Lucas R. de Freitas

Quantidades iniciais de variação intraespecífica influenciam na persistência de populações em paisagens degradadas e/ou fragmentadas?

Do initial amounts of adaptive intraspecific variation matter for the persistence of populations in fragmented landscapes?

São Paulo

2022

Lucas R. de Freitas

Quantidades iniciais de variação intraespecífica influenciam na persistência de populações em paisagens degradadas e/ou fragmentadas?

Do initial amounts of adaptive intraspecific variation matter for the persistence of populations in fragmented landscapes?

Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Mestre em 2022, na Área de Ecologia.

Orientador(a): Paulo Inácio de Knegt López de Prado

São Paulo

2022

Comissão Julgadora:

_____

Prof(a). Dr(a).   Prof(a). Dr(a).

_____

Prof(a). Dr.(a).

_____

Orientador(a)

To my last two brain cells

Epígrafe

KC Green

(http://kcgreendotcom.com/index.html)

Agradecimentos:

Primeiramente agradeço ao PI, que além de desempenhar TODAS as funções acadêmicas esperadas de um orientador, é um espécime exemplar de ser humano. Você me inspira a querer ser melhor Paulo.

Em segundo, agradeço aos meus membros do comitê de acompanhamento, DeMarco e Dan, pelas sugestões sempre pertinentes e que certamente incorporaram bastante a qualidade da tese.

Agradeço também ao Felipe e a Melina pelas ajudas operacionais em diversas ocasiões.

Agradeço, ainda, a todos os membros do Programa de Pós Graduação em Ecologia da USP.

(em especial a Vera que carrega esse programa nas costas)

Agradeço imensamente a todos que tiveram qualquer grau de envolvimento na confecção deste trabalho, assim como a CAPES (Nº 88887.339537/2019-00) e a FAPESP (Nº 2019/24355-9) que pagaram minhas contas de água e luz .

Finalmente, agradeço à minha família pelo amparo necessário durante toda a minha vida, sem o qual não poderia ter tido essa oportunidade.

Índice

Do initial amounts of adaptive intraspecific variation matter for the persistence of populations in fragmented landscapes?

Do initial amounts of adaptive intraspecific variation matter for the persistence of populations in fragmented landscapes?

Master 's student: Lucas R. de Freitas (Graduate Program in Ecology, USP), Academic Supervisor: Paulo Inácio de Knegt López de Prado (Biosciences Institute, USP) Committee Advisors: Daniel I. Bolnick (Universidade de Connecticut) & Paulo De Marco Júnior (Federal University of Goiás)

Abstract

The preexisting variation within a population, as well as its heritability, are fundamental prerequisites to the persistence of the population suffering from disturbance events. Of the many anthropic sources of wildlife extinction, habitat loss has proven itself to be one of major importance. Moreover, the spatial configuration of how habitat remains on the landscape may bear significance beyond simply the amount of habitat removed. Several explanations for the persistence of populations focus on the existence of species whose traits mitigate the effects of habitat loss and fragmentation while overlooking that those favorable traits may arise at the individual level as a consequence of preexisting intraspecific variation in resource usage. Thus, the interaction between quantitative heritable variation and landscape populational dynamics falls at the interface between ecological and evolutionary processes, a hot topic for both theoretical and empirical developments. We used computer simulations to systematically explore the logical consequences of varying initial amounts of intraspecific variation in the extinction time of populations in the events of varying amounts of both habitat loss and fragmentation. We found that higher initial amounts of intraspecific variation generally increase the persistence of populations under most instances of habitat destruction, but also that this relationship is not monotonous. We also found that, although higher amounts of habitat loss are objectively more hazardous for populations, its association with lower degrees of fragmentation may be especially detrimental to individual types (and analogous species with narrow niche widths), while its association with higher fragmentation is more harmful to the populational survival.

Resumo

A variação preexistente dentro de uma população, bem como sua herdabilidade, são pré-requisitos fundamentais para a persistência da população que sofre eventos de perturbação. Das muitas fontes antrópicas de extinção da vida selvagem, a perda de habitat provou-se de grande importância. Além disso, a configuração espacial de como o habitat permanece na paisagem pode ter significado além da simples quantidade de habitat removido. Várias explicações para a persistência das populações concentram-se na existência de espécies cujas características atenuam os efeitos da perda e fragmentação do habitat, ignorando que essas características favoráveis podem surgir no nível individual como consequência da variação intraespecífica preexistente no uso dos recursos. Assim, a interação entre a variação quantitativa hereditária e

a dinâmica populacional da paisagem situa-se na interface entre os processos ecológicos e evolutivos, um tema quente para desenvolvimentos teóricos e empíricos. Usamos simulações de computador para explorar sistematicamente as consequências lógicas de quantidades iniciais variáveis de variação intraespecífica no tempo de extinção de populações em eventos de quantidades variáveis de perda e fragmentação de habitat. Descobrimos que quantidades iniciais mais altas de variação intraespecífica geralmente aumentam a persistência das populações na maioria dos casos de destruição de habitat, mas também que essa relação não é monótona. Também descobrimos que, embora maiores quantidades de perda de habitat sejam objetivamente mais perigosas para as populações, sua associação com menores graus de fragmentação pode ser especialmente prejudicial para tipos individuais (e espécies análogas com larguras de nicho estreitas), enquanto sua associação com maior fragmentação é mais prejudiciais à sobrevivência da população.

Keywords: computer simulations, individual-based models, habitat loss, habitat fragmentation, individual variation, spatially explicit models.

Introduction

The preexisting variation within a population, as well as its heritability, are fundamental prerequisites to the persistence of the population under events of disturbances (MACCOLL, 2011; ORR; SMITH, 1998). Individuals of a population do not perceive nor exploit a given environment in the same way (SOBERÓN; NAKAMURA, 2009). As a consequence, habitat loss and fragmentation may favor some individuals which may be linked to a particular set of traits that are capable of mitigating the effects of habitat degradation. Most of the research on this topic has focused on both dispersal capability and/or recruitment power (CLAUDINO; GOMES; CAMPOS, 2015; HYLANDER; EHRLÉN, 2013). Dispersal capacity enhances an individual's ability to dislocate between patches of the landscape, and recruitment power facilitates establishing new populations in unoccupied patches, thus rescuing a population that crashed. Those and more traits, usually linked to the persistence of populations in face of disturbances, are generally analyzed under the assumption that the individuals within a given species interact similarly with their environments (YANG *et al.*, 2021). This assumption supports researchers to use trait averages for a population that doesn't even depict biologically realistic values (CHESSON, 1996, 1998, 2001).Therefore, most of the literature overlooks that those favorable individual traits may arise as a consequence of preexisting intraspecific variation in resource usage by the individuals of a single species (BOLNICK *et al.*, 2003). The persistent variability of adaptive traits depends on the viability of stable polymorphisms, which in turn is extremely dependent on both environmental heterogeneity and the grain scale of the individuals

(LEVINS, 1968; WIENS, 1989). Environmental heterogeneity is important as it creates conditions where several trait-related optimum values can exist for the same population. However, it is also determinant that individuals actively pursue favorable environments (e.g. habitat selection) and that those different patches of habitat are large enough for individuals to linger in a single patch for most of their lives (e.g coarse-grained) (HAMILTON, 2017). So that different biotypes may be selected and maintained within a population in a patched, or heterogeneous environment (LEVINS, 1968; WIENS, 1989). Stable polymorphisms may also arise as a consequence of frequency-dependent selection, independently of spatial structure (LEVENE, 1953; SLOAN WILSON; TURELLI, 1986). Initial poorly adapted morphs may be favored by their ability to utilize resources previously unexploited by their population (e.g. occupying previously "empty niches"), a phenomenon that is commonly associated with evolutionary irradiation events (COLLINS; DE MEAUX; ACQUISTI, 2007).

There are several selection pressures capable of poaching genetic variation culminating in the extinction of species, but habitat loss is the primary source of the disappearance of wildlife species in our modern setting (TILMAN *et al.*, 9 1994). Understanding the particularities of how different types of habitat destruction may affect the myriad of species populations under its influence is a pressing matter for landscape ecology. The spatial configuration of how patches of habitat remain on the landscape as habitat is removed may also affect the populations in ways beyond the effects of the amount of habitat loss (FAHRIG, 11 2003). Real world habitat fragmentation is an aspect of the process of habitat destruction in the sense that it not only spresses habitat loss but also discontinues the habitat (i.g. breaks the amount of remaining habitat across different patches) and potentially enhances the isolation between these patches (REFERENCE)(KUHN, 7 2014; PRUGH *et al.*, 12 2008). Habitat loss and habitat fragmentation can affect the biodiversity of a given area by either (i) diminishing the total suitable area available for individuals or (ii) reducing the overall suitability/quality of the patches generated by the fragmentation process (e.g. edge effects, isolation of patches (FAHRIG, 4 2002). Therefore, how individuals of a given species can cope with these effects ultimately determines the species' persistence in fragmented landscapes. Much has been done to estimate the effects of both habitat loss and fragmentation on populations without acknowledging that populations are often composed of different subsets of individual types (ARAÚJO; BOLNICK; LAYMAN, 2011; BOLNICK *et al.*, 2007). Therefore, a very necessary next step is to explore how changes in the amount and distribution of habitat being removed affect populations with different amounts of initial adaptive interspecific variation. Polymorphic populations may be more prone to persist in events of disturbances (HAIRSTON *et al.*, 2005), but it may depend on the previously available variation within a populational gene pool of the area. Populational trajectories may depend on the capability of the regional gene pool of generating and maintaining individual variants that can survive and reproduce under the new landscape conditions generated by a disturbance event. Yet, even in the instance of viable individuals being selected within a population the sudden reduction in population size may entail mechanisms that bound the population to ultimately suffer local extinction (e.g. allee effect, demography stochastic, and negative edge effects) (COLLINGE; FORMAN, 2009; COURCHAMP; BEREC; GASCOIGNE, 2 2008; LANDE, 1993; RYBICKI; HANSKI, 5

2013). On another account, the fragmentation of continuous habitats is generally perceived as a threat to the persistence of populations as it diminishes the amount of gene flow between the remaining patches (BROWNE; KARUBIAN, 8 2018; YOUNG; BOYLE; BROWN, 10 1996).

Although relatively scarce, there has been some effort to evaluate the effect that trait variance has on the persistence of populations in events of habitat fragmentation empirically (MATESANZ *et al.*, 2017; YE *et al.*, 1 2014). Analyzing systems under the lens of individual variation is a challenging but necessary step for a better understanding of real complex eco-evolutionary dynamics and their possible implications for biology and conservation (BOLNICK *et al.*, 2011). Likewise, understanding aggravations and particularities associated with the ever-growing problem of habitat loss and fragmentation generated by anthropic action have never been more necessary. Examining this through the simulation of "virtual species" allows us to understand the complexity of the system and differentiate between its composing effects in a way that would be difficult to achieve in the field. Therefore, we aim to add to both those growing literature by analyzing how simulated artificial populations created under different initial amounts of initial intraspecific variation fare under varying combinations of both habitat loss and habitat fragmentation. We found that although higher amounts of initial intraspecific variation enhance the persistence of populations after habitat fragmentation, under most landscapes this relationship is not linear or monotonic. We also found that habitat loss is unsurprisingly the most detrimental landscape determinant for the survival of populations and that habitat fragmentation has a substantially weaker effect on population persistence, which can be either positive or negative depending on its intensity.

Methods

Model

We implemented a spatially explicit individual-based model (IBM) to simulate the dynamics of populations with different initial amounts of intraspecific variation in landscapes that undergo processes of both habitat destruction and fragmentation. The model was built upon the already established TWoLife project (http://pilaboratory.github.io/TWoLife) that runs exact simulations of reaction-diffusion stochastic dynamics with the Gillespie Algorithm (GILLEPSIE, 1976). In TWoLife at any moment in time an individual residing in the landscape either (i) dies, (ii) disperses, or (iii) reproduces. To explore our hypothesis, we included in the simulation landscape heterogeneity, individual fitness, as well as their consequences, namely differential mortality, and habitat selection, as detailed below. The current version of the TwoLife code is also publicly available in a version-control repository and fully documented (https://github.com/DeFreitasLR/TWoLife).

Landscape Heterogeneity

The initial condition of our simulations is a population with stable polymorphisms in undisturbed landscapes. To achieve this, we replicated the conditions which theoretically can both produce and maintain such situations (HEDRICK, 1986, 2006), namely a coarse-grained gradient-like landscape, that is, a landscape with patches along a continuum of habitat types where individuals usually spend most of their lives within a single patch of habitat (GILLESPIE, 1973, 1974). In addition, our landscapes have enough heterogeneity (e.g different habitat types) to allow the existence and coexistence of the population variants simultaneously. Therefore, the landscapes of our model are composed of sufficiently large discrete patches of habitat in a grid of cells. Each of those cells is categorized by a habitat type represented by a number that corresponds to a relative value within a continuous hypothetical environmental gradient (HEG) that represents an abstract environmental variable. Individuals have preferred values within the HEG spectrum and actively pursue them via habitat selection behavior (MONTGOMERY; ROLOFF, 2013).

