassall and Thompson, 2012; Sarremejane et al., 2017). Thereby, management measures should particularly focus - as presented above - on patch density and landscape permeability.

Process-based models can generally improve effective habitat management (Cuddington et al., 2013; Evans, 2012; Jacoby and Freeman, 2016; Petchey et al., 2015; Saura et al., 2014). For example, a simplified version of our model revealed information on the minimum time required to colonize habitat patches added to an existing network (Heer et al., 2019).

The presented model has the potential to be parameterized with species-specific traits and, in combination with real-world landscapes, streams and habitat patch assemblages, may serve, for instance, to support future site-specific habitat management planning. Moreover, it can be adopted in future studies to simulate how singular and periodic (e.g. resulting of an increased likelihood of drought events caused by climate change) or permanent effects (e.g. resulting from land-use change) on patch quality affects meta-population persistence.

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AUTHOR CONTRIBUTIONS

All authors contributed to the development of the conceptual model; L.S. programmed the model and analyzed the data; R.B.S, M.K. and H.H. provided critical feedback and helped shape the research and analysis; and L.S. led the writing with contributions from all other authors.

DECLARATION OF INTEREST

The authors declare that they have no competing interests. The funding source B•M•U Graduate Academy of the University of Koblenz-Landau was not involved in the collection, analysis and interpretation of data; in the writing; and in the decision to submit the article for publication.

APPENDIX A

We developed the following formula to calculate the specific fraction $F_t(x,y)$ of $N_{em,t}(x)$ per t that a habitat patch y directly connected to a source patch x receives:

$$F_t(x, y) = \frac{C^3_{red}(x,y)}{\sum_{(x,y)\epsilon S_{con}(x)} C^3_{red}(x,y)} \qquad \text{(A.1)}$$

where $S_{con}(x)$ represents the set of all direct connections from a source habitat patch x to all empty or not fully colonized patches. $C_{red}(x,y)$ is calculated as follows:

$$C_{red}(x, y) = C_{max}(x) - C(x, y) + C_{min}(x) \qquad \text{(A.2)}$$

where $C(x,y)$ are the costs of the connection form source habitat patch x to patch y. $C_{max}(x)$ is the maximum and $C_{min}(x)$ is the minimum cost of all connections in $S_{con}(x)$. Once patch y is fully colonized ($N_t(y) = K(y)$), the connection from x to y is removed from $S_{con}(x)$. However, the specific connection is added again to $S_{con}(x)$ as soon as the patch population of y decreases due to dispersal in the following t.

APPENDIX B

Supplementary material (Python code plus Input-Data) for this publication can be found online at: https://github.com/luclucky/HabitatConnectivity_Colonization

REFERENCES

Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., Matthysen, E., 2003. The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning 64, 233–247. https://doi.org/10.1016/S0169-2046(02)00242-6

Amarasekare, P., 2004. The role of density-dependent dispersal in source-sink dynamics. Journal of Theoretical Biology 226, 159–168. https://doi.org/10.1016/j.jtbi.2003.08.007

Anderson, K.E., Hayes, S.M., 2018. The effects of dispersal and river spatial structure on asynchrony in consumer–resource metacommunities. Freshwater Biology 63, 100–113. https://doi.org/10.1111/fwb.12998

Avon, C., Bergès, L., 2016. Prioritization of habitat patches for landscape connectivity conservation differs between least-cost and resistance distances. Landscape Ecology 31, 1551–1565. https://doi.org/10.1007/s10980-015-0336-8

Baguette, M., Van Dyck, H., 2007. Landscape connectivity and animal behavior: Functional grain as a key determinant for dispersal. Landscape Ecology 22, 1117–1129. https://doi.org/10.1007/s10980-007-9108-4

Bocedi, G., Palmer, S.C.F., Pe'er, G., Heikkinen, R.K., Matsinos, Y.G., Watts, K., Travis, J.M.J., 2014. RangeShifter: A platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. Methods in Ecology and Evolution 5, 388–396. https://doi.org/10.1111/2041-210X.12162

Bowler, D.E., Benton, T.G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80, 205–225. https://doi.org/10.1017/S1464793104006645

Brink, P.J. van den, Baird, D.J., Baveco, H., Focks, A., 2013. The use of traits-based approaches and eco(toxico)logical models to advance the ecological risk assessment framework for chemicals. Integrated Environmental Assessment and Management 9, e47–e57. https://doi.org/10.1002/ieam.1443

Brown, B.L., Swan, C.M., Auerbach, D.A., Campbell Grant, E.H., Hitt, N.P., Maloney, K.O., Patrick, C., 2011. Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. Journal of the North American Benthological Society 30, 310–327. https://doi.org/10.1899/10-129.1

Burgess, S.C., Treml, E.A., Marshall, D.J., 2012. How do dispersal costs and habitat selection influence realized population connectivity? Ecology 93, 1378–1387. https://doi.org/10.1890/11-1656.1

Chisholm, C., Lindo, Z., Gonzalez, A., 2011. Metacommunity diversity depends on connectivity and patch arrangement in heterogeneous habitat networks. Ecography 34, 415–424. https://doi.org/10.1111/j.1600-0587.2010.06588.x

Corbet, P.S., 1963. A biology of dragonflies. Quadrangle Books.

Córdoba-Aguilar, A., 2008. Dragonflies and Damselflies. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199230693.001.0001

Cuddington, K., Fortin, M.-J.M.J., Gerber, L.R., Hastings, A., Liebhold, A., O'Connor, M., Ray, C., 2013. Process-based models are required to manage ecological systems in a changing world. Ecosphere 4, art20. https://doi.org/10.1890/ES12-00178.1

Didham, R.K., Blakely, T.J., Ewers, R.M., Hitchings, T.R., Ward, J.B., Winterbourn, M.J., 2012. Horizontal and vertical structuring in the dispersal of adult aquatic insects in a fragmented landscape. Fundamental and Applied Limnology / Archiv für Hydrobiologie 180, 27–40. https://doi.org/10.1127/1863-9135/2012/0243

Doerr, V.A.J., Barrett, T., Doerr, E.D., 2011. Connectivity, dispersal behaviour and conservation under climate change: A response to Hodgson et al. Journal of Applied Ecology 48, 143–147. https://doi.org/10.1111/j.1365-2664.2010.01899.x

Eros, T., Campbell Grant, E.H., 2015. Unifying research on the fragmentation of terrestrial and aquatic habitats: patches, connectivity and the matrix in riverscapes. Freshwater Biology 60, 1487–1501. https://doi.org/10.1111/fwb.12596

Etherington, T.R., Holland, E.P., O'Sullivan, D., 2015. NLMpy: A python software package for the creation of neutral landscape models within a general numerical framework. Methods in Ecology and Evolution 6, 164–168. https://doi.org/10.1111/2041-210X.12308

Evans, M.R., 2012. Modelling ecological systems in a changing world. Philosophical Transactions of the Royal Society B: Biological Sciences 367, 181–190. https://doi.org/10.1098/rstb.2011.0172

Evans, M.R., Norris, K.J., Benton, T.G., 2012. Predictive ecology: Systems approaches. Philosophical Transactions of the Royal Society B: Biological Sciences 367, 163–169. https://doi.org/10.1098/rstb.2011.0191

Fahrig, L., 2017. Ecological Responses to Habitat Fragmentation Per Se. Annual Review of Ecology, Evolution, and Systematics 48, annurev-ecolsys-110316-022612. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fahrig, L., Merriam, G., 1994. Conservation of Fragmented Populations. Source: Conservation Biology Conservation Biology 8, 50–59. https://doi.org/10.1046/j.1523-1739.1994.08010050.x

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16, 265–280. https://doi.org/10.1111/j.1466-8238.2007.00287.x

Forbes, V.E., Calow, P., Sibly, R.M., 2008. The extrapolation problem and how population modeling can help. Environmental Toxicology and Chemistry 27, 1987. https://doi.org/10.1897/08-029.1

Frissell, C.A., Liss, W.J., Warren, C.E., Hurley, M.D., 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. Environmental Management 10, 199–214. https://doi.org/10.1007/BF01867358

Galpern, P., Manseau, M., Fall, A., 2011. Patch-based graphs of landscape connectivity: A guide to construction, analysis and application for conservation. Biological Conservation 144, 44–55. https://doi.org/10.1016/j.biocon.2010.09.002

GDAL/OGR, 2018. GDAL - Geospatial Data Abstraction Library: Version 2.2.1.

Gustafson, E.J., 2013. When relationships estimated in the past cannot be used to predict the future: Using mechanistic models to predict landscape ecological dynamics in a changing world. Landscape Ecology 28, 1429–1437. https://doi.org/10.1007/s10980-013-9927-4

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., De Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12. https://doi.org/10.1371/journal.pone.0185809

Hanski, I., 2011. Habitat Loss, the Dynamics of Biodiversity, and a Perspective on Conservation. AMBIO 40, 248–255. https://doi.org/10.1007/s13280-011-0147-3

Hanski, I., 1999. Habitat Connectivity, Habitat Continuity, and Metapopulations in Dynamic Landscapes. Oikos 87, 209. https://doi.org/10.2307/3546736

Hanski, I., 1994. A Practical Model of Metapopulation Dynamics. The Journal of Animal Ecology 63, 151. https://doi.org/10.2307/5591

Hanski, I., 1989. Metapopulation dynamics: Does it help to have more of the same? Trends in Ecology and Evolution 4, 113–114. https://doi.org/10.1016/0169-5347(89)90061-X

Hassall, C., Thompson, D.J., 2012. Study design and mark-recapture estimates of dispersal: A case study with the endangered damselfly Coenagrion mercuriale. Journal of Insect Conservation 16, 111–120. https://doi.org/10.1007/s10841-011-9399-2

Heer, H., Streib, L., Kattwinkel, M., Schäfer, R.B., Ruzika, S., 2019. Optimisation Model of a Distribution Prediction Model. Manuscript sumbitted for publication.

Heino, J., 2013. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. Biological Reviews 88, 166–178. https://doi.org/10.1111/j.1469-185X.2012.00244.x

Heino, J., Alahuhta, J., Ala-Hulkko, T., Antikainen, H., Bini, L.M., Bonada, N., Datry, T., Erős, T., Hjort, J., Kotavaara, O., Melo, A.S., Soininen, J., 2017. Integrating dispersal proxies in ecological and environmental research in the freshwater realm. Environmental Reviews 25, 334–349. https://doi.org/10.1139/er-2016-0110

Heino, M., Hanski, I., 2001. Evolution of Migration Rate in a Spatially Realistic Metapopulation Model. The American Naturalist 157, 495–511. https://doi.org/10.1086/319927

Hepenstrick, D., Holderegger, R., Keller, D., 2012. Monitoring von Populationen der Helm-Azurjungfer Coenagrion mercuriale (Odonata : Coenagrionidae): Was taugen zwei Begehungen pro Saison? Entomo Helvetica 5, 139–145.

Hepenstrick, D., Koch, B., Monnerat, C., 2014. Merkblätter Arten – Libellen – Coenagrion mercuriale.

Hodgson, J.A., Moilanen, A., Wintle, B.A., Thomas, C.D., 2011. Habitat area, quality and connectivity: Striking the balance for efficient conservation. Journal of Applied Ecology 48, 148–152. https://doi.org/10.1111/j.1365-2664.2010.01919.x

Jacoby, D.M.P., Freeman, R., 2016. Emerging Network-Based Tools in Movement Ecology. Trends in Ecology and Evolution 31, 301–314. https://doi.org/10.1016/j.tree.2016.01.011

Kastner, F., Buchwald, R., Willen, M., 2015. Artenhilfsprogramme für die FFH-Libellenarten Aeshna viridis, Coenagrion mercuriale und Coenagrion ornatum in NW-Deutschland. Unveröffentlichter Abschlussbericht zum gleichnamigen DBU-Projekt, Oldenburg.

Keitt, T., Urban, D.L., Milne, B.T., 1997. Detecting Critical Scales in Fragmented Landscapes. Conservation Ecology 1, art4. https://doi.org/10.5751/ES-00015-010104

Keller, D., Holderegger, R., 2013. Damselflies use different movement strategies for short- and long-distance dispersal. Insect Conservation and Diversity 6, 590–597. https://doi.org/10.1111/icad.12016

Keller, D., Seidl, I., Forrer, C., Home, R., Holderegger, R., 2013. Schutz der Helm-Azurjungfer Coenagrion mercuriale (Odonata : Coenagrionidae) am Beispiel des Smaragd-Gebiets Oberaargau. Entomo Helvetica 6, 87–99.

Keller, D., Van Strien, M.J., Holderegger, R., 2012. Do landscape barriers affect functional connectivity of populations of an endangered damselfly? Freshwater Biology 57, 1373–1384. https://doi.org/10.1111/j.1365-2427.2012.02797.x

King, A.W., With, K.A., 2002. Dispersal success on spatially structured landscapes: When do spatial pattern and dispersal behavior really matter? Ecological Modelling 147, 23–39. https://doi.org/10.1016/S0304-3800(01)00400-8

Laita, A., Kotiaho, J.S., Mönkkönen, M., 2011. Graph-theoretic connectivity measures: What do they tell us about connectivity? Landscape Ecology 26, 951–967. https://doi.org/10.1007/s10980-011-9620-4

Lakens, D., 2013. Calculating and reporting effect sizes to facilitate cumulative science: A practical primer for t-tests and ANOVAs. Frontiers in Psychology 4, 1–12. https://doi.org/10.3389/fpsyg.2013.00863

Lakovic, M., Mitesser, O., Hovestadt, T., 2017. Mating timing, dispersal and local adaptation in patchy environments. Oikos 1–11. https://doi.org/10.1111/oik.04369

Lechner, A.M., Brown, G., Raymond, C.M., 2015. Modeling the impact of future development and public conservation orientation on landscape connectivity for conservation planning. Landscape Ecology 30, 699–713. https://doi.org/10.1007/s10980-015-0153-0

Lechner, A.M., Sprod, D., Carter, O., Lefroy, E.C., 2017. Characterising landscape connectivity for conservation planning using a dispersal guild approach. Landscape Ecology 32, 99–113. https://doi.org/10.1007/s10980-016-0431-5

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lüdecke, D., 2018. sjstats: Statistical Functions for Regression Models (Version 0.17.1). https://doi.org/10.5281/zenodo.1284472

Luque, S., Saura, S., Fortin, M.-J., 2012. Landscape connectivity analysis for conservation: insights from combining new methods with ecological and genetic data. Landscape Ecology 27, 153–157. https://doi.org/10.1007/s10980-011-9700-5

Marquet, P.A., Allen, A.P., Brown, J.H., Dunne, J.A., Enquist, B.J., Gillooly, J.F., Gowaty, P.A., Green, J.L., Harte, J., Hubbell, S.P., O'Dwyer, J., Okie, J.G., Ostling, A., Ritchie, M., Storch, D., West, G.B., 2014. On theory in ecology. BioScience 64, 701–710. https://doi.org/10.1093/biosci/biu098

Masters, Z., Peteresen, I., Hildrew, A.G., Ormerod, S.J., 2007. Insect dispersal does not limit the biological recovery of streams from acidification. Aquatic Conservation: Marine and Freshwater Ecosystems 17, 375–383. https://doi.org/10.1002/aqc.794

Matisziw, T.C., Murray, A.T., 2009. Connectivity change in habitat networks. Landscape Ecology 24, 89–100. https://doi.org/10.1007/s10980-008-9282-z

Matthysen, E., 2005. Density-dependent dispersal in birds and mammals. Ecography 28, 403–416. https://doi.org/10.1111/j.0906-7590.2005.04073.x

Milko, L.V., Haddad, N.M., Lance, S.L., 2012. Dispersal via stream corridors structures populations of the endangered St. Francis' satyr butterfly (Neonympha mitchellii francisci). Journal of Insect Conservation 16, 263–273. https://doi.org/10.1007/s10841-011-9413-8

Minor, E.S., Urban, D.L., 2008. A graph-theory framework for evaluating landscape connectivity and conservation planning. Conservation Biology 22, 297–307. https://doi.org/10.1111/j.1523-1739.2007.00871.x

Moilanen, A., Nieminen, M., 2002. Simple connectivity measure in spatial ecology. Ecology 83, 1131–1145.

Murdoch, W.W., Oaten, A., 1975. Predation and Population Stability. Advances in Ecological Research 9, 1–131. https://doi.org/10.1016/S0065-2504(08)60288-3

Nouhuys, S. van, Hanski, I., 2002. Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. Journal of Animal Ecology 71, 639–650. https://doi.org/10.1046/j.1365-2656.2002.00627.x

Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation 117, 285–297. https://doi.org/10.1016/j.biocon.2003.12.008

Pascual-Hortal, L., Saura, S., 2006. Comparison and development of new graph-based landscape connectivity indices: Towards the priorization of habitat patches and corridors for conservation. Landscape Ecology 21, 959–967. https://doi.org/10.1007/s10980-006-0013-z

Petchey, O.L., Pontarp, M., Massie, T.M., Kéfi, S., Ozgul, A., Weilenmann, M., Palamara, G.M., Altermatt, F., Matthews, B., Levine, J.M., Childs, D.Z., McGill, B.J., Schaepman, M.E., Schmid, B., Spaak, P., Beckerman, A.P., Pennekamp, F., Pearse, I.S., 2015. The ecological forecast horizon, and examples of its uses and determinants. Ecology Letters 18, 597–611. https://doi.org/10.1111/ele.12443

Pinto, N., Keitt, T.H., 2009. Beyond the least-cost path: Evaluating corridor redundancy using a graph-theoretic approach. Landscape Ecology. https://doi.org/10.1007/s10980-008-9303-y

Purse, B.V., Hopkins, G.W., Day, K.J., Thompson, D.J., 2003. Dispersal characteristics and management of a rare damselfly. Journal of Applied Ecology 40, 716–728. https://doi.org/10.1046/j.1365-2664.2003.00829.x

Python Core Team, 2021. Python.

R Core Team, 2018. R: A Language and Environment for Statistical Computing.

Rankin, M.A., Burchsted, J.C.A., 1992. The cost of migration in insects. Annual Review of Entomology 37, 533–39. https://doi.org/10.1146/annurev.en.37.010192.002533

Ricketts, T.H., 2001. The Matrix Matters: Effective Isolation in Fragmented Landscapes. The American Naturalist 158, 87–99. https://doi.org/10.1086/320863

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., 2019. MASS: Support Functions and Datasets for Venables and Ripley’s MASS, ’Modern Applied Statistics with S’.

Rouquette, J.R., 2005. Conservation requirements of the southern damselfly in chalkstream and fen habitats. Environment Agency UK, Bristol.

Salcher, M., Schiel, F., 2015. Neunachweise der Helm-Azurjungfer (Coenagrion mercuriale) bei Tübingen (Odonata: Coenagrionidae). Mercuriale 5–12.

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Sarremejane, R., Mykrä, H., Bonada, N., Aroviita, J., Muotka, T., 2017. Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. Freshwater Biology 62, 1073–1082. https://doi.org/10.1111/fwb.12926

Saura, S., Bodin, Ö., Fortin, M.-J.J., 2014. EDITOR’S CHOICE: Stepping stones are crucial for species’ long-distance dispersal and range expansion through habitat networks. Journal of Applied Ecology 51, 171–182. https://doi.org/10.1111/1365-2664.12179

Saura, S., Martínez-Millán, J., 2000. Landscape patterns simulation with a modified random clusters method Santiago. Landscape Ecology 15, 661–678. https://doi.org/10.1023/a:1008107902848

Saura, S., Pascual-Hortal, L., 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. Landscape and Urban Planning 83, 91–103. https://doi.org/10.1016/j.landurbplan.2007.03.005

Simmons, B.I., Balmford, A., Bladon, A.J., Christie, A.P., De Palma, A., Dicks, L.V., Gallego-Zamorano, J., Johnston, A., Martin, P.A., Purvis, A., Rocha, R., Wauchope, H.S., Wordley, C.F.R., Worthington, T.A., Finch, T., 2019. Worldwide insect declines: An important message, but interpret with caution. Ecology and Evolution 9, 3678–3680. https://doi.org/10.1002/ece3.5153

Smith, R.F., Alexander, L.C., Lamp, W.O., 2009. Dispersal by terrestrial stages of stream insects in urban watersheds: a synthesis of current knowledge. Journal of the North American Benthological Society 28, 1022–1037. https://doi.org/10.1899/08-176.1

Strien, M.J. van, Grêt-Regamey, A., 2016. How is habitat connectivity affected by settlement and road network configurations? Results from simulating coupled habitat and human networks. Ecological Modelling 342, 186–198. https://doi.org/10.1016/j.ecolmodel.2016.09.025

Sutherland, W.J., Norris, K., 2002. Behavioural models of population growth rates: implications for conservation and prediction. Phylosophical Transactions of the Royal Society B: Biological Science 357, 1273–1284. https://doi.org/10.1098/rstb.2002.1127

Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H., Brotons, L., 2016. Biodiversity scenarios neglect future land-use changes. Global change biology 22, 2505–2515. https://doi.org/10.1111/gcb.13272

Tonkin, J.D., Altermatt, F., Finn, D.S., Heino, J., Olden, J.D., Pauls, S.U., Lytle, D.A., S. Finn, D., Heino, J., Olden, J.D., Pauls, S.U., Lytle, D.A., Finn, D.S., Heino, J., Olden, J.D., Pauls, S.U., Lytle, D.A., S. Finn, D., Heino, J., Olden, J.D., Pauls, S.U., Lytle, D.A., 2018a. The role of dispersal in river network metacommunities: Patterns, processes, and pathways. Freshwater Biology 63, 141–163. https://doi.org/10.1111/fwb.13037

Tonkin, J.D., Heino, J., Altermatt, F., 2018b. Metacommunities in river networks: The importance of network structure and connectivity on patterns and processes. Freshwater Biology 63, 1–5. https://doi.org/10.1111/fwb.13045

Travis, J.M.J., Murrell, D.J., Dytham, C., 1999. The evolution of density–dependent dispersal. Proceedings of the Royal Society of London. Series B: Biological Sciences 266, 1837–1842. https://doi.org/10.1098/rspb.1999.0854

Tsoularis, A., Wallace, J.B., 2002. Analysis of logistic growth models. Mathematical Biosciences 179, 21–55. https://doi.org/10.1016/S0025-5564(02)00096-2

Urban, D.L., 2005. MODELING ECOLOGICAL PROCESSES ACROSS SCALES. Ecology 86, 1996–2006. https://doi.org/10.1890/04-0918

Urban, M.C., Bocedi, G., Hendry, A.P., Mihoub, J.B., Pe'er, G., Singer, A., Bridle, J.R., Crozier, L.G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J.J., Holt, R.D., Huth, A., Johst, K., Krug, C.B., Leadley, P.W., Palmer, S.C.F., Pantel, J.H., Schmitz, A., Zollner, P.A., Travis, J.M.J., 2016. Improving the forecast for biodiversity under climate change. Science 353. https://doi.org/10.1126/science.aad8466

Van den Brink, P.J., (Hans) Baveco, J.M., Verboom, J., Heimbach, F., 2007. An individual-based approach to model spatial population dynamics of invertebrates in aquatic ecosystems after pesticide contamination. Environmental Toxicology and Chemistry 26, 2226. https://doi.org/10.1897/07-022R.1

Villard, M.A., Metzger, J.P., 2014. Beyond the fragmentation debate: A conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology 51, 309–318. https://doi.org/10.1111/1365-2664.12190

Vos, C.C., Goedhart, P.W., Lammertsma, D.R., Annemarieke, M., Sluijs, S.D., 2006. Matrix permeability of agricultural landscapes: an analysis of movements of the common frog (Rana temporaria). Conservation Biology.

Walt, S. van der, Schönberger, J.L., Nunez-Iglesias, J., Boulogne, F., Warner, J.D., Yager, N., Gouillart, E., Yu, T., 2014. scikit-image: image processing in Python. PeerJ 2, e453. https://doi.org/10.7717/peerj.453

Watts, P.C., Rouquette, J.R., Saccheri, I.J., Kemp, S.J., Thompson, D.J., 2004. Molecular and ecological evidence for small-scale isolation by distance in an endangered damselfly, Coenagrion mercuriale. Molecular Ecology 13, 2931–2945. https://doi.org/10.1111/j.1365-294X.2004.02300.x

Watts, P.C., Saccheri, I.J., Kemp, S.J., Thompson, D.J., 2006. Population structure and the impact of regional and local habitat isolation upon levels of genetic diversity of the endangered damselfly Coenagrion mercuriale (Odonata: Zygoptera). Freshwater Biology 51, 193–205. https://doi.org/10.1111/j.1365-2427.2005.01478.x

Wilson, M.C., Richard, X.C., Didham, R.K., Ding, P., Holt, R.D., Holyoak, M., Hu, G., Hughes, A.C., Jiang, L., Laurance, W.F., Liu, J., Pimm, S.L., Robinson, S.K., Russo, S.E., Si, X., Wilcove, D.S., Wu, J., Yu, M., 2016. Habitat fragmentation and biodiversity conservation : key findings and future challenges. Landscape Ecology 31, 219–227. https://doi.org/10.1007/s10980-015-0312-3

Ye, X., Wang, T., Skidmore, A.K., 2013. Spatial pattern of habitat quality modulates population persistence in fragmented landscapes. Ecological Research 28, 949–958. https://doi.org/10.1007/s11284-013-1077-2

Zeller, K.A., McGarigal, K., Whiteley, A.R., 2012. Estimating landscape resistance to movement: A review. Landscape Ecology 27, 777–797. https://doi.org/10.1007/s10980-012-9737-0

3. SPATIOTEMPORAL DYNAMICS DRIVE SYNERGISM OF LAND USE AND CLIMATIC EXTREME EVENTS IN INSECT META-POPULATIONS

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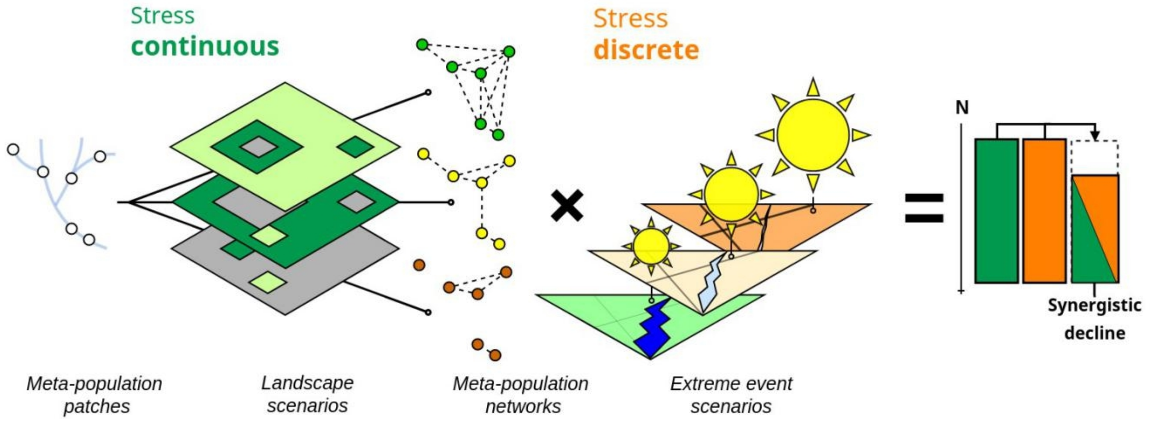
GRAPHICAL ABSTRACT



ABSTRACT

Ecosystems are increasingly threatened by co-occurring stressors associated with anthropogenic global change. Spatial stressor patterns range from local to regional to global, and temporal stressor patterns from discrete to continuous.

To date, most multiple stressor studies covered short periods and focused on local effects and interactions. However, it remains largely unknown how stressors with different spatiotemporal profiles interact in their effects over longer periods. In particular, at higher spatial scales, biotic dynamics in ecological networks complicate the understanding of stressor interactions.

We used a spatially explicit meta-population model for a generic freshwater insect, parameterized based on traits of the European damselfly *Coenagrion mercuriale*, to simulate scenarios of discrete climatic extreme events and continuous land use-related stress. Climatic extreme events were modeled as repetitive mortality in all patches, whereas land use permanently influenced meta-populations via patch qualities and network connectivity.

We found that the risk of discrete climatic extreme events to meta-populations depended strongly on the proportion of land use types, with effects ranging from negligible to extinction. Land use-related stress limited recovery and thereby buffering of the effects of climatic extreme events in meta-populations, resulting in synergistic stressor interactions. Moreover, the spatial configuration of land use type influenced the combined stressor effects with clustered configurations resulting in lower effects compared to a random configuration. Finally, we found that stressor effects and interactions can vary with the time point at which they were determined, indicating that inconclusive results in multiple stressor research can partly be due to differences in the time of determination.

We conclude that conservation should focus on regional landscape management to mitigate risks on meta-populations from future, intensified extreme climate events. Reducing land use effects, thus improving patch quality and network connectivity, can buffer the effects of additional discrete stressors and, in turn, synergistic interactions.

KEYWORDS

Global change; Multiple stressors; Meta-population networks; Spatiotemporal patterns; Stressor interactions

1 INTRODUCTION

Ecosystems are increasingly threatened by stressors associated with climate and land use change (IPCC, 2019; Orr et al., 2020), where a stressor is defined as an environmental variable outside of its normal range with adverse ecological effects (Brown et al., 2013). Stressors vary in their spatial and temporal patterns. Spatial patterns range from locally (e.g., chemical pollution), to regionally (e.g., reduced habitat connectivity), to globally acting stressors (e.g., global climate change) (Brown et al., 2014; Côté et al., 2016). Temporal patterns range from discrete, short stressor events (e.g., climatic extreme events) to continuous, permanent stressor presence (e.g., modified micro-climates) (Cash et al., 2006; IPCC, 2019; Pinek et al., 2020).