Pre-disturbance Landscape

The initial configuration of the landscape (pre-disturbance configuration) is composed of patches with HEG values that vary within a pre-selected range. To achieve this, we adjusted landscapes created by the GradientLand software (CAMBUI *et al.*, 2015) to our pre-disturbance populational requirements. It is important to note that at this stage of the simulation we used GradientLand to build the pre-disturbance environmental gradient of the undisturbed landscape. This is a different use of this software, which was originally created to simulate only habitat loss and fragmentation. GradientLand uses the "midpoint displacement—DPM" algorithm to open disturbed areas in landscapes by creating a tridimensional surface that is then sectioned perpendicularly at different levels to generate island-like fragments. The level (e.g. height) of this section represents the amount of habitat being removed. The cells below this level are assigned as matrix pixels and the grid cells above this level represent the remaining patches of habitat. This landscape simulation has a fractal dimension parameter H that controls the relief of the surface and determines the spatial autocorrelation of the disturbed patches. Thus, H acts as a proxy of fragmentation and allows the simulation of different degrees of spatial autocorrelation of habitat state. The software generates binary outputs of the landscape at intervals between the desired amounts of total landscape coverage. To convert the binary outputs produced by the GradientLand into continuous values of HEG we standardize the three-dimensional surfaces generated by the software between intervals of interest. This process takes advantage of the H parameter of the software to generate landscapes with a spatially explicit environmental continuum that can be fitted to the desired HEG range. That in this instance represents the usable niche width of a population. Thus, to create the pre-disturbance landscapes we first generate square landscapes, whose sides are equal to a hundred pixels, and are spatially autocorrelated by a fractal dimension parameter of H =

0.6. We then standardize the surfaces constructed under this software between the upper and lower bounds of the pre-disturbance HEG interval. By using the standardized height of the generated surface as HEG values, we are left with a gradient-like landscape that reflects a natural landscape with a moderate degree of environmental distance-decay and contains only HEG pixel values that will be usable by at least a member of the original population.

Habitat Destruction and Fragmentation:

In our model, habitat destruction is represented by the reduction of habitat quality of patches of grid cells. This is represented by reducing the cell's HEG value and is achieved by subtracting the environmental values of each pixel value in the pre-disturbance landscape matrix from a value for each pixel taken from a habitat destruction matrix. Therefore, we defined a "habitat degradation surface" independently of the surface that defined the distribution of HEG in the pristine landscapes (described in the previous section). Although the initial condition of HEG should span over a wide range of values, events of habitat disturbance can produce patches of habitat with extreme values beyond the original HEG gradient, and therefore, are outside the tolerance range of any individual in the population. Similar to our method for generating the pre-disturbance landscapes, we used the GradientLand software to create independent landscape surfaces with the desired amounts of habitat loss and fractal dimension to be reduced from the pre-disturbance landscapes. We implemented habitat destruction and fractal dimension as a cross-factor phenomenon with each varying across three degrees of intensity (that is, all combinations of loss and H values of 0.1, 0.5, and 0.9).

To generate each post-disturbance landscape we first use GradientLand to independently generate three square landscapes with the same dimensions as the pre-disturbed landscapes, whose pixels are all deteriorated to some degree and are spatially autocorrelated by each of our fractal dimensions "H" of interest, acting as a proxy for the spatial autocorrelation of habitat degradation (that is, habitat fragmentation degree). We then standardize the lower and upper bounds of those landscape surfaces around 0 and 1 and subsequently sectioned them under the three habitat loss amount classes. This resulted in nine habitat destruction matrices that are each subtracted from their pre-disturbance landscapes and configures in a simulation block (Figure 1). Therefore, each simulation block consists of nine habitat matrices that were obtained from different habitat destruction treatments that were applied to the same pristine landscape.

Individual Fitness

We simulated the relative fitness of individuals in the landscape as Gaussian distributions that represent how well individuals fare within a cell of a given HEG value. This distribution can be interpreted as the fitness scores of each individual under each of the HEG values. The individual's fitness distribution in function of HEG is therefore composed of (i) an individual mean (IM), and (ii) a standard deviation (SD). The IM represents the optimum value of HEG for that individual (e.g. the habitat type in which it has the lowest mortality rates) and the SD expresses how generalist that individual is (e.g. the rate at which the change in HEG corresponds to a decrease in that individual's fitness). As each individual within a population possess an individual fitness curve it also perceives the landscape in a singular manner (Figure 2)

Obtaining Individual fitness components

To decompose the components of individual fitness we use an approach similar to Bolnick's model of partitioning a population's total niche width into within-individual and between-individual niche width variance (BOLNICK *et al.*, 6 2010). Likewise, the population's total fitness variance is composed of both within and between individual components, such that TNW = BIC + WIC. The total niche width (TNW) determines the fraction of the HEG values under which the collective of individuals of the population is capable of surviving, consequently, it also defines the pre-disturbance HEG range (Figure 3). The between-individual component (BIC) portrays the maximum difference between individual means or how generalist the population is as a whole. The within-individual component (WIC) represents how generalist a single individual in our simulation is. Thus, each individual's IM is drawn from the BIC interval and each individual's SD is determined as half the WIC and is the same for each individual in the population. By fixating a given WIC while altering the BIC (and consequently TNW) we determine the specific role that different amounts of intraspecific variation have in the population dynamics of our model.

The Algorithm - Population dynamics

We used the Gillespie algorithm, which is the exact algorithmic model to simulate realizations of stochastic dynamics in continuous time (GILLESPIE, 1977). In our case, we applied this algorithm to allow that in our simulations, at any moment, any individual can either (i) die, (ii) disperse, or (iii) asexually reproduce. The probabilities associated with each of those events are parameters of the simulation. The time at a given event is carried out by an individual is drawn from an exponential distribution of waiting times for each event. The individual fitness components are used for determining the probability of one of those events happening to an individual in response to the HEG value of the cell that the individual is currently on (Figure

4). The mortality rate of an individual is based on the result of the probability density function where x is the HEG value of the cell the individual is currently on, μ is that individual's IM, and σ is its SD (Equation 1).

```
Equation 1: Mortality rate = DR · MM(1 − N(x,σ² )/N(μ,σ²))
```

Here DR is the basal death rate of individuals, MM is the number of times the mortality is higher on "matrix patches" (pixels with HEG values outside of the tolerance range of the individual), $N(x, σ²)$ and $N(μ, σ²)$ are probability density functions that determine the fitness scores of that individual at its current residing pixel and best possible HEG value, respectively.

Both the probability of dispersal and how an individual acts in the face of such an event (e.g. movement length and angle) are also influenced by the mortality probability density function, as to reflect the reluctance or willingness of individuals to leave an area based on how well an individual would perform on it. This translates to a process of habitat selection by our individuals. To achieve this, when an event of dispersion takes place, an individual samples P points (here set to 10) within its dispersal kernel and drafts between them according to weights in respect of how well it would fare on them. This sorting is done using a softmax function that normalizes the sampled points into a probability density function that attributes odds inversely to the mortality rate that the individual would have on the sampled points (GAO; PAVEL, 2017).

The birth rates of the individuals are not directly affected by the HEG value of their current cell, but are instead locally density-dependent, by decreasing linearly with the number of neighbors within a radius. In the event of reproduction, the offspring inherits its parent's IM and SD and spawns at the same coordinates. Whenever an action is performed time is added to the world clock. The simulation algorithm repeats the steps of drafting individuals and determining their actions until either the world clock reaches an inputted limit or until there are no remaining individuals in the simulation.

Simulation Parameters

We used the Latin hypercube sampling (LHS) to sample nine of our parameters directly, and another two were analytically solved using them. Our LHS implementation, found on the pse R Package (https://CRAN.R-project.org/package=pse) is capable of estimating the importance of several parameter values by sampling from within their parameter space a finite amount of non-redundant parameter combinations, therefore, diminishing the number of models runs. This is achieved as the technique partitions a predefined parameter space (defined as either a range or a distribution) into equiprobable intervals, promoting a stratified sampling between combinations of intervals. So that each interval within a parameter is

sampled only once, which reduces the redundancy of both proximate values within a parameter and the repetitiveness of combinations between parameters. We uniformly sampled a total of 30 hypercube combinations of the following parameters.

- Maximum birth rates (BR): the birth rate of individuals in their best possible conditions (that is, under its optimum HEG value)
- Basal death rates (DR): the death rate of individuals in their best possible conditions
- Density dependence radius (r): the radius of a circular area centered in each individual used to compute how many individuals influence density-dependent events for an individual performing an action
- Landscape carrying capacity (K): Constant used for setting the maximum populational size within R
- Dispersal lengths (DL): maximum distance traveled during dispersal events
- Movement rates (MR): the rate at which dispersal events happen complementary to both death and birth events
- Matrix mortality (MM): the number of times the mortality rate is higher outside of an individual's tolerance range
- Total niche width (TNW): How generalist a population is a whole
- Between individual components (BIC): The maximum distance between trait optimums of individuals of the same population
- Within individual component (WIC): The percentage of the TNW that constitutes the niche of an individual

To achieve biologically meaningful parameter values we opted for basing the sampling ranges of four of our parameters on compilations of real-world avian databases. Maximum birth rates (BR), Basal death rates (DR), Landscape carrying capacity (K), and dispersal lengths (DL) ranges were obtained from probability density functions obtained by fitting compilations of empirical avian data distributions (Table 3, similarly to Chapter 4, (MANDAI, 2016). Maximum birth rates, the birth rate of individuals under the best possible conditions (e.g. having no other individuals within its density dependence radius), were estimated based on the compilation of the approximate number of eggs produced per year by individuals of species sampled in six Atlantic forest landscapes under both continuous and fragmented conditions (BANKS-LEITE *et al.*, 2011). Basal death rates, the mortality rate of individuals residing on their preferred habitat patches (e.g. residing on a pixel with a HEG value equal to its trait mean), were computed as the inverse of the longevity rates of the individuals of the same compilation of studies. Carrying capacities, used for computing the density dependence inclination parameters, were based on population densities of 25 bird species from Panama and were re-scaled for our study area (BRAWN; KARR; NICHOLS, 1995). The dispersal length distances and maximum distance traveled during dispersal events, of our individuals are based on the compilation of neonatal dispersal events of 45 bird species from all across the globe (SUTHERLAND *et al.*, 2000). Probability distributions were adjusted for each of the four traits described (Chapter 4, (MANDAI, 2016). For each of those parameters, we stipulated intervals within their 0,05 and 0,95 lognormal distribution quantiles to be sampled, to contemplate a wide range of interesting scenarios.

The remaining parameters, movement rates (MR), density dependence radius (R), matrix mortality, TNW, and WIC were either chosen to comprehensively represent their biological counterparts or were computed as a consequence of the empirically defined parameters. For the sake of generality, we opted for exploring varying movement rates (MR), the rate at which dispersal events happen complementary to both death and birth events, between a more conservative scenario (one) and ten average dispersal events in an individual's lifetime. We set the density dependence radius (R), the radius used to define the number of individuals who influence density-dependent events for an individual acting, ranging from zero to the length of a landscaped side. This is sure to contemplate both extremes of real density-dependent relationships and their in-between. Matrix mortality (MM), the number of times the mortality rate of individuals outside of their tolerance interval is higher than their BD, ranges between one and five. Generational time lengths, the amount of simulational "time" required for the passing of a generation, was computed as a function of both BR and DR. Finally, our population variation component (TNW) and our within individual components (WIC) are both sampled between 0,05% and 0,95%. WIC in this instance is measured as a percentage of TNW and both are subsequently used for computing the BIC.

Initial Conditions

Our starting conditions are simulated populations with stable polymorphisms in landscapes preceding disturbance events. We attained such initial conditions by running simulations in undisturbed landscapes until a near-equilibrium state is reached. We define this equilibrium as a point in time at which the unfit individual types have been selected out of the population, and therefore, each remaining individual has the same fitness. The undisturbed landscapes consisted of a pre-disturbance landscape configuration and an initial oversaturation of randomly placed individuals. The initial landscape oversaturation leads to a selection process resulting in the logistic decay of the population size towards the landscape carrying capacity. We compare operational variables' for individuals' fitness at different points in time until we find the earliest amount of simulation runtime required for it to stabilize. This can be interpreted as an indication that no substantial trait selection affects the individuals within the time interval. Therefore, we can consider the population at equilibrium.

This is achieved by comparing the reproductive successes of the remaining surviving lineages up to a given time to their success after an arbitrarily large amount of time. We tested a total of 30 reference times between 1 and 180 generations. Each equilibrium interval test then consists of simulating reaching the desired generational time being tested, storing the current state of the population (e.g. individual coordinates and fitness components), then using it to run 20 nested replicate simulations that continue these "initial" conditions until 1000 generations have passed. Through the use of an output analysis algorithm, we obtain a table containing each individual that lived within the time interval of interest and how many offspring they

generated. This way we can evaluate, for each time interval of each LHS parameter combination, the reproductive success of the remaining trait classes between the reference time and the end of the simulation.

If the reproductive success data of a reference time produces a null effect GLM that has at least the same explanatory capacity as a GLM that takes into account the trait differences between individuals, we consider that the population is no longer under relevant selective pressures and treat it as in equilibrium. As, in this instance, the number of living individuals of a given type can be perceived as the major driver of what offspring is being generated, instead of being defined by the trait values of their parent individuals. To do so, we use the reproduction success data tables as response variables for two sets of competing GLM models adjusted for Poisson distributions (NELDER; WEDDERBURN, 5 1972). The first set of models uses the trait differences between individuals as explanatory variables. The second set treats each individual as being of the same trait class, a null effect model. While comparing the Akaike Information Criterion (AIC) produced under both competing models if we find that their difference (DeltaAIC = Trait effect model - Null effect Model) is of a least "-2" we conclude that the reproductive success of the individuals that were alive within the period can be explained without the need to attest for their trait classes (JOHNSON; OMLAND, 2 2004). Therefore, we obtained the Delta AICs of each time interval for each LHS parameter combination to determine the amount of time required for our populations to reach equilibrium. We ran the previously mentioned procedure for a total of 10 replicates and took averages of the minimum amounts of time necessary for obtaining Delta AIC values higher or equal to "-2" for a given LHS parameter combination and used them as our cut-off times.