In most ecosystems stressors co-occur spatially and temporally (Birk et al., 2020; Schäfer et al., 2016). The effects of co-occurring, interacting stressors are broadly classified into (1) additive (combined effect = sum individual effects), (2) antagonistic (combined effect < sum individual effects), or (3) synergistic (combined effect > sum individual effects) (Birk et al., 2020; Côté et al., 2016). Particularly synergistic effects have attracted attention in conservation and ecosystem management, as they can produce disproportional, long-term losses in biodiversity and ecosystem functioning by amplifying biotic and abiotic feedbacks (Brook et al., 2008; Côté et al., 2016). In this context, previously stable ecosystems can be pushed beyond their tipping points, resulting in abrupt, possibly irreversible shifts (Dakos et al., 2019; Oliver and Morecroft, 2014). For example, landscape degradation can slow down the dynamics of populations or communities to the extent that brief additional stress events, which previously caused minor short-term effects, can trigger sharp declines up to extinction.

From a practical perspective, local and regional stressors are often addressed by management measures, whereas global stressors, such as climate change, are largely beyond the control of ecosystem management (Brown et al., 2014; Oliver and Morecroft, 2014). Reducing the level of local and regional stressors may mitigate the effects of increasing global stressors, thereby buffering against crossing tipping points (Brown et al., 2013; Côté et al., 2016; Woodward et al., 2016). Indeed, for ecological networks, the optimization of the landscape matrix can enhance the resilience to temporary climatic extreme events by higher patch reproduction and network connectivity (Cid et al., 2020). Given limited resources, conservation requires knowledge on the implementation of landscape-related measures, i.e., to improve the entire matrix moderately or selected areas strongly (Grass et al., 2019; Kremen and Merenlender, 2018; Van Teeffelen et al., 2012).

Most previous manipulative stressor studies focused exclusively on the local scale, e.g., microcosm or mesocosm experiments. Furthermore, studies rarely considered the temporal dynamics of multiple stressor events (Jackson et al., 2021). Accordingly, comparatively little is known on how stressors with different spatial and temporal profiles interact (Birk et al., 2020; Hunting et al., 2019; Jackson et al., 2021) and a framework to predict their effects is missing (Oliver and Morecroft, 2014; Rillig et al., 2021). At the landscape scale, the spatial profile of the stressor may determine the dynamics in ecological networks (Gonzalez et al., 2017; Schiesari et al., 2019) and alter the resilience to discrete events of an additional stressor. The long-term effects for networks depend on whether repetitive short-term local effects of a discrete stressor are compensated over time (Schäfer et al., 2017), e.g., if extinct patches can continuously be recolonized. An improved understanding of co-occurring stressors with different spatial and temporal profiles is critical to address future risks to ecosystems (Oliver and Morecroft, 2014).

Spatially explicit, process-based models, based on ecological theory, can enhance our understanding by simulating future risks for ecological networks in multiple stressor environments (Cuddington et al., 2013; Evans et al., 2012; Petchey et al., 2015). However, previous studies with meta-population models focused mainly on extinction-recolonization dynamics as well as patch distribution and number but ignored the influence of the landscape on patch qualities or network connectivity (Howell et al., 2018; Schooley and Branch, 2011; Titeux et al., 2016).

To examine the effects for meta-populations we simulated scenarios of co-occurring stressors. We used a modified version of a meta-population model for a generic, hemimetabolous freshwater insect with a terrestrial life-stage parameterized based on traits of the European damselfly *Coenagrion mercuriale* (Streib et al., 2020). As stressors, we selected land use and climatic extreme events, implemented with different profiles. Land use scenarios, defined by different proportions of three land use types in three spatial configurations, determined patch qualities and network connectivity. Climatic extreme event scenarios, defined by different mortalities and frequencies, repetitively reduced the population of all patches of a meta-population. We compared the effects of scenarios with co-occurring stressors to a baseline scenario. The baseline scenario corresponded to optimal landscape conditions, without extreme events, where the landscape exhibited the highest patch qualities and lowest dispersal costs. Moreover, we examined the influence of the spatial land use configuration (i.e., random or clustered in two different forms) on the findings at identical stressor scenarios. As suggested by previous meta-analyses on landscape management (Côté et al., 2016; Oliver and Morecroft, 2014), we hypothesized that low land use-related stress can buffer the long-term effects of extreme climatic events, preventing synergies.

2 MATERIAL & METHODS

We used the meta-population model of Streib et al. (2020) to (1) set up generic meta-population networks and, subsequently, (2) to simulate population dynamics and dispersal in the networks. In addition to Streib et al. (2020), we further incorporated land use-related patch qualities, influencing the specific carrying capacity and extinction risk, and multiple scenarios of temporary extreme events (Fig. 1).

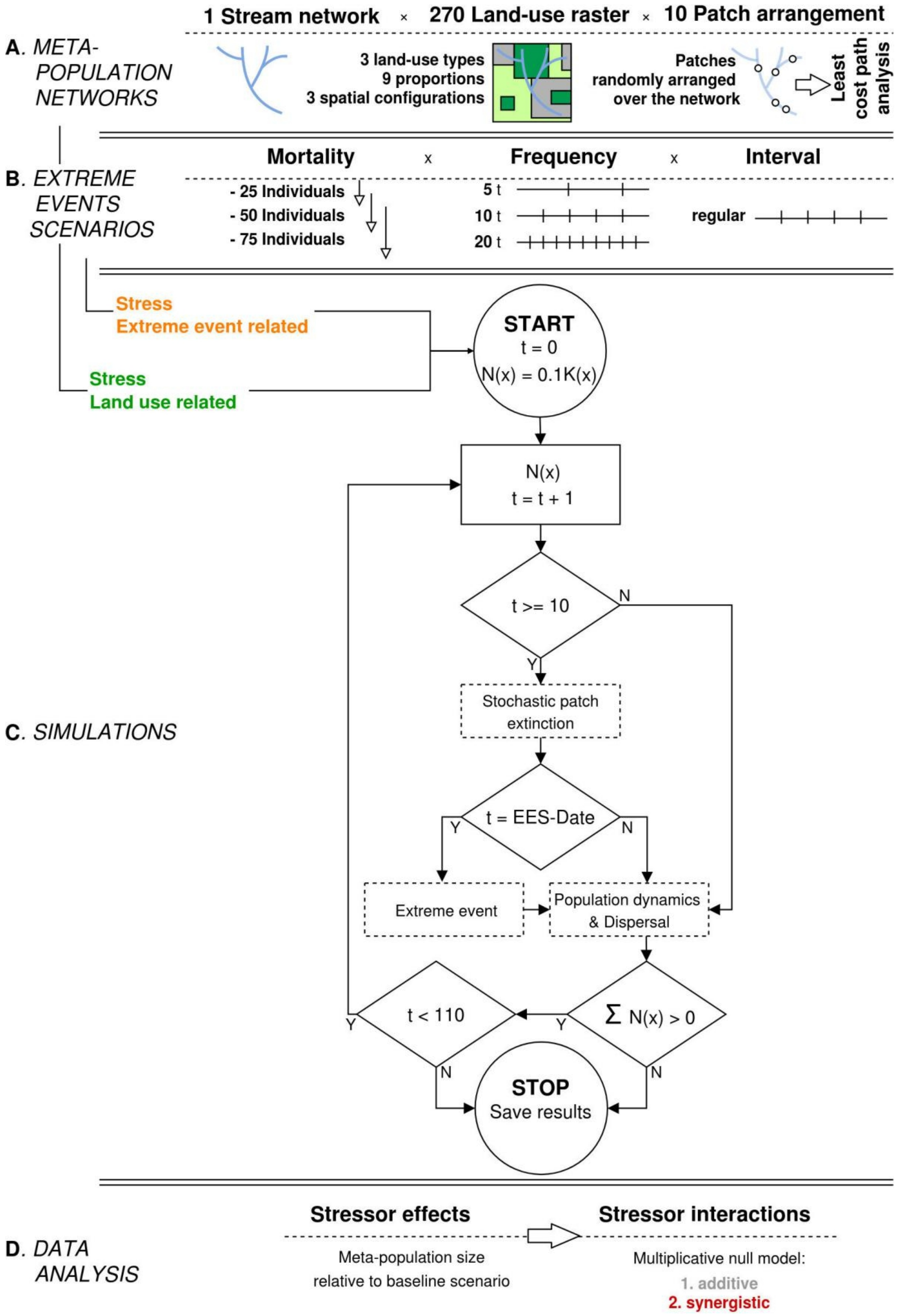


Figure 1: Overview of the simulation process, i.e., **A.** the set-up of meta-population networks MPNs, **B.** the set-up of extreme event scenarios EES, **C.** the simulation process, and **D.** the data analysis approach. **A.**: MPNs were set up by 270 land use scenarios (resulting of a stream network combined with 3 land use types in 9 different distributions and 3 spatial configurations) combined with 10 random patch arrangement scenarios using least-cost path analysis. **B.**: EES were set up by combining 3 mortalities with 3 frequencies occurring at regular intervals. **C.**: Stylized simulation process for one MPN over 110 time steps *t*. START: The initial population size N per patch *x* is set to 10 % of its carrying capacity *K(x)*. time steps *t* 1-10: Simulation of population dynamics and dispersal without local patch extinction and extreme events to arrive at an initially stable state. *t* 11-110 (or until Σ*N(x)* == 0): Simulation of population dynamics and dispersal with local patch extinction and specific extreme events. END **D.**: Calculation of stressor effects in terms of population decline relative to baseline scenarios. The effects of the stressors were subsequently quantified and classified regarding their interaction type, using a multiplicative null model.

2.1 Set up of meta-population networks

We set up multiple meta-population networks based on (1) land use scenarios combined with (2) patch arrangement scenarios, using least-cost path analysis (Adriaensen et al., 2003; Lechner et al., 2017). The resulting meta-population networks consist of quality-assigned patches and the most cost-efficient connections between those. Patches were only connected when the dispersal costs were below a given maximum (Barthélemy et al., 2005); for details see Streib et al. (2020).

A landscape scenario is a raster with a cell size of 25 x 25 m and an area of 12.5 km x 12.5 km, composed of three terrestrial land use types (LT; LT1 = extensive agriculture, LT2 = forestry, and LT3 = intensive agriculture) and a section of a real stream network (LT4 = aquatic). The proportion of each terrestrial LT varied from 0 to 100 % in steps of 50 %, with the remaining proportion distributed equally among the other two terrestrial LT. This resulted in 9 different distributions of LT. Moreover, to study the influence of the spatial configuration, each of this LT distribution was arranged in three spatial configurations using the neutral landscape model (NLM) algorithms (1) random (*nlmr*), (2) random element nearest-neighbour (*nlmre*), and (3) random cluster nearest-neighbour (*nlmrc*)

(Etherington et al., 2015). (1) resulted in land use scenarios with a random LT configuration, (2) in regularly shaped but unevenly sized fragmented LT clusters, and (3) in irregularly shaped but evenly sized aggregated LT clusters (Etherington et al., 2015) (Fig. 2).

Each LT was associated with species-specific qualities and dispersal costs. Land use-related qualities represent a proxy for pollution caused by intensive agriculture (LT3), reducing patch quality if present upstream (Allan, 2004; Feld, 2013; Sweeney and Newbold, 2014). The (numeric) dispersal costs represent the permeability of the LTs (LT1 = 50, LT2 = 75, LT3 = 50, LT 4 = 25) because the dispersal of the model species predominantly occurs by aerial movement as an adult, where elevated structures impede dispersal (Streib et al., 2020). Higher dispersal costs per connection result in enhanced dispersal mortality (Chaput-Bardy et al., 2010; Córdoba-Aguilar, 2008).

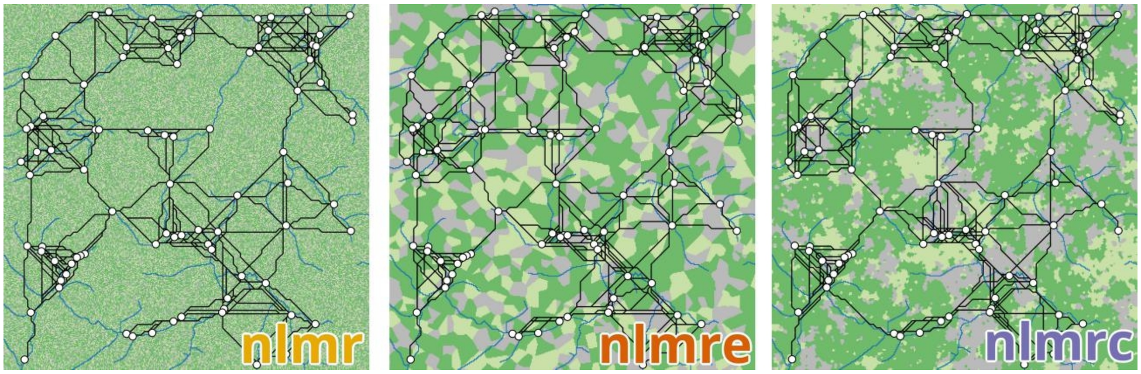


Figure 2: Examples of three land use scenarios (LSs), based on a 50 % proportion of land use type 2, combined with a random patch arrangement scenario (PA), and the resulting three meta-population networks (MPNs). MPNs consist of both, patches, represented as white points, and the most cost-efficient connections represented as black lines. The left LS with a random configuration was set up by the neutral landscape model algorithm random (*nlmr*), the center LS consisting of fragmented clusters by random element nearest-neighbour (*nlmre*), and the right LS consisting of aggregated clusters by random cluster nearest-neighbour (*nlmrc*). Light-green colored pixels represent land use type 1 (extensive agriculture), dark-green pixels land use type 2 (forestry), gray pixels land use type 3 (intensive agriculture), and blue pixels land use type 4 (aquatic).

The patch arrangement scenarios were set up by randomly selecting 10% of the LT4 (aquatic) cells of the central inner 10 km x 10 km landscape scenario area as eligible meta-population patches (Fig. 2). Thereby, we assumed that only the selected cells of the stream network provide suitable conditions for larval development.

To minimize bias, we created 10 land use scenarios for each proportion and configuration of LT and 10 random patch arrangement scenarios.

2.1.1 Derivation of patch quality

Following Richards and Host (1994) and Lammert and Allan (1999), the quality Q_P of the patches in a meta-population network was determined by the upstream land use composition in a catchment. We created a two-sided upstream buffer (width: 0.1 km, maximal length: 10 km) as the catchment area for each patch *x* within a meta-population network; for technical details see Appendix B.

We set Q_P for a patch *x* to 1 in the absence of intensive agriculture in the upstream catchment (i.e., 0% LT3). Otherwise, we reduced Q_P linearly, with a minimum value of 0.25 for 100% LT3:

$$Q_P(x) = 1.0 - \frac{A_{\mathrm{LT3}}}{A_{\mathrm{B}} - A_{\mathrm{LT4}}} * 0.75 \quad (1)$$

where A_B is the total area of the buffer. A_{LT4} the area covered by LT 4 aquatic and A_{LT3} the area covered by LT3.

2.2 Simulation of meta-population dynamics

The simulation of meta-population dynamics within each network is detailed in Streib et al. (2020). Briefly, the simulation includes (1) population growth (using the classic Verhulst model; e.g., Tsoularis and Wallace (2002); Ross (2009)), (2) potential stress events resulting in population decline (Section 2.3), and (3) dispersal processes between meta-population patches. Reproduction in a colonized patch results in positive density-dependent dispersal in terms of the emigration of individuals into connected patches. Here, the dispersal costs per connection, determined by the land use between two connected patches, act in two ways. First, patches connected via low costs receive a higher proportion of dispersing individuals. Second, dispersal mortality increases with connection costs.

2.3 Stressor scenarios

We simulated (1) land use-related stress (LUS) and (2) extreme event-related stress (EES). LUS affected a meta-population through permanent effects on patch quality and network connectivity. EES resulted in temporary, extreme events of mortality reducing the population of all meta-population patches.

2.3.1 Land use-related stress (LUS)

The landscape scenario, combining the distribution between LTs and their spatial configuration, affects the related meta-population on the regional scale through patch qualities Q_P and network connectivity (Fig. A-1 LUS).

The local patch quality Q_P represents the impact of land use on the water quality of a patch (see 2.1.1). Low-quality patches were assumed to have smaller carrying capacities, thereby having lower reproduction and being more susceptible to environmental, genetic, or demographic stochasticity (Hodgson et al., 2009; Oliver and Morecroft, 2014; Schooley and Branch, 2007). Hence, we defined the carrying capacity K and the stochastic extinction probability P_E of a patch x as a function of $Q_P(x)$:

$$K(x) = Q_P(x) \cdot Ab_{max} \quad (2)$$

The probability P_E of a patch x, i.e., the probability that the patch population $N(x)$ is set to 0, was defined to linearly decrease with Q_P from 0.1 for the minimum Q_P (0.25) to 0.01 for the maximum Q_P (1):

$$P_E(x) = 0.12 * (1 - Q_P(x)) + 0.01 \quad (3)$$

The network connectivity decreases with the proportion of LT2 (forestry) in a landscape scenario (Streib et al., 2020). LT2 has the highest dispersal cost (Section 2.1) and results in meta-populations with a lower number and also more cost-intensive connections.

2.3.2 Extreme event-related stress (EES)

Global environmental change will very likely increase the intensity and frequency of extreme events in most non-marine ecosystems (IPCC, 2019; Ummenhofer and Meehl, 2017). Most extreme events are likely to act temporarily at the regional scale (e.g., droughts, or floods) (Harrison, 1991; Schooley and Branch, 2007) and reduce the size of entire meta-populations (Bergen et al., 2020; Lande, 1998).

Thus, we extended the meta-population model by temporary scenarios of extreme events that impact all patches in a network simultaneously (Fig. A-1 EES). The EES scenarios were set up by three mortalities (high = 75.0, medium = 50.0, and low = 25.0 individuals) in three frequencies (high = 5, medium = 10, and low = 20 time steps), occurring at regular intervals, i.e., at the last time step of a frequency.

2.4 Model application

At the start of a simulation for a meta-population network, the initial population per patch *x* was set to 10 % of its specific carrying capacity *K(x)*. Subsequently, population dynamics for patches and dispersal in the network (Streib et al. (2020): Section 2.2.1 - 2.2.3) were simulated for the first 10 time steps, i.e., reproductive periods. Local patch extinction and extreme events were omitted to ensure an initially stable state. Then, over the following 100 time steps *t* or until complete extinction of the meta-population, patch-related stochastic extinction was simulated in each time step, in addition to population dynamics and dispersal. We used the algorithm 'numpy.random.choice' of the Python package 'NumPy v1.18' (NumPy, 2020) to determine whether a patch will become extinct based on its specific $P_E(x)$. Mortality resulting from extreme events was simulated according to the specific design (mortality and date) of an EES scenario. Overall, we ran 27.000 simulations based on 3.000 meta-population networks (10 land use proportions x 3 NLM algorithms x 10 random spatial configurations x 10 random patch arrangements; Section 2.1) combined or non-combined with 9 extreme event scenarios (3 mortalities x 3 frequencies; Section 2.3.2).

2.5 Data analysis

2.5.1 Quantification of stressor effects

The effect size E_s of stressors was determined as the mean population decline of all meta-population networks related to one LT configuration *y* (LUS_y; Section 2.1), without (EES_0) or with one of the 9 extreme event scenarios *z* (EES_z; Section 2.3). E_s was calculated at the final time step with respect to baseline meta-population networks, based on the optimal LT configuration (LUS_1, i.e., 100 % LT1) without extreme events (i.e., EES_n):

$$E_s(LUS_y, EES_{0 \vee z}) = 1 - \frac{\overline{N}_{110}(LUS_y, EES_{0 \vee z})}{\overline{N}_{110}(LUS_1, EES_0)} \qquad (4)$$

where $\bar{N}_{110}(LUS_y, EES_{0 \vee z})$ is the mean population size (i.e., out of 300 replicates per LUS-EES combination) at the final time step 110 for one specific LUS-EES combination, i.e., the sum of individuals in all meta-population networks divided by the number of meta-population networks.

Note that including additional extreme events in baseline meta-population networks would lead to very similar results because they had negligible long-term effects (Section 3.1.2).

Land use type configuration

To determine the influence of the LT configuration at identical LT proportions and extreme event scenarios, we quantified stressor effects differentiated by the three NLM algorithms used to arrange a specific LT proportion (i.e., 3 x 100 meta-population networks per LUS-EES combination; Section 2.1). We discuss the results in the case of deviations, defined as a standard deviation greater than 0.01.

2.5.2 Assessment of stressor interactions

To classify stressor interactions as additive or synergistic, we compared the simulated joint effects of a stressor combination to its predicted joint effects using a multiplicative null model, given mortality as the ecological response (Côté et al., 2016; Schäfer and Piggott, 2018). In the case of two co-occurring, but independently acting stressor effects E_1 and E_2, the multiplicative null model (also known as Bliss Independence, Response Multiplication, or Response Addition) assumes additivity in terms of the probabilistic sum of the individual effects (Schäfer and Piggott, 2018):

$$E_p(E_1, E_2) = E_1 + E_2 - (E_1 * E_2) \quad (5)$$

where E_1 is equivalent to $E_s(LUS_y, EES_0)$, E_2 is equivalent to $E_s(LUS_1, EES_z)$ and $E_p(E_1, E_2)$ is the predicted, additive effect resulting from their interaction. Following the concept of model deviation ratio, we used the ratio of predicted effects E_p to simulated effects E_s to evaluate stressor interactions (Belden et al., 2007). A ratio > 1 is defined as antagonistic and a ratio < 1 as synergistic interaction. To discriminate noise in the data and minor interaction effects, we only considered interactions as non-additive, where the absolute difference between E_s and E_p was greater than 0.05.

Time point of determination

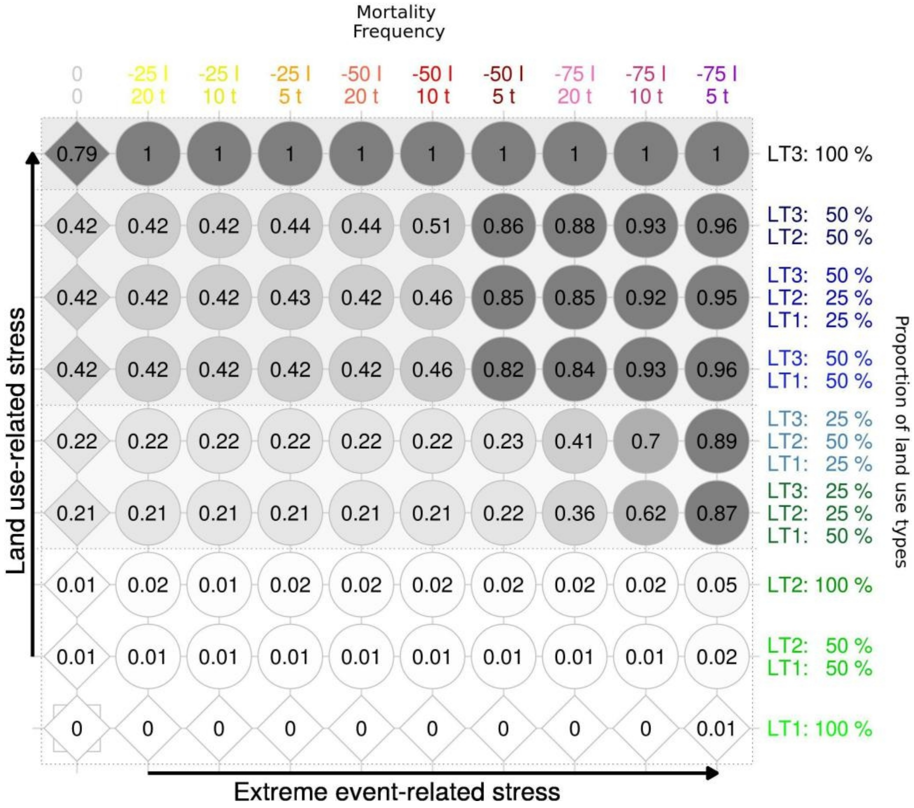
In experimental studies, the time point of the determination of the interaction effect varies across studies but may have a strong influence on the results. To evaluate the influence of this time point, we also classified stressor effects and interactions for time steps directly before and after an extreme event. For this purpose, we compared the results for time steps 90 and 91. These were the last to allow such a comparison across all stressor combinations simultaneously, as our simulation always ended with an extreme event at time step 110.

3 RESULTS

3.1 Individual effects of land use-related and extreme event-related stress

Land use-related stress (LUS) was almost exclusively driven by the proportion of intensive agriculture (LT3). The effect of LUS was negligible in the absence of LT3 (Fig. 3), but higher proportions of LT3 resulted in higher effect sizes (Fig. 3 - first column; Appendix Fig. A-1). For the scenario of only intensive agriculture the LUS effect size peaked with 0.79 (i.e., on average 79% lower meta-population size compared to the baseline scenario).

By contrast, extreme event-related stress (EES) alone, i.e., extreme events simulated at optimal LUS scenario featuring 100% extensive agriculture (LT1), led to no or negligible effects (Fig. 3 - bottom row; Appendix Fig. A-2).



0 0	-25 I 20 t	-25 I 10 t	-25 I 5 t	-50 I 20 t	-50 I 10 t	-50 I 5 t	-75 I 20 t	-75 I 10 t	-75 I 5 t	
0.79	1	1	1	1	1	1	1	1	1	LT3: 100 %
0.42	0.42	0.42	0.44	0.44	0.51	0.86	0.88	0.93	0.96	LT3: 50 % LT2: 50 %
0.42	0.42	0.42	0.43	0.42	0.46	0.85	0.85	0.92	0.95	LT3: 50 % LT2: 25 % LT1: 25 %
0.42	0.42	0.42	0.42	0.42	0.46	0.82	0.84	0.93	0.96	LT3: 50 % LT1: 50 %
0.22	0.22	0.22	0.22	0.22	0.22	0.23	0.41	0.7	0.89	LT3: 25 % LT2: 50 % LT1: 25 %
0.21	0.21	0.21	0.21	0.21	0.21	0.22	0.36	0.62	0.87	LT3: 25 % LT2: 25 % LT1: 50 %
0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.05	LT2: 100 %
0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	LT2: 50 % LT1: 50 %
0	0	0	0	0	0	0	0	0	0.01	LT1: 100 %

Figure 3: Effects of land use-related stress (LUS) and extreme event-related stress (EES). On the x-axis, mortality corresponds to the number of individuals *I* that the extreme events reduced

patch populations, and frequency to the number of s *t* in which the events were simulated; on the y-axis, the proportion is given by the area covered by land use types LT 1, 2, and 3. The bottom left (star shape) represents the baseline, i.e., 100% extensive agriculture LT1) and no EES (0, 0). The diamonds represent the individual stressor effects for LUS and EES, and the points represent the stressor effects for a LUS-EES combination. Labels and color saturation visualize the effect size, i.e., the higher the number or more saturated the shapes are, the greater is the effect size. The intensity of the background coloring of the rows reflects the proportion of intensive agriculture (LT3). Land use type configurations were not considered, i.e., results represent the average across the configurations.

3.2 Effects of combined stressors

The combination of EES and LUS led to stronger declines in meta-population size compared to individual LUS (Figure 3). However, in the absence of intensive agriculture (LT3), LUS scenarios buffered even the highest EES scenarios. By contrast, LUS scenarios featuring intensive agriculture and high EES scenarios resulted in strong declines in meta-population sizes.

At the highest LUS scenario of 100% intensive agriculture, the first extreme event at any EES scenario resulted in an effect size of 1, which means instant meta-population extinction. For intermediate LUS scenarios featuring 50% or 25% intensive agriculture, only EES scenarios with high mortalities (50.0 or 75.0 individuals per patch) led to combined effects exceeding the individual LUS effect, with effect size increasing with EES frequency.

LUS scenarios with a constant proportion of intensive agriculture resulted in meta-populations with patches of similar quality. However, shifts in the distribution of land use proportions between extensive agriculture (LT1) and forestry (LT2) translated to changes in dispersal costs and in turn network connectivity. Hence, a comparison of these scenarios (i.e., same LT3 but different proportions of LT1 and LT2) allowed for assessing the effect of network connectivity for meta-populations persistence. However, for a constant EES scenario, the difference in effect sizes was mostly minor (Fig. 3; maximum difference of 0.08).

Land use configuration

Our analysis shows a clear influence of landscape configuration on the effects (and the resulting interactions) for LUS scenarios with multiple land uses. At equal proportions of land use types, we found strong differences in the effect sizes (Fig. 4; Appendix A Fig. A-5).

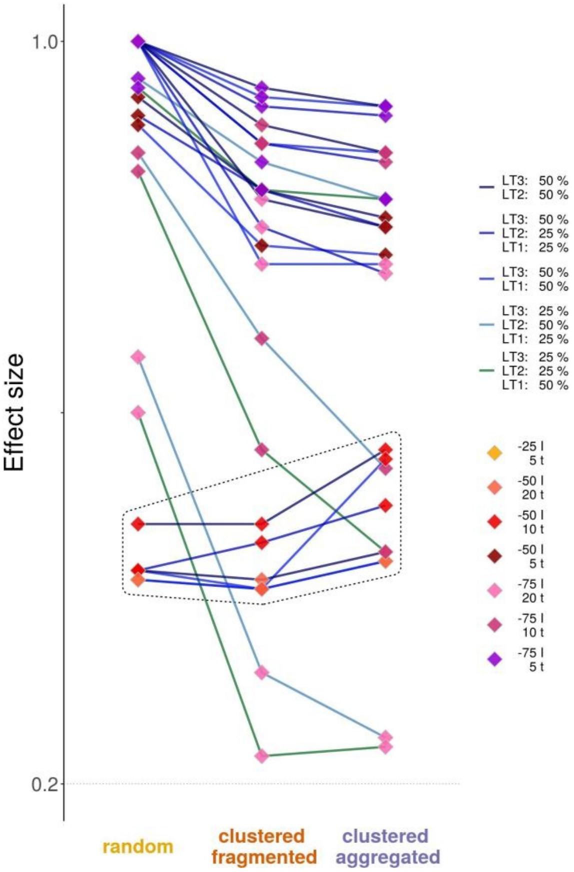
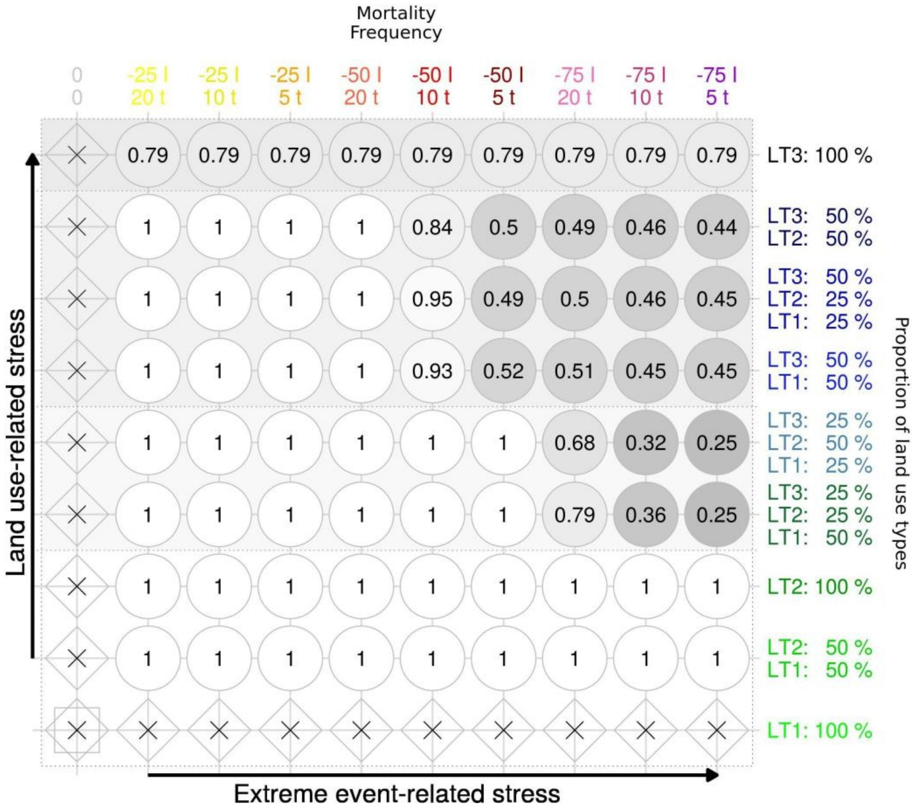


Figure 4: Effects of land use-related stress (LUS) and extreme event-related stress (EES) differentiated by the three land use type configurations, i.e., random (without autocorrelation), fragmented clusters, and aggregated clusters. Only LUS-EES combinations are displayed, where a standard deviation greater than 0.01 was detected. The coloring of lines (LUS) and points (EES) corresponds to the label colors in Fig. 3. The dotted box shows all combinations where a random land use type configuration resulted in lower effect sizes than a configuration with aggregated clusters. For details on land use-related stress and extreme event-related stress scenarios see Fig. 3 caption.

Land use scenarios with a random configuration of land use type had higher effect sizes in 92% and 75% of cases than scenarios with fragmented clusters and aggregated clusters, respectively. Scenarios with fragmented clusters had higher effect sizes than aggregated clusters in 67% of cases.

3.3 Interactions of combined stressors

We used the multiplicative null model to evaluate the interaction of combined stressors. Interactions of LUS and EES were either additive or synergistic (Fig. 4).



	0 0	-25 l 20 t	-25 l 10 t	-25 l 5 t	-50 l 20 t	-50 l 10 t	-50 l 5 t	-75 l 20 t	-75 l 10 t	-75 l 5 t
LT3: 100 %	×	0.79	0.79	0.79	0.79	0.79	0.79	0.79	0.79	0.79
LT3: 50 % LT2: 50 %	×	1	1	1	1	0.84	0.5	0.49	0.46	0.44
LT3: 50 % LT2: 25 % LT1: 25 %	×	1	1	1	1	0.95	0.49	0.5	0.46	0.45
LT3: 50 % LT1: 50 %	×	1	1	1	1	0.93	0.52	0.51	0.45	0.45
LT3: 25 % LT2: 50 % LT1: 25 %	×	1	1	1	1	1	1	0.68	0.32	0.25
LT3: 25 % LT2: 25 % LT1: 50 %	×	1	1	1	1	1	1	0.79	0.36	0.25
LT2: 100 %	×	1	1	1	1	1	1	1	1	1
LT2: 50 % LT1: 50 %	×	1	1	1	1	1	1	1	1	1
LT1: 100 %	×	×	×	×	×	×	×	×	×	×

Figure 5: Model deviation ratio of the predicted to observed interaction effects of stress (LUS) and extreme event-related stress (EES), not differentiated by land use type configuration. The color saturation and labels of the points give the model deviation ratio. Color saturation and labeling visualize the size of the effect, i.e., the lower the number or the more saturated the

shapes are, the greater is the synergistic effect. For details on land use-related stress and extreme event-related stress scenarios see Fig. 3 caption.

All EES scenarios interacted additively in combination with LUS scenarios without intensive agriculture. Also, EES scenarios with a mortality of 25 individuals per patch interacted additively with all LUS scenarios, except for the highest LUS scenario with only intensive agriculture, where the interaction was roughly 20% higher than predicted (synergism).

In contrast, synergistic interactions emerged for LUS scenarios with 25% intensive agriculture combined with EES scenarios with a mortality of 75 individuals and for LUS scenarios with 50% intensive agriculture combined with EES scenarios with a mortality of 50 and 75 individuals. The strongest synergy occurred at the highest EES scenario with a mortality of 75 individuals and a frequency of 5 time steps in combination with LUS scenarios featuring 25% intensive agriculture.

Time point of determination

The time points of determining the stressor effects and interactions considerably affected the results for several scenarios (Fig. 6).

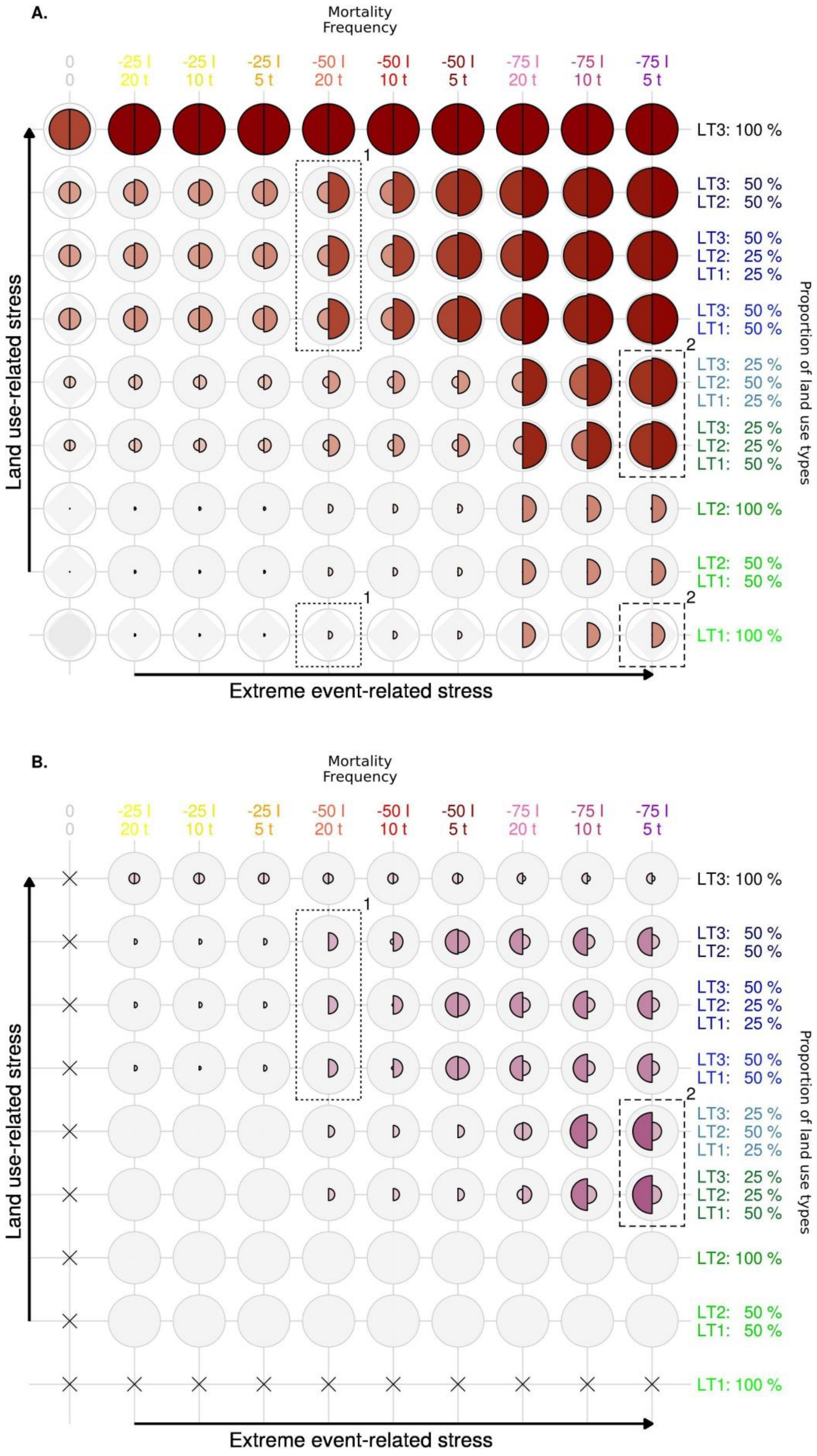

A.
Mortality
Frequency
0
0
-25 l
20 t
-25 l
10 t
-25 l
5 t
-50 l
20 t
-50 l
10 t
-50 l
5 t
-75 l
20 t
-75 l
10 t
-75 l
5 t
1
2
LT3: 100 %
LT3: 50 %
LT2: 50 %
LT3: 50 %
LT2: 25 %
LT1: 25 %
LT3: 50 %
LT1: 50 %
LT3: 25 %
LT2: 50 %
LT1: 25 %
LT3: 25 %
LT2: 25 %
LT1: 50 %
LT2: 100 %
LT2: 50 %
LT1: 50 %
LT1: 100 %
Land use-related stress
Extreme event-related stress
Proportion of land use types
B.
Mortality
Frequency
0
0
-25 l
20 t
-25 l
10 t
-25 l
5 t
-50 l
20 t
-50 l
10 t
-50 l
5 t
-75 l
20 t
-75 l
10 t
-75 l
5 t
1
2
LT3: 100 %
LT3: 50 %
LT2: 50 %
LT3: 50 %
LT2: 25 %
LT1: 25 %
LT3: 50 %
LT1: 50 %
LT3: 25 %
LT2: 50 %
LT1: 25 %
LT3: 25 %
LT2: 25 %
LT1: 50 %
LT2: 100 %
LT2: 50 %
LT1: 50 %
LT1: 100 %
Land use-related stress
Extreme event-related stress
Proportion of land use types

Figure 6: Impacts of time point of determination on effects **A.** and interactions **B.** of land use-related stress (LUS; y-axis) and extreme event-related stress (EES; x-axis). The half circles represent values calculated directly before (left part, time step 90) and after (right part, time step 91) an extreme event. Color saturation and size per half circle visualize effect size (underlying shaded circles represent the maximum of 1) and interaction size (underlying shaded circles represent the minimum of 0). Dotted and dashed boxes show examples discussed in Section 4.2. For details on land use-related stress and extreme event-related stress scenarios see Fig. 3 caption.

For all stressor combinations except for those causing meta-population extinction, we found that effect sizes calculated directly after (i.e., for time step 91) an extreme event were consistently higher than those calculated directly before (i.e., for time step 90). In contrast, the response of interactions after an extreme event was inconsistent. Besides consistent additive interactions, we found changes from additive to synergistic interactions as well as stronger and weaker synergistic interactions.

4. DISCUSSION

4.1 Stressor effects and interactions

Individual effects

We modeled the effects of stress related to land use and extreme climatic events on insect meta-populations and found that increased land use-related stress individually resulted in severe meta-population declines. In contrast, climatic extreme events had no negative effects when simulated individually, i.e., for optimal landscapes featuring 100% extensive agriculture (detailed discussion in next section).

Our findings on land use-related stress are consistent with recent studies that linked global declines and extinctions of insect populations to intensified agriculture (Benton et al., 2021; Raven and Wagner, 2021; Seibold et al., 2019).

For example, a study on twelve streams found that intensive agricultural land use in the catchment was a major determinant of local population declines of stream invertebrates (Wahl et al., 2013). For ecological networks, a review of Van Teeffelen et al. (2012) identified landscape as the main factor determining the size of meta-populations, meaning that land use stress would cause meta-population decline.

In our model, intensive agriculture governed mean patch quality and, thereby, primarily the individual effect of land use-related stress. Intensive agriculture negatively impacted patch quality (Appendix A Fig. A-4) and, thus, reduced the mean carrying capacity and increased extinction risks in a meta-population. Reduced carrying capacities had a major impact, as it lowered the potential meta-population size and inevitably increased the effect size. In contrast, the additional effect of stochastic patch extinction was lower, yet also evident. With the start of simulated patch extinction at time step 10, we detected a clear drop in population size (Appendix A Fig. A-1). We assume that high reproduction and network connectivity within a network buffered most patch extinctions via recolonization from connected patches, i.e., through mass effects (Leibold et al., 2004). The effect likely resulted from extinctions shortly before the determination (i.e., time step 110), and isolated patches that failed to recolonize. Furthermore, despite an expected strong effect (Moilanen and Nieminen, 2002; Van Teeffelen et al., 2012), we found that lower network connectivity at higher proportions of forestry, but equal proportions of intensive agriculture had little additional effect. We hypothesize that even for meta-populations split into multiple, disconnected parts (Streib et al., 2020) the number of colonized patches was sufficient to largely compensate for stochastic patch extinctions.

Combined effects

The combined effects of extreme event-related and land use-related stress were mainly governed by land use via the proportion of intensive agricultural land use (Figure 4). Similar to the optimal landscape scenario, extreme events had little to no effect in the absence of intensive agriculture. For landscapes containing intensive agriculture, combined effects generally increased with its proportion, up to 1, i.e., meta-population extinction.

Our finding that the landscape can buffer extreme climate events match a review by Woodward et al. (2016) on the effects of climatic variability and extreme events on stream ecosystems, suggesting that land use at catchment scale often exacerbates local effects of extreme events. For meta-populations, Oliver and Morecroft (2014) also indicated that (besides network area) the optimization of a landscape can buffer extreme events by improving patch quality and connectivity. Based on field survey data for butterflies, Oliver et al. (2013) or Piessens et al. (2009) showed empirically that the landscape determined responses to extreme droughts and meta-population decline were lower with better quality. Using a monitoring dataset and climate data from the UK, Newson et al. (2014) found also that meta-populations of birds inhabiting high-quality landscapes recovered quickly from climatic extreme events.

Accordingly, extreme events had no to little effect on meta-populations consisting of only high-quality patches resulting from land use scenarios without intensive agriculture. Temporary population losses in all patches were compensated rapidly by local recovery in any extreme event scenario. However, increased land use stress resulted in lower mean patch qualities making a meta-population vulnerable to extreme events. As theoretically expected for ecosystems (Dai et al., 2012), with higher continuous stress level, i.e., higher proportion of intensive agriculture, the resilience against additional, temporary events decreased. The landscape no longer allowed full recovery between extreme events at the patch and, in turn, meta-population level. Increasingly more patches had populations that were extirpated by the extreme event mortality. We assume that, both, the failure to recolonize isolated extinct patches and insufficient neighboring mass effects contributed to meta-populations declined and consequently to the determined effects. However, effect sizes varied depending on patch quality, network connectivity, and time available for recovery (Dai et al., 2013; Schooley and Branch, 2007). For equal extreme event scenarios, effects increased with lower mean patch quality, i.e., a higher proportion of intensive agriculture. For example, we found no effects for landscapes with 25% agricultural land use, but clear effects for landscapes with 50% agricultural land use for events with a mortality of at least 50 individuals at a frequency of 10 or 5 time steps (Fig. 3). Fewer patch populations survived and, in turn, recolonization via mass effects was lower and compensated less for patch extinctions. Worst case landscapes featuring 100% intensive agriculture resulted in meta-populations of patches with small populations. Hence, the first extreme event at any scenario resulted in the extinction of all patches instantly. Reduced network connectivity likely lowered recolonization further via fewer patch connections but higher dispersal losses and explains the (slight) differences between land use scenarios with the same intensive agriculture but higher forestry. Time available for recovery was determined by extreme event frequency and, thus, we found higher effects for scenarios with the same mortality, but higher frequency. This matches a study of Johansson et al. (2020) for meta-populations of an endangered butterfly using post-drought turnover data. For the same mortality, high frequency resulted in strong additional effects, with no or little additional effects at low frequency.

Land use configuration

We found for most extreme event scenarios that land use scenarios based on clustered land use configurations resulted in lower effects than those based on a random configuration. For the former, a dominant presence of one land-use type was likely in the individual patch catchments, resulting in heterogeneous patch qualities in the associated meta-populations, whereas for the latter, the distribution of types was mostly uniform across patch catchments, resulting in homogeneous patch qualities (Appendix A - Fig. A-4).

Land use at catchment scale drives the local responses to extreme events (Woodward et al., 2016). Oliver and Morecroft (2014) and Van Teeffelen et al. (2012) found evidence that meta-populations with patches of heterogeneous quality are likely to perform better against temporary stressors than meta-populations with homogeneous patches. They described that single high-quality patches can promote more stable population dynamics by surviving events of temporary mortality and, thus, driving recovery processes afterward. Also, two empirical studies showed for butterfly species in the UK (Oliver et al., 2010) and Finland (Bergen et al., 2020) that in heterogeneous meta-populations persistent, high-quality patches can buffer against climatic extreme events. These are more stable than meta-populations with homogeneous patches, which are vulnerable to extreme events due to the lack of resilient patches.

The outlined mechanisms also apply to our model. The difference was generally highest for scenarios with aggregated land use clusters, as more high-quality patches resulted form scenarios with fragmented land use clusters. For the few stressor combinations where random configurations resulted in lower effect sizes (Fig. 3: dotted box), we assume that all patches in the associated meta-populations survived the extreme events, whereas patches with lower quality, found only at clustered configurations, became extinct, and were incompletely recolonized.

4.2 Stressor interactions

The interacting effects of combined stressors were largely additive. However, synergism occurred when a meta-population did not recover between extreme events, i.e., for those stressor combinations where both stressors or land use-related stress was high.

Similarly, a review on interactions between climate change and land use change (Oliver and Morecroft, 2014) suggested that the type and size of the stressor interaction are determined by the continuous stressor (e.g., the landscape). This defines if an additional, discrete stressor (e.g., extreme events) is buffered over time, thereby preventing a synergistic effect. Moreover, a recent empirical study of habitat loss and climate change effects on population dynamics of birds in the US found that, in the absence of land use change, the landscape prevented meta-population declines by climate change (Northrup et al., 2019).

In the absence of intensive agriculture, meta-populations remained stable in the long term against any extreme event scenario and stressor interactions were additive. However, with increasing land use-related stress, even low extreme event-related stress scenarios resulted in (partly high) effects and synergistic interactions emerged.

An analysis by Côté et al. (2016) pointed out that multiple stressors often interact antagonistically at the community or ecosystem level. For example, altered species communities and thus reduced competition (Sage, 2020) or increasing tolerance of individuals through evolutionary adaptation or phenotypic plasticity (Stoks et al., 2014; Walter et al., 2013) may result in antagonism. Notwithstanding, we expect antagonism to be less likely at the (meta)-population level that our model represents (Orr et al., 2020). Future studies should expand our approach to the community or ecosystem level.

Time point of determination

The stressor effects and interactions varied, i.e., depending on whether determined directly after or directly before an extreme event. For the former, effects were consistently higher, whereas responses for interactions were mixed.

Based on data from long-term studies on global change in terrestrial ecosystems, Leuzinger et al. (2011) found that effects of combined land-use and climatic stressors can decline over time. This indicates that the time point of determination, depending on whether and how much it accounts for recovery, can affect effect size and, thus, alter the type and size of stressor interactions. For example, the interaction type changed from additive to synergistic when complete recovery over time was not ignored (Fig. 6: dotted boxes, 1), or lower interaction sizes resulted when recovery for the optimal landscape scenario was stronger than for an associated stressor combination (e.g., Fig. 6: dashed boxes, 2).

In environments with repetitive discrete stress events, a determination covering only one or very few events may lead to biased evaluations of stressor effects and interactions. Moreover, our results caution against regarding interaction types as constant over time. Our results show that multiple discrete events can lead to increasing synergy (e.g., Appendix A - Fig. A-3: steady decline for extreme event scenario ‘50 5’). The continuous stochastic extinction of high-quality patches amplified the, otherwise constant, effects over time.

Overall, to become more predictive, we suggest that multiple stressor studies should have a stronger focus on potential temporal discontinuities in effects and interaction types.

4.3 Limitations of the modeling approach

Process-based simulation models represent a trade-off between simplicity and complexity. More complex models require approximating a higher number of parameter values incurring higher uncertainty. Limitations of the current model have been discussed in Streib et al. (2020). Besides, our scenarios included only two static stressors for one species. In real world ecosystems, a wider range of stressors may occur (Sage, 2020) and stressor profiles may change over time (Jackson et al., 2021). Additional stressors would probably exacerbate the effects, as populations may further decline (e.g., invasive species reducing the population size of another species). Different stressor profiles may lead to different dynamics but are beyond the scope of the current study. For example, we expect the buffering capacity of a meta-population to vary in changing landscapes, hence events with equal mortality may have variable effects over time. Or, extreme events with irregular frequency may produce stronger meta-population declines, as the recovery time occasionally is shortened. We argue that the consideration of multiple species and more stressors would complicate the interpretation of results (Leuzinger et al., 2011), but findings regarding the relevance of the continuous stressor and recovery dynamics would likely be similar. Moreover, altered life-history and dispersal traits may quantitatively modify our findings. However, we suggest that the general principles and mechanisms underlying our findings would remain valid. Nevertheless, implementing dynamic stressor scenarios may lead to qualitatively novel insights (Jackson et al., 2021).

5. CONCLUSION FOR MANAGEMENT

In line with Oliver and Morecroft (2014) and Côté et al. (2016), our study demonstrates the effectiveness of regional landscape management to compensate for global stressors. Management that reduces a continuous stressor, thus improving patch quality (and connectivity) can mitigate or prevent long-term additional effects of intensified extreme events, potentially preventing synergistic interactions. This conclusion is supported by Johansson et al. (2020), who recently found that active landscape management can almost completely mitigate drought effects on a threatened butterfly species in Sweden. However, if only limited landscape optimization is possible, we expect measures focused on single high-value patches to be more effective than a moderate upgrade of the entire landscape.

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AUTHOR CONTRIBUTIONS

Lucas Streib: Conceptualization, Methodology, Data Curation, Model programming, Formal analysis, Visualization, Writing - Original draft preparation

Noel Juvigny-Khenafou: Conceptualization, Writing - Original draft preparation, Writing - Reviewing & Editing

Henriette Heer: Conceptualization, Writing - Reviewing & Editing

Mira Kattwinkel: Conceptualization, Writing - Reviewing & Editing

Ralf B. Schäfer: Conceptualization, Writing - Original draft preparation, Writing - Reviewing & Editing, Supervision

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests. The funding source B•M•U Graduate Academy of the University of Koblenz-Landau was not involved in the analysis, and interpretation of data; in the writing; and in the decision to submit the article for publication.

APPENDIX A

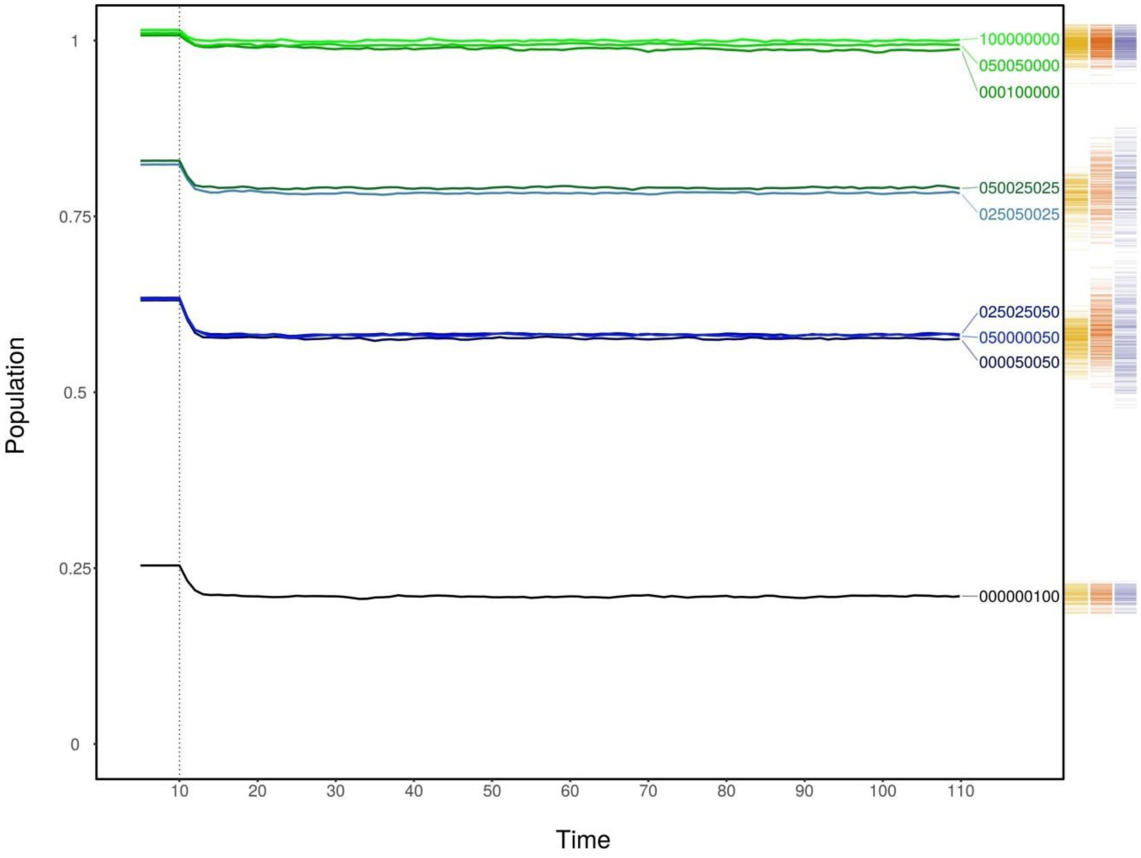


Figure A-1: Individual effects of land use-related stress (LUS) on meta-population population size from time step 5 to time step 110, i.e., simulation without extreme events. LUS scenarios are labeled at the specific line-end, here, the first three digits stand for the proportion of land use type 1, the following three for land use type 2, and the last three for land use type 3. Colored lines represent the mean of all 300 meta-population networks related to one LUS scenario, not differentiate by land use configuration. The vertical dotted line at time step 10 represents the start of simulation of local patch extinction. The dashes on the right outside the figure (3 x 100) represent the final meta-population population size of all simulations split according to the neutral landscape model algorithm: dark-yellow dashes represent the results for land use scenarios of a random LT configuration, red-orange dashes represent the results for scenarios of fragmented LT clusters, and dark-violet dashes represent the results for scenarios of aggregated LT clusters.