Block Runtimes and Reference Model:

We then took each simulation that reaches an equilibrium polymorphic population (henceforth "equilibrium") and use it to construct a simulation block containing all disturbance classes. For each block, we take the surviving population and subject its initial pre-disturbance landscape to the nine classes of the combining levels of habitat loss and habitat fractality. Each of the nested simulations within a block is then continued for an arbitrarily large amount of time (e.g. 1000 generations), or until there are no remaining individuals left in the simulation. This way the time of the last performed action is either the time of the populational extinction event or a censored observation, whether it happened before or after the maximum simulation runtime. The persistence times, time of the last performed action, and status of our populations as well as the parameters used for their generation are stored for statistical analysis.

Each simulation had a reference counterpart in which each individual's fitness curve is the average of all individual's fitness curves initially contained within its pair main simulation, meaning that each individual in that population has the same degree of generalism as the population as a whole. This null scenario

discriminates between population and individual generalism. We ran 100 simulation modules for each LHS parameter combination, and therefore we ended up with 27000 simulations plus the same amount of reference model runs.

Statistical Analysis:

As a first graphical exploration, we used a Kaplan–Meier's survival analysis (CRAWLEY, 2007; HOSMER; LEMESHOW; MAY, 2008). to estimate the persistence time of populations in the function of fragmentation loss and specialization The simulations were grouped according to the parameters used for constructing each given simulation (e.g. TNW level, WIC level, Fractal dimension, and habitat degradation Ranks) to express the different "treatments" populations were subjected to. The values of WIC were expressed as proportions of TNW, for easier interpretation and to make all of our predictor variables range between 0 and 1. The simulation outputs consist of the resulting persistence time of each simulation (e.g. time of the last performed action in generations and the populational death status) and represent the degree of death risk associated with the treatments populations were subjected to. We feed both simulation inputs and outputs to survival analysis as explanatory and response variables, respectively, to create persistence curves. This exploratory analysis provided survival curves for populations grouped by different combinations of the predictor variables.

To formally test the effects of the explanatory variables we also used Cox proportional Hazard models (CPH), a semiparametric generalized linear model of the survival analysis family that allows us to estimate the effects of explanatory variables on hazard rates (THERNEAU; GRAMBSCH, 2000). Hazard rates here represent how likely a given population is to become extinct given the treatments (e.g. landscape condition and individual variation) it was subject to. In this model, the logarithm of the resulting hazard rate of a population at any given time follows a linear additive model and is the result of the sum of additive effects of each of the parameters used in its implementation. We tested for all second-order interactions among our explanatory variables, including the parabolic behavior of both populational variation components (TNW and WIC). We then fitted the selected model formulation to a Mixed effect CPH model to control the random effect of our modules, since each module shares the same initial conditions (THERNEAU, 2015). Through information-based model selection, we determined the version of the CPH model which was best supported by our data (JOHNSON; OMLAND, 2 2004). Finally, used the log-hazard ratios predicted by the selected models to describe the joint of the habitat loss, fragmentation, TNW, and WIC on persistence times of the simulated populations.

Results

Persistence Curves:

Here we represent the proportion of populations that persisted through time as survival curves (Figure 5a). These curves represent the probability associated with the extinction time of the population subjected to a given treatment. Across all simulations, there is a very steep initial extinction of populations, with about 35% of all populations becoming extinct within the first 10 generations. We broke down our data into groups of interest for further graphical analysis. Separating the data by the degree of habitat loss shows distinct groups of extinction curves (Figure 6a). The degree of loss is inversely related to the persistence times of the populations subjected to them. For instance, in simulated landscapes with 10% of habitat loss, on average more than 60% of the populations persisted up to 400 generations, while about 46% of the populations persisted under 90% of habitat loss, meaning a relative risk of 1.76 diference between the two groups. In contrast, separating our data between degrees of fractal dimension of landscape degradation creates much less clear groups (Figure 6b). The survival curves for low and intermediate amounts of habitat fragmentation are practically the same up until 300 generations have passed and the one for strong fragmentation is only slightly lower than the other two. Breaking the data between the nine combinations of both loss and fractal dimension levels delineates the interactions between the two parameters (Figure 6c). We can see nine survival curves that fall into the three general shapes of their respective habitat loss classes group and increasing the habitat fragmentation value with a group dislocates each curve within a group. Under moderate and high amounts of habitat loss, increasing fragmentation decreases the height of the survival curves. However, under low amounts of loss increasing fragmentation, above its minimum, value lifts the curves values. Therefore, under very low amounts of habitat loss, moderate to high fractality enhances population persistence.

As a next graphical examination, we grouped our data by classes of small, intermediate, and large intervals of each of their individual specialization parameters, setting the threshold cuts at 0.3 and 0.6 respectively. For the total niche width (TNW) parameter values we obtain a survival curve for large values with much higher survival values than the remaining two (Figure 7a). The curve for the intermediate amounts of TNW initially has smaller values than those attributed to the small amounts of TNW up until a hundred generations. Past that, the two curves become very similar for about 30 generations then return to the previous pattern. Therefore, there are two initially distinct groups, with larger TNW values producing populations with much lower hazard rates than the others, but as we progress in time populations with smaller TNW values persist longer than those of intermediate values. The relationship between persistence and WIC is not monotonous and resembles a concave up quadratic function. Now for the within-individual component (WIC) parameters, we obtain three distinct curves that never overlap within the analyzed interval (Figure 7b). The curve for intermediate WIC has the highest values, followed closely by the one for large amounts of WIC, and the one for small amounts much more distanced from the rest. Therefore, the intermediate values of

WIC produce populations with higher survivability, followed by those of large WIC values, and finally by the ones with small WIC values. This suggests that the relationship between the persistence of populations and WIC, once again, is not monotonous and resembles a now concave down quadratic.

Fitted Model Parameters:

Our fitted mixed-effects Cox proportional hazard model (CPH) identified that the model that best supports our data includes TNW, TNW^2, BIC, BIC^2, loss, and fractal dimension levels, as well as most of their second-order interactions (Equation 2). As there is no sense in separating the standard individual specialization terms from their quadratic ones, they are presented together (Table 1). Thus, for each of those parameters and interactions, we obtain the response variable as the predicted log-hazard rate coefficient that when exponentiated measures how likely a population with a given parameter value is to become extinguished at any given time, in comparison with its standard rate of zero. Those response variables are estimated in the function of the persistence times of lineage populations, censored or otherwise. The expected values are then obtained by a linear predictor function, whose variables are the sum of the effects of the predictor parameters and their interactions. In the next section, we explore the cumulative hazard scores resulting from the myriad of combinations each of those hazard ratios can express.

Equation 2:

$$Linear\ Predictor \sim TNW\ +\ WIC\ +\ Frag\ +\ Loss\ +\ TNW^2\ +\ WIC^2\ +\ Frag{:}Loss\ +\ \dots$$
$$TNW{:}Frag\ +\ Loss{:}WIC^2\ +\ WIC{:}Loss\ +\ TNW{:}WIC\ +\ TNW^2{:}WIC^2\ +\ \dots$$
$$TNW{:}Loss\ +\ Loss{:}TNW^2\ +\ Frag{:}TNW^2\ +\ Random\ effects$$

Here ":" represents the interactions between two parameters

Heat Map Hazards:

We constructed heat maps that show how tampering with the parameter space of our four variables influences the cumulative hazard rates estimated for each simulated population (BOJKO, 2009). Cumulative hazard rates are the sum of the hazard rates associated with the values of each of the four simulation parameters. Therefore, each pixel in a heatmap represents the cumulative hazard score computed under varying degrees of combinations of the variables in the X and Y axes (TNW and BIC in figure 8, fractal dimension, and habitat loss in figure 9). Thus, figures 8 to 9 are sets of nine heatmaps each, spotlighting the populational or landscape parameters. Darker pixel colors represent higher cumulative hazard rates, that is,

lower persistence times or higher extinction hazards. The color scale is the same for graphs of the same panel. Each individual graph in a panel consists of the full variation of two quantitative parameters along the x/y-axis and each row and column has a fixed value level for the remaining parameters. The first panel is made by fixing habitat loss and fractal dimension to the same values used when running simulations (e.g. 0.1, 0.5, and 0.9). Thus these graphs allow evaluation of how the interaction between our two populational variation parameters affects extinction risks (hazard rates) across nine different classes of landscape degradation (Figure 8). The second panel is achieved by fixing TNW and BIC values instead, to evaluate how the interaction between increasingly larger degrees of both types of landscape deterioration affects the hazard scores of populations subjected to them (Figure 9). For consistency, we also decided to fix the populational diversity parameters in this instance at their extremes and intermediate values (0.1, 0.5, and 0.9).

The first set of heat maps (Figure 8) shows that the predicted cumulative hazards are more sensitive to the TNW variation than WIC. Most of the variation contained within every single graph is represented by horizontal layers along the y-axis, and therefore, can be attributed to the TNW parameter. The curvature and concavity of these horizontal layers are modulated, however, by the amount of habitat loss and fragmentation associated with them. Increasing the habitat loss parameter (going through each column in the figure) shows that higher levels of loss produce parameter space combinations with higher cumulative hazard values overall, with each column of graphs producing pixels with increasingly darker color intervals. There are increasingly lighter pixels as one goes from the bottom to the top on the heatmaps fixed for low amounts of habitat loss. For the remaining classes of loss, this pattern is slightly altered as the bottommost pixels are lighter than the lower intermediate ones. Now for increasing amounts of habitat fragmentation, we can see an expansion of the darker areas on the heatmaps. These shape patterns overall translate into the cumulative hazard rates peeking under small to intermediate TNW rates and steadily decreasing as we move from that range. Nonetheless, we can see that the darker areas in each heatmap that have either habitat loss or fragmentation set to their most severe form are restricted to elliptical shapes located mid-section. In the remaining set of heatmaps, the darkest areas are close to their left margin (that is, under small values ofWIC). Consequently, there is an influence of the WIC parameter on extinction hazards as some of the central to lower horizontal layers in these heatmaps have vertical delimitations, forming elliptical shapes. Therefore, the WIC parameter seems to be particularly important to decrease, or dislocate, the peak hazard rates produced under critical TNW values of populations suffering from sufficient habitat disturbances. Since moderate amounts of it reduce hazard ratios for those populations.

Now for the landscape parameters, the heatmaps show that across all graphs populations are more sensitive to habitat loss than habitat fractality (figure 9). Most of the total variation within heatmaps is represented by vertical layers with increasingly higher hazard rates. The darkest regions of each heatmap can always be found in the rightmost areas of the x-axis, indicating a monotonic effect of habitat loss on extinction risk. However, the two parameters strongly interact as some values of fractal dimension bend those

vertical layers towards either side. If it were a mere additive effect we would be left with diagonal, yet straight lines. How the fractal dimension parameter seems to influence the hazard scores is mostly defined by the very own habitat loss parameter. For high amounts of habitat loss, increasing the fractal parameter (e.g. top right corners) results in overwhelmingly darker pixels. While increasing fractality in association with lower habitat loss (e.g. top left corners) has the potential to lighten the pixels resulting from the combination. Ultimately, the fractal dimension potentialized the expected effect of the degree of habitat fragmentation associated with it. Going through each row, increasing the fixed amount of TNW, lightens the color of the heatmaps. It also modifies the shape of the interaction between loss and fractality. For the first row, the beneficial effect of fractality is mostly absent but it can be seen in both the second and third ones. Going through each three-panel column in figure 9, we can see that increasing the fixed amount of WIC modifies the range of the pixel values being fit within a single heatmap. This results in the first column fitting the least amount of pixel variation and the middle one the most.

Discussion

Using an individual-based simulation of stochastic reaction-diffusion population dynamics in heterogeneous landscapes we have addressed the relative importance of prior individual specialization components and landscape characteristics on the persistence of the populations subjected to them. We have partitioned the components of individual specialization under TNW, populational niche width, and WIC, individual niche width, and we found that populational generalism (TNW) is more critical than individual niche variation (WIC) for the persistence of populations facing varying combinations of habitat loss and habitat fragmentation. Populational generalism tends to increase the persistence of populations, but this relationship is not monotonic, as in some cases the population persistence peaked at intermediate values of TNW. In addition, despite having a comparatively smaller effect, individual specialization influences populations' persistence under some circumstances. Notably, the importance of the WIC component on persistence increases as both landscape deterioration components are enhanced. Our simulated landscapes ventured beyond the standard comfortable binary notion of habitat and matrix patches, commonly used in landscape ecology, breaking down landscape cells in a continuum of habitat classes and examining how different degrees of habitat loss and habitat fragmentation affect them. Habitat loss is a very straightforward concept as it merely measures the proportion of the initial landscape that has been degraded, and particularly in this instance, the reduction in the overall quality of a habitat. Habitat fragmentation, however, is a more theoretically challenging concept, for which there is no unique or consensual form of measurement. We thus used the spatial fractality of the habitat loss as our proxy of fragmentation, to express the spatial autocorrelation of degraded areas (MILNE, 1992). In doing so, we have found support for the growing idea that, while habitat loss is the most important landscape driver of populational extinction, habitat fragmentation can either potentialize or mitigate its effects depending on its intensity and degree of ecological specialization of the affected populations. We further discuss each of these findings in order below.