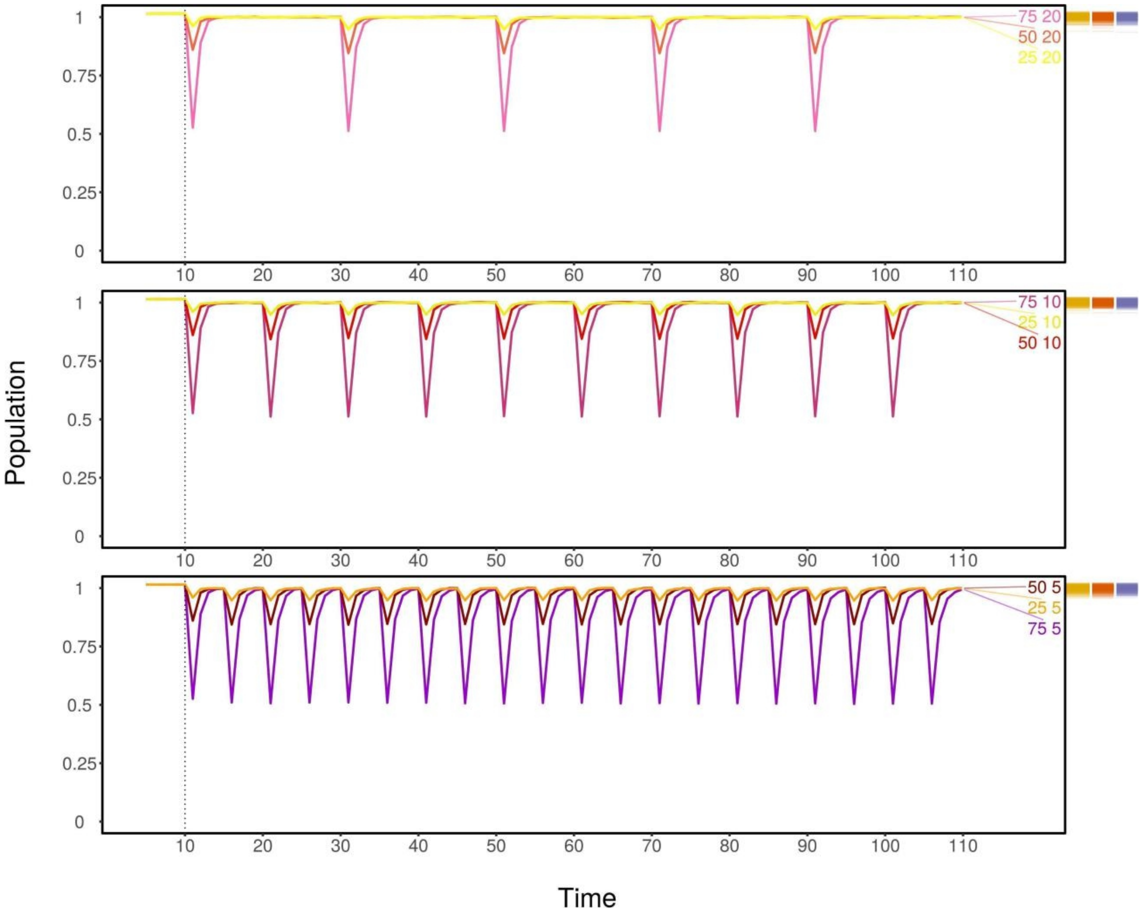


Figure A-2: Individual effects of extreme event-related stress (EES) on meta-population population size from time step 5 to time step 110, i.e., simulated for the optimal land use scenarios of 100 % land use type 1 (extensive agriculture). EES scenarios are labeled at the end of the line, where the first number represents intensity and the second frequency. Colored lines represent the mean of all related 300 meta-population networks, not differentiate by land use configuration. The vertical dotted line at time step 10 represents the start of local patch extinction and extreme events simulation. The vertical dotted line at time step 10 represents the start of simulation of local patch extinction and extreme events. The dashes on the right outside the figure (3 x 100) represent the final meta-population population size of all simulations split according to the neutral landscape model algorithm: dark-yellow dashes represent the results for land use scenarios of a random LT configuration, red-orange dashes represent the results for scenarios of fragmented LT clusters, and dark-violet dashes represent the results for scenarios of aggregated LT clusters.

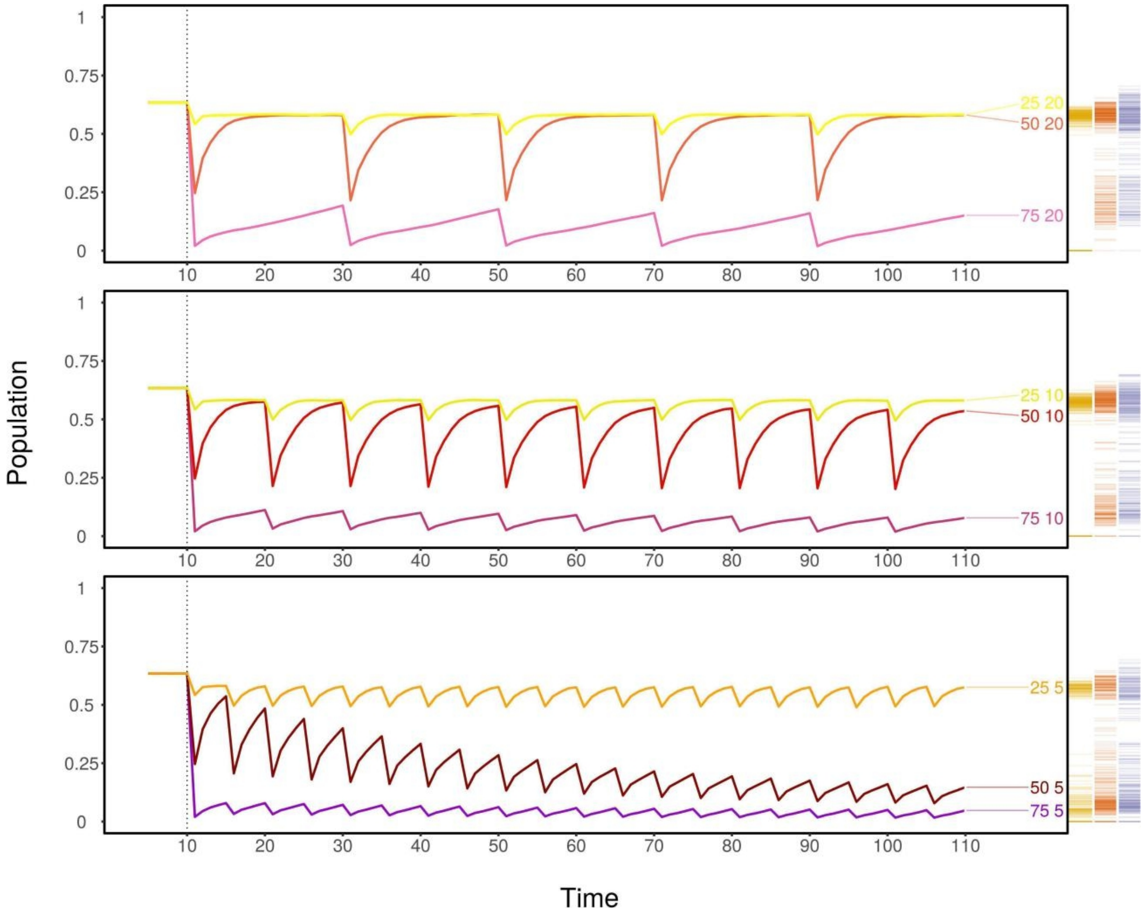


Figure A-3: Combined effects of land use-related stress (LUS) resulting from a land use proportion of 25 % land use type 1, 25 % land use type 2, & 50 % land use type 3 and extreme event-related stress (EES) on meta-population population size from time step 5 to time step 110. EES scenarios are labeled at the end of the line, where the first number represents intensity and the second frequency. Colored lines represent the mean of all related 300 meta-population networks, not differentiate by land use configuration. The vertical dotted line at time step 10 represents the start of local patch extinction and extreme events simulation. The vertical dotted line at time step 10 represents the start of simulation of local patch extinction and extreme events. The dashes on the right outside the figure (3 x 100) represent the final meta-population population size of all simulations split according to the neutral landscape model algorithm: dark-yellow dashes represent the results for land use scenarios of a random LT configuration, red-orange dashes represent the results for scenarios of fragmented LT clusters, and dark-violet dashes represent the results for scenarios of aggregated LT clusters.

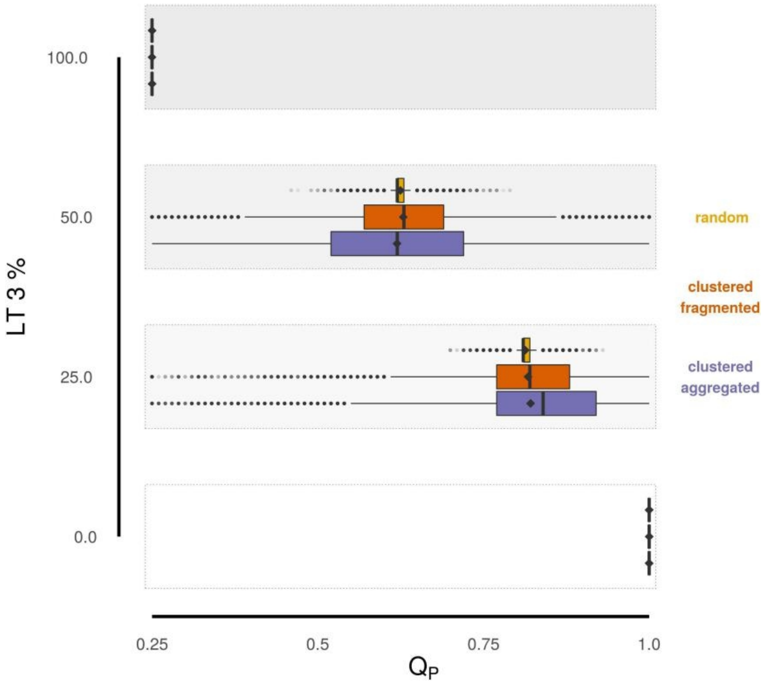
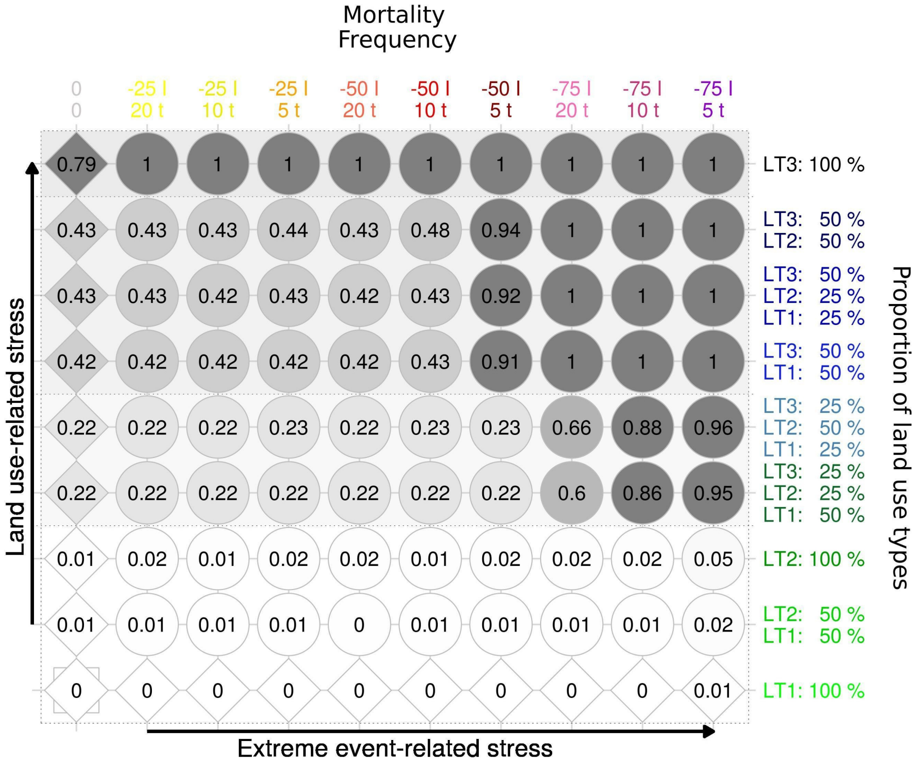


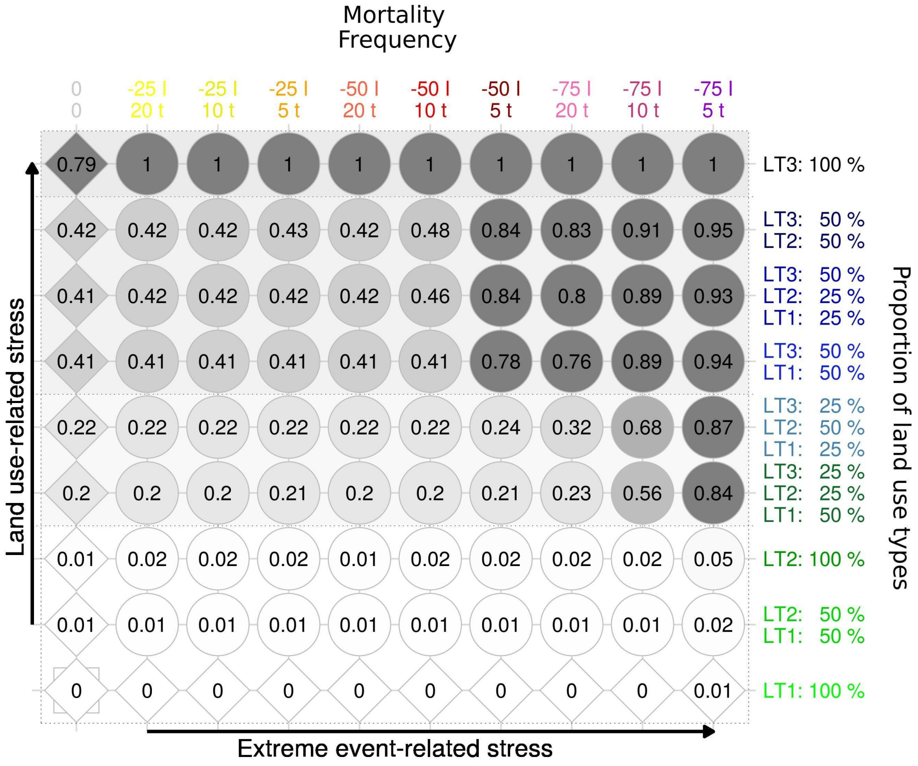
Figure A-4: Box-whisker plots with an additional mean (diamond) showing ranges of patch quality in meta-population networks differentiated by the three land use type configurations for identical proportions of land use type 3 (intensive agriculture, LT 3). The boxes are colored according to the configuration: *random* represent the results for land use scenarios of a random LT configuration, *clustered - fragmented* scenarios of fragmented LT clusters, and *clustered - aggregated* scenarios of aggregated LT clusters.

random



	0 0	-25 l 20 t	-25 l 10 t	-25 l 5 t	-50 l 20 t	-50 l 10 t	-50 l 5 t	-75 l 20 t	-75 l 10 t	-75 l 5 t
LT3: 100 %	0.79	1	1	1	1	1	1	1	1	1
LT3: 50 % LT2: 50 %	0.43	0.43	0.43	0.44	0.43	0.48	0.94	1	1	1
LT3: 50 % LT2: 25 % LT1: 25 %	0.43	0.43	0.42	0.43	0.42	0.43	0.92	1	1	1
LT3: 50 % LT1: 50 %	0.42	0.42	0.42	0.42	0.42	0.43	0.91	1	1	1
LT3: 25 % LT2: 50 % LT1: 25 %	0.22	0.22	0.22	0.23	0.22	0.23	0.23	0.66	0.88	0.96
LT3: 25 % LT2: 25 % LT1: 50 %	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.6	0.86	0.95
LT2: 100 %	0.01	0.02	0.01	0.02	0.02	0.01	0.02	0.02	0.02	0.05
LT2: 50 % LT1: 50 %	0.01	0.01	0.01	0.01	0	0.01	0.01	0.01	0.01	0.02
LT1: 100 %	0	0	0	0	0	0	0	0	0	0.01

clustered - fragmented



	0 0	-25 l 20 t	-25 l 10 t	-25 l 5 t	-50 l 20 t	-50 l 10 t	-50 l 5 t	-75 l 20 t	-75 l 10 t	-75 l 5 t
LT3: 100 %	0.79	1	1	1	1	1	1	1	1	1
LT3: 50 % LT2: 50 %	0.42	0.42	0.42	0.43	0.42	0.48	0.84	0.83	0.91	0.95
LT3: 50 % LT2: 25 % LT1: 25 %	0.41	0.42	0.42	0.42	0.42	0.46	0.84	0.8	0.89	0.93
LT3: 50 % LT1: 50 %	0.41	0.41	0.41	0.41	0.41	0.41	0.78	0.76	0.89	0.94
LT3: 25 % LT2: 50 % LT1: 25 %	0.22	0.22	0.22	0.22	0.22	0.22	0.24	0.32	0.68	0.87
LT3: 25 % LT2: 25 % LT1: 50 %	0.2	0.2	0.2	0.21	0.2	0.2	0.21	0.23	0.56	0.84
LT2: 100 %	0.01	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.05
LT2: 50 % LT1: 50 %	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02
LT1: 100 %	0	0	0	0	0	0	0	0	0	0.01

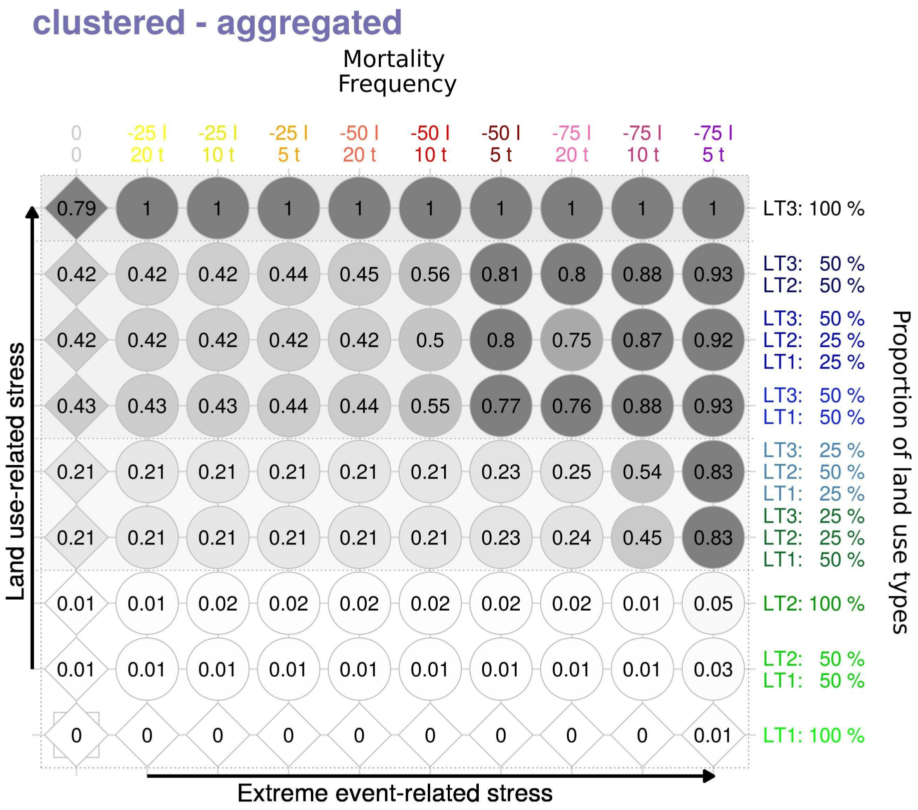


Figure A-5: Effects of combined land use-related stress (LUS) and extreme event-related stress (EES), differentiated by land use type (LT) configuration. **random** represents the results for land use scenarios without spatial autocorrelation of LT, **clustered - fragmented** for scenarios of fragmented LT clusters, and **clustered - aggregated** for scenarios of aggregated LT clusters. In the matrix plots, the points represent the stressor interactions for a LUS-EES combination. Color saturation and labels visualize the interaction size. The intensity of the plot-background coloring reflects the proportion of land use type 3 (intensive agriculture). For details on land use-related stress and extreme event-related stress scenarios see Fig. 3 caption.

APPENDIX B

Further supplementary material (software-framework, input-data, code & additional graphs for all LUS-EES combinations) can be found at the corresponding GitHub repository: https://github.com/luclucky/LUSEES

REFERENCES

Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., Matthysen, E., 2003. The application of ’least-cost’ modelling as a functional landscape model. Landscape and Urban Planning 64, 233–247. https://doi.org/10.1016/S0169-2046(02)00242-6

Allan, J.D., 2004. Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. Annual Review of Ecology, Evolution, and Systematics 35, 257–284. https://doi.org/10.1146/annurev.ecolsys.35.120202.110122

Barthélemy, M., Barrat, A., Pastor-Satorras, R., Vespignani, A., 2005. Characterization and modeling of weighted networks. Physica A: Statistical Mechanics and its Applications 346, 34–43. https://doi.org/10.1016/j.physa.2004.08.047

Belden, J.B., Gilliom, R.J., Lydy, M.J., 2007. How well can we predict the toxicity of pesticide mixtures to aquatic life? Integrated environmental assessment and management 3, 364–372. https://doi.org/10.1897/1551-3793(2007)3[364:HWCWPT]2.0.CO;2

Benton, T., Bieg, C., Harwatt, H., Pudassaini, R., Wellesley, L., 2021. Food system impacts on biodiversity loss.

Bergen, E., Dallas, T., DiLeo, M.F., Kahilainen, A., Mattila, A.L.K., Luoto, M., Saastamoinen, M., 2020. The effect of summer drought on the predictability of local extinctions in a butterfly metapopulation. Conservation Biology 0, 1–9. https://doi.org/10.1111/cobi.13515

Birk, S., Chapman, D., Carvalho, L., Spears, B.M., Andersen, H.E., Argillier, C., Auer, S., Baattrup-Pedersen, A., Banin, L., Beklioğlu, M., Bondar-Kunze, E., Borja, A., Branco, P., Bucak, T., Buijse, A.D., Cardoso, A.C., Couture, R.-M., Cremona, F., Zwart, D. de, Feld, C.K., Ferreira, M.T., Feuchtmayr, H., Gessner, M.O., Gieswein, A., Globevnik, L., Graeber, D., Graf, W., Gutiérrez-Cánovas, C., Hanganu, J., Işkın, U., Järvinen, M., Jeppesen, E., Kotamäki, N., Kuijper, M., Lemm, J.U., Lu, S., Solheim, A.L., Mischke, U., Moe, S.J., Nõges, P., Nõges, T., Ormerod, S.J., Panagopoulos, Y., Phillips, G., Posthuma, L., Pouso, S., Prudhomme, C., Rankinen, K., Rasmussen, J.J., Richardson, J., Sagouis, A., Santos, J.M., Schäfer, R.B., Schinegger, R., Schmutz, S., Schneider, S.C., Schülting, L., Segurado, P., Stefanidis, K., Sures, B., Thackeray, S.J., Turunen, J., Uyarra, M.C., Venohr, M., Ohe, P.C. von der, Willby, N., Hering, D., 2020. Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. Nature Ecology & Evolution. https://doi.org/10.1038/s41559-020-1216-4

Brook, B.W., Sodhi, N.S., Bradshaw, C.J., 2008. Synergies among extinction drivers under global change. Trends in Ecology and Evolution 23, 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Brown, C.J., Saunders, M.I., Possingham, H.P., Richardson, A.J., 2014. Interactions between global and local stressors of ecosystems determine management effectiveness in cumulative impact mapping. Diversity and Distributions 20, 538–546. https://doi.org/10.1111/ddi.12159

Brown, C.J., Saunders, M.I., Possingham, H.P., Richardson, A.J., 2013. Managing for Interactions between Local and Global Stressors of Ecosystems. PLoS ONE 8. https://doi.org/10.1371/journal.pone.0065765

Cash, D.W., Adger, W.N., Berkes, F., Garden, P., Lebel, L., Olsson, P., Pritchard, L., Young, O., 2006. Scale and Cross-Scale Dynamics: Governance and Information in a Multilevel World. Ecology and Society 11. https://doi.org/10.5751/es-01759-110208

Chaput-Bardy, A., Grégoire, A., Baguette, M., Pagano, A., Secondi, J., 2010. Condition and phenotype-dependent dispersal in a damselfly, Calopteryx splendens. PLoS ONE 5, e10694. https://doi.org/10.1371/journal.pone.0010698

Cid, N., Bonada, N., Heino, J., Cañedo-Argüelles, M., Crabot, J., Sarremejane, R., Soininen, J., Stubbington, R., Datry, T., 2020. A Metacommunity Approach to Improve Biological Assessments in Highly Dynamic Freshwater Ecosystems. BioScience 70, 427–438. https://doi.org/10.1093/biosci/biaa033

Córdoba-Aguilar, A., 2008. Dragonflies and Damselflies. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199230693.001.0001

Côté, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B: Biological Sciences 283, 20152592. https://doi.org/10.1098/rspb.2015.2592

Cuddington, K., Fortin, M.-J.M.J., Gerber, L.R., Hastings, A., Liebhold, A., O'Connor, M., Ray, C., 2013. Process-based models are required to manage ecological systems in a changing world. Ecosphere 4, art20. https://doi.org/10.1890/ES12-00178.1

Dai, L., Korolev, K.S., Gore, J., 2013. Slower recovery in space before collapse of connected populations. Nature 496, 355–358. https://doi.org/10.1038/nature12071

Dai, L., Vorselen, D., Korolev, K.S., Gore, J., 2012. Generic indicators for loss of resilience before a tipping point leading to population collapse. Science 336, 1175–1177. https://doi.org/10.1126/science.1219805

Dakos, V., Matthews, B., Hendry, A.P., Levine, J., Loeuille, N., Norberg, J., Nosil, P., Scheffer, M., De Meester, L., 2019. Ecosystem tipping points in an evolving world. Nature Ecology and Evolution 3, 355–362. https://doi.org/10.1038/s41559-019-0797-2

Etherington, T.R., Holland, E.P., O’Sullivan, D., 2015. NLMpy: A python software package for the creation of neutral landscape models within a general numerical framework. Methods in Ecology and Evolution 6, 164–168. https://doi.org/10.1111/2041-210X.12308

Evans, M.R., Norris, K.J., Benton, T.G., 2012. Predictive ecology: Systems approaches. Philosophical Transactions of the Royal Society B: Biological Sciences 367, 163–169. https://doi.org/10.1098/rstb.2011.0191

Feld, C.K., 2013. Response of three lotic assemblages to riparian and catchment-scale land use: Implications for designing catchment monitoring programmes. Freshwater Biology 58, 715–729. https://doi.org/10.1111/fwb.12077

Gonzalez, A., Thompson, P., Loreau, M., 2017. Spatial ecological networks: planning for sustainability in the long-term. Current Opinion in Environmental Sustainability 29, 187–197. https://doi.org/10.1016/j.cosust.2018.03.012

Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A., Klaus, F., Riechers, M., Rosa, J., Tiede, J., Udy, K., Westphal, C., Wurz, A., Tscharntke, T., 2019. Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. People and Nature 262–272. https://doi.org/10.1002/pan3.21

Harrison, S., 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42, 73–88. https://doi.org/10.1111/j.1095-8312.1991.tb00552.x

Hodgson, J.A., Moilanen, A., Thomas, C.D., 2009. Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. Ecology 90, 1608–1619. https://doi.org/10.1890/08-1227.1

Howell, P.E., Muths, E., Hossack, B.R., Sigafus, B.H., Chandler, R.B., 2018. Increasing connectivity between metapopulation ecology and landscape ecology. Ecology 99, 1119–1128. https://doi.org/10.1002/ecy.2189

Hunting, E.R., Bundschuh, M., Schrama, M., 2019. Editorial: Multiple Stressors Across Ecosystem Boundaries. Frontiers in Environmental Science 7, 171–176. https://doi.org/10.3389/fenvs.2019.00098

IPCC, 2019. Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. In press.

Jackson, M.C., Pawar, S., Woodward, G., 2021. The Temporal Dynamics of Multiple Stressor Effects: From Individuals to Ecosystems. Trends in Ecology & Evolution 36, 402–410. https://doi.org/10.1016/j.tree.2021.01.005

Johansson, V., Kindvall, O., Askling, J., Franzén, M., 2020. Extreme weather affects colonization–extinction dynamics and the persistence of a threatened butterfly. Journal of Applied Ecology 57, 1068–1077. https://doi.org/10.1111/1365-2664.13611

Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. Science 362. https://doi.org/10.1126/science.aau6020

Lammert, M., Allan, J.D., 1999. Assessing biotic integrity of streams: Effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environmental Management 23, 257–270. https://doi.org/10.1007/s002679900184

Lande, R., 1998. Anthropogenic, Ecological and Genetic Factors in Extinction and Conservation. Researches on Population Ecology 40, 259–269. https://doi.org/10.1007/BF02763457

Lechner, A.M., Sprod, D., Carter, O., Lefroy, E.C., 2017. Characterising landscape connectivity for conservation planning using a dispersal guild approach. Landscape Ecology 32, 99–113. https://doi.org/10.1007/s10980-016-0431-5

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Leuzinger, S., Luo, Y., Beier, C., Dieleman, W., Vicca, S., Körner, C., 2011. Do global change experiments overestimate impacts on terrestrial ecosystems? Trends in Ecology and Evolution 26, 236–241. https://doi.org/10.1016/j.tree.2011.02.011

Moilanen, A., Nieminen, M., 2002. Simple connectivity measure in spatial ecology. Ecology 83, 1131–1145.

Newson, S.E., Oliver, T.H., Gillings, S., Crick, H.Q., Morecroft, M.D., Duffield, S.J., Macgregor, N.A., Pearce-Higgins, J.W., 2014. Can site and landscape-scale environmental attributes buffer bird populations against weather events? Ecography 37, 872–882. https://doi.org/10.1111/ecog.00575

Northrup, J.M., Rivers, J.W., Yang, Z., Betts, M.G., 2019. Synergistic effects of climate and land-use change influence broad-scale avian population declines. Global Change Biology 25, 1561–1575. https://doi.org/10.1111/gcb.14571

NumPy, 2020. NumPy Reference - Release 1.18.1.

Oliver, T.H., Brereton, T., Roy, D.B., 2013. Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. Ecography 36, 579–586. https://doi.org/10.1111/j.1600-0587.2012.07665.x

Oliver, T.H., Morecroft, M.D., 2014. Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. Wiley Interdisciplinary Reviews: Climate Change 5, 317–335. https://doi.org/10.1002/wcc.271

Oliver, T., Roy, D.B., Hill, J.K., Brereton, T., Thomas, C.D., 2010. Heterogeneous landscapes promote population stability. Ecology Letters 13, 473–484. https://doi.org/10.1111/j.1461-0248.2010.01441.x

Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle, C., Brink, P.J. van den, Laender, F. de, Stoks, R., Holmstrup, M., Matthaei, C.D., Monk, W.A., Penk, M.R., Leuzinger, S., Schäfer, R.B., Piggott, J.J., 2020. Towards a unified study of multiple stressors: Divisions and common goals across research disciplines. Proceedings of the Royal Society B: Biological Sciences 287. https://doi.org/10.1098/rspb.2020.0421

Petchey, O.L., Pontarp, M., Massie, T.M., Kéfi, S., Ozgul, A., Weilenmann, M., Palamara, G.M., Altermatt, F., Matthews, B., Levine, J.M., Childs, D.Z., McGill, B.J., Schaepman, M.E., Schmid, B., Spaak, P., Beckerman, A.P., Pennekamp, F., Pearse, I.S., 2015. The ecological forecast horizon, and examples of its uses and determinants. Ecology Letters 18, 597–611. https://doi.org/10.1111/ele.12443

Piessens, K., Adriaens, D., Jacquemyn, H., Honnay, O., 2009. Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. Oecologia 159, 117–126. https://doi.org/10.1007/s00442-008-1204-x

Pinek, L., Mansour, I., Lakovic, M., Ryo, M., Rillig, M.C., 2020. Rate of environmental change across scales in ecology. Biological Reviews 95, 1798–1811. https://doi.org/10.1111/brv.12639

Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. Proceedings of the National Academy of Sciences of the United States of America 118, 1–6. https://doi.org/10.1073/PNAS.2002548117

Richards, C., Host, G., 1994. EXAMINING LAND USE INFLUENCES ON STREAM HABITATS AND MACROINVERTEBRATES: A GIS APPROACH. Journal of the American Water Resources Association 30, 729–738. https://doi.org/10.1111/j.1752-1688.1994.tb03325.x

Rillig, M.C., Ryo, M., Lehmann, A., 2021. Classifying human influences on terrestrial ecosystems. Global Change Biology gcb.15577. https://doi.org/10.1111/gcb.15577

Ross, J.V., 2009. A note on density dependence in population models. Ecological Modelling 220, 3472–3474. https://doi.org/10.1016/j.ecolmodel.2009.08.024

Sage, R.F., 2020. Global change biology: A primer. Global Change Biology 26, 3–30. https://doi.org/10.1111/gcb.14893

Schäfer, R.B., Kühn, B., Hauer, L., Kattwinkel, M., 2017. Assessing recovery of stream insects from pesticides using a two-patch metapopulation model. Science of the Total Environment 609, 788–798. https://doi.org/10.1016/j.scitotenv.2017.07.222

Schäfer, R.B., Kühn, B., Malaj, E., König, A., Gergs, R., 2016. Contribution of organic toxicants to multiple stress in river ecosystems. Freshwater Biology 61, 2116–2128. https://doi.org/10.1111/fwb.12811

Schäfer, R.B., Piggott, J.J., 2018. Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. Global Change Biology 24, 1817–1826. https://doi.org/10.1111/gcb.14073

Schiesari, L., Matias, M.G., Prado, P.I., Leibold, M.A., Albert, C.H., Howeth, J.G., Leroux, S.J., Pardini, R., Siqueira, T., Brancalion, P.H., Cabeza, M., Coutinho, R.M., Diniz-Filho, J.A.F., Fournier, B., Lahr, D.J., Lewinsohn, T.M., Martins, A., Morsello, C., Peres-Neto, P.R., Pillar, V.D., Vázquez, D.P., 2019. Towards an applied metaecology. Perspectives in Ecology and Conservation 17, 172–181. https://doi.org/10.1016/j.pecon.2019.11.001

Schooley, R.L., Branch, L.C., 2011. Habitat quality of source patches and connectivity in fragmented landscapes. Biodiversity and Conservation 20, 1611–1623. https://doi.org/10.1007/s10531-011-0049-5

Schooley, R.L., Branch, L.C., 2007. Spatial heterogeneity in habitat quality and cross-scale interactions in metapopulations. Ecosystems 10, 846–853. https://doi.org/10.1007/s10021-007-9062-7

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671–674. https://doi.org/10.1038/s41586-019-1684-3

Stoks, R., Geerts, A.N., De Meester, L., 2014. Evolutionary and plastic responses of freshwater invertebrates to climate change: Realized patterns and future potential. Evolutionary Applications 7, 42–55. https://doi.org/10.1111/eva.12108

Streib, L., Kattwinkel, M., Heer, H., Ruzika, S., Schäfer, R.B., 2020. How does habitat connectivity influence the colonization success of a hemimetabolous aquatic insect? - A modeling approach. Ecological Modelling 416, 108909. https://doi.org/10.1016/j.ecolmodel.2019.108909

Sweeney, B.W., Newbold, J.D., 2014. Streamside forest buffer width needed to protect stream water quality, habitat, and organisms: A literature review. Journal of the American Water Resources Association 50, 560–584. https://doi.org/10.1111/jawr.12203

Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H., Brotons, L., 2016. Biodiversity scenarios neglect future land-use changes. Global change biology 22, 2505–2515. https://doi.org/10.1111/gcb.13272

Tsoularis, A., Wallace, J.B., 2002. Analysis of logistic growth models. Mathematical Biosciences 179, 21–55. https://doi.org/10.1016/S0025-5564(02)00096-2

Ummenhofer, C.C., Meehl, G.A., 2017. Extreme weather and climate events with ecological relevance: A review. Philosophical Transactions of the Royal Society B: Biological Sciences 372. https://doi.org/10.1098/rstb.2016.0135

Van Teeffelen, A.J., Vos, C.C., Opdam, P., 2012. Species in a dynamic world: Consequences of habitat network dynamics on conservation planning. Biological Conservation 153, 239–253. https://doi.org/10.1016/j.biocon.2012.05.001

Wahl, C.M., Neils, A., Hooper, D., 2013. Impacts of land use at the catchment scale constrain the habitat benefits of stream riparian buffers. Freshwater Biology 58, 2310–2324. https://doi.org/10.1111/fwb.12211

Walter, J., Jentsch, A., Beierkuhnlein, C., Kreyling, J., 2013. Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. Environmental and Experimental Botany 94, 3–8. https://doi.org/10.1016/j.envexpbot.2012.02.009

Woodward, G., Bonada, N., Brown, L.E., Death, R.G., Durance, I., Gray, C., Hladyz, S., Ledger, M.E., Milner, A.M., Ormerod, S.J., Thompson, R.M., Pawar, S., 2016. The effects of climatic fluctuations and extreme events on running water ecosystems. Philosophical Transactions of the Royal Society B: Biological Sciences 371. https://doi.org/10.1098/rstb.2015.0274

4. THE SPATIOTEMPORAL PROFILE AND ADAPTATION DETERMINE THE JOINT EFFECTS AND INTERACTIONS OF MULTIPLE STRESSORS

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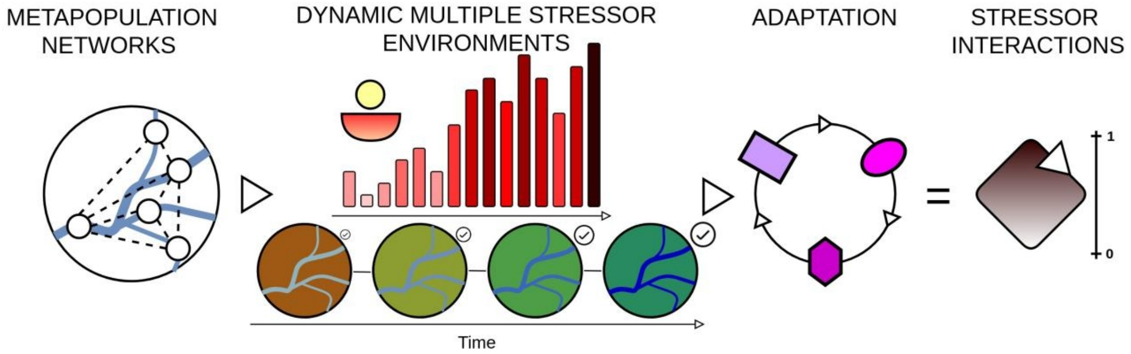
The content of this chapter corresponds to a draft in preparation.

GRAPHICAL ABSTRACT



ABSTRACT

Background: Biodiversity is declining worldwide as ecosystems are increasingly threatened by multiple stressors associated with anthropogenic global change. Stressors frequently co-occur across scales spatially and temporally, resulting in joint effects that are additive or non-additive, i.e., antagonism or synergism. Forecasting and counteracting threats from intensifying stressors requires improved mechanistic understanding of joint effects, which is currently relatively low. To date, research on multiple stressors has been biased toward simplified scenarios, emphasized classification of interactions over realized joint effects, and mostly ignored adaptation (i.e., phenotypic plasticity or evolving life-history traits) of organisms. We modified a spatially explicit meta-population model for a generic freshwater insect to simulate different, hypothetical spatiotemporal profiles of a continuous and a discrete stressor and evaluated their joint effects and interactions. Land use represented the continuous stressor impacting meta-population patch quality and network connectivity and related scenarios implied different trajectories. Climatic events represented the discrete stressor impacting all patches simultaneously by temporary mortality events, with related scenarios implying different event severity. Adaptation mitigated the effects of climatic events based on previous events.

Results: Excluding adaption, we found that at higher levels of the discrete stressor (i.e., strong and frequent climatic events) strongly dominates the joint effects, while at a low level (i.e., weak and infrequent climatic events) of the discrete stressor, the continuous stressor (i.e., land use) dominates. Yet, the continuous stressor always defined the interaction type, with decreasing land use stress leading to antagonism, and increasing land use stress leading to synergism. Adaptation reduced joint effects under decreasing land use stress, yet had little compensatory influence under increasing land use stress. Moreover, adaptation changed the interaction classification inconsistently across the different land use and climate scenarios.

Conclusions: We highlight that complex stressor scenarios are critical for a mechanistic understanding of how species respond to global change. To our knowledge, this is the first modeling study to show that stressor interactions depend on spatiotemporal stressor profiles and adaptation, following general principles.

KEYWORDS

Global change · Multiple stressors · Spatiotemporal patterns · Joint effects · Interaction classification

BACKGROUND

Worldwide terrestrial, marine and freshwater biodiversity is declining at an accelerating rate (Newbold et al., 2015; Reid et al., 2019). Many ecosystems and their species are threatened by intensifying stressors associated with anthropogenic global change, including climate and land use change (IPCC, 2019). Stressors frequently co-occur at different spatial and temporal scales, resulting in joint effects on ecosystems (Jackson et al., 2021). Spatially, stressors may occur locally (e.g., pollution by point sources), regionally (e.g., droughts), or globally (e.g., ocean acidification) (Moe et al., 2013). Temporally, stressors may have many profiles ranging from discrete events (e.g., single climatic extremes) to continuous (e.g., constant discharge of toxic chemicals) (IPCC, 2019; Pinek et al., 2020). Multiple co-occurring stressors can result in additive effects (joint effect = sum of individual effects), but also in non-additive effects, i.e., antagonisms (joint effect < sum of individual effects) or synergisms (joint effect > sum of individual effects) (Birk et al., 2020; Côté et al., 2016). Non-additive effects can result from mechanistic stressor interactions (i.e., one stressor alters organisms' response to a second stressor), but also from other factors (e.g., nonlinear stressor-response relationships, choice of the null model predicting joint effect, and experimental duration) (Hunsicker et al., 2016; Schäfer and Piggott, 2018; Turschwell et al., 2022). The prevalence of additive and non-additive interactions is forecasted to change significantly in response to global anthropogenic changes (Jackson et al., 2021; Woodward et al., 2016). Notably, synergisms, considered to produce rapid, disproportionate losses of biodiversity and ecosystem functions (Côté et al., 2016; Ratajczak et al., 2018; Turner et al., 2020), are forecasted to occur more frequently and with higher intensity in the future (Sage, 2020).

However, research on multiple stressors has been criticized for emphasizing interaction classification, thereby neglecting mechanistic understanding of joint effects (De Laender, 2018; Simmons et al., 2021a). Nevertheless, the capacity to forecast, and counteract the threats from intensifying stressor regimes requires such predictive understanding, which is currently relatively low (Côté et al., 2016;

Kaunisto et al., 2016; Maxwell et al., 2019). Indeed, meta-analyses of experimental studies with multiple stressors have yielded few consistent findings (Côté et al., 2016; Simmons et al., 2021b). Partly, this owes to a bias in previous experimental studies toward simplified scenarios resulting in distorted, if not false, assessments of joint effects and interactions when extrapolated to real-world scenarios (Catford et al., 2022; Jackson et al., 2021; Rillig et al., 2021).

Process-based simulation models can simulate realistic spatiotemporal stressor profiles and, thereby, significantly contribute to a better mechanistic understanding of joint effects and related interactions across scales (Jackson et al., 2021; Orr et al., 2024; Turschwell et al., 2021). In addition, they support the development of corresponding theory (Simmons et al., 2021a; Stock et al., 2023). Compared to data-based models, which rely on empirical information, often are very specific, and make fewer assumptions, process-based models have a high general predictive power, yet also structural uncertainty and associated risk of bias, e.g., potentially resulting from inappropriate assumptions (Baker et al., 2018; Pirotta et al., 2022). Process-based models support predictions beyond the range of observed stressors and allow for broader extrapolation, as they do not necessarily have to replicate real-world systems or pre-determined developments; it is also reasonable to apply such models based on hypothetical scenarios, focusing on the identification of general principles (Grimm and Railsback, 2005; Pirotta et al., 2022; Stock et al., 2023). However, process-based models in multiple stressor research are rare, although related studies can support future management and thereby optimize species conservation by assessing and predicting joint effects and related interactions (Patrick et al., 2021; Pirotta et al., 2022; Turschwell et al., 2022).

By contrast, large-scale empirical experiments with multiple stressors are technically difficult to realize (Brooks and Crowe, 2019; Simmons et al., 2021). Therefore, in experiments, multiple stressors have mostly been implemented with static profiles, where stressors are temporally constant or synchronous in pulses, and spatially homogeneous (Jackson et al., 2021; Ogle et al., 2015). However, at the landscape scale and beyond, multiple stressors typically occur discontinuously, i.e., intensities vary in space and time (Hughes et al., 2019; Turschwell et al., 2021). Complex spatiotemporal stressor regimes (Brooks and Crowe, 2019; Ryo et al., 2019) and thus associated complex patterns of joint effects and interactions emerge (Jackson et al., 2021; Turner et al., 2020). For example, a variable spatial intensity of a stressor together with another, regionally uniform stressor creates locally dissimilar joint effects (Oliver and Morecroft, 2014; Van Teeffelen et al., 2012). Yet, biotic exchange processes between patches within ecological networks, e.g., driven by the dispersal of organisms, can in turn compensate for local differences over time (Bruder et al., 2019; Schiesari et al., 2019). Moreover, changes in the temporal stressor intensity, in the interval between or the frequency of stress events, can also modify the joint effects by altering the available recovery time (Côté et al., 2016; Falk et al., 2019).

Another shortcoming in multiple stressor research is that adaptation processes of organisms to stressors, likely modifying their effects and interactions, have been largely unconsidered in most previous experimental and modeling studies (Boyd et al., 2018; Orr et al., 2021; Ryo et al., 2019). Adaptation through phenotypic plasticity (Bush et al., 2016) or the evolution of life-history traits (Orr et al., 2021) can enable species to cope with changing stressor regimes. Consequently, future stress of similar intensity may have a lower effect on adapted individuals, populations, and communities, respectively (Jackson et al., 2021; Patrick et al., 2021). Moreover, adaptation can determine the response to additional stressors, for instance, through co-tolerance or trade-offs (Siddique et al., 2021; Vinebrooke et al., 2004).

We aimed to identify how complex spatiotemporal stressor profiles and adaptation influence the joint effects and thereby interactions of multiple stressors at the landscape scale compared to simplified scenarios. Hereto, we used a spatially explicit, process-based meta-population model (Streib et al., 2021, 2020) to simulate hypothetical scenarios of two stressors considering potential adaptation to one stressor. Land use and climatic events were implemented as continuous and discrete stressors, respectively, as these are key global change stressors likely to have strong future impacts on ecosystems (Aspin et al., 2019; Northrup et al., 2019). Land use-related stress continuously affected patch qualities and was incorporated with multiple temporal profiles; i.e., steady ramping, and abrupt stepwise (positive or negative). Climate scenarios resulted in numerous, irregularly timed mortality events, with the frequency and intensity of events randomly drawn from three skewed normal probability distributions. Adaptation was considered as different levels of adaptability to climatic events based on previous events. Finally, we determined the response (i.e., joint effect and interaction type and size) of meta-populations to multiple combinations of stressors and adaptation levels.

Following recent conceptual studies (Jackson et al., 2021; Turner et al., 2020), we hypothesize that scenarios incorporating complex spatiotemporal stressor profiles and adaption profoundly change joint effects and interactions of multiple stressors compared to simplified scenarios, specifically altering the frequency of additive and non-additive effects. Given the lack of data, we had no specific expectations regarding the directional change of the joint effects concerning the multiple, interacting parameters that most likely either increase (e.g., random discrete events) or decrease (e.g., adjustment) the effect sizes.

METHODS

We used a spatially explicit meta-population model for a generic hemimetabolous freshwater insect, parameterized based on traits of the European damselfly Coenagrion mercuriale (Streib et al., 2021, 2020), to simulate hypothetical scenarios incorporating complex, dynamic spatiotemporal profiles of a continuous (land use) and a discrete stressor (repetitive climatic events), considering adaptation. Compared to Streib et al. (2021), where we used the model previously to examine multiple stressor interactions, the scenarios were modified as follows:

i. Various scenarios of land use change are incorporated instead of constant land use

ii. Various scenarios of episodic climatic extreme events with random mortality are employed instead of synchronous events with constant mortality

iii. Adaptation to climatic events in different levels is now considered

iv. Stochastic patch extinction was removed to simplify understanding of climate scenario impacts

In the following, we provide an overview of the model, i.e., the set up of meta-population networks and the simulation process of population dynamics (i.e., reproduction and dispersal) within these, as well as introduce the stressor scenarios and the implementation of adaptation. The technical details of the model are described in Streib et al. (2020) and Streib et al. (2021), respectively; the software-framework as well as supplementary data and material used for the present study is provided in a GitHub repository.

Meta-population networks and population dynamics

Meta-population networks

Meta-population networks form the basis for the simulation process and were set up on a 12.5 km x 12.5 km landscape raster and consist of quality-assigned patches and interpatch connections. The landscape raster was extracted from real-world geospatial data, i.e., land cover data (OpenStreetMap.Contributors, 2021) around a stream network section (GeoPortal.rlp, 2017) from South-West Germany. We classified the land cover data into three terrestrial types ‘Urban’ (LT1), ‘Forestry’ (LT2), and ‘Agriculture’ (LT3) and assigned the cells intersecting the stream network as the aquatic land cover type ‘Stream’ (LT4) (Fig. 1-A). Each type was associated with (numeric) dispersal costs (LT1 = 100, LT2 = 75, LT3 = 50, LT 4 = 25), representing species-specific landscape permeability.

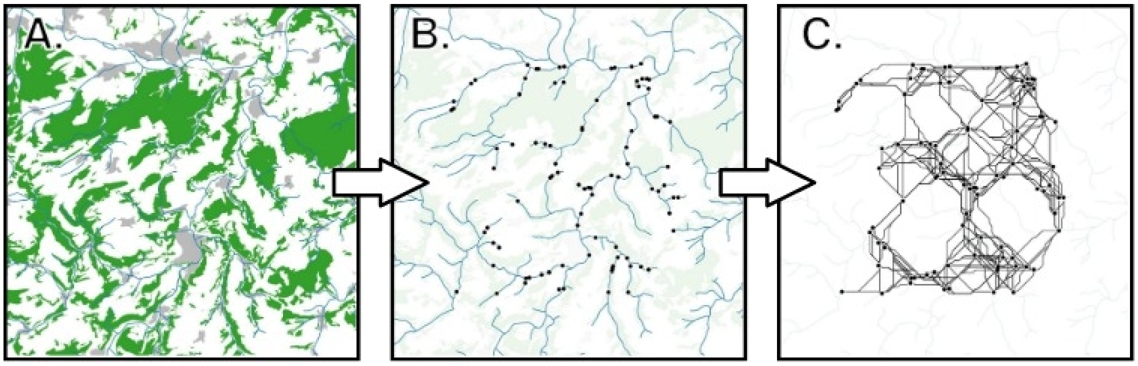


Figure 1: Flow of the set-up of meta-population networks - **A.** Landscape raster extracted from real-world geospatial data, with following land cover types: grey = 'Urban' (LT1), green = 'Forestry' (LT2), white = 'Agriculture' (LT3), and blue = 'Stream' (LT4). **B.** Random patch arrangement scenarios along LT4 of the landscape raster, patches are represented as 'black' points. **C.** Meta-population networks determined via least-cost path analysis based on **A** and **B**; networks consist of patches, represented by 'black' points, and the most cost-efficient connections, represented as 'black' lines.

The meta-population patches were defined by randomly selecting 10 % of LT4 cells from the inner 10 km x 10 km landscape area as suitable meta-population patches (Fig. 1-B). The (most cost-efficient) interpatch connections (Fig.1-C) were identified based on the patches and the LT-specific dispersal costs in the landscape raster using least-cost path analysis (Adriaensen et al., 2003), considering only connections below a maximum connectivity cost threshold (Streib et al., 2020). To minimize bias because of the random patch distributions along the stream network, we created a total of ten meta-population networks for simulation.

To capture the land use scenario, simulating different shifts of 'Agriculture', starting from an initial 50/50 split of LT3 into intensive (LT3-i) and extensive (LT3-e) use, patch quality was determined time-step specific. Thereto, we considered the terrestrial land cover composition in the complete upstream catchment AP Total and set the specific quality for a patch QP to its maximum 1.0 in the absence of 'Urban' and intensive 'Agriculture'; else, we linearly reduced the QP as a function of proportion to a minimum value of 0.0 for 100% LT1 and LT3-i land cover in the catchment of a patch AP:

$$Q_P = 1 - (A_{PLT1} + A_{PLT3-i}) / A_{PTotal} \qquad (1)$$

Population dynamics

Within each meta-population network, we simulated the following population dynamics: (1) Reproduction in each patch up to the maximum carrying capacity KP, and (2) inter-patch dispersal based on positive density-dependent emigration. KP depended on time-step specific patch quality and linearly increased with quality from 0 to 100 individuals (i.e., KP = QP x 100). Density-dependent dispersal within the network, i.e., the emigration of individuals, occurred when (directly) connected patches were not fully colonized, i.e., were below their maximum KP due to prior mortality by climatic events. The outcome of dispersal was determined by connection costs: dispersal mortality increased with cost, which represented higher risks and reduced energy reserves, and more dispersers were emitted to patches with lower costs when multiple patches were connected (based on higher colonization probability).

Stressor scenarios and adaptation

Land use scenarios

Land use represented a continuous stressor. We assumed that intensification or extensification of agricultural land use in a catchment results in reduced or increased patch qualities, respectively, and thereby reduced carrying capacities of patches (Oliver and Morecroft, 2014). As we aimed to show general patterns, we implemented four different, hypothetical scenarios of agricultural land use change based on simple temporal profiles of a continuous stressor as suggested in Jackson et al. (2021): steady ramping shifts (Fig. 2), or abrupt stepwise shifts (Fig. A.1) to 100% extensive (LT3-e) or intensive (LT3-i) agricultural land use, respectively, starting from 50% LT3-e and 50% LT3-i agricultural land use in the landscape grid.

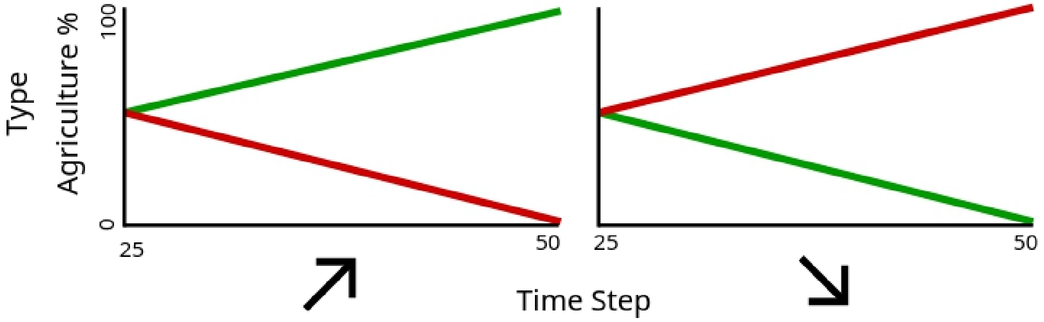


Figure 2: Temporal profile associated with the land use scenario for the ‘ramping’ scenario. Here, the red lines show the trend of intensive agriculture (LT3-i), and the green lines show the trend of extensive agriculture (LT3-e).

For both profiles, results were highly similar at the end of the simulation. Therefore, we mainly present results for the ‘ramping’ scenarios, and differences for the ‘stepwise’ scenarios profile are discussed only briefly (see Appendix A - Fig. A.2 & A.3).

Climate scenarios

We implemented climate scenarios as discrete stressor events of mortality resulting in population declines (i.e., reduction by an integer number of individuals) in a colonized meta-population patch, assuming the same effect is present at the regional scale, uniformly across all meta-population patches.

We used normal probability distribution functions (PDFs; Figueiredo and Gomes (2013)) with different skewness α to sample event mortality M in a range from 0 to 100 individuals for every time step. The PDFs provided probability weights for M sampling based on a logarithmic vector between log(0.01) and log(10) with e as the base and values rounded to integers. Three scenarios were simulated: (1) 'moderate' (α = 0), (2) 'severe' (α = -2.5), and (3) 'intense' (α = -5) (Fig. 3). Thus, event mortality increased on average with the scenarios.

Figure 3: Probability density functions to sample event mortality associated with the climate scenarios. Here, curves represent the skewed normal probability density functions; the lightgreen curve shows the 'moderate' climate scenario with a skewness α of 0, the orange curve the 'severe' climate scenario with a skewness α of -2.5, and the red curve the 'intense' climate scenario with a skewness α of -5. The bar chart below shows the mortality corresponding to the respective probabilities in a range from 0 to 100.

To minimize bias, we sampled ten random sequences of climatic events (i.e., mortalities per time-step over the simulation) per climate scenario.

Adaptation

Adaptation comprises evolutionary or non-evolutionary processes and phenotypic plasticity by which species can possibly adapt to changing environmental conditions (Jackson et al., 2021; Stoks et al., 2014). We implemented adaptation in a greatly simplified form as a generic concept, using a hypothetical approach. Thereto, climatic event-induced mortality *M* for a time step *t* was buffered based on the mean mortality of the last five time steps $M_{t\text{-}5}$ in percentage terms, with a factor *A* controlling the power of the buffering:

$$M_{t_A} = int\ (M_t * (1 - A * \frac{\overline{M}_{t-5}}{100})) \qquad (2)$$

Overall, we simulated three levels of A: ‘no’ adaption (A = 0), ‘low’ adaption (A = 0.5), and ‘high’ adaption (A = 1).

Simulation process

The simulation included the population dynamics under different land use and climate scenarios as well as adaptation to the latter. 75 time steps were simulated, starting from a fully colonized meta-population network, i.e., an initial population of 100% of the carrying capacity K of all patches. Land use scenarios and the resulting changes in patch qualities were simulated between time steps 25 and 50. Accordingly, patch qualities remained stable in the first and the last 25 time steps, so a stable initial and final state was achieved.