Firstly we compare the relative effects of both individual variation components used to generate our populations in their pristine landscapes, that is, the initial imputed values of both TNW and BIC. Unsurprisingly, initial populational generalism (TNW) was the most important factor contributing to the persistence of our simulated populations. This is a somewhat straightforward consequence of wider populational niches resulting in a set of individuals that are as a whole better able to utilize a greater range of habitats, expressed as different HEG values of the landscape pixels. As a consequence, higher values of initial TNW enhance the probability of populations containing individuals that are capable of utilizing the habitat patches remaining from both the processes of habitat loss and habitat fragmentation effectively mitigating their effect. This happens as habitat loss events decrease the environmental value of pixels but their subsequent resulting HEG value may still be within the TNW range of the initial population, and the probability of this happening increases as TNW increases. Acting similarly to the portfolio effect, the high initial range variance of individual types within a population may diversify the resource usage of habitats in ways that both make its population more resilient to local extinction and enhance productivity (ABBOTT; DOAK; PETERSON, 4 2017). Populational generalism is, therefore, responsible for preventing the decrease of the carrying capacity of a population in the post-disturbance landscape. That is, higher initial amounts of TNW result in populations that are larger overall, while in equilibrium in the post-disturbance landscape, and thus have lower extinction risks due to stochasticity. However, we found out that this relationship, at least in our model, is not always monotonic, because, under some combinations of the other parameters, lower to intermediate values of TNW lead to extinction risk rates that are higher than those obtained at lower TNW values. A possible contributor to an explanation may rely on some TNW values effectively goading individuals into falling into some form of an ecological trap in our initial conditions, which would result in populations that lack the potential diversity to cope with the conditions generated by our landscape disturbances (SCHLAEPFER; RUNGE; SHERMAN, 10 2002).

An ecological trap is usually attributed to the situation when individuals, while selected by some form of environmental change, settle for habitats that do not maximize their long-term fitness (HALE; SWEARER, 2 2016). In our model, there are ultimately two distinct sources of selective pressures affecting our individuals, the pre-disturbance landscape and the post-disturbance landscape. As a consequence, the filtering of lineages in the first stage may reduce the variability needed for populations to thrive under the second one. The initial landscape acts as a source of strong purifying selection, and how the pre-disturbance landscape filters the initially inputted individuals often results in few lineages spaced out through the BIC range in a way that very much resembles Macarthur's maximum niche similarity hypothesis (HALE; SWEARER, 2 2016; MACARTHUR; LEVINS, 9 1967; SCHEFFER; VAN NES, 4 2006; SZABÓ *et al.*, 3 2006). Our simulation explores short-term evolution (e.g. response to rapid environmental variation) so our individuals cannot mutate, differently from similar studies, and therefore populations evolve only because the genetic variability is directly lost throughout the simulations (HAIRSTON *et al.*, 2005). Therefore, to achieve our initial conditions of stable polymorphism at levels defined by the values of TNW and WIC set in each simulation, only a few individual lineages are selected and proceed in the simulation. In these cases, TNW decreases (as does BIC), which of course means that once lineages are lost in the simulation the

variation of the population as a whole is irreparably diminished. Meaning, that oftentimes the initial conditions TNW is in general lower than the initially input TNW value. On the other hand, like WIC, the degree of individual generalism is a fixed trait that is shared by all individuals within a population, and therefore is independent of the loss of individuals, remaining the same as simulation proceeds and generations succeed. Therefore, there is a delicate balance between trait mismatch and demographic effects that dictates the number of lineages that remain after the landscape achieves equilibrium. As this initial poach of diversity is completely unrelated to the new selection pressures that will arise from our subsequent landscape degradation, the variational loss in the first stage may hinder a population's ability to thrive in the second stage. And this relationship seems to be particularly relevant for some combinations of WIC and TNW values. So, a possible mechanism is that for a few intermediate values of TNW, the pre-disturbance selection process maximizes the fitness of the individuals in the initial landscape, thus excluding competing lineages and, as a consequence, reducing the individual variability that could allow populations to thrive in the post-disturbance landscape. Therefore it may be that some pre-disturbance conditions ensue in populations with relatively high TNW values but without enough individual variability to contain individuals capable of thriving under the now disturbed landscape. As a consequence, there is a lower minimum threshold TNW value that makes it valuable for populations to be generalists, as there is a required amount of investment in the trait variation range that makes the tradeoff between different resource utilization and better resource exploitation that generates positive net fitness scores for populations. Below this threshold, and especially under minimum TNW values, the emerging conditions approximate the simulation to a binary matrix landscape condition, making it so that any event of degradation makes a pixel unsuitable for individuals to persist.

The idea that trait variation among individuals does not necessarily translate into higher persistence rates is counterintuitive at first but has a few real-world corner cases such as the enhancement of the genetic load of a population (LANDE; SHANNON, 1996). For instance, a population that has functional trait variation may be ill-suited to the current environment habitats. Ultimately, having a low trait mismatch between individuals and their current environments is what enhances the survival of individuals, and therefore, the persistence of populations (GIBERT, 2016; GIBERT; DELONG, 10 2017, 2015). That, of course, means the persistence of populations is only enhanced by the variability of resource usage of its composing individual if the landscape is accordingly heterogeneous, as phenotypes whose optimum lay beyond existing patches are doomed to become extinct (FAGAN; HOLMES, 1 2006). However, as the pre-disturbance landscape of our simulations is constructed in a way to contain at least some pixels whose HEG values are suitable for each phenotype in the population, at least for the initial landscape there should be few to no trait mismatch after the stable polymorphic equilibrium has been reached in the pre-disturbance stage. It is still unclear what is the precise causal mechanism in which lower to intermediate values of TNW generate populations that are more affected by habitat degradation-induced mortality and thus have lower persistence rates than populations with lower variation, and thus, further investigation is needed for a more robust conclusion. A detailed dive into simulations with a thoughtful examination of the demographic rates of each phenotype, lineage loss through time, and trait mismatch mappings are important future steps.

On the other hand, variation at the individual level played a substantially less critical role in population persistence, with individual generalism seemingly being the best strategy across the overwhelming majority of combinations of habitat fragmentation and loss. Therefore, our results indicate that it is overall better for each individual to be able to utilize a wider range of landscape HEG values than having higher benefits from a few particular ones on most occasions. However, there are exceptions as being a generalist implies having a lower maximum fitness than specialist individuals, as enhancing standard deviations results in lowering the frequency of the average value on normal distributions. Under harsher landscape conditions (high degrees of loss and fragmentation), higher levels of individual specialization (that is, the highest values of WIC) result in extinction rates that are just as low as individual generalism (lowest values of WIC) does for the same conditions. The mechanism of the enhanced survival of specialist-composed populations, but only under higher degrees of habitat loss probably lies in the fact that, as there are fewer usable pixels in the landscape, and as a consequence a lesser range of usable HEG values, it becomes substantially more important to have higher fitness values, and consequently, the lowest possible mortality rates. For the instance of high fragmentation values, the discontinuities of the initial pristine landscape auto-correlated gradient values results in there being less advantage for individuals to have a wider range of proximate values of resource usage (with exception of the very extreme cases). As, the decrease in spatial autocorrelation of the habitat being removed, and consequently of the environmental values of the pixels in the landscape would result in a much more homogeneous landscape. At the extreme of habitat loss and fragmentation events, we are left with effectively small island-like areas of usable patches scattered throughout the landscape. As there is an initial gradient associated with the pre-disturbance landscape each of the resulting fragments is bound to be composed of very homogeneous HEG values. This in turn would favor individuals on the sole basis of having a lower mortality rate (e.g. higher fitness) on particularly preferred pixels instead of a variety of HEG values at its disposal.

Now we compare the relative effects that both landscape degradation processes (habitat loss and fragmentation) produce on the individuals of our simulated landscapes. The environmental values of each cell pixel are influenced by the simulated degrees of habitat loss, (e.g. the reduction of the pixel value of HEG, which is equivalent to habitat degradation in our simulation) and habitat fragmentation (e.g. the spatial autocorrelation of the degradation process). The landscape deterioration variable that mostly diminished the persistence of our populations was, unsurprisingly, habitat loss. This is a consequence of the availability of suitable patches on the landscape being the most important driver of individual survival, and thus of the carrying capacity of the landscape. Therefore, as we reduce the quality of patches of land beyond the conditions its original residents were adapted to, most of its original inhabitants will die (SOBERON; PETERSON, 1 2005). The reduction of habitat quality has theoretical consequences at both the population and individual levels. Each of the individual types in a population experiences habitat loss differently but the averaged effect of habitat loss for the whole population can be reasonably estimated by the remaining amount of usable habitat, particularly so for higher degrees of loss that push all patches out of populational niche width. Therefore, at the population level, the effect of habitat loss reduces the amount of remaining suitable habitat in the post-disturbance landscape, thus decreasing the overall carrying capacity of the

affected population, and as a consequence, enhancing the probability of the population being extinguished (MORRIS; DOAK,). This average effect would approach the outcome of our model to the classic binary matrix-habitat model, especially for higher intensities of habitat loss. This would happen as any sufficiently degraded areas would have the HEG values of their composing cells ranging outside the tolerance range of any of the individuals in the population. Effectively dichotomizing the landscape into pristine habitat (e.g. habitat) and affected patches (e.g. matrix). However, due to the nature of our algorithm, the average effect is not always representative, either due to the intrinsic stochasticity associated with the survival of the individuals or the fact that as TNW increases the probability of individuals surviving extreme scenarios also increases. As a consequence, there is an individual effect to the habitat loss process and for moderate to low degrees of habitat loss understanding how individuals cope with the changing environment becomes required to understand the whole process.

As aforementioned, at any given time individuals will either (i) die, (ii) reproduce, or (iii) perform a migratory event. Assuming an event of habitat loss that encompasses the location of a given individual, will heavily increase the probability of death while decreasing the probability of birth events (as both, in conjunction with migration, are complementary probabilities). Therefore, the individuals "sampled" by a degradation event will most likely die unless i) they are currently present within a pixel that's still within its tolerance range or; ii) if they perform a successful migratory event to a nearby tolerable pixel. The relationship between habitat loss and successful migratory events however is modulated by the degree of fragmentation associated with the loss event. This means, of course, that individuals sampled by strong degradation events will have their survival defined by their ability to find suitable habitat patches before being stochastically eliminated, and this, in turn, is affected by their distance to the nearest suitable habitat patch. Therefore, the spatial configuration of how habitat is removed from the landscape bears very important consequences for each individual's survival (FAHRIG, 11 2017). The effect that habitat fragmentation on itself exerts on a population can be either positive or negative depending on its interaction with the remaining factors . Moreover, there is a minimum amount of habitat loss necessary to bear any ill consequences for populations (SWIFT; HANNON, 2010; VAN DER HOEK; ZUCKERBERG; MANNE, 1 2015). Accordingly, under small amounts of habitat loss most effects that habitat fragmentation would bear become somewhat negligible. Beneath this minimum habitat loss threshold, the effects of habitat fragmentation may even become positive, increasing individual survival, in comparison with other predicted degradation scenarios (FAHRIG *et al.*, 2019). This pattern is likely a consequence of the reduction in pixel habitat quality being so spatially spread out throughout the whole of the landscape that it fails to represent an important threat to any of the affected individuals. As any of the individuals sampled by a loss event are easily able to find suitable pixels to survive in their immediate proximity (as the original landscape is self-correlated). Habitat fragmentation under low habitat loss, therefore, fails to enable a degradation event that locally encompasses most or all suitable patches of a biotype that could be possible under a high spatial self-correlated degradation process (e.g. very low fragmentation).

Habitat loss directly impacts an individual's survival in a very straightforward and negative way while habitat fragmentation homogenizes the landscape conditions (ARAÚJO *et al.*, 2022). Most, if not all, of the detrimental effects of fragmentation, are associated with moderate to high habitat loss amounts and arrive as a consequence of the habitat loss being sufficiently spatially diluted in small patches in a fashion that endangers the population unproportionally to the extent of land being modified (SWIFT; HANNON, 2010). This would happen if the remaining pixels of usable habitat were not able to locally support individuals of a biotype even if its total area allowed for it at landscape capacity (e.g. in a non spatially explicit landscape). Making it so that previously stable areas become unable to sustain the number of individuals one could. Our results support this hypothesis since under the majority of scenarios the increase in spatial fractality over moderate to high habitat loss made populations more prone to extinction. Another possible explanation is that the individuals who find themselves sampled by a degradation event are not reliably able to perform migratory events to tolerable conditions before being stochastically eliminated by the matrix-like conditions of the landscape. The mechanism by which this occurs is likely a consequence of the homogenization of habitat quality in a significantly negative way interfering with the equilibrium achieved by our individuals on the pre-disturbance landscape. The overall homogenization of the landscape has an inherent problem for diverse populations that evolved in a previously heterogeneous landscape. The portfolio effect, the diversification of "investments" the populations do on different individuals, makes it so they become very resilient to either small habitat loss events or strong habitat loss events that are spatially aggregated (ABBOTT; DOAK; PETERSON, 4 2017; MIMURA *et al.*, 2 2017; MORAN; HARTIG; BELL, 1 2016). Populations with bigger niche widths, independent of the degree of individual specialization, are less affected by habitat loss in general. Since individuals have preferred environmental values that range within a spectrum, the HEG values of pixels are still likely to be tolerable to some members of a population under lower amounts of habitat loss. However, if degradation events are sufficiently strong, it will certainly modify the pixel's HEG to a value outside the tolerance of any individual in the population. Therefore, the homogenization of the landscape in a sufficiently negative way completely outweighs the populational advantages of having great individual diversity. And although this is also true for populations suffering from high amounts of habitat loss, the additional effect of sufficiently large habitat fragmentation diminishes the threshold amount of habitat being lost needed for the population's extinction. Ultimately, a possible generalization is that while higher amounts of habitat loss are objectively more hazardous for populations its association with a lower degree of fragmentation may be detrimental to individual types (and analogous species with narrow niche widths), and its association with higher degrees of fragmentation is harmful to the population survival as a whole.