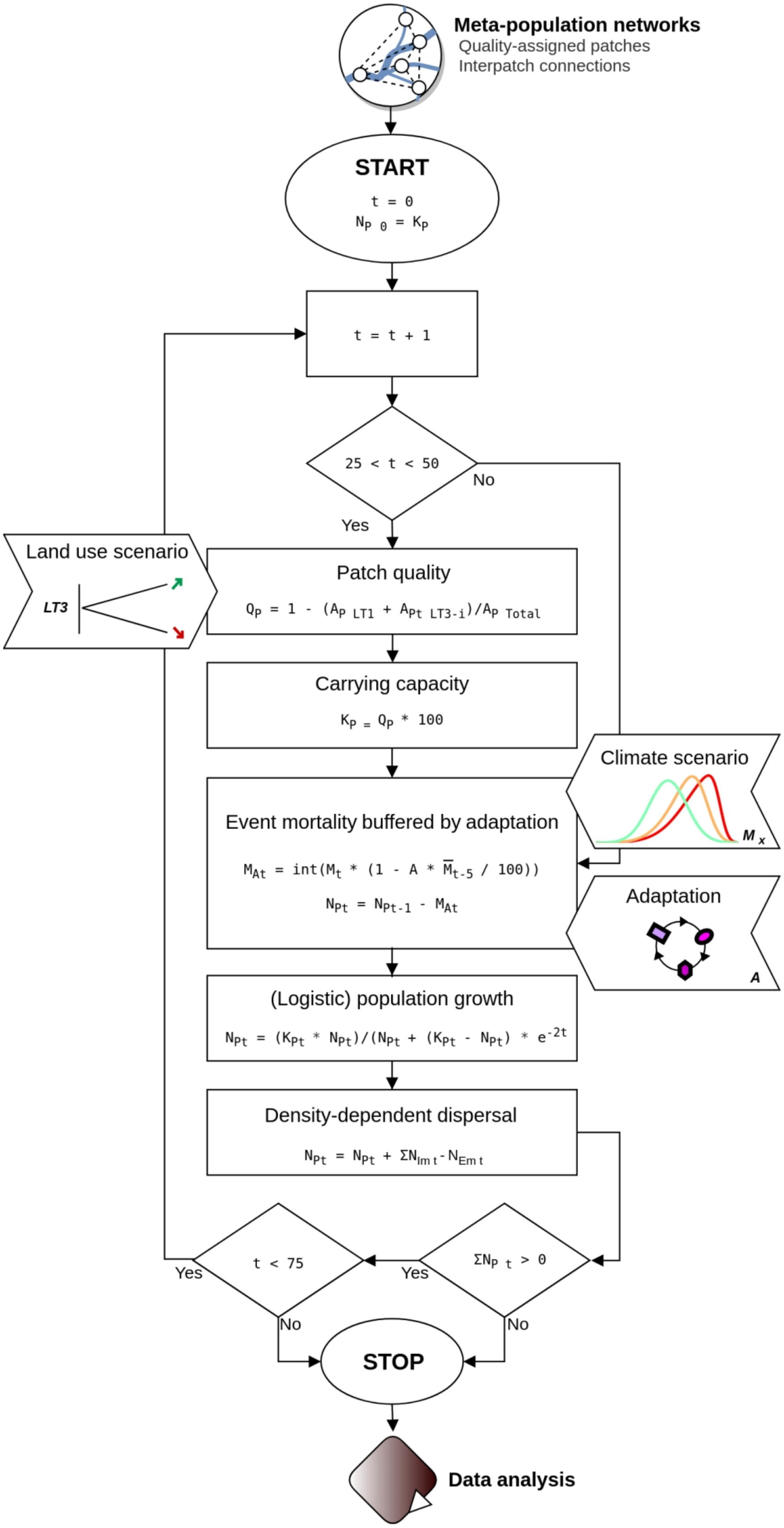

Meta-population networks
Quality-assigned patches
Interpatch connections
START
$t = 0$
$N_{P\ 0} = K_P$
$t = t + 1$
$25 < t < 50$
No
Yes
Land use scenario
LT3
Patch quality
$Q_P = 1 - (A_{P\ LT1} + A_{Pt\ LT3-i})/A_{P\ Total}$
Carrying capacity
$K_P = Q_P * 100$
Climate scenario
M_x
Event mortality buffered by adaptation
$M_{At} = \mathrm{int}(M_t * (1 - A * \overline{M}_{t-5} / 100))$
$N_{Pt} = N_{Pt-1} - M_{At}$
Adaptation
A
(Logistic) population growth
$N_{Pt} = (K_{Pt} * N_{Pt})/(N_{Pt} + (K_{Pt} - N_{Pt}) * e^{-2t}$
Density-dependent dispersal
$N_{Pt} = N_{Pt} + \Sigma N_{Im\ t} - N_{Em\ t}$
$t < 75$
Yes
No
$\Sigma N_{P\ t} > 0$
Yes
No
STOP
Data analysis

Figure 4: Flowchart of the stylized simulation process for one meta-population network. START: The initial population size N per meta-population patch P is set to its carrying capacity K_P. SIMULATION: Population dynamics and dispersal, discrete mortality events based on one climate scenario are simulated over 75 time steps t or until an entire meta-population is extinct (i.e., $\Sigma N_t==0$); between time steps 25 and 49, land use scenario related shifts in agricultural land 'LT3' use are simulated. The event mortality M_{At} of a time step is buffered over the respective adaptation level A and subtracted from a patch population N_{Pt-1}. Based on the resulting N_{Pt} (logistic) population growth is simulated; in the time steps concerned, the land use scenario modifies the carrying capacity KP via the patch quality Q_P, determined as a function of the proportion of 'urban' $A_{P\ LT1}$ and intensive 'agricultural' $A_{P\ LT3\text{-}i}$ land use in a catchment A_P Total. Dispersal-driven processes are next simulated and result in changes in N_{Pt} based on the difference of immigrants N_{EMt} from directly connected patches and emigrants N_{IMt}; for clarity, the processes to calculate immigration and emigration are not shown here - these are described in detail in Streib et al. (2020). STOP: Store and export the results for subsequent data analysis.

The latter was done to capture long-term land use impacts, i.e., whether joint effects remain stable over time. Climate scenario-induced mortality events were simulated over the entire simulation process and reduced the patch populations depending on the adaptation level.

In total, we ran 4500 simulations based on 10 meta-population networks, 5 land use scenarios, 10 sequences for each of the 3 climate scenarios, and 3 adaptation levels. Accordingly, 100 runs (10 meta-population networks x 10 climate scenario sequences) were simulated for each combination of land use and climate scenario and adaptation, and the mean value was determined.

Data analysis

Quantification of joint effects

The joint effect *E* for a scenario combination *S* (i.e., land use x climatic events x adaptation) was calculated as the mean change in meta-population size relative to a baseline. The baseline *B* was defined as static land use (i.e., no land use change), excluding the simulation of climatic events and, thus, adaptation. This baseline provided an easily interpretable comparison between the discrete and continuous stressor. In addition, stressor levels were generic and defined to systematically study the effect levels of a discrete and continuous stressor rather than to represent a current or past climate scenario.

The meta-population size corresponded to the sum of individuals in all patches at the end of a simulated time step *i*. For all 100 simulation runs (i.e., 10 meta-population networks x 10 climatic events sequences) related to a scenario combination, we determined the deviation of the resulting mean population size N_S from the mean population size of all baseline simulations N_B at all simulated time steps *i* and calculated *E(i)* as:

$$E(i) = 1 - \frac{N_S(i)}{N_B(i)} \qquad (3)$$

2.5.2 Assessment of stressor interactions

The type and size of a stressor interaction for a scenario combination *S* were calculated using the multiplicative null model (also termed Response Addition), given mortality as the ecological response (Côté et al., 2016; Schäfer and Piggott, 2018). We compared the simulated effect *E(i)* of a land use and climate scenario combination to predicted effects *P(i)*, i.e., the probabilistic sum of their individual effects:

$$P(i) = E_c(S) + E_d(S) - E_c(S) * E_d(S) \qquad (4)$$

where E_c and E_d of a scenario combination *S* are the individual effects of the continuous (i.e., simulated for one specific land use scenario without climatic events) and discrete (i.e., simulated for one specific climatic event-scenario and the ‘static’ land use scenario) stressor alone.

Following the concept of model deviation ratio *MDR* (Belden et al., 2007), we defined interactions *I(i)* by the ratio of predicted to simulated effect (i.e., *(1 + P(i)) / (1 + E(i))*). A ratio of 1.0 corresponds to an additive, a ratio > 1.0 to a antagonistic, and a ratio < 1.0 to a synergistic interaction. Consequently, the magnitude of non-additive (antagonistic or synergistic) interactions increases with departure from 1.0.

RESULTS

The present study intended to identify how complex spatiotemporal profiles and adaptation influence joint effects and interactions of two stressors on meta-populations. Excluding adaptation, we found that the discrete stressor (i.e., climatic events) primarily dominated joint effects, whereas the continuous stressor (i.e., land use change) always dominated the interaction type. Adaptation lowered joint effects but changed interaction classification inconsistently across land use and climate scenarios; for decreasing land use stress, adaptation (partly considerably) reduced meta-population declines, yet had little effect for increasing land use stress. Details are presented below.

Joint effects

In the absence of adaptation, severe and intense climate stress dominated the joint effects in any related scenario combination, with major declines or extinctions of the meta-population (Fig. 5). Even for decreasing land use stress (i.e., decreasing intensive agriculture), the joint effects were only slightly lower at 0.8 (i.e., 80% meta-population size reduction) than for increasing land use stress (i.e., increasing intensive agriculture) at 0.95. However, for moderate climate stress, the land use scenario dominated the joint effects.

Adaptation had negligible influence on the trajectory of joint effects in the moderate scenario, but significant influence in the severe and intense climate scenarios (Fig. 5). Here, adaptation slowed down meta-population decline for increasing land use stress, yet declines over time were still severe, virtually resulting in extinction. For decreasing land use stress, however, adaptation had a pronounced positive influence; high adaptation even yielded a slight recovery close to the baseline in the moderate climate scenario.

The land use scenarios of the ‘stepwise’ profile showed qualitatively similar patterns, resulting in comparable levels of meta-population sizes at the end of the simulation (Fig. A1).

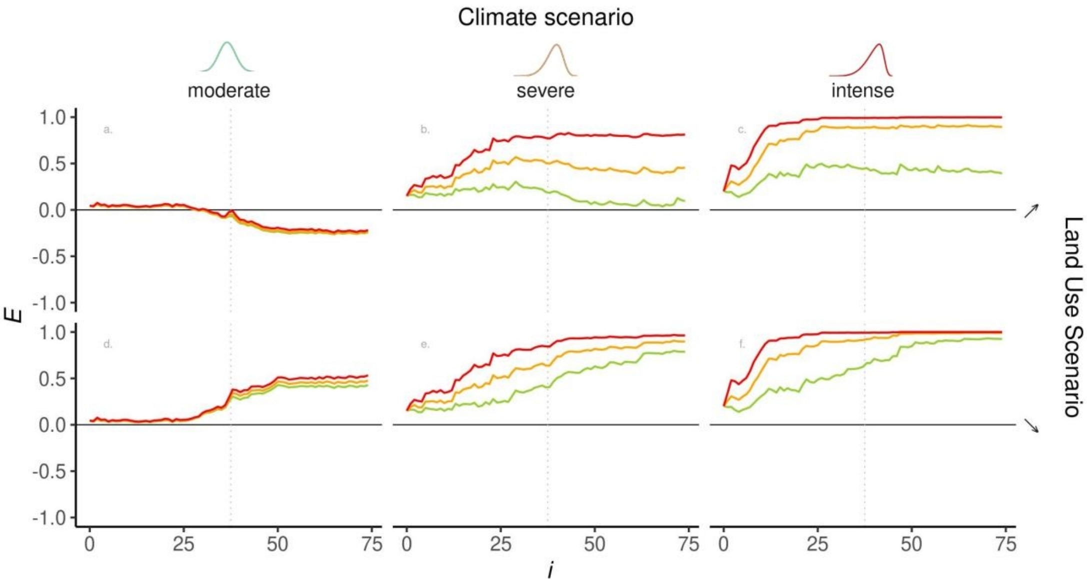


Figure 5: Development of joint stressor effects (y-axis) compared to the baseline B (black line) over the simulation period (x-axis) for all stressor scenarios-adaptation level combinations, with lines corresponding to the mean over 100 simulation runs per combination. Joint effects sizes > 0.0 imply a lower mean population size compared to B, and < 0.0 imply a higher mean population size compared to B. The climate scenario is labeled at the top of the figure, and the land use scenario at the right, where ↗ represents ‘ramping’ increasing extensive agricultural land use, and ↘ ‘ramping’ decreasing extensive agricultural land use. The adaptation level is coded by the line color: red is ‘no’, orange is ‘low’ adaptation, and green is ‘high’ adaptation.

Interactions

In general, we found that non-additive interactions emerged over time triggered by land use change (Fig. 6); however, no and low adaptation resulted in additive interactions for the intense climatic scenario or close to additive interactions for the severe climatic scenario. Antagonistic interactions progressively developed with increasing land use stress and synergistic interactions with decreasing land use stress. For any given stressor combination, adaptation changed the interaction sizes, but changes depended on the climate scenario. The interactions inconsistently decreased in the moderate climate scenario with adaptation levels but increased in the severe and intense. As a result, for severe climate stress low adaptation resulted in a similarly strong antagonism as high adaptation and severe climate stress at decreasing land use stress, but in much lower synergism at increasing land use stress (Fig. 6, I5). By contrast, in low climate scenarios, the interaction size of synergism and antagonism decreased consistently across land use scenarios with adaptation levels.

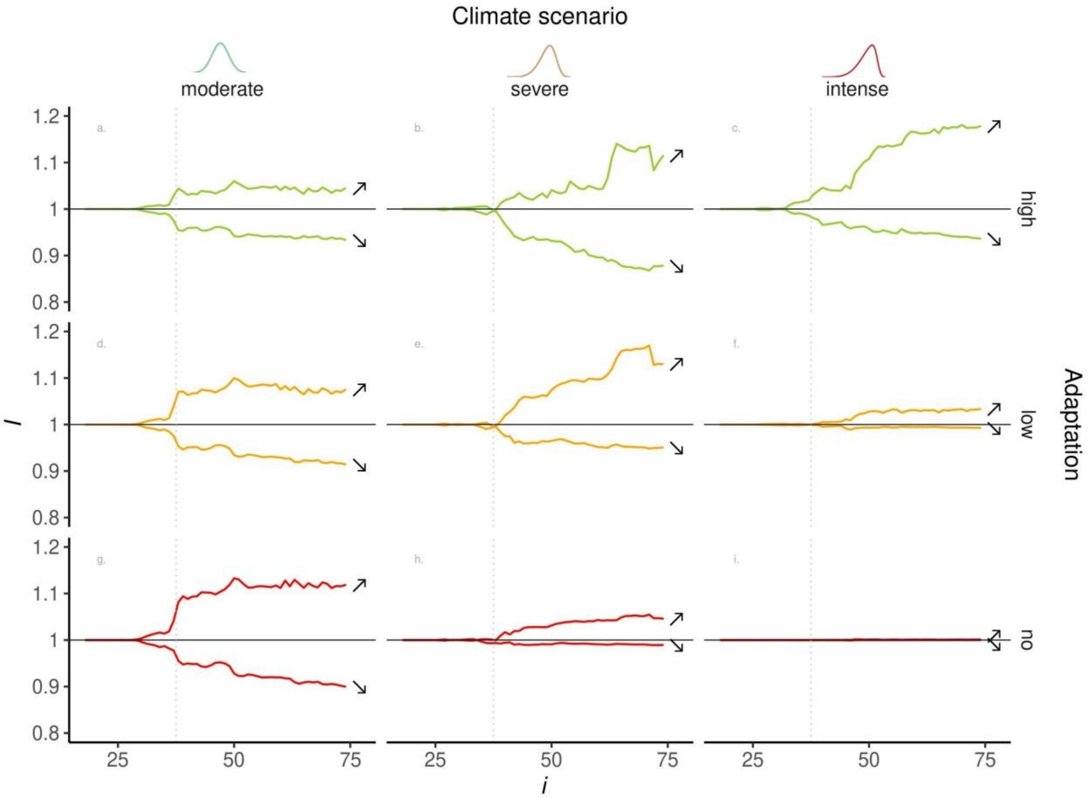


Figure 6: Interaction size (y-axis) over the simulation period (x-axis) for all stressor scenarios-adaptation level combinations, with lines corresponding to the mean over 100 simulation runs per combination. Interaction sizes > 1.0 indicate antagonism, and < 1.0 synergism. The climate scenario is labeled at the top of the figure, and the adaptation level is at the right and color-coded: red is 'no', orange is 'low' adaptation, and green is 'high' adaptation. For the land use scenario, ↗ represents 'ramping' increasing extensive agriculture (i.e., decreasing land use stress), and ↘ 'ramping' decreasing extensive agriculture (i.e., increasing land use stress).

DISCUSSION

We simulated two stressors (i.e., land use and climate) with complex spatiotemporal profiles in varying scenarios and evaluated their effect on meta-populations of a freshwater insect. Compared to a static baseline scenario, we found that joint effects and interactions developed fairly differently over time, depending on the stressor levels and dynamics. Adaptation to climatic stress reduced joint effects and modified interactions.

To our knowledge, this is the first modeling study to show that interactions depend on spatiotemporal stressor profiles and adaptation, supporting previous calls to place less emphasis on stressor classification as additive or non-additive. We conclude that static stressor scenarios over short periods, as often used in experiments, without including potential adaptation, may be insufficient to reliably predict the joint effects and interactions of multiple stressors under real-world conditions. Below we discuss our results in detail.

Relevance of discrete and continuous stressors under dynamic scenarios in the absence of adaptation

We found that moderate climate stress had no or only negligible long-term impact on meta-populations, yet became dominant for severe and intense stress. For moderate climate stress, land use dominated the joint effects and a relatively strong antagonism developed with increasing land use stress, whereas decreasing land use stress resulted in synergism. For severe and intense climate stress, the joint effects were largely or completely disjointed from land use, thus only minor non-additive (‘severe’ scenario) or additive (‘intense’ scenario) interactions emerged.

Côté et al. (2016) showed that management of a regional continuous stressor to seagrass populations in multiple stressor environments lowered mortality and thereby led to higher populations, in turn resulting in antagonism. Consequently, higher continuous stress likely can have the opposite effect, i.e., synergism via higher mortality and thus lower population sizes. Furthermore, optimizing land use can mitigate long-term impacts from more severe extreme events and thereby strong joint effects, as shown in a review of climate and land use change feedbacks (Oliver and Morecroft, 2014). However, positive benefits from land use optimization are only to expect if climatic stress remains below a certain level and sufficient time for recovery is provided, as shown in a study on dry coniferous forests in western North America under rapid climate change and altered disturbance regimes (Falk et al., 2019). Otherwise, the discrete stressor dominates, resulting in additive interactions as the benefits of managing a continuous stressor become minimal (Côté et al., 2016). This matches also a recent review on abrupt changes in ecological systems, indicating that in multiple stressor environments a strong increase of a discrete stressor likely results in additive interactions (Ratajczak et al., 2018).

Under moderate climate stress, the dominant role of land use for the joint effects is explained by intensive agriculture in the catchment, determining the mean patch quality in the meta-population networks. Positive land use change resulted in antagonism, whereas negative land use change resulted in synergism, as higher patch qualities produced higher meta-populations based on increased carrying capacities, while lower qualities produced lower meta-populations. Here, extreme climatic events resulted only in temporal population declines, as mean event mortality was on average low and, simultaneously, meta-populations had sufficient time to fully recover between events (Bruder et al. (2019); for details on underlying general processes see Streib et al. (2021)). For severe and intense climate stress recovery after individual events may be incomplete and insufficient to survive subsequent events, given that with more intense climatic extreme events: (1) mean event mortality increased and (2) time to the next intense events decreased; notably, a random event sequence, compared to a synchronous, non-realistic sequence, can result in very short intervals (Jackson et al., 2021). This produced strong joint effects that were predominantly or entirely driven by climate stress, as events became so severe that even improved patch quality with decreasing land use stress failed to prevent the extinction of most or all patches over time (Fig. A.4.1 & A.4.2). Consequently, weak non-additive interactions emerged for severe climate stress and additive interactions emerged for intense climate stress, as meta-populations became extinct or were reduced to almost zero.

Role of adaptation on joint stressor effects and interactions under dynamic scenarios

Adaptation reduced the joint effects for all scenario combinations. Consequently, non-additive interactions decreased with adaption for the moderate climate scenario, as the dominant impact of land use became even stronger. However, non-additive interactions increased or emerged for the severe and intense scenarios, as with adaptation climate stress no longer dominated, and joint effects were strongly reduced. Here, antagonistic interactions based on decreasing land use stress increased more than synergistic interactions based on increasing land use stress, indicating that land use optimization may provide more positive outcomes than to expect.

Our findings support the idea that adaptation needs to be considered in predicting joint effects and interactions of multiple stressors (Hughes et al., 2019; Orr et al., 2021). As theoretically outlined by Bush et al. (2016) or Jackson et al. (2021), reduced joint effects by adaption are expected, when ecosystems or species have sufficient time to adapt to single or multiple changed environmental stressors. In the best case, stressor effects are even reduced despite more intense events. Hughes et al. (2019) showed empirically that adaptation alleviated the effects of marine heat waves on coral reefs. Adapted corals were significantly less affected by a second heat wave, albeit this was more intense. The effect of joint stressors may be overestimated if not considering adaptation as demonstrated in a modeling study on fruit flies (Bush et al., 2016). Furthermore, beneficial impacts by management, e.g., land use optimization, may be missed. Our second major finding, that adaptation produces higher interactions in intensified stressor regimes despite strongly reduced joint effects, is initially surprising yet supported by a recent study by Orr et al. (2021). Using data from an evolutionary experiment with the rotifer *Brachionus calyciflorus*, they showed that higher interaction sizes can emerge if adaptation reduces both individual and joint effects compared to control. A change in interactions from antagonism to synergism followed when the reduction in individual effects was greater than the reduction in joint effects. For management, this implies that actions should focus on reducing joint effects based on a mechanistic, predictive understanding of interactions (Pirotta et al., 2022), rather than automatically seeking to prevent synergies (Orr et al., 2021; Schäfer and Piggott, 2018). However, adaptation to new stressor regimes is difficult to predict (Bush et al., 2016; Hoffmann and Sgró, 2011), making predictions of joint stressor effects and thus interactions challenging (Bush et al., 2016; Hoffmann and Sgró, 2011). While adaptation may occur in many species, the speed and strength of adaptation remain unclear (Hill et al., 2011). Moreover, species may also respond positively to an increasing stressor if the environment shifts toward their niche optimum, or if competition or predation is reduced by removing more vulnerable species, thereby increasing their robustness to other stressors (MacLennan and Vinebrooke, 2021; Vinebrooke et al., 2004).

The changes observed in joint effects and interactions are explained by the reduced extreme event mortality associated with adaptation. Notably under severe and intense climate stress, meta-populations were more resilient as single patches survived short intervals of high mortality more frequently and in higher numbers when adaption is present allowing them and, subsequently, the meta-population to recover. Compared to the absence of adaptation, it turns out that the recovery potential is highly dependent on land use, as improved patch quality now prevents more patches from extinction over time with decreasing (Fig. A.4.1) than with increasing land-use stress (Fig. A.4.2). Consequently, (both under ‘low’ and ‘high’) adaptation produced relatively stronger reductions in joint effects and thereby stronger non-additive interactions for reduced land use stress.

CONCLUSIONS

We provide theoretical evidence that scenarios of complex spatiotemporal dynamics and adaptation are critical to understanding how species respond to modified multiple stressor regimes under global change. Albeit the approach is primarily hypothetical we are confident that this work contributes to the mechanistic understanding of how multiple stressors in real-world environments act across space and time by demonstrating and explaining general principles.

Analysis of simplified static regimes at local scales over short periods is likely insufficient for reliable prediction of future joint effects and interactions, notably since recovery processes are not sufficiently considered. Moreover, adaptation likely reduces joint effects and, thereby, can alter interactions with inconsistent direction and size. We expect that these findings could be tested in an experimental setting with moderate effort.

Consequently, regarding management, actions should focus on reducing the strongest individual or joint effects, rather than placing too much emphasis on interactions. Not considering adaptation can result in overestimating joint effects and potentially missing beneficial management outcomes.

DECLARATIONS

Acknowledgments

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Authors‘ contributions

LS: Conceptualization, Methodology, Data Curation, Model programming, Formal analysis, Visualization, Writing - Original draft preparation. JWS: Conceptualization, Writing - Reviewing & Editing. MK: Writing - Reviewing & Editing. RBS: Conceptualization, Writing - Reviewing & Editing, Supervision. All authors read and approved the manuscript.

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Availability of data and materials

Supplementary data and material (software-framework, input-data, code & additional graphs) for the publication are provided in the corresponding GitHub repository: https://github.com/luclucky/StPAd_JEIn

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors consented to the publication of this work.

Competing interests

The authors declare that they have no competing interests.

APPENDIX A

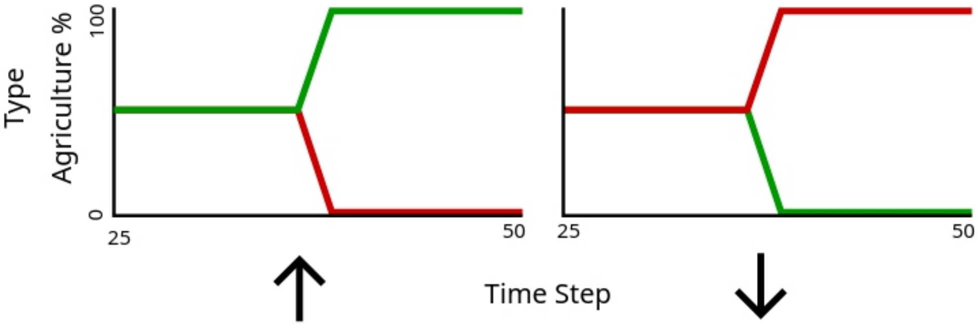

***Figure A.1:** Temporal profile associated with the land use scenario for the 'stepwise' scenario. Here, the red lines show the trend of intensive agriculture (LT3-i), and the green lines show the trend of extensive agriculture (LT3-e).*

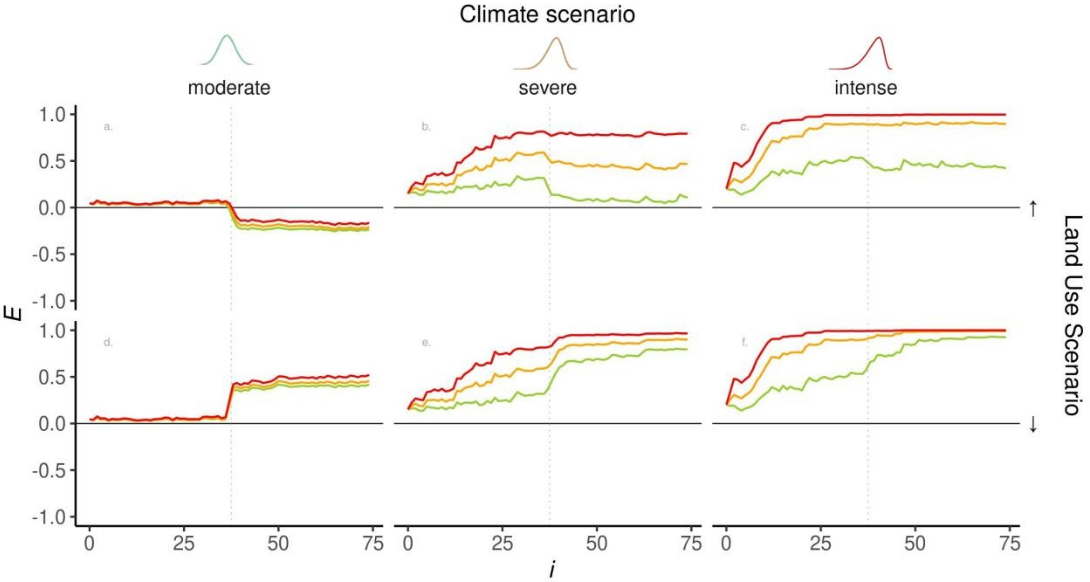

Figure A.2: Development of joint stressor effects (y-axis) compared to the baseline B (black line) over the simulation period (x-axis) for all stressor scenarios-adaptation level combinations, with lines corresponding to the mean over 100 simulation runs per combination. Joint effects sizes > 0.0 imply a lower mean population size compared to B, and < 0.0 imply a higher mean population size compared to B. The climate scenario is labeled at the top of the figure, and the land use scenario at the right, where ↑ represents 'stepwise' increasing extensive agricultural land use, and ↓ 'stepwise' decreasing extensive agricultural land use. The adaptation level is coded by the line color: red is 'no', orange is 'low' adaptation, and green is 'high' adaptation.

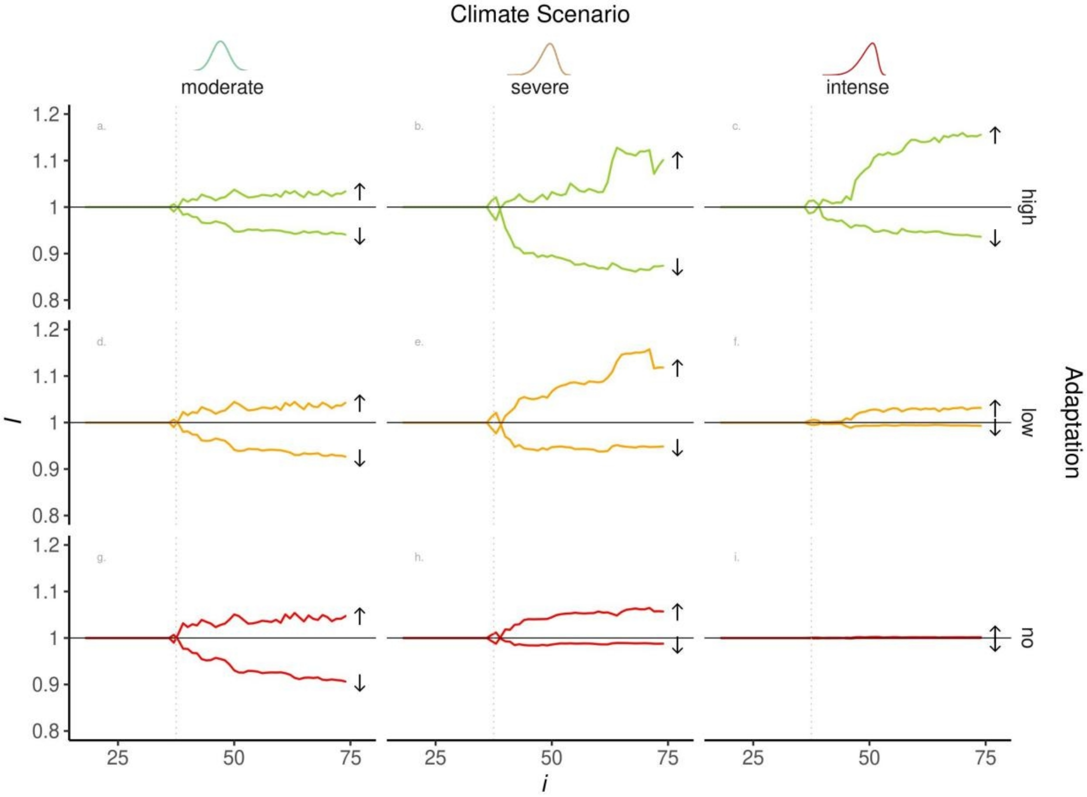

Figure A.3: Interaction size (y-axis) over the simulation period (x-axis) for all stressor scenarios-adaptation level combinations. Interaction sizes > 1.0 indicate antagonism, and < 1.0 synergism. The climate scenario is labeled at the top of the figure, and the adaptation level at the right and color-coded: red is 'no', yellow is 'low' adaptation, and green is 'high' adaptation. For land use scenario, ↑ represents 'stepwise' increasing extensive agriculture (i.e., decreasing land use stress), and ↓ 'stepwise' decreasing extensive agriculture (i.e., increasing land use stress).