As often is the case for in-silico projects our findings have to be analyzed under the scrutiny of a few limitations. Firstly, we use a mixture of empirically measured and theoretically speculative parameters. This opens the possibility of revisiting a similar study when more empirically challenging estimations of

real-world population traits become available. Second, simulational studies are always limited by how their developers decided to represent reality, in our instance, due to already dealing with challenging eco-evolutionary dynamics under non-binary habitat patches, we opted to simplify the genetic structure of our individuals. Thus, assortative mating, elaborated inheritance mechanisms, and mutation seem to be important contributors to some of the dynamics that explain why some real populations persist under landscape deterioration and others don't and are interesting future steps to be taken from where we left (GODWIN *et al.*, 8 2020). Throughout the history of the ecological sciences, most authors lump together all individuals of a population or species as completely identical. Similarly, most landscape ecologists lump together landscape patches as either habitat patches, in which individuals can fully thrive, or matrix patches, where individuals can all but die, with the notable exception of the use of edge effects (GALLÉ *et al.*, 1 2022; SCHLAEPFER; RUNGE; SHERMAN, 10 2002; STODDARD, 2010). In a desire to elaborate on either of those crutches not comprehensively representing the associated complexity of either case we designed this work to shed some light on this eco-evolutionary dynamics across several landscape types on individual specialization. We found results that supported that populational generalism is the important driver of persistence in a wide range of scenarios while that individual specialization plays a secondary role whose importance is completely mediated by landscape quality. Arising as a consequence of more diverse strategies entailing higher populational fitness, and thus making the population more resilient, under the majority of landscape scenarios while extreme degradation scenarios can favor higher specialization strategies due to the lack of variety within the landscape itself. Even the shortcomings of our findings revealed that the relationship between populational variation and persistence of populations is not as trivial as one might have guessed and brings out the necessity of clarification under a more rigorous lens. We also add to the growing debate of habitat fragmentation not being objectively a bad thing for ecosystems (FLETCHER *et al.*, 2018). Finally, understanding individual variation alters the consequences of anthropic actions is not exclusive to habitat destruction and fragmentation. We hope to inspire other scientists to embrace and explore the complexity of both of its central topics and, consequently, help us disentangle the causal mechanisms that rule the natural world.

References

ABBOTT, R. E.; DOAK, D. F.; PETERSON, M. L. Portfolio effects, climate change, and the persistence of small populations: analyses on the rare plant Saussurea weberi. **Ecology**, v. 98, p. 1071–1081, 4 2017.

ARAÚJO, F. de C.; MENDES, C. N.; SOUZA, C. R. de; MIRANDA, K. F.; MORELLI, M. C. M.; COELHO, P. A.; FIGUEIREDO, M. A. P.; CARVALHO, W. A. C.; CASTRO, G. C. de; FONTES, M. A. L.; SANTOS, R. M. dos. Fragmentation Effects on Beta Diversity of Fragmented and Conserved Landscapes: Insights about Homogenization and Differentiation Processes. **Acta botanica Brasilica**, v. 36, 15 abr. 2022. Disponível em: <https://www.scielo.br/j/abb/a/YDrDh6K3Rm8y77BvD4hbjbz/>. Acesso em: 22 jul. 2022.

ARAÚJO, M. S.; BOLNICK, D. I.; LAYMAN, C. A. The ecological causes of individual specialisation. **Ecology letters**, v. 14, p. 948–958, 2011.

BANKS-LEITE, C.; EWERS, R. M.; KAPOS, V.; MARTENSEN, A. C.; METZGER, J. P. Comparing species and measures of landscape structure as indicators of conservation importance. **The Journal of applied ecology**, v. 48, p. 706–714, 2011.

BOJKO, A. Informative or misleading? Heatmaps deconstructed. **Lecture notes in computer science**, v. 5610 LNCS, p. 30–39, 2009.

BOLNICK, D. I.; AMARASEKARE, P.; ARAÚJO, M. S.; BÜRGER, R.; LEVINE, J. M.; NOVAK, M.; RUDOLF, V. H. W.; SCHREIBER, S. J.; URBAN, M. C.; VASSEUR, D. A. **Why intraspecific trait variation matters in community ecologyTrends in Ecology and Evolution**Howard Hughes Medical Institute, 2011. Disponível em: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC3088364>.

BOLNICK, D. I.; INGRAM, T.; STUTZ, W. E.; SNOWBERG, L. K.; LAU, O. L.; PAULI, J. S. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Em: 6 2010, [...]. The Royal Society, 6 2010. v. 277, p. 1789–1797.

BOLNICK, D. I.; SVANBÄCK, R.; ARAÚJO, M. S.; PERSSON, L. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. **Proceedings of the National Academy of Sciences of the United States of America**, v. 104, p. 10075–10079, 2007.

BOLNICK, D. I.; SVANBÄCK, R.; FORDYCE, J. A.; YANG, L. H.; DAVIS, J. M.; HULSEY, C. D.; FORISTER, M. L. The ecology of individuals: Incidence and implications of individual specialization. **The American naturalist**, v. 161, p. 1–28, 2003.

BRAWN, J. D.; KARR, J. R.; NICHOLS, J. D. Demography of birds in a neotropical forest: Effects of allometry, taxonomy, and ecology. **Ecology**, v. 76, p. 41–51, 1995.

BROWNE, L.; KARUBIAN, J. Habitat loss and fragmentation reduce effective gene flow by disrupting seed dispersal in a neotropical palm. **Molecular ecology**, v. 27, p. 3055–3069, 8 2018.

CAMBUI, E. C. B.; NOGUEIRA DE VASCONCELOS, R.; BOSCOLO, D.; BERNARDO DA ROCHA, P. L.; MIRANDA, J. G. V. GradientLand Software: A landscape change gradient generator. **Ecological informatics**, v. 25, p. 57–62, 2015.

CHESSON, P. **Matters of scale in the dynamics of populations and communities** (R. B. Floyd, A. W. Sheppard, P. J. de Barro). **Frontiers of Population Ecology**CSIRO, 1996.

CHESSON, P. **Making sense of spatial models in ecology** (J. Bascompte, R. Sole). **Modelling Spatiotemporal Dynamics in Ecology**Academic Press, 1998.

CHESSON, P. **Metapopulations** (S. A. Levin). **Encyclopedia of Biodiversity**Academic Press, 2001.

CLAUDINO, E. S.; GOMES, M. A. F.; CAMPOS, P. R. A. Extinction debt and the role of static and dynamical fragmentation on biodiversity. **Ecological Complexity**, v. 21, p. 150–155, 2015.

COLLINGE, S. K.; FORMAN, R. T. T. **Ecology of fragmented landscapes**. [s.l.] Johns Hopkins University Press, 2009.

COLLINS, S.; DE MEAUX, J.; ACQUISTI, C. Adaptive walks toward a moving optimum. **Genetics**, v. 176, p. 1089–1099, 2007.

COURCHAMP, F.; BEREC, L.; GASCOIGNE, J. **Allee Effects in Ecology and Conservation**. [s.l.] Oxford University Press, 2 2008.

CRAWLEY, M. J. **The R Book**. [s.l: s.n.]

FAGAN, W. F.; HOLMES, E. E. Quantifying the extinction vortex. **Ecology letters**, v. 9, p. 51–60, 1 2006.

FAHRIG, L. Effects of Habitat Fragmentation on Biodiversity. **Annual review of ecology, evolution, and systematics**, v. 34, p. 487–515, 11 2003.

FAHRIG, L. Effect of Habitat Fragmentation on the Extinction Threshold: A Synthesis. **Ecological applications: a publication of the Ecological Society of America**, v. 12, p. 346, 4 2002.

FAHRIG, L. Ecological Responses to Habitat Fragmentation per Se. **Annual review of ecology, evolution, and systematics**, v. 48, p. 1–23, 11 2017.

FAHRIG, L.; ARROYO-RODRÍGUEZ, V.; BENNETT, J. R.; BOUCHER-LALONDE, V.; CAZETTA, E.; CURRIE, D. J.; EIGENBROD, F.; FORD, A. T.; HARRISON, S. P.; JAEGER, J. A. G.; KOPER, N.; MARTIN, A. E.; MARTIN, J.-L.; METZGER, J. P.; MORRISON, P.; RHODES, J. R.; SAUNDERS, D. A.; SIMBERLOFF, D.; SMITH, A. C.; TISCHENDORF, L.; VELLEND, M.; WATLING, J. I. Is habitat fragmentation bad for biodiversity? **Biological conservation**, v. 230, p. 179–186, 1 fev. 2019.

FLETCHER, R. J.; DIDHAM, R. K.; BANKS-LEITE, C.; BARLOW, J.; EWERS, R. M.; ROSINDELL, J.; HOLT, R. D.; GONZALEZ, A.; PARDINI, R.; DAMSCHEN, E. I.; MELO, F. P. L.; RIES, L.; PREVEDELLO, J. A.; TSCHARNTKE, T.; LAURANCE, W. F.; LOVEJOY, T.; HADDAD, N. M. Is habitat fragmentation good for biodiversity? **Biological conservation**, v. 226, p. 9–15, 2018.

GALLÉ, R.; TÖLGYESI, C.; TORMA, A.; BÁTORI, Z.; LÖRINCZI, G.; SZILASSI, P.; GALLÉ-SZPISJAK, N.; KAUR, H.; MAKRA, T.; MÓDRA, G.; BATÁRY, P. **A Broader Ecological Context to Habitat Fragmentation: Why Matrix Habitat Is More Important than We Thought on JSTORPerspectives in Ecology and Conservation**Elsevier, 1 2022. Disponível em: <https://www.jstor.org/stable/3236524#metadata_info_tab_contents>.

GAO, B.; PAVEL, L. **On the properties of the softmax function with application in game theory and reinforcement learningarXiv**arXiv, 2017. Disponível em: <http://arxiv.org/abs/1704.00805>.

GIBERT, J. P. The effect of phenotypic variation on metapopulation persistence. **Population Ecology**, v. 58, n. 3, p. 345–355, 1 jul. 2016.

GIBERT, J. P.; DELONG, J. P. Phenotypic variation explains food web structural patterns. **Proceedings of the National Academy of Sciences of the United States of America**, v. 114, p. 11187–11192, 10 2017.

GIBERT, J. P.; DELONG, J. P. Chapter Three - Individual Variation Decreases Interference Competition but Increases Species Persistence. *Em*: PAWAR, S.; WOODWARD, G.; DELL, A. I. **Advances in Ecological Research**. [s.l.] Academic Press, 2015. p. 45–64.

GILLEPSIE, D. T. A General Method for Numerically Simulating the Stochastic Time Evolution of Coupled Chemical Reactions. **Journal of computational physics**, v. 22, p. 403–434, 1976.

GILLESPIE, D. T. **Exact stochastic simulation of coupled chemical reactions**. [s.l.] American Chemical Society, 1977. v. 812340-2361 p.

GILLESPIE, J. Polymorphism in random environments. **Theoretical population biology**, v. 4, p. 193–195, 1973.

GILLESPIE, J. The role of environmental grain in the maintenance of genetic variation. **The American**

naturalist, v. 108, p. 831–836, 1974.

GODWIN, J. L.; LUMLEY, A. J.; MICHALCZYK, Ł.; MARTIN, O. Y.; GAGE, M. J. G. Mating patterns influence vulnerability to the extinction vortex. **Global change biology**, v. 26, p. 4226–4239, 8 2020.

HAIRSTON, N. G.; ELLNER, S. P.; GEBER, M. A.; YOSHIDA, T.; FOX, J. A. Rapid evolution and the convergence of ecological and evolutionary time. **Ecology letters**, v. 8, p. 1114–1127, 2005.

HALE, R.; SWEARER, S. E. Ecological traps: current evidence and future directions. **Proceedings of the Royal Society B: Biological Sciences**, v. 283, 2 2016. Disponível em: <http://dx.doi.org/10.1098/RSPB.2015.2647>.

HAMILTON, I. M. Habitat Selection ☆. **Reference Module in Life Sciences**, 2017. Disponível em: <http://dx.doi.org/10.1016/B978-0-12-809633-8.01151-1>.

HEDRICK, P. W. Genetic Polymorphism in Heterogeneous Environments: A Decade Later. **Annual review of ecology and systematics**, v. 17, p. 535–566, 1986.

HEDRICK, P. W. Genetic Polymorphism in Heterogeneous Environments: The Age of Genomics. **Annual review of ecology, evolution, and systematics**, v. 37, p. 67–93, 2006.

HOSMER, D. W.; LEMESHOW, S.; MAY, S. **Applied survival analysis : regression modeling of time-to-event data**. [s.l.] Wiley-Interscience, 2008.

HYLANDER, K.; EHRLÉN, J. The mechanisms causing extinction debts. **Trends in ecology & evolution**, v. 28, p. 341–346, 2013.

JOHNSON, J. B.; OMLAND, K. S. Model selection in ecology and evolution. **Trends in ecology & evolution**, v. 19, p. 101–108, 2 2004.

KUHN, A. Fragmentation and Isolation. **Encyclopedia of Natural Resources: Land**, p. 230–237, 7 2014.

LANDE, R. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. **The American naturalist**, v. 142, p. 911–927, 1993.

LANDE, R.; SHANNON, S. THE ROLE OF GENETIC VARIATION IN ADAPTATION AND POPULATION PERSISTENCE IN A CHANGING ENVIRONMENT. **Evolution; international journal of organic evolution**, v. 50, p. 434–437, 1996.

LEVENE, H. Genetic Equilibrium When More Than One Ecological Niche is Available. **The American naturalist**, v. 87, p. 331–333, 1953.

LEVINS, R. **Evolution in changing environments : some theoretical explorations**. [s.l.] Princeton University Press, 1968. 120 p.

MACARTHUR, R.; LEVINS, R. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. **The American naturalist**, v. 101, p. 377–385, 9 1967.

MACCOLL, A. D. C. The ecological causes of evolution. **Trends in ecology & evolution**, v. 26, p. 514–522, 2011.

MANDAI, C. Y. Simulações Computacionais em Ecologia de Comunidades: uma Interface Intuitiva entre Modelos Verbais e Matemáticos. 2016. Disponível em: <http://www.teses.usp.br/teses/disponiveis/41/41134/tde-01022016-085828/>.

MATESANZ, S.; TESO, M. L. R.; GARCÍA-FERNÁNDEZ, A.; ESCUDERO, A. Habitat fragmentation differentially affects genetic variation, phenotypic plasticity and survival in populations of a gypsum endemic. **Frontiers in plant science**, v. 8, p. 843, 2017.

MILNE, B. T. Spatial aggregation and neutral models in fractal landscapes. **The American naturalist**, v.

139, n. 1, p. 32–57, 1992.

MIMURA, M.; YAHARA, T.; FAITH, D. P.; VÁZQUEZ-DOMÍNGUEZ, E.; COLAUTTI, R. I.; ARAKI, H.; JAVADI, F.; NÚÑEZ-FARFÁN, J.; MORI, A. S.; ZHOU, S.; HOLLINGSWORTH, P. M.; NEAVES, L. E.; FUKANO, Y.; SMITH, G. F.; SATO, Y. I.; TACHIDA, H.; HENDRY, A. P. Understanding and monitoring the consequences of human impacts on intraspecific variation. **Evolutionary applications**, v. 10, p. 121–139, 2 2017.

MONTGOMERY, R. A.; ROLOFF, G. J. Habitat Selection. **Encyclopedia of Biodiversity: Second Edition**, p. 59–69, 2013.

MORAN, E. V.; HARTIG, F.; BELL, D. M. Intraspecific trait variation across scales: implications for understanding global change responses. **Global change biology**, v. 22, p. 137–150, 1 2016.

MORRIS, W. F.; DOAK, D. F. **QUANTITATIVE CONSERVATION BIOLOGY THEORY AND PRACTICE OF POPULATION VIABILITY ANALYSIS** [s.d.]

NELDER, J. A.; WEDDERBURN, R. W. M. Generalized Linear Models. **Journal of the Royal Statistical Society. Series A** , v. 135, p. 370, 5 1972.

ORR, M. R.; SMITH, T. B. Ecology and speciation. **Trends in ecology & evolution**, v. 13, p. 502–506, 1998.

PRUGH, L. R.; HODGES, K. E.; SINCLAIR, A. R. E.; BRASHARES, J. S. Effect of habitat area and isolation on fragmented animal populations. **Proceedings of the National Academy of Sciences of the United States of America**, v. 105, p. 20770–20775, 12 2008.

RYBICKI, J.; HANSKI, I. Species-area relationships and extinctions caused by habitat loss and fragmentation. **Ecology letters**, v. 16, p. 27–38, 5 2013.

SCHEFFER, M.; VAN NES, E. H. Self-organized similarity, the evolutionary emergence of groups of similar species. **Proceedings of the National Academy of Sciences of the United States of America**, v. 103, p. 6230–6235, 4 2006.

SCHLAEPFER, M. A.; RUNGE, M. C.; SHERMAN, P. W. (PDF) Habitat Fragmentation and Role of Matrix. **Trends in ecology & evolution**, v. 17, p. 474–480, 10 2002.

SLOAN WILSON, D.; TURELLI, M. Stable underdominance and the evolutionary invasion of empty niches. **The American naturalist**, v. 127, p. 835–850, 1986.

SOBERÓN, J.; NAKAMURA, M. Niches and distributional areas: Concepts, methods, and assumptions. **Proceedings of the National Academy of Sciences of the United States of America** , v. 106, p. 19644–19650, 2009.

SOBERON, J.; PETERSON, A. T. Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas. **Biodiversity Informatics**, v. 2, 1 2005. Disponível em: <https://journals.ku.edu/index.php/jbi/article/view/4>.

STODDARD, S. T. Continuous versus binary representations of landscape heterogeneity in spatially-explicit models of mobile populations. **Ecological modelling**, v. 221, n. 19, p. 2409–2414, 1 set. 2010. . Acesso em: 22 jul. 2022.

SUTHERLAND, G. D.; HARESTAD, A. S.; PRICE, K.; LERTZMAN, K. P. Analysis of Survival Data - D.R. Cox, David Oakes - Google Books. **Ecology and Society**, v. 4, 2000. Disponível em: <http://dx.doi.org/10.5751/es-00184-040116>.

SWIFT, T. L.; HANNON, S. J. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. **Biol. Rev**, v. 85, p. 35–53, 2010.

SZABÓ, P.; MESZÉNA, G.; SZABÓ, P.; MESZÉNA, G. **Limiting similarity revisitedOikos**John Wiley & Sons, Ltd, 3 2006. Disponível em: <http://dx.doi.org/10.1111/J.0030-1299.2006.14128.X>.

THERNEAU, T. M. coxme: Mixed Effects Cox Models. **R-package description.**, p. 1–14, 2015.

THERNEAU, T. M.; GRAMBSCH, P. M. **Modeling Survival Data: Extending the Cox Model | Terry M. Therneau | Springer**. [s.l: s.n.]

TILMAN, D.; MAY, R. M.; LEHMAN, C. L.; NOWAK, M. A. Habitat destruction and the extinction debt. **Nature**, v. 371, p. 65–66, 9 1994.

VAN DER HOEK, Y.; ZUCKERBERG, B.; MANNE, L. L. **Application of habitat thresholds in conservation: Considerations, limitations, and future directionsGlobal Ecology and Conservation**Elsevier, 1 2015. Disponível em: <http://dx.doi.org/10.1016/J.GECCO.2015.03.010>.

WIENS, J. A. Spatial Scaling in Ecology. **Functional ecology**, v. 3, p. 385, 1989.

YANG, J.; LU, J.; WANG, R. R.; WANG, X.; LI, S.; SHEN, G. Importance and benefit of incorporating the responses of species mean trait values in trait-based community assembly. **Ecological indicators**, v. 130, 2021. Disponível em: <http://dx.doi.org/10.1016/J.ECOLIND.2021.108095>.

YE, Q.; TANG, F.; WEI, N.; YAO, X. Molecular and quantitative trait variation within and among small fragmented populations of the endangered plant species Psilopeganum sinense. **Annals of botany**, v. 113, p. 79–86, 1 2014.

YOUNG, A.; BOYLE, T.; BROWN, T. The population genetic consequences of habitat fragmentation for plants. **Trends in ecology & evolution**, v. 11, p. 413–418, 10 1996.

Figures
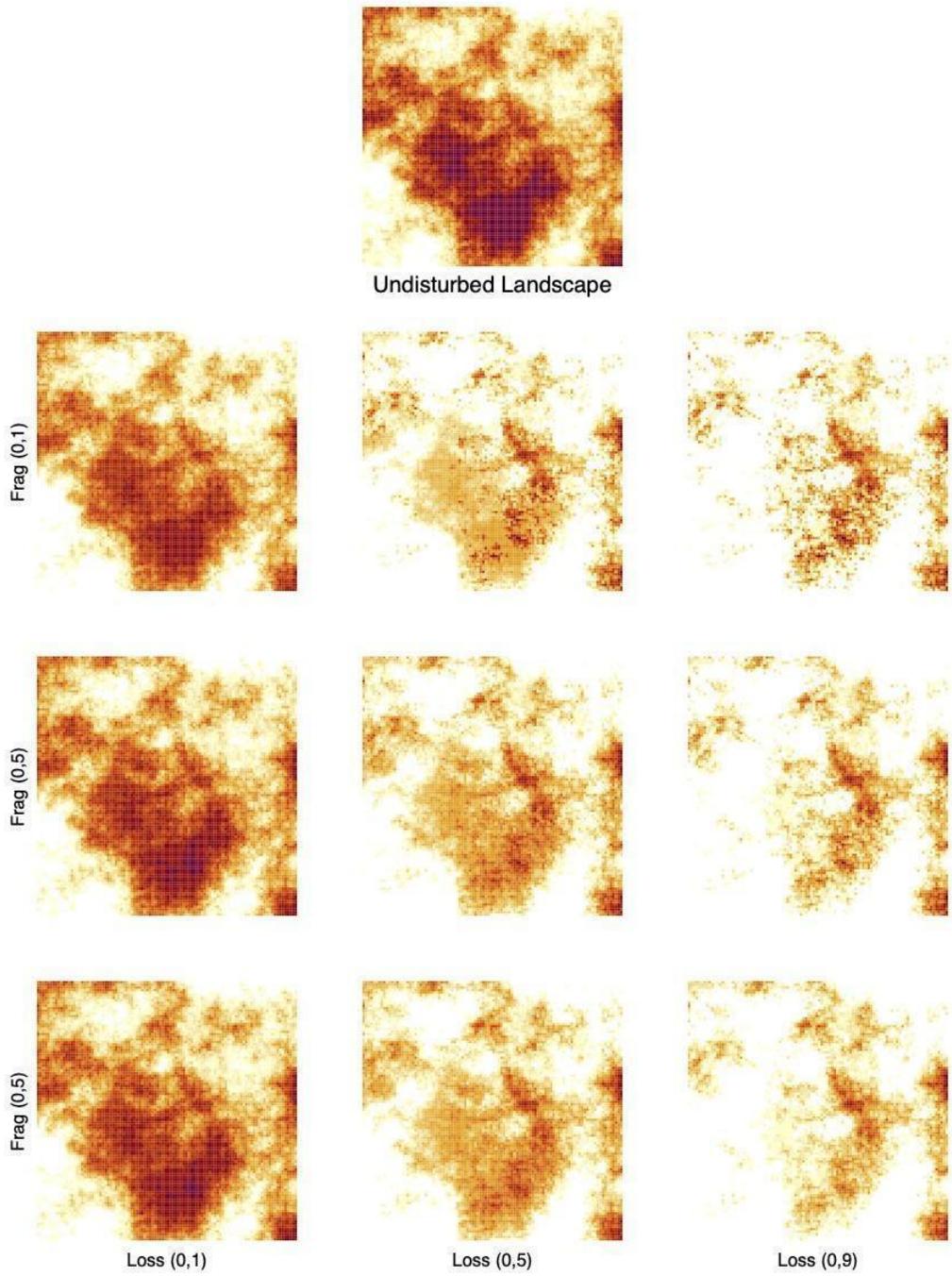
Figure 1: Landscape configuration module example. Each graph represents the spatial distributions of the HEG pixels of a given landscape. Darker pixels represent higher HEG values for a pixel. The top landscape graph represents a pre-disturbance landscape composed only of HEG values contained within the TNW range of its corresponding population. Bottom landscape graphs represent the nine resulting landscape classes of the cross factorial combination of fragmentation loss amounts. Each column of graphs varies the habitat loss amount and each row of graphs varies fragmentation levels.