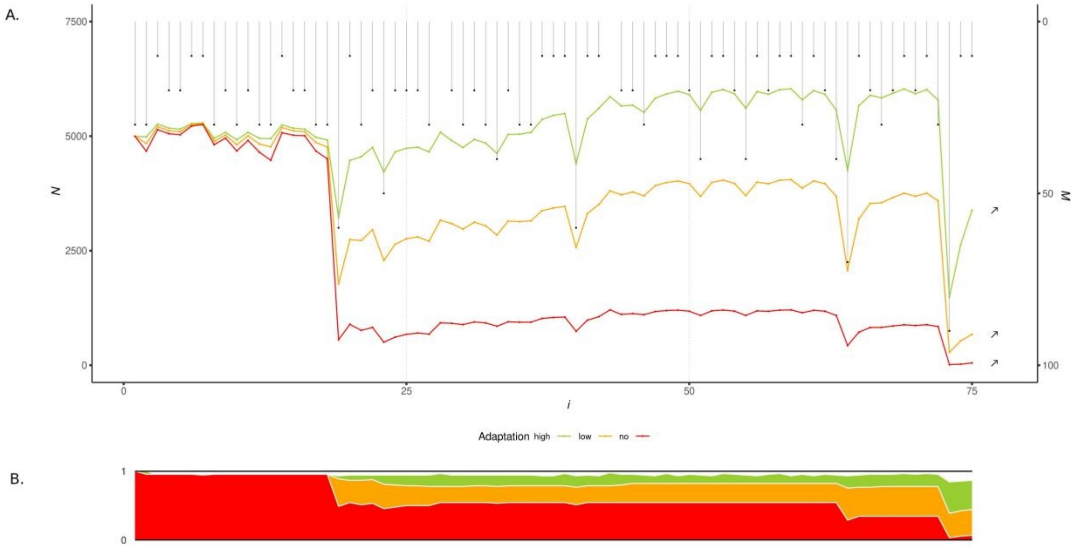

Figure A.4.1: Exemplary representation of **A.** total population size N and **B.** rate of colonized patches (y-axis) over time i (x-axis; i.e., 75 time steps) for one meta-population network simulated for one sequence of the severe climate scenario and the 'ramping' land use scenario with decreasing intensive agriculture ↗. Event mortality M (secondary y-axis; i.e., population decline per patch in the range of 0 to 100) per time step is represented by black lines vertically downward from the top. In **A.** the red line shows the results for N with 'no' adaptation, the orange line with 'low' adaptation, and the green line with 'high' adaptation. In **B.** the red area shows the rate of colonized patches in the range between 0 to 1 with 'no' adaptation, the orange area with 'low' adaptation, and the green area with 'high' adaptation; note that the red area is displayed in front of the orange area, which is displayed in front of the green area.

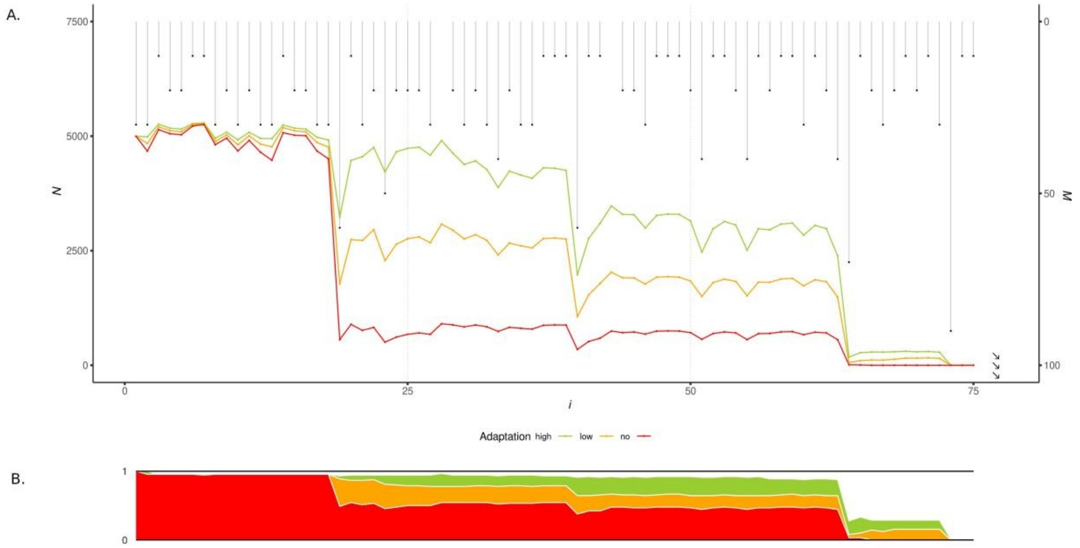

Figure A.4.2: Exemplary representation of **A.** total population size N and **B.** rate of colonized patches (y-axis) over time i (x-axis; i.e., 75 time steps) for one meta-population network simulated for one sequence of the severe climate scenario and the ‘ramping’ land use scenario with increasing intensive agriculture ↘. Event mortality M (secondary y-axis; i.e., population decline per patch in the range of 0 to 100) per time step is represented by black lines vertically downward from the top. In **A.** the red line shows the results for N with ‘no’ adaptation, the orange line with ‘low’ adaptation, and the green line with ‘high’ adaptation. In **B.** the red area shows the rate of colonized patches in the range between 0 to 1 with ‘no’ adaptation, the orange area with ‘low’ adaptation, and the green area with ‘high’ adaptation; note that the red area is displayed in front of the orange area, which is displayed in front of the green area.

Notes on the graphs shown in Figures A.4.1 & A.4.2

Successive mortality events with low to medium mortality in the first time steps result in only small changes in the meta-population size (~ -80%) and rate of colonized patches (~ -50%). However, without adaption, a high mortality event in time step 19 sharply reduces meta-population size and the rate of colonized patches, with levels remaining relatively constant in the following; with adaption, reduction in meta-population size and the number of colonized patches is less severe, with a partial recovery following (more pronounced for ‘high’ relative to ‘low’). The effects of the land use scenarios simulated from time step 25 to time step 50 are only pronounced with adaptation. Here, despite a high mortality event on time step 40, decreasing intensive agriculture (Fig. A.4.1) generally results in progressively increasing meta-population size and a constant colonization rate (both, ‘low’ and ‘high’ adaptation), while increasing intensive agriculture (Fig. A.4.2) results in decreasing meta-population size and colonization rate (both, ‘low’ and ‘high’ adaptation). Consequently, without adaptation population sizes and colonization rates are comparable for both land use scenarios, but with adaptation they are clearly higher under decreasing land use stress. After time step 50, the long-term effects of the land use scenarios become clear, i.e., high mortality events in time steps 64 and 73 result in meta-population extinction under increasing land use stress, whereas the meta-populations survive and recover subsequently under decreasing land use stress.

REFERENCES

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning 64, 233–247. doi:10.1016/S0169-2046(02)00242-6

Aspin TWH, Khamis K, Matthews TJ, Milner AM, O'Callaghan MJ, Trimmer M, Woodward G, Ledger ME (2019) Extreme drought pushes stream invertebrate communities over functional thresholds. Global Change Biology 25, 230–244. doi:10.1111/gcb.14495

Baker RE, Peña JM, Jayamohan J, Jérusalem A (2018) Mechanistic models versus machine learning, a fight worth fighting for the biological community? Biology Letters 14, 1–4. doi:10.1098/rsbl.2017.0660

Belden JB, Gilliom RJ, Lydy MJ (2007) How well can we predict the toxicity of pesticide mixtures to aquatic life? Integrated environmental assessment and management 3, 364–372. doi:10.1897/1551-3793(2007)3[364:HWCWPT]2.0.CO;2

Birk S, Chapman D, Carvalho L, Spears BM, Andersen HE, Argillier C, Auer S, Baattrup-Pedersen A, Banin L, Beklioğlu M, Bondar-Kunze E, Borja A, Branco P, Bucak T, Buijse AD, Cardoso AC, Couture RM, Cremona F, de Zwart D, Feld CK, Ferreira MT, Feuchtmayr H, Gessner MO, Gieswein A, Globevnik L, Graeber D, Graf W, Gutiérrez-Cánovas C, Hanganu J, Işkın U, Järvinen M, Jeppesen E, Kotamäki N, Kuijper M, Lemm JU, Lu S, Solheim AL, Mischke U, Moe SJ, Nõges P, Nõges T, Ormerod SJ, Panagopoulos Y, Phillips G, Posthuma L, Pouso S, Prudhomme C, Rankinen K, Rasmussen JJ, Richardson J, Sagouis A, Santos JM, Schäfer RB, Schinegger R, Schmutz S, Schneider SC, Schülting L, Segurado P, Stefanidis K, Sures B, Thackeray SJ, Turunen J, Uyarra MC, Venohr M, von der Ohe PC , Willby N, Hering D (2020) Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. Nature Ecology & Evolution. doi:10.1038/s41559-020-1216-4

Boyd PW, Collins S, Dupont S, Fabricius K, Gattuso JP, Havenhand J, Hutchins DA, Riebesell U, Rintoul MS, Vichi M, Biswas H, Ciotti A, Gao K, Gehlen M, Hurd CL, Kurihara H, McGraw CM, Navarro JM, Nilsson GE, Passow U, Pörtner HO (2018) Experimental strategies to assess the biological ramifications of multiple drivers of global ocean change—A review. Global Change Biology 24, 2239–2261. doi:10.1111/gcb.14102

Brooks PR, Crowe TP (2019) Combined Effects of Multiple Stressors: New Insights Into the Influence of Timing and Sequence. Frontiers in Ecology and Evolution 7. doi:10.3389/fevo.2019.00387

Bruder A, Frainer A, Rota T, Primicerio R (2019) The importance of ecological networks in multiple-stressor research and management. Frontiers in Environmental Science 7, 1–7. doi:10.3389/fenvs.2019.00059

Bush A, Mokany K, Catullo R, Hoffmann A, Kellermann V, Sgrò C, McEvey S, Ferrier S (2016) Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. Ecology Letters 19, 1468–1478. doi:10.1111/ele.12696

Catford JA, Wilson JRU, Pyšek P, Hulme PE, Duncan RP (2022) Addressing context dependence in ecology. Trends in Ecology and Evolution 37, 158–170. doi:10.1016/j.tree.2021.09.007

Côté IM, Darling ES, Brown CJ (2016) Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B: Biological Sciences 283, 20152592. doi:10.1098/rspb.2015.2592

De Laender F (2018) Community- and ecosystem-level effects of multiple environmental change drivers: Beyond null model testing. Global Change Biology 24, 5021–5030. doi:10.1111/gcb.14382

Falk DA, Watts AC, Thode AE (2019) Scaling Ecological Resilience. Frontiers in Ecology and Evolution 7, 1–16. doi:10.3389/fevo.2019.00275

Figueiredo F, Gomes MI (2013) The skew-normal distribution in SPC. Revstat Statistical Journal 11, 83–104.

GeoPortal.rlp (2017) Gewässernetz (gesamt), Wasserwirtschaftsverwaltung Rheinland-Pfalz.

Grimm V, Railsback SF, (2005) Individual-based Modeling and Ecology, STU - Stud. ed. Princeton University Press.

Hill JK, Griffiths HM, Thomas CD (2011) Climate change and evolutionary adaptations at species' range margins. Annual Review of Entomology 56, 143–159. doi:10.1146/annurev-ento-120709-144746

Hoffmann AA, Sgró CM (2011) Climate change and evolutionary adaptation. Nature 470, 479–485. doi:10.1038/nature09670

Hughes, TP, Kerry, JT, Connolly, SR, Baird, AH, Eakin, CM, Heron, SF, Hoey, AS, Hoogenboom, MO, Jacobson, M, Liu, G, Pratchett, MS, Skirving, W, Torda, G (2019) Ecological memory modifies the cumulative impact of recurrent climate extremes. Nature Climate Change 9, 40–43. doi:10.1038/s41558-018-0351-2

Hunsicker ME, Kappel CV, Selkoe KA, Halpern BS, Scarborough C, Mease L, Amrhein A (2016) Characterizing driver-response relationships in marine pelagic ecosystems for improved ocean management. Ecological Applications 26, 651–663. doi:10.1890/14-2200/suppinfo

IPCC (2019) Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. In press.

Jackson MC, Pawar S, Woodward G (2021) The Temporal Dynamics of Multiple Stressor Effects: From Individuals to Ecosystems. Trends in Ecology & Evolution 36, 402–410. doi:10.1016/j.tree.2021.01.005

Kaunisto S, Ferguson LV, Sinclair BJ (2016) Can we predict the effects of multiple stressors on insects in a changing climate? Current Opinion in Insect Science 17, 55–61. doi:10.1016/j.cois.2016.07.001

MacLennan MM, Vinebrooke RD (2021) Exposure order effects of consecutive stressors on communities: the role of co-tolerance. Oikos 130, 2111–2121. doi:10.1111/oik.08884

Maxwell SL, Butt N, Maron M, McAlpine CA, Chapman S, Ullmann A, Segan DB, Watson JEM (2019) Conservation implications of ecological responses to extreme weather and climate events. Diversity and Distributions 25, 613–625. doi:10.1111/ddi.12878

Moe SJ, De Schamphelaere K, Clements WH, Sorensen MT, Van den Brink PJ, Liess M (2013) Combined and interactive effects of global climate change and toxicants on populations and communities. Environmental Toxicology and Chemistry 32, 49–61. doi:10.1002/etc.2045

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Börger L, Bennett DJ, Choimes A, Collen B, Day J, De Palma A, Díaz S, Echeverria-Londoño S, Edgar MJ, Feldman A, Garon M, Harrison MLK, Alhusseini T, Ingram DJ, Itescu Y, Kattge J, Kemp V, Kirkpatrick L, Kleyer M, Correia DLP, Martin CD, Meiri S, Novosolov M, Pan Y, Phillips HRP, Purves DW, Robinson A, Simpson J, Tuck SL, Weiher E, White HJ, Ewers RM, Mace GM, Scharlemann JPW, Purvis A (2015) Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. doi:10.1038/nature14324

Northrup JM, Rivers JW, Yang Z, Betts MG (2019) Synergistic effects of climate and land-use change influence broad-scale avian population declines. Global Change Biology 25, 1561–1575. doi:10.1111/gcb.14571

Ogle K, Barber JJ, Barron-Gafford GA, Bentley LP, Young JM, Huxman TE, Loik ME, Tissue DT (2015) Quantifying ecological memory in plant and ecosystem processes. Ecology Letters 18, 221–235. doi:10.1111/ele.12399

Oliver TH, Morecroft MD (2014) Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. Wiley Interdisciplinary Reviews: Climate Change 5, 317–335. doi:10.1002/wcc.271

OpenStreetMap.Contributors (2021) OpenStreetMap.

Orr JA, Bussi G, Hughes JMR, Whitehead PG, Jackson MC (2024) Modelling the potential for local management practices to offset climate change impacts on freshwater macroinvertebrate communities. Freshwater Biology 1–15. doi:10.1111/fwb.14222

Orr JA, Luijckx P, Arnold, J, Jackson AL, Piggott JJ (2021) Rapid evolution generates synergism between multiple stressors: linking theory and an evolution experiment. Global Change Biology 1–13. doi:10.1111/gcb.15633

Patrick CJ, McCluney KE, Ruhi A, Gregory A, Sabo J, Thorp JH (2021) Multi-scale biodiversity drives temporal variability in macrosystems. Frontiers in Ecology and the Environment 19, 47–56. doi:10.1002/fee.2297

Pinek L, Mansour I, Lakovic M, Ryo M, Rillig MC (2020) Rate of environmental change across scales in ecology. Biological Reviews 95, 1798–1811. doi:10.1111/brv.12639

Pirotta E, Thomas L, Costa DP, Hall AJ, Harris CM, Harwood J, Kraus SD, Miller PJO, Moore MJ, Photopoulou T, Rolland RM, Schwacke L, Simmons SE, Southall BL, Tyack PL (2022) Understanding the combined effects of multiple stressors: A new perspective on a longstanding challenge. Science of the Total Environment 821, 153322. doi:10.1016/j.scitotenv.2022.153322

Ratajczak Z, Carpenter SR, Ives AR, Kucharik CJ, Ramiadantsoa T, Stegner MA, Williams JW, Zhang J, Turner MG (2018) Abrupt Change in Ecological Systems: Inference and Diagnosis. Trends in Ecology and Evolution 33, 513–526. doi:10.1016/j.tree.2018.04.013

Reid, AJ, Carlson, AK, Creed, IF, Eliason, EJ, Gell, PA, Johnson, PTJ, Kidd, KA, MacCormack, TJ, Olden, JD, Ormerod, SJ, Smol, JP, Taylor, WW, Tockner, K, Vermaire, JC, Dudgeon, D, Cooke, SJ (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 94, 849–873. doi:10.1111/brv.12480

Rillig MC, Ryo M, Lehmann A (2021) Classifying human influences on terrestrial ecosystems. Global Change Biology gcb.15577. doi:10.1111/gcb.15577

Ryo M, Aguilar-Trigueros CA, Pinek L, Muller LAH, Rillig MC (2019) Basic Principles of Temporal Dynamics. Trends in Ecology and Evolution 34, 723–733. doi:10.1016/j.tree.2019.03.007

Sage RF (2020) Global change biology: A primer. Global Change Biology 26, 3–30. doi:10.1111/gcb.14893

Schäfer RB, Piggott JJ (2018) Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. Global Change Biology 24, 1817–1826. doi:10.1111/gcb.14073

Schiesari L, Matias MG, Prado PI, Leibold MA, Albert CH, Howeth JG, Leroux SJ, Pardini R, Siqueira T, Brancalion PHS, Cabeza M, Coutinho RM, Diniz-Filho JAF, Fournier B, Lahr DJG, Lewinsohn TM, Martins A, Morsello C, Peres-Neto PR, Pillar VD, Vázquez DP (2019) Towards an applied metaecology. Perspectives in Ecology and Conservation 17, 172–181. doi:10.1016/j.pecon.2019.11.001

Siddique A, Shahid N, Liess M (2021) Multiple Stress Reduces the Advantage of Pesticide Adaptation. Environmental Science and Technology 55, 15100–15109. doi:10.1021/acs.est.1c02669

Simmons BI, Blyth PSA, Blanchard JL, Clegg T, Delmas E, Garnier A, Griffiths CA, Jacob U, Pennekamp F, Petchey OL, Poisot T, Webb TJ, Beckerman AP (2021) Refocusing multiple stressor research around the targets and scales of ecological impacts. Nature Ecology and Evolution 5, 1478–1489. doi:10.1038/s41559-021-01547-4

Stock A, Murray CC, Gregr EJ, Steenbeek J, Woodburn E, Micheli F, Christensen V, Chan KMA (2023) Exploring multiple stressor effects with Ecopath, Ecosim, and Ecospace: Research designs, modeling techniques, and future directions. Science of the Total Environment 869, 161719. doi:10.1016/j.scitotenv.2023.161719

Stoks R, Geerts AN, De Meester L (2014) Evolutionary and plastic responses of freshwater invertebrates to climate change: Realized patterns and future potential. Evolutionary Applications 7, 42–55. doi:10.1111/eva.12108

Streib L, Juvigny-Khenafou N, Heer H, Kattwinkel M, Schäfer RB (2021) Spatiotemporal dynamics drive synergism of land use and climatic extreme events in insect meta-populations. Science of The Total Environment 814, 152602. doi:10.1016/j.scitotenv.2021.152602

Streib L, Kattwinkel M, Heer H, Ruzika S, Schäfer RB (2020) How does habitat connectivity influence the colonization success of a hemimetabolous aquatic insect? - A modeling approach. Ecological Modelling 416, 108909. doi:10.1016/j.ecolmodel.2019.108909

Turner, MG, Calder, WJ, Cumming, GS, Hughes, TP, Jentsch, A, LaDeau, SL, Lenton, TM, Shuman, BN, Turetsky, MR, Ratajczak, Z, Williams, JW, Williams, AP, Carpenter, SR (2020) Climate change, ecosystems and abrupt change: Science priorities. Philosophical Transactions of the Royal Society B: Biological Sciences 375. doi:10.1098/rstb.2019.0105

Turschwell MP, Connolly RM, Dunic JC, Sievers M, Buelow CA, Pearson RM, Tulloch VJD, Cote IM, Unsworth RKF, Collier CJ, Brown CJ (2021) Anthropogenic pressures and life history predict trajectories of seagrass meadow extent at a global scale. Proceedings of the National Academy of Sciences of the United States of America 118, 1–11. doi:10.1073/pnas.2110802118

Turschwell MP, Connolly SR, Schäfer RB, De Laender F, Campbell MD, Mantyka-Pringle C, Jackson MC, Kattwinkel M, Sievers M, Ashauer R, Côté IM, Connolly RM, van den Brink PJ, Brown CJ (2022) Interactive effects of multiple stressors vary with consumer interactions, stressor dynamics and magnitude. Ecology Letters 25, 1483–1496. doi:10.1111/ele.14013

Van Teeffelen AJA, Vos CC, Opdam P (2012) Species in a dynamic world: Consequences of habitat network dynamics on conservation planning. Biological Conservation 153, 239–253. doi:10.1016/j.biocon.2012.05.001

Vinebrooke RD, Cottingham KL, Norberg J, Scheffer M, Dodson SI, Maberly SC, Sommer U (2004) Impacts of multiple stressors on biodiversity and ecosystem functioning: The role of species co-tolerance. Oikos 104, 451–457. doi:10.1111/j.0030-1299.2004.13255.x

Woodward G, Bonada N, Brown LE, Death RG, Durance I, Gray C, Hladyz S, Ledger ME, Milner AM, Ormerod SJ, Thompson RM, Pawar S (2016) The effects of climatic fluctuations and extreme events on running water ecosystems. Philosophical Transactions of the Royal Society B: Biological Sciences 371. doi:10.1098/rstb.2015.0274

5. DISCUSSION & OUTLOOK

5.1 DISCUSSION

Overall, the results of the studies presented (Chapters 2-4) provide strong theoretical evidence that an improved mechanistic understanding of co-occurring stressors is needed to adequately assess how (hemimetabolous) species respond to global change-related stressors. Scenarios with complex spatiotemporal profiles of multiple stressors considering how space and time combine, together with adaptation, are critical to predicting how joint stressor effects and interactions develop.

5.1.1 CHANGING HABITAT CONNECTIVITY DRIVEN BY GLOBAL CHANGE

The modeling study presented in Chapter 2 clearly demonstrates that habitat connectivity has positive effects on the resilience of meta-populations to decreasing landscape permeability and fragmentation (Streib et al., 2020). Global change is likely to reduce the connectivity of many terrestrial habitats, increasing dispersal mortality within meta-populations as inter-patch connections degrade (Strien and Grêt-Regamey, 2016), or worst case, are lost entirely (Baguette and Van Dyck, 2007; King and With, 2002). The extinction risk of meta-populations will thereby be increased (Chisholm et al., 2011; Heino et al., 2017; Wilson et al., 2016), as they rely on the capability of individuals to disperse between sub-populations in sufficient numbers to recolonize extinct patches (Bocedi et al., 2014; Moilanen and Nieminen, 2002) or maintain genetic variability (Hanski, 1989; Watts et al., 2006). Consequently, understanding spatial patterns shaping habitat connectivity (Didham et al., 2012; Purse et al., 2003; Saura et al., 2014) is crucial for future management of terrestrial or semi-terrestrial species (Laita et al., 2011; Wilson et al., 2016).

Similar to terrestrial species, aside from landscape permeability and fragmentation, habitat connectivity for freshwater hemimetabolous species is primarily determined by the number of patches, but also by spatial patch arrangement (Hanski, 1989; Hodgson et al., 2011; Lechner et al., 2017); however, for these species, which rely on aquatic and terrestrial sites, the spatial structuring of the dendritic stream network additionally influences connectivity significantly, determining the potential spatial distribution of patches (Streib et al., 2020; Tonkin et al., 2018). The results indicate that management needs (besides local actions) to focus on the landscape scale and, thereby, on the preservation or improvement of habitat connectivity Lechner et al. (2017); Hodgson et al. (2011); Hanski (1989); Watts et al. (2006)]. Here, Heer et al. (2019) demonstrated, based on a simplified version of the presented model, that mathematical optimization methods can be useful tools to identify highly suitable habitat sites to enhance connectivity and thus plan management actions in an effective way.

5.1.2 IMPACT OF SPATIOTEMPORAL STRESSOR PROFILE ON JOINT EFFECTS AND INTERACTIONS

In Chapter 3, using an extended version of the meta-population model, it was shown that the joint effects and, thereby, interactions of a discrete stressor (extreme events) and a continuous stressor (land use) were mainly determined by the latter (Streib et al., 2022). For meta-populations, the risk of a discrete stressor (ranging from negligible to extinction) depends strongly on patch quality and habitat connectivity, which determine the recovery potential following temporary mortality (Newson et al., 2014; Oliver and Morecroft, 2014; Piessens et al., 2009); increasing land use stress makes a meta-population more vulnerable to extreme events (Dai et al., 2012). The study also showed that (under overall comparable conditions) meta-populations in environments where land use stress is homogeneously distributed are expected to perform worse against an additional (discrete) stressor than ones in environments where stress is heterogeneously distributed. Regional landscape homogeneity likely produces meta-populations of patches with similar quality, while regional heterogeneity promotes single, high-quality patches. These are more resilient to temporary mortality and, therefore more likely to survive and, thus, can promote more stable population dynamics by maintaining and driving recovery processes, e.g., recolonization of extinct patches (Oliver and Morecroft, 2014; Van Teeffelen et al., 2012). Moreover, it appeared that the size of joint effects and interaction (classification) strongly depended on the determination time. The more time for recovery, the lower the joint effects, and thereby the interactions may decrease (Leuzinger et al., 2011) possibly changing even the classification from non-additive to additive.

The study demonstrates the potential of regional landscape management in counteracting the risks of stressors associated with global change. Management that mitigates a continuous stressor, i.e., improves patch quality and habitat connectivity, can likely reduce or prevent joint effects and synergistic interactions from a co-occurring discrete stressor (Côté et al., 2016; Oliver and Morecroft, 2014). Here, actions focused on single high-quality patches are likely more effective than moderate improvements across all patches (Bergen et al., 2020; Oliver et al., 2010). However, when evaluating risks, a sharp focus regarding potential temporal discontinuities in joint effects and interactions is needed; joint effects and interaction (classification) do not necessarily remain stable over time.

5.1.3 MORE REALISTIC SCENARIO DESIGNS INCORPORATING DYNAMIC STRESSOR PROFILES AND ADAPTATION

Following, in chapter 4 potential changes by more realistic stressor scenarios designs, i.e., dynamic stressor profiles plus adaptation, were investigated. It appeared that joint effects and interactions developed fairly differently over time compared to a static baseline, moreover, adaptation reduced joint effects, changing interactions inconsistently (Streib et al., 2023). Dynamic profiles can produce rapid climatic event sequences preventing recovery processes within meta-populations, so the discrete stressor drives the joint effects, resulting in additive interactions (Falk et al., 2019; Ratajczak et al., 2018). Otherwise, the continuous stressor determines the interaction classification, as lower or higher land-use stress results in increased or decreased recovery, producing antagonism or synergism, respectively (Côté et al., 2016). Adaptation to the discrete stress reduced joint effects under decreasing continuous stress, yet had little compensatory influence under increasing stress. Reduced joint effects are likely if ecosystems or species adapt to changing environmental stressors (Bush et al., 2016; Jackson et al., 2021). However, this only applies unless another stressor simultaneously increases, offsetting gains by adaptation. Moreover, adaptation was found to produce higher interaction sizes despite reduced concurrent joint effects, thereby, albeit counter-intuitive, inconsistently changing the interaction classification. Here, even shifts from antagonism to synergism can occur, if adaptation produces a greater reduction in individual effects compared to joint effects (Orr et al., 2021).

The results imply that predicting joint effects and interactions of multiple stressors under real-world conditions based on static, short-term stressor scenarios without considering adaptations is likely unreliable (Jackson et al., 2021). It has also been shown that the management of a continuous stressor is ineffective once a discrete stressor dominates (Côté et al., 2016). Ignoring adaptation can, moreover, result in an incorrect assessment of potential management, e.g., actions can be incorrectly considered ineffective if adaptation will result in joint effects being lower in reality than expected. Also, adaptation can increase the interaction size, thereby inconsistently changing the classification, e.g., additive interactions may shift to non-additive interactions. Consequently, future management of threatened species should focus on reducing joint effects based on a mechanistic understanding of joint effects, rather than trying to prevent (high) synergies (Orr et al., 2021; Schäfer et al., 2023; Schäfer and Piggott, 2018).

5.2 OUTLOOK

The present study shows that process-based simulation models can generate an advanced (theoretical) understanding of how multiple stressors associated with anthropogenic global change act across space and time. Such models always make a trade-off between simplicity and complexity, so the scenarios of the studies presented reflected one or two stressors for one species with specific characteristics only. In real ecosystems, typically more stressors are present (Sage, 2020) with mostly very complex patterns (Jackson et al., 2021).

Recent research reveals that current technological developments in IT allow new models to become more complex. High-performance computing environments provide growing capabilities to apply computationally intensive statistical models, e.g., Bayesian methods, and to process large data sets so model uncertainties can be reduced and efficient calibration of complex process-based models is possible (Fer et al., 2018). Deep learning algorithms are evolving in their ability to automatically extract spatio-temporal features, thereby allowing improved modeling of long-range spatial patterns across multiple time scales (Reichstein et al., 2019). Also, a growing number of species trait databases have been published in recent years (Gallagher et al., 2020), enabling models to be parameterized for multiple species with low effort. These developments will reduce the need to control the complexity of a model framework and allow for parameterization that relies less on approximations or estimates in the absence of precise values. Thus, the (primarily hypothetical) presented modeling approaches have the potential to be applied to a wide variety of real-world species and habitats based on probabilistic scenarios in the future. Here, we are confident that the outlined principles of the mechanistic mode of action of multiple stressors generally apply, so they continue to hold under increasing complexity. This will likely allow these models to be used to identify individual risks to species and thus support specific management planning in the real world and, furthermore, potentially increase the acceptance of model results in the (broader) scientific community (Grimm and Railsback, 2011).

In summary, although primarily theoretical, the presented findings will (at a minimum) support further expanding the conceptual framework of research on multiple stressors in the future, thereby contributing to the conservation of the Earth's threatened biodiversity. Nevertheless, conservation efforts will only be successful if society and politics take the risks of anthropogenic global change seriously and act consequently to limit its environmental effects to the maximum extent possible.

6 REFERENCES

Anderson, K.E., Hayes, S.M., 2018. The effects of dispersal and river spatial structure on asynchrony in consumer–resource metacommunities. Freshwater Biology 63, 100–113. https://doi.org/10.1111/fwb.12998

Baguette, M., Van Dyck, H., 2007. Landscape connectivity and animal behavior: Functional grain as a key determinant for dispersal. Landscape Ecology 22, 1117–1129. https://doi.org/10.1007/s10980-007-9108-4

Baker, R.E., Peña, J.M., Jayamohan, J., Jérusalem, A., 2018. Mechanistic models versus machine learning, a fight worth fighting for the biological community? Biology Letters 14, 1–4. https://doi.org/10.1098/rsbl.2017.0660

Bergen, E., Dallas, T., DiLeo, M.F., Kahilainen, A., Mattila, A.L.K., Luoto, M., Saastamoinen, M., 2020. The effect of summer drought on the predictability of local extinctions in a butterfly metapopulation. Conservation Biology 0, 1–9. https://doi.org/10.1111/cobi.13515

Birk, S., Chapman, D., Carvalho, L., Spears, B.M., Andersen, H.E., Argillier, C., Auer, S., Baattrup-Pedersen, A., Banin, L., Beklioğlu, M., Bondar-Kunze, E., Borja, A., Branco, P., Bucak, T., Buijse, A.D., Cardoso, A.C., Couture, R.-M., Cremona, F., Zwart, D. de, Feld, C.K., Ferreira, M.T., Feuchtmayr, H., Gessner, M.O., Gieswein, A., Globevnik, L., Graeber, D., Graf, W., Gutiérrez-Cánovas, C., Hanganu, J., Işkın, U., Järvinen, M., Jeppesen, E., Kotamäki, N., Kuijper, M., Lemm, J.U., Lu, S., Solheim, A.L., Mischke, U., Moe, S.J., Nõges, P., Nõges, T., Ormerod, S.J., Panagopoulos, Y., Phillips, G., Posthuma, L., Pouso, S., Prudhomme, C., Rankinen, K., Rasmussen, J.J., Richardson, J., Sagouis, A., Santos, J.M., Schäfer, R.B., Schinegger, R., Schmutz, S., Schneider, S.C., Schülting, L., Segurado, P., Stefanidis, K., Sures, B., Thackeray, S.J., Turunen, J., Uyarra, M.C., Venohr, M., Ohe, P.C. von der, Willby, N., Hering, D., 2020. Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. Nature Ecology & Evolution. https://doi.org/10.1038/s41559-020-1216-4

Bocedi, G., Palmer, S.C.F., Pe’er, G., Heikkinen, R.K., Matsinos, Y.G., Watts, K., Travis, J.M.J., 2014. RangeShifter: A platform for modelling spatial eco-evolutionary dynamics and species’ responses to environmental changes. Methods in Ecology and Evolution 5, 388–396. https://doi.org/10.1111/2041-210X.12162

Boyd, P.W., Collins, S., Dupont, S., Fabricius, K., Gattuso, J.P., Havenhand, J., Hutchins, D.A., Riebesell, U., Rintoul, M.S., Vichi, M., Biswas, H., Ciotti, A., Gao, K., Gehlen, M., Hurd, C.L., Kurihara, H., McGraw, C.M., Navarro, J.M., Nilsson, G.E., Passow, U., Pörtner, H.O., 2018. Experimental strategies to assess the biological ramifications of multiple drivers of global ocean change—A review. Global Change Biology 24, 2239–2261. https://doi.org/10.1111/gcb.14102

Brooks, P.R., Crowe, T.P., 2019. Combined Effects of Multiple Stressors: New Insights Into the Influence of Timing and Sequence. Frontiers in Ecology and Evolution 7. https://doi.org/10.3389/fevo.2019.00387

Bruder, A., Frainer, A., Rota, T., Primicerio, R., 2019. The importance of ecological networks in multiple-stressor research and management. Frontiers in Environmental Science 7, 1–7. https://doi.org/10.3389/fenvs.2019.00059

Bush, A., Mokany, K., Catullo, R., Hoffmann, A., Kellermann, V., Sgrò, C., McEvey, S., Ferrier, S., 2016. Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. Ecology Letters 19, 1468–1478. https://doi.org/10.1111/ele.12696

Catford, J.A., Wilson, J.R.U., Pyšek, P., Hulme, P.E., Duncan, R.P., 2022. Addressing context dependence in ecology. Trends in Ecology and Evolution 37, 158–170. https://doi.org/10.1016/j.tree.2021.09.007

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. Science Advances 1, 9–13. https://doi.org/10.1126/sciadv.1400253

Ceballos, G., Ehrlich, P.R., Raven, P.H., 2020. Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. Proceedings of the National Academy of Sciences of the United States of America 117, 13596–13602. https://doi.org/10.1073/pnas.1922686117

Chisholm, C., Lindo, Z., Gonzalez, A., 2011. Metacommunity diversity depends on connectivity and patch arrangement in heterogeneous habitat networks. Ecography 34, 415–424. https://doi.org/10.1111/j.1600-0587.2010.06588.x

Côté, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B: Biological Sciences 283, 20152592. https://doi.org/10.1098/rspb.2015.2592

Dai, L., Vorselen, D., Korolev, K.S., Gore, J., 2012. Generic indicators for loss of resilience before a tipping point leading to population collapse. Science 336, 1175–1177. https://doi.org/10.1126/science.1219805

De Laender, F., 2018. Community- and ecosystem-level effects of multiple environmental change drivers: Beyond null model testing. Global Change Biology 24, 5021–5030. https://doi.org/10.1111/gcb.14382

Didham, R.K., Blakely, T.J., Ewers, R.M., Hitchings, T.R., Ward, J.B., Winterbourn, M.J., 2012. Horizontal and vertical structuring in the dispersal of adult aquatic insects in a fragmented landscape. Fundamental and Applied Limnology / Archiv für Hydrobiologie 180, 27–40. https://doi.org/10.1127/1863-9135/2012/0243

Falk, D.A., Watts, A.C., Thode, A.E., 2019. Scaling Ecological Resilience. Frontiers in Ecology and Evolution 7, 1–16. https://doi.org/10.3389/fevo.2019.00275

Fer, I., Kelly, R., Moorcroft, P.R., Richardson, A.D., Cowdery, E.M., Dietze, M.C., 2018. Linking big models to big data: Efficient ecosystem model calibration through Bayesian model emulation. Biogeosciences 15, 5801–5830. https://doi.org/10.5194/bg-15-5801-2018

Gallagher, R.V., Falster, D.S., Maitner, B.S., Salguero-Gómez, R., Vandvik, V., Pearse, W.D., Schneider, F.D., Kattge, J., Poelen, J.H., Madin, J.S., Ankenbrand, M.J., Penone, C., Feng, X., Adams, V.M., Alroy, J., Andrew, S.C., Balk, M.A., Bland, L.M., Boyle, B.L., Bravo-Avila, C.H., Brennan, I., Carthey, A.J.R., Catullo, R., Cavazos, B.R., Conde, D.A., Chown, S.L., Fadrique, B., Gibb, H., Halbritter, A.H., Hammock, J., Hogan, J.A., Holewa, H., Hope, M., Iversen, C.M., Jochum, M., Kearney, M., Keller, A., Mabee, P., Manning, P., McCormack, L., Michaletz, S.T., Park, D.S., Perez, T.M., Pineda-Munoz, S., Ray, C.A., Rossetto, M., Sauquet, H., Sparrow, B., Spasojevic, M.J., Telford, R.J., Tobias, J.A., Violle, C., Walls, R., Weiss, K.C.B., Westoby, M., Wright, I.J., Enquist, B.J., 2020. Open Science principles for accelerating trait-based science across the Tree of Life. Nature Ecology and Evolution 4, 294–303. https://doi.org/10.1038/s41559-020-1109-6

Griffen, B.D., Belgrad, B.A., Cannizzo, Z.J., Knotts, E.R., Hancock, E.R., 2016. Rethinking our approach to multiple stressor studies in marine environments. Marine Ecology Progress Series 543, 273–281. https://doi.org/10.3354/meps11595

Grigoropoulou, A., Hamid, S.A., Acosta, R., Akindele, E.O., Al-Shami, S.A., Altermatt, F., Amatulli, G., Angeler, D.G., Arimoro, F.O., Aroviita, J., Astorga-Roine, A., Bastos, R.C., Bonada, N., Boukas, N., Brand, C., Bremerich, V., Bush, A., Cai, Q., Callisto, M., Chen, K., Cruz, P.V., Dangles, O., Death, R., Deng, X., Domínguez, E., Dudgeon, D., Eriksen, T.E., Faria, A.P.J., Feio, M.J., Fernández-Aláez, C., Floury, M., García-Criado, F., García-Girón, J., Graf, W., Grönroos, M., Haase, P., Hamada, N., He, F., Heino, J., Holzenthal, R., Huttunen, K.L., Jacobsen, D., Jähnig, S.C., Jetz, W., Johnson, R.K., Juen, L., Kalkman, V., Kati, V., Keke, U.N., Koroiva, R., Kuemmerlen, M., Langhans, S.D., Ligeiro, R., Van Looy, K., Maasri, A., Marchant, R., Garcia Marquez, J.R., Martins, R.T., Melo, A.S., Metzeling, L., Miserendino, M.L., Moe, S.J., Molineri, C., Muotka, T., Mustonen, K.R., Mykrä, H., Cavalcante do Nascimento, J.M., Valente-Neto, F., Neu, P.J., Nieto, C., Pauls, S.U., Paulson, D.R., Rios-Touma, B., Rodrigues, M.E., de Oliveira Roque, F., Salazar Salina, J.C., Schmera, D., Schmidt-Kloiber, A., Shah, D.N., Simaika, J.P., Siqueira, T., Tachamo-Shah, R.D., Theischinger, G., Thompson, R., Tonkin, J.D., Torres-Cambas, Y., Townsend, C., Turak, E., Twardochleb, L., Wang, B., Yanygina, L., Zamora-Muñoz, C., Domisch, S., 2023. The global EPTO database: Worldwide occurrences of aquatic insects. Global Ecology and Biogeography 32, 642–655. https://doi.org/10.1111/geb.13648

Grimm, V., Railsback, S.F., 2011. Pattern-oriented modelling: a ‘multi-scope’ for predictive systems ecology. Philosophical Transactions of the Royal Society B 367, 298–310. https://doi.org/10.1098/rstb.2011.0180

Guerry, A.D., Polasky, S., Lubchenco, J., Chaplin-Kramer, R., Daily, G.C., Griffin, R., Ruckelshaus, M., Bateman, I.J., Duraiappah, A., Elmqvist, T., Feldman, M.W., Folke, C., Hoekstra, J., Kareiva, P.M., Keeler, B.L., Li, S., McKenzie, E., Ouyang, Z., Reyers, B., Ricketts, T.H., Rockström, J., Tallis, H., Vira, B., 2015. Natural capital and ecosystem services informing decisions: From promise to practice. Proceedings of the National Academy of Sciences of the United States of America 112, 7348–7355. https://doi.org/10.1073/pnas.1503751112

Hanski, I., 1989. Metapopulation dynamics: Does it help to have more of the same? Trends in Ecology and Evolution 4, 113–114. https://doi.org/10.1016/0169-5347(89)90061-X

Heer, H., Streib, L., Kattwinkel, M., Schäfer, R.B., Ruzika, S., 2019. Optimisation Model of Dispersal Simulations on a Dendritic Habitat Network. Scientific Reports 9, 1–11. https://doi.org/10.1038/s41598-019-44716-z

Heino, J., Alahuhta, J., Ala-Hulkko, T., Antikainen, H., Bini, L.M., Bonada, N., Datry, T., Erős, T., Hjort, J., Kotavaara, O., Melo, A.S., Soininen, J., 2017. Integrating dispersal proxies in ecological and environmental research in the freshwater realm. Environmental Reviews 25, 334–349. https://doi.org/10.1139/er-2016-0110

Hodgson, J.A., Moilanen, A., Wintle, B.A., Thomas, C.D., 2011. Habitat area, quality and connectivity: Striking the balance for efficient conservation. Journal of Applied Ecology 48, 148–152. https://doi.org/10.1111/j.1365-2664.2010.01919.x

Hunsicker, M.E., Kappel, C.V., Selkoe, K.A., Halpern, B.S., Scarborough, C., Mease, L., Amrhein, A., 2016. Characterizing driver-response relationships in marine pelagic ecosystems for improved ocean management. Ecological Applications 26, 651–663. https://doi.org/10.1890/14-2200/suppinfo

Jackson, M.C., Pawar, S., Woodward, G., 2021. The Temporal Dynamics of Multiple Stressor Effects: From Individuals to Ecosystems. Trends in Ecology & Evolution 36, 402–410. https://doi.org/10.1016/j.tree.2021.01.005

Jackson, M., Voulvoulis, N., Woodward, G., 2018. Multiple stressors in freshwater ecosystems: biocides and climate change. Imperial College paper 27, 10.

Jager, T., Barsi, A., Hamda, N.T., Martin, B.T., Zimmer, E.I., Ducrot, V., 2014. Dynamic energy budgets in population ecotoxicology: Applications and outlook. Ecological Modelling 280, 140–147. https://doi.org/10.1016/j.ecolmodel.2013.06.024

Jørgensen, S.E., 1994. Models as instruments for combination of ecological theory and environmental practice. Ecological Modelling 75-76, 5–20. https://doi.org/10.1016/0304-3800(94)90003-5

King, A.W., With, K.A., 2002. Dispersal success on spatially structured landscapes: When do spatial pattern and dispersal behavior really matter? Ecological Modelling 147, 23–39. https://doi.org/10.1016/S0304-3800(01)00400-8

Laita, A., Kotiaho, J.S., Mönkkönen, M., 2011. Graph-theoretic connectivity measures: What do they tell us about connectivity? Landscape Ecology 26, 951–967. https://doi.org/10.1007/s10980-011-9620-4

Lakovic, M., Mitesser, O., Hovestadt, T., 2017. Mating timing, dispersal and local adaptation in patchy environments. Oikos 1–11. https://doi.org/10.1111/oik.04369

Lechner, A.M., Sprod, D., Carter, O., Lefroy, E.C., 2017. Characterising landscape connectivity for conservation planning using a dispersal guild approach. Landscape Ecology 32, 99–113. https://doi.org/10.1007/s10980-016-0431-5

Leuzinger, S., Luo, Y., Beier, C., Dieleman, W., Vicca, S., Körner, C., 2011. Do global change experiments overestimate impacts on terrestrial ecosystems? Trends in Ecology and Evolution 26, 236–241. https://doi.org/10.1016/j.tree.2011.02.011

McCallum, M.L., 2015. Vertebrate biodiversity losses point to a sixth mass extinction. Biodiversity and Conservation 24, 2497–2519. https://doi.org/10.1007/s10531-015-0940-6

Moilanen, A., Nieminen, M., 2002. Simple connectivity measure in spatial ecology. Ecology 83, 1131–1145.

Newson, S.E., Oliver, T.H., Gillings, S., Crick, H.Q.P., Morecroft, M.D., Duffield, S.J., Macgregor, N.A., Pearce-Higgins, J.W., 2014. Can site and landscape-scale environmental attributes buffer bird populations against weather events? Ecography 37, 872–882. https://doi.org/10.1111/ecog.00575

Oliver, T.H., Morecroft, M.D., 2014. Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. Wiley Interdisciplinary Reviews: Climate Change 5, 317–335. https://doi.org/10.1002/wcc.271

Oliver, T., Roy, D.B., Hill, J.K., Brereton, T., Thomas, C.D., 2010. Heterogeneous landscapes promote population stability. Ecology Letters 13, 473–484. https://doi.org/10.1111/j.1461-0248.2010.01441.x

Orr, J.A., Luijckx, P., Arnoldi, J., Jackson, A.L., Piggott, J.J., 2021. Rapid evolution generates synergism between multiple stressors: linking theory and an evolution experiment. Global Change Biology 1–13. https://doi.org/10.1111/gcb.15633

Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-pringle, C., Van den Brink, P.J., De Laender, F., Stoks, R., Holmstrup, M., Matthaei, C.D., Monk, W.A., Penk, M.R., Leuzinger, S., Schäfer, R.B., Piggott, J.J., 2020. Towards a unified study of multiple stressors : divisions and common goals across research disciplines. Proceedings of the Royal Society B: Biological Sciences 20200421. https://doi.org/10.1098/rspb.2020.0421

Patrick, C.J., McCluney, K.E., Ruhi, A., Gregory, A., Sabo, J., Thorp, J.H., 2021. Multi-scale biodiversity drives temporal variability in macrosystems. Frontiers in Ecology and the Environment 19, 47–56. https://doi.org/10.1002/fee.2297

Payne, J.L., Aswad, J.A.A., Penn, J.L., Deutsch, C., 2023. Selectivity of mass extinctions : Patterns , processes , and future directions 1–11.

Piessens, K., Adriaens, D., Jacquemyn, H., Honnay, O., 2009. Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. Oecologia 159, 117–126. https://doi.org/10.1007/s00442-008-1204-x

Pievani, T., 2014. The sixth mass extinction: Anthropocene and the human impact on biodiversity. Rendiconti Lincei 25, 85–93. https://doi.org/10.1007/s12210-013-0258-9

Piggott, J.J., Townsend, C.R., Matthaei, C.D., 2015. Reconceptualizing synergism and antagonism among multiple stressors. Ecology and Evolution 5, 1538–1547. https://doi.org/10.1002/ece3.1465

Pirotta, E., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J., Kraus, S.D., Miller, P.J.O., Moore, M.J., Photopoulou, T., Rolland, R.M., Schwacke, L., Simmons, S.E., Southall, B.L., Tyack, P.L., 2022. Understanding the combined effects of multiple stressors: A new perspective on a longstanding challenge. Science of the Total Environment 821, 153322. https://doi.org/10.1016/j.scitotenv.2022.153322

Purse, B.V., Hopkins, G.W., Day, K.J., Thompson, D.J., 2003. Dispersal characteristics and management of a rare damselfly. Journal of Applied Ecology 40, 716–728. https://doi.org/10.1046/j.1365-2664.2003.00829.x

Ratajczak, Z., Carpenter, S.R., Ives, A.R., Kucharik, C.J., Ramiadantsoa, T., Stegner, M.A., Williams, J.W., Zhang, J., Turner, M.G., 2018. Abrupt Change in Ecological Systems: Inference and Diagnosis. Trends in Ecology and Evolution 33, 513–526. https://doi.org/10.1016/j.tree.2018.04.013

Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. Proceedings of the National Academy of Sciences of the United States of America 118, 1–6. https://doi.org/10.1073/PNAS.2002548117

Reichstein, M., Camps-Valls, G., Stevens, B., Jung, M., Denzler, J., Carvalhais, N., Prabhat, 2019. Deep learning and process understanding for data-driven Earth system science. Nature 566, 195–204. https://doi.org/10.1038/s41586-019-0912-1

Rillig, M.C., Ryo, M., Lehmann, A., 2021. Classifying human influences on terrestrial ecosystems. Global Change Biology gcb.15577. https://doi.org/10.1111/gcb.15577

Ryo, M., Aguilar-Trigueros, C.A., Pinek, L., Muller, L.A.H., Rillig, M.C., 2019. Basic Principles of Temporal Dynamics. Trends in Ecology and Evolution 34, 723–733. https://doi.org/10.1016/j.tree.2019.03.007

Sage, R.F., 2020. Global change biology: A primer. Global Change Biology 26, 3–30. https://doi.org/10.1111/gcb.14893

Saura, S., Bodin, Ö., Fortin, M.-J.J., 2014. EDITOR'S CHOICE: Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. Journal of Applied Ecology 51, 171–182. https://doi.org/10.1111/1365-2664.12179

Schäfer, R.B., Jackson, M., Juvigny-Khenafou, N., Osakpolor, S.E., Posthuma, L., Schneeweiss, A., Spaak, J., Vinebrooke, R., 2023. Chemical Mixtures and Multiple Stressors: Same but Different? Environmental Toxicology and Chemistry 00, 1–22. https://doi.org/10.1002/etc.5629

Schäfer, R.B., Piggott, J.J., 2018. Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. Global Change Biology 24, 1817–1826. https://doi.org/10.1111/gcb.14073

Simmons, B.I., Blyth, P.S.A., Blanchard, J.L., Clegg, T., Delmas, E., Garnier, A., Griffiths, C.A., Jacob, U., Pennekamp, F., Petchey, O.L., Poisot, T., Webb, T.J., Beckerman, A.P., 2021b. Refocusing multiple stressor research around the targets and scales of ecological impacts. Nature Ecology & Evolution 5, 1478–1489. https://doi.org/10.1038/s41559-021-01547-4

Simmons, B.I., Blyth, P.S.A., Blanchard, J.L., Clegg, T., Delmas, E., Garnier, A., Griffiths, C.A., Jacob, U., Pennekamp, F., Petchey, O.L., Poisot, T., Webb, T.J., Beckerman, A.P., 2021a. Refocusing multiple stressor research around the targets and scales of ecological impacts. Nature Ecology and Evolution 5, 1478–1489. https://doi.org/10.1038/s41559-021-01547-4

Streib, L., Kloft, M., Schäfer, R.B., 2023. The spatiotemporal profile and adaptation determine the joint effects and interactions of multiple stressors. [Unpublished manuscript]. iES - Institute for Environmental Sciences, RPTU Kaiserslautern-Landau.

Streib, L., Juvigny-Khenafou, N., Heer, H., Kattwinkel, M., Schäfer, R.B., 2022. Spatiotemporal dynamics drive synergism of land use and climatic extreme events in insect meta-populations. Science of The Total Environment 814, 152602. https://doi.org/10.1016/j.scitotenv.2021.152602

Streib, L., Kattwinkel, M., Heer, H., Ruzika, S., Schäfer, R.B., 2020. How does habitat connectivity influence the colonization success of a hemimetabolous aquatic insect? - A modeling approach. Ecological Modelling 416, 108909. https://doi.org/10.1016/j.ecolmodel.2019.108909

Strien, M.J. van, Grêt-Regamey, A., 2016. How is habitat connectivity affected by settlement and road network configurations? Results from simulating coupled habitat and human networks. Ecological Modelling 342, 186–198. https://doi.org/10.1016/j.ecolmodel.2016.09.025

Tonkin, J.D., Altermatt, F., Finn, D.S., Heino, J., Olden, J.D., Pauls, S.U., Lytle, D.A., S. Finn, D., Heino, J., Olden, J.D., Pauls, S.U., Lytle, D.A., Finn, D.S., Heino, J., Olden, J.D., Pauls, S.U., Lytle, D.A., S. Finn, D., Heino, J., Olden, J.D., Pauls, S.U., Lytle, D.A., 2018. The role of dispersal in river network metacommunities: Patterns, processes, and pathways. Freshwater Biology 63, 141–163. https://doi.org/10.1111/fwb.13037

Turner, M.G., Calder, W.J., Cumming, G.S., Hughes, T.P., Jentsch, A., LaDeau, S.L., Lenton, T.M., Shuman, B.N., Turetsky, M.R., Ratajczak, Z., Williams, J.W., Williams, A.P., Carpenter, S.R., 2020. Climate change, ecosystems and abrupt change: Science priorities. Philosophical Transactions of the Royal Society B: Biological Sciences 375. https://doi.org/10.1098/rstb.2019.0105

Turschwell, M.P., Connolly, R.M., Dunic, J.C., Sievers, M., Buelow, C.A., Pearson, R.M., Tulloch, V.J.D., Cote, I.M., Unsworth, R.K.F., Collier, C.J., Brown, C.J., 2021. Anthropogenic pressures and life history predict trajectories of seagrass meadow extent at a global scale. Proceedings of the National Academy of Sciences of the United States of America 118, 1–11. https://doi.org/10.1073/pnas.2110802118

Turschwell, M.P., Connolly, S.R., Schäfer, R.B., De Laender, F., Campbell, M.D., Mantyka-Pringle, C., Jackson, M.C., Kattwinkel, M., Sievers, M., Ashauer, R., Côté, I.M., Connolly, R.M., Brink, P.J. van den, Brown, C.J., 2022. Interactive effects of multiple stressors vary with consumer interactions, stressor dynamics and magnitude. Ecology Letters 25, 1483–1496. https://doi.org/10.1111/ele.14013

Tynan, J., 1986. Earth History. Thought 8, 515–518. https://doi.org/10.5840/thought19338341

Van den Brink, P.J., (Hans) Baveco, J.M., Verboom, J., Heimbach, F., 2007. An individual-based approach to model spatial population dynamics of invertebrates in aquatic ecosystems after pesticide contamination. Environmental Toxicology and Chemistry 26, 2226. https://doi.org/10.1897/07-022R.1

Van Teeffelen, A.J.A., Vos, C.C., Opdam, P., 2012. Species in a dynamic world: Consequences of habitat network dynamics on conservation planning. Biological Conservation 153, 239–253. https://doi.org/10.1016/j.biocon.2012.05.001

Watts, P.C., Saccheri, I.J., Kemp, S.J., Thompson, D.J., 2006. Population structure and the impact of regional and local habitat isolation upon levels of genetic diversity of the endangered damselfly Coenagrion mercuriale (Odonata: Zygoptera). Freshwater Biology 51, 193–205. https://doi.org/10.1111/j.1365-2427.2005.01478.x

Wilson, M.C., Richard, X.C., Didham, R.K., Ding, P., Holt, R.D., Holyoak, M., Hu, G., Hughes, A.C., Jiang, L., Laurance, W.F., Liu, J., Pimm, S.L., Robinson, S.K., Russo, S.E., Si, X., Wilcove, D.S., Wu, J., Yu, M., 2016. Habitat fragmentation and biodiversity conservation : key findings and future challenges. Landscape Ecology 31, 219–227. https://doi.org/10.1007/s10980-015-0312-3

Woodward, G., Bonada, N., Brown, L.E., Death, R.G., Durance, I., Gray, C., Hladyz, S., Ledger, M.E., Milner, A.M., Ormerod, S.J., Thompson, R.M., Pawar, S., 2016. The effects of climatic fluctuations and extreme events on running water ecosystems. Philosophical Transactions of the Royal Society B: Biological Sciences 371. https://doi.org/10.1098/rstb.2015.0274

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PAPER 1: HOW DOES HABITAT CONNECTIVITY INFLUENCE THE COLONIZATION SUCCESS OF A HEMIMETABOLOUS AQUATIC INSECT? - A MODELING APPROACH

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PAPER 2: SPATIOTEMPORAL DYNAMICS DRIVE SYNERGISM OF LAND USE AND CLIMATIC EXTREME EVENTS IN INSECT META-POPULATIONS

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PAPER 3: THE SPATIOTEMPORAL PROFILE AND ADAPTATION DETERMINE THE JOINT EFFECTS AND INTERACTIONS OF MULTIPLE STRESSORS

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AUTHORSHIP DECLARATION

I, Lucas Santichai Streib, hereby certify that the work presented in this Ph.D. thesis has been interdependently prepared without the use of any generative models (artificial intelligence). The thesis includes no material accepted or submitted for the award of any other degree at any university or other scientific institution. Supporting materials, references, and the contribution of co-authors are clearly specified. I am aware that any violation of the contents of this declaration will result in legal consequences.

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Diploma thesis

Title	Risks of climatic impact for grassland areas - future scenarios from GIS-based yield modelling in Rhineland-Palatinate
Context	Research project "Klim-LandRP: Klima- und Landschaftswandel in Rheinland- Pfalz" of the (former) Department for Environment, Food, Agriculture, Viticul- ture and Forestry Rhineland-Palatinate

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