28
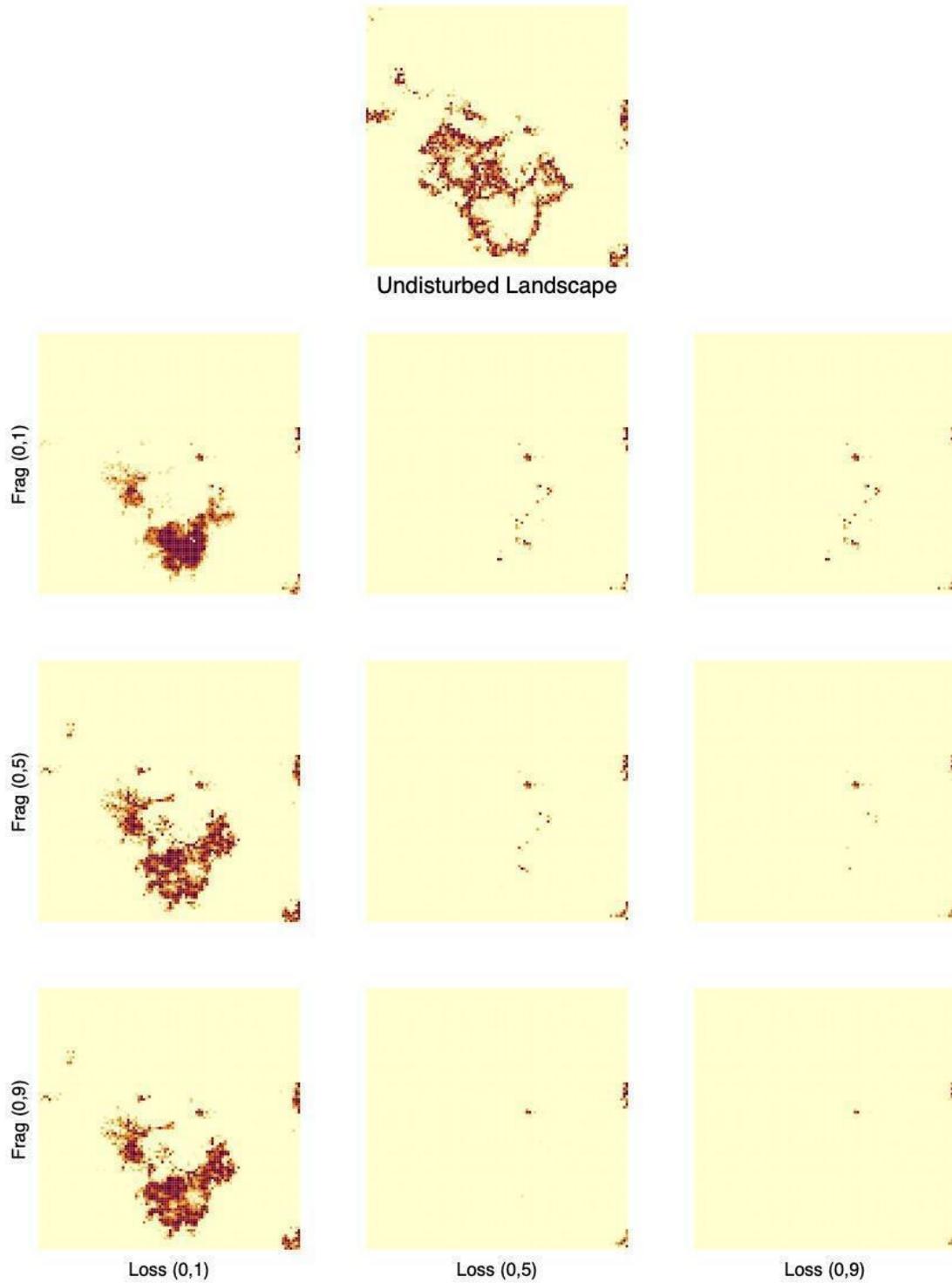
Figure 2: Relative fitness of an individual on a landscape. Each graph represents the spatial distributions of the fitness scores of an example individual through the landscape module in figure1. The fitness score is a consequence of the individual fitness curve as the pixel values of the landscape. Darker pixels represent that the individual has a higher fitness score in that location.
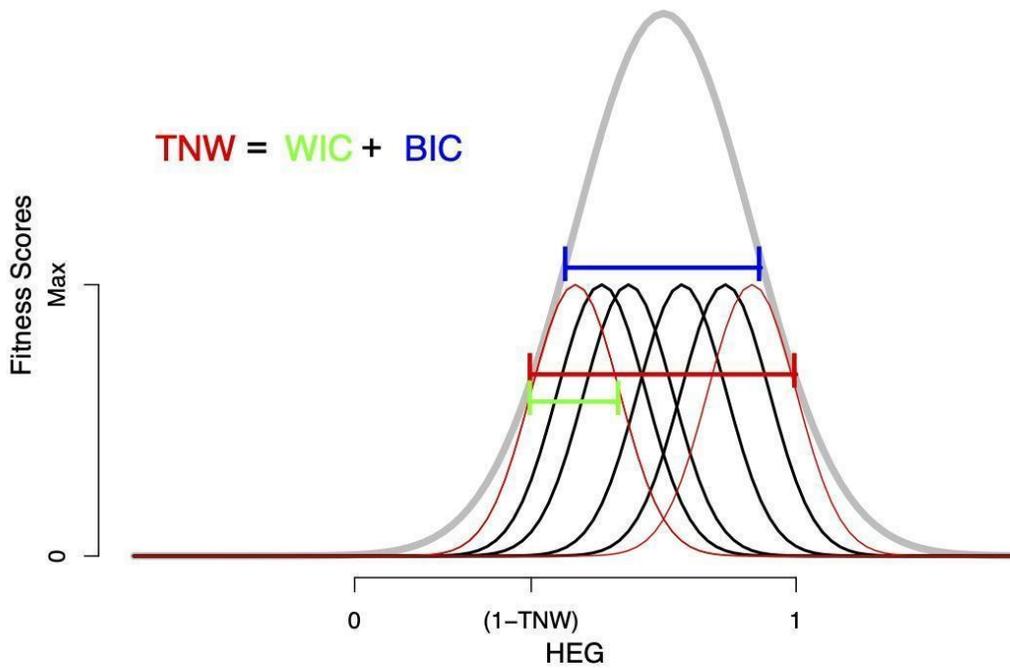
Figure 3: Populational fitness components. The schematization of how the individual's fitness curves are computed. The WIC (green), the within-individual component, determines how generalist each individual of the population is (and it's the same for all individuals). The BIC (blue), the between-individual component, determines the maximum difference between individual fitness curve means in a population. The TNW (red), the total niche width of a population, is the sum of the previous components and defines the ranges of HEG values in which individuals can persist.
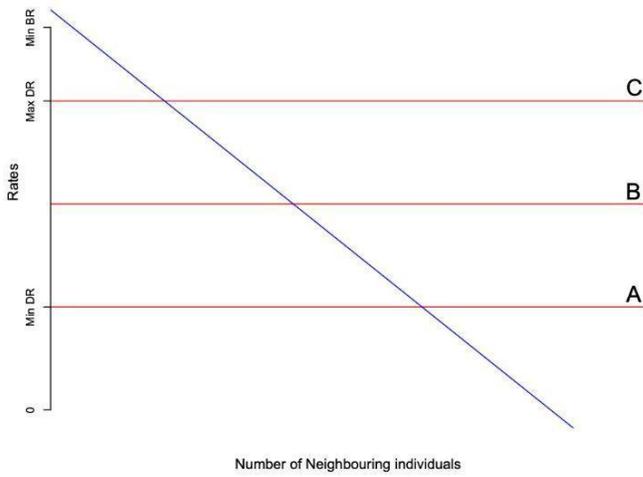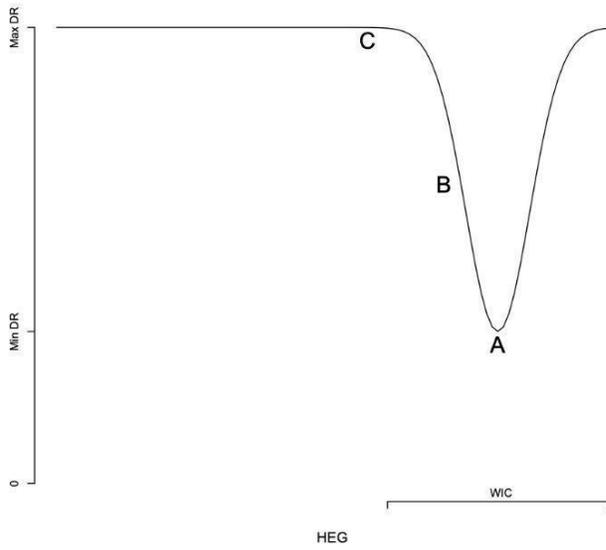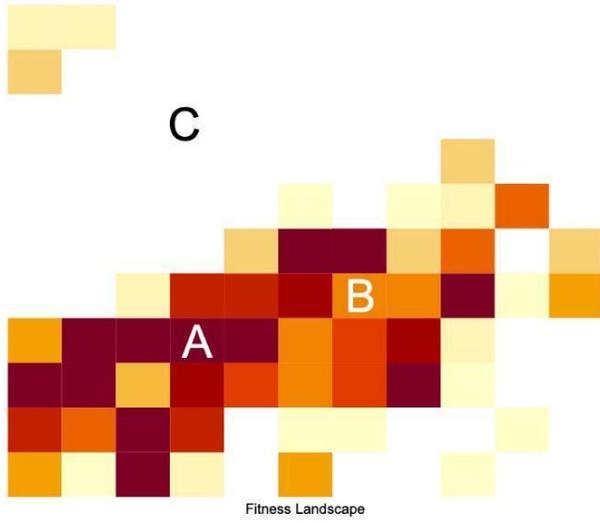
Fitness Landscape

Figure 4: Differential Mortality. The first panel is the fitness scores of an individual in a given landscape. The second panel is the resulting differential mortality curve that an individual has based on its fitness curve along the HEG gradient. The third panel is the interaction between the resulting locally fixed death rates of an individual and the density-dependent birth rate. Therefore, A, B, and C represent the relative fitness scores, relative death rates, and locally fixed death rates of an individual, respectively, for a given HEG value.
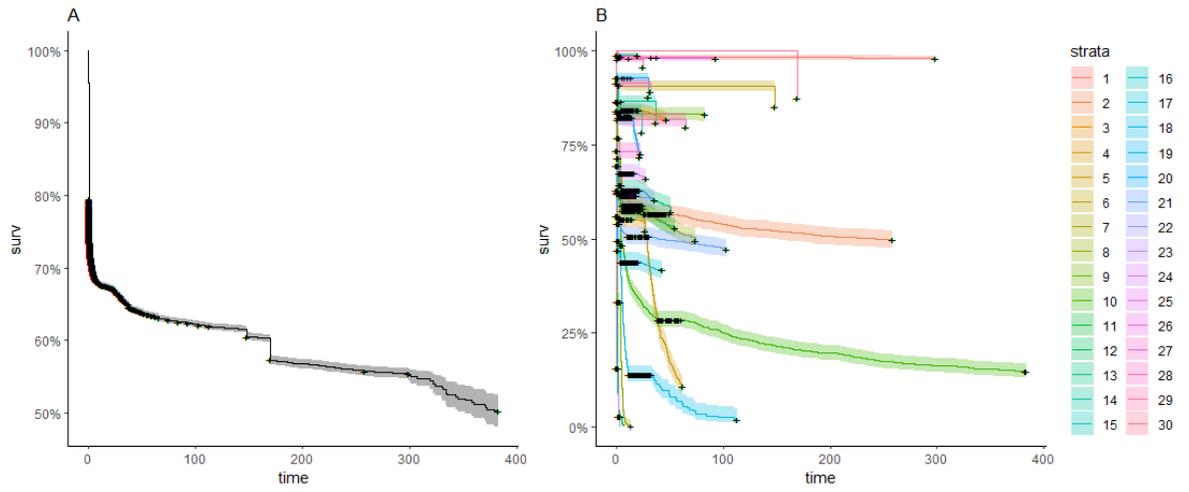
Figure 5: a) Persistence curve of all the datasets. The proportion of surviving individuals on the Y-axis and time in generations of the populations on the X-axis. **b) Persistence curve of all the datasets divided by LHS.** The proportion of surviving individuals on the Y-axis and time in generations of the populations on the X-axis. each line represents onde of the LHS parameter combinations run by us.
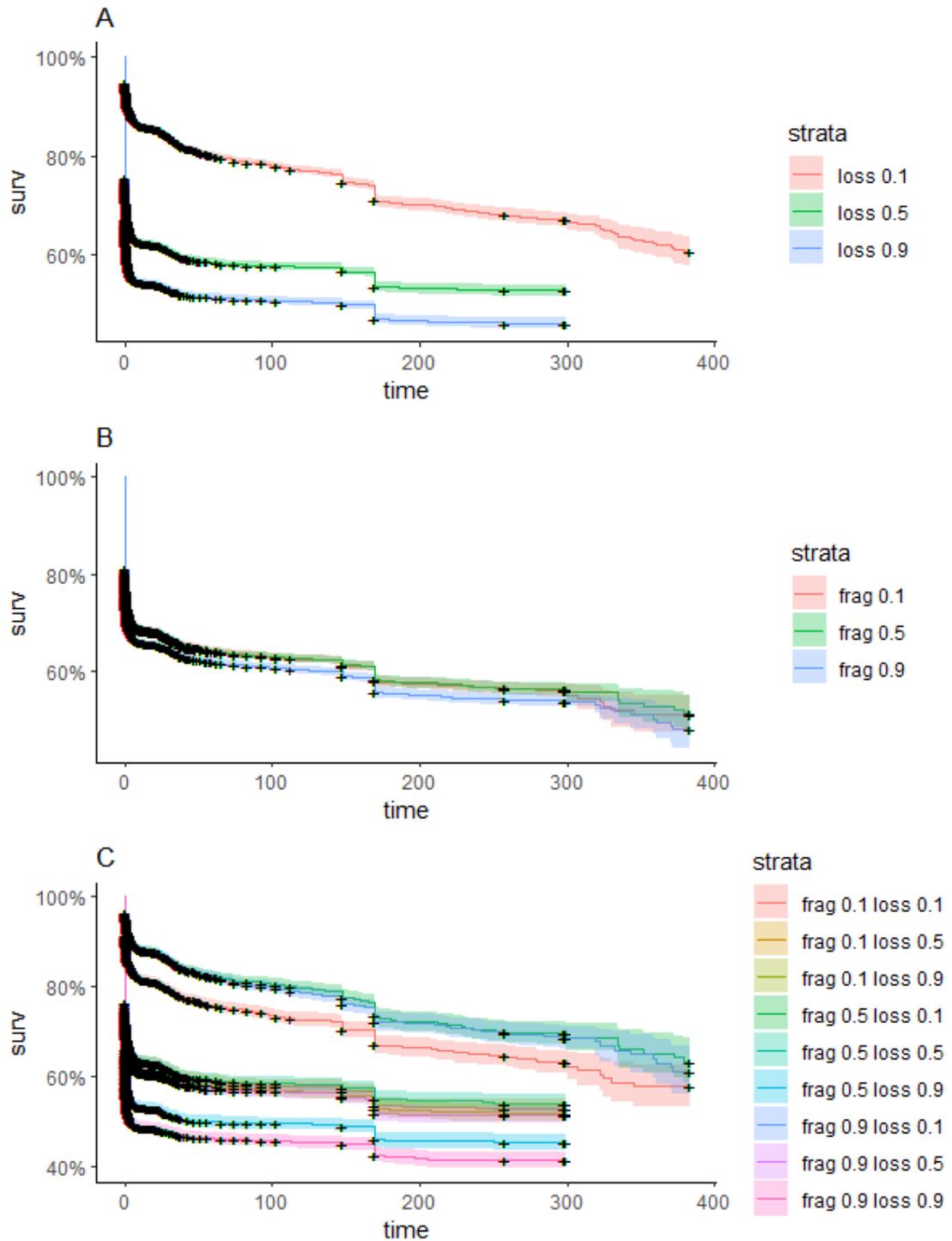
Figure 6: a) Persistence curves divided by habitat loss. Persistence curves here are divided under the simulated factorial categorical amounts of habitat loss (0.1 in red, 0.5 in green, and 0.9 in blue). The proportion of surviving individuals in the Y-axis and time in generations of the populations in X. **b) Persistence curves divided by habitat fragmentation.** Persistence curves here are divided under the simulated factorial categorical amounts of habitat fragmentation (0.1 in red, 0.5 in green, and 0.9 in blue). The proportion of surviving individuals in the Y-axis and time in generations of the populations in X. **c) Persistence curves divided by the landscape treatments.** Persistence curves here are divided under the simulated landscape module, the cross factorial landscape treatment as combinations of habitat loss and fragmentation. The proportion of surviving individuals in the Y-axis and time in generations of the populations in X.
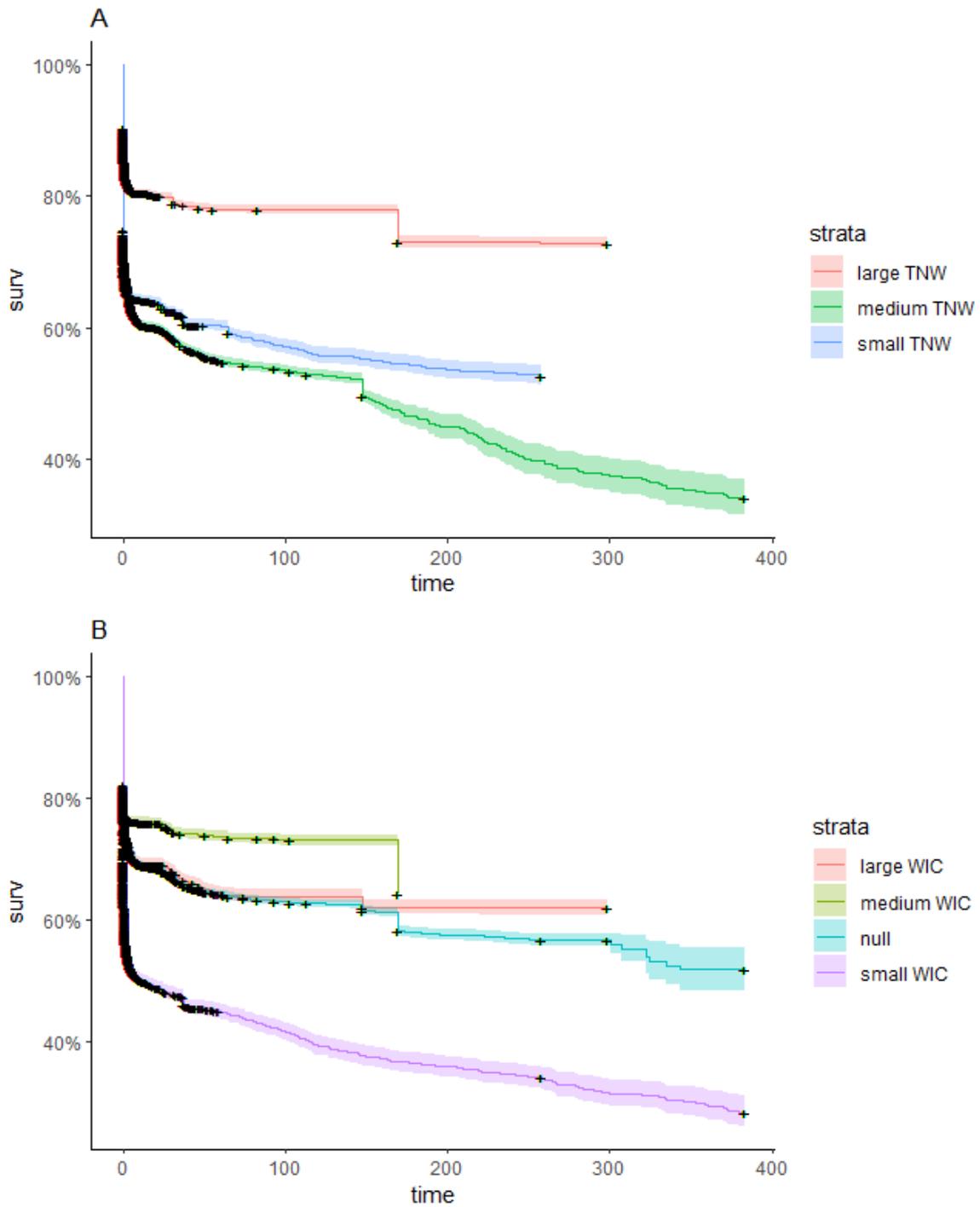
Figure 7: a) Persistence curves divided by TNW. Persistence curves here are divided under threshold values of the simulated TNW parameter. The threshold intervals are determined as 0.3 and 0.6 and discriminate small, intermediate, and high amounts of total niche width. The proportion of surviving individuals in the Y-axis and time in generations of the populations in X. **b) Persistence curves divided by WIC.** Persistence curves here are divided under threshold values of the simulated WIC parameter. The threshold intervals are determined as 0.3 and 0.6 and discriminate between small, intermediate, and high amounts of within-individual variation. The proportion of surviving individuals in the Y-axis and time in generations of the populations in X.
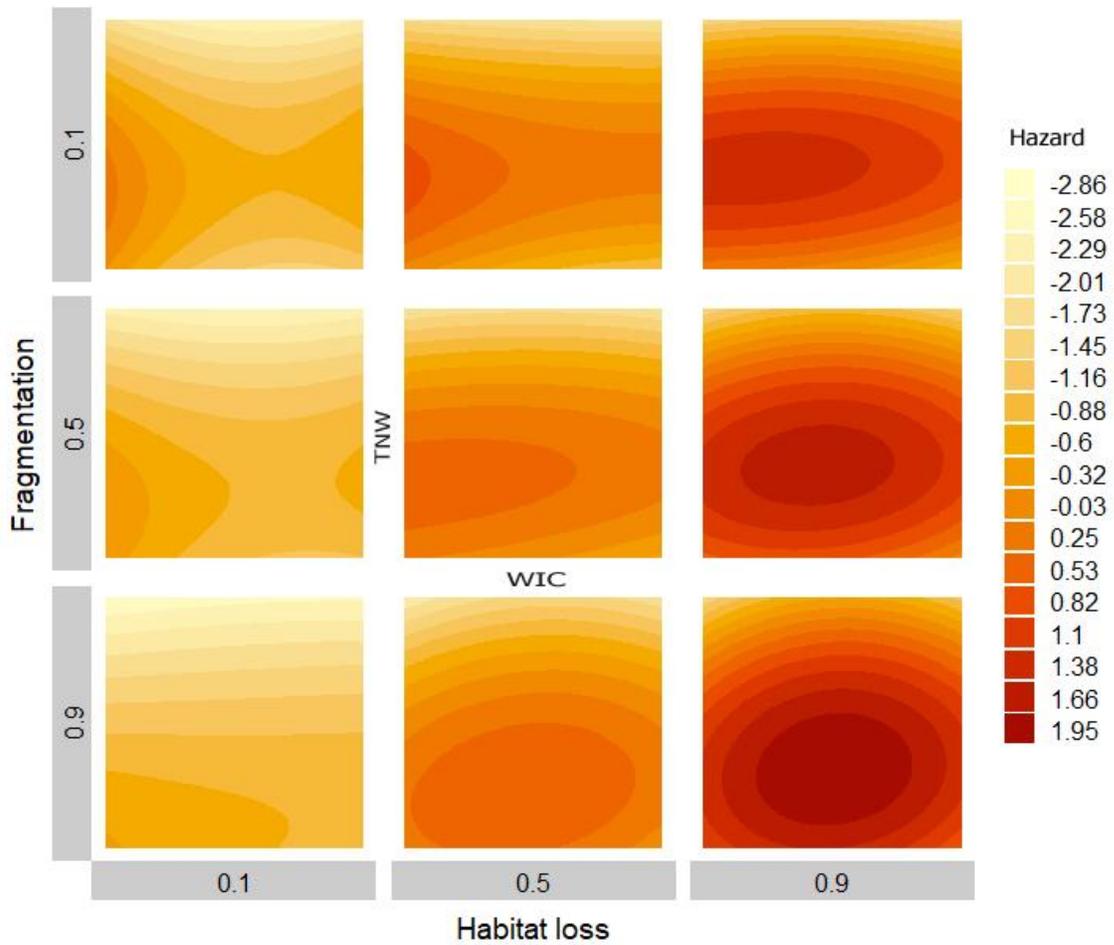
Figure 8: Heatmaps for fixated amounts of landscape components and varying amounts of TNW and WIC. A subset of nine graphs that shows the variation of TNW and WIC along the XY axis under cross factorial combinations of habitat loss (rows) and fragmentation (columns) as two fixed parameters on three levels each. Each pixel in a graph represents the hazard rate score computed for the combination of our four parameters. The color scale for the pixels is shared across graphs of the same group.
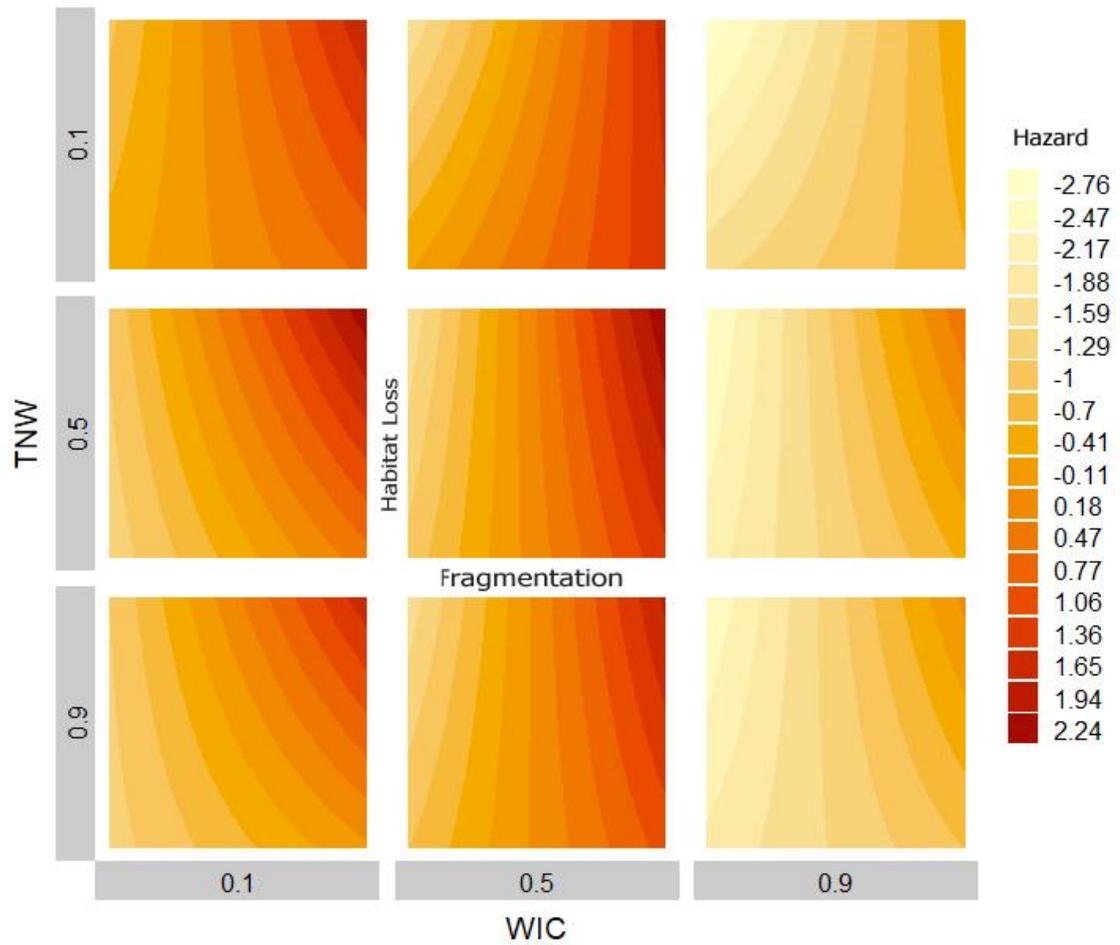
Figure 9: Heatmaps for fixed amounts of individual specialization components and varying amounts of habitat loss and fragmentation. A subset of nine graphs that show the variation of fragmentation and loss along the XY axis under cross factorial combinations of TNW (rows) and WIC (columns) as two fixed parameters on three levels each. Each pixel in a graph represents the hazard rate score computed for the combination of our four parameters. The color scale for the pixels is shared across graphs of the same group.

Tables

Parameter	coef	exp(coef)
TNW	-1,64	0,1939800423
WIC	-1,29	0,2752707831
Frag	-0,51	0,6004955788
Loss	0,35	1,419067549
Frag:Loss	1,71	5,528961478
TNW:WIC	0,75	2,117000017
TNW:Frag	-1,04	0,353454682
WIC:Loss	0,22	1,246076731
TNW:Loss	-0,2	0,8187307531
WIC:Frag	0,87	2,386910854

Table1: Table containing the parameters resulting from the mixed-effects Cox proportional hazard model.