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Habitat loss causes non-linear genetic erosion in specialist species

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ABSTRACT

Habitat loss can lead to non-linear declines in species abundance once the amount of landscape-wide habitat is reduced to a critical value. Previous studies have suggested that such non-linear responses to landscape-wide habitat loss might also exist in genetic variation, and an in-depth understanding of non-linear habitat loss effects on all levels of biodiversity levels is vital to take appropriate conservation actions.

Using individual-based simulations we evaluated the existence of generic non-linear responses in three different response variables and across different combinations of traits related to dispersal and population density. We simulated habitat loss scenarios by incrementally reducing the landscape-wide habitat amount within a previously undisturbed landscape and monitored population abundance, genetic diversity and differentiation of populations within constant sampling areas over time. We found aside from population abundance, genetic variation also responded non-linearly to habitat loss across all scenarios. Importantly, the populations that persisted in remaining habitat fragments experienced genetic erosion before a noticeable effect on local abundance occurred. The observed increase in genetic differentiation and the decrease in genetic diversity of remaining populations are likely caused by the indirect effects of landscape-wide habitat loss on effective patch isolation. Thus, genetic data might have the potential to detect indirect effects of landscape-wide habitat loss before it directly affects the size of a population. Since indirect effects of habitat loss might go unnoticed when extinction risk is estimated from abundance data alone, we argue that an improved understanding of genetic effects is crucial to anticipate and ultimately prevent the negative effects of habitat loss.

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1. Introduction

Habitat loss and fragmentation are major global threats to species diversity and ecosystem functions (Fahrig, 2003; Haddad et al., 2015; Pardini et al., 2017). Populations affected by habitat loss and fragmentation are often small and isolated, thus showing increased extinction probabilities because they are vulnerable to demographic variability, inbreeding depression, and environmental stochasticity (Frankham, 2005; Shaffer, 1981).

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For population density and abundance, previous conceptual, simulation and empirical studies suggest that habitat loss often leads to sharp population declines and hence increased extinction rates when the amount of remaining habitat drops below 10–50% within a landscape (Andrén, 1994; Banks-Leite et al., 2014; Swift et al., 2010). This non-linear response to increasing habitat loss is sometimes called an ‘extinction threshold’ (Ovaskainen and Hanski, 2003; With and King, 1999), and challenges the prediction about the future persistence of species, as even small additional amounts of habitat loss can cause rapid extinction and potentially irreversible regime shifts (Pardini et al., 2010). Extinction thresholds are often used to develop simple guidelines for how much habitat has to remain for a species to persist in a disturbed landscape.

Despite the appealing nature of a simple habitat extinction threshold, empirical studies have found mixed and species-dependent evidence for the occurrence of such a threshold (Swift et al., 2010). For example, threshold values for species diversity in mammals and birds ranged between 10 and 30% of native habitat cover (Andrén, 1994), and for Amazonian mammals’ and birds’ species richness between 19 and 43% (Ochoa-Quintero et al., 2015). Richness in Australian forest-dependent bird species declined dramatically when habitat cover reached a threshold of 10% (Radford et al., 2005). Other studies have even concluded that abundance or species richness did not at all show a threshold response to decreasing habitat (Lindenmayer et al., 2005). Because of this variability, the use of simple general habitat thresholds in practical conservation has been repeatedly criticized (Johnson, 2013; Lindenmayer and Luck, 2005; van der Hoek et al., 2015), and the general existence of sudden, non-linear responses to decreasing habitat (i.e., thresholds effects) remains highly controversial.

In addition to species-dependence, the existence or magnitude of a non-linear response may also depend on the measured population response. While most studies on habitat thresholds focus on population abundances, densities or species richness as response variables, habitat loss effects on genetic variation are underrepresented. Habitat loss in general can directly lead to a reduction in genetic diversity when it reduces the size of sampled patches, as this leads to a reduction of local population sizes and an associated direct loss of alleles. Landscape-wide habitat loss can also indirectly affect genetic variation, when decreasing habitat amount in the surrounding landscape reduces gene flow among populations, thus increasing their effective isolation (Jackson and Fahrig, 2016, 2014). A few empirical studies suggest that genetic variation, similar to the more typical response variables, can sometimes show sudden changes when the amount of landscape-wide habitat drops below a certain threshold (Balkenhol et al., 2013; Lange et al., 2010). However, empirical studies are always limited with respect to the number of landscapes they can consider and the time scale at which analyses are conducted. Thus, the general existence of non-linear genetic responses to landscape-wide habitat loss remains to be tested.

Here, we used simulations to test the hypothesis that genetic variation can respond non-linearly to continuous, landscape-wide habitat loss and compare the responses of genetic diversity and differentiation to that of population abundance. Simulations are by definition only a simplified proxy of reality, however, they allow us to control scenarios of habitat loss in many landscapes and to observe and compare changes in population responses over long time periods. We approximated situations where a study species is constantly monitored over several generations in the same localities (i.e., focal populations), while experiencing increasing habitat loss in the surrounding landscape. Since we used binary landscapes with a hostile matrix, our scenario corresponds best to specialist species, which are expected to be most sensitive to habitat loss (Bommarco et al., 2010; Keinath et al., 2017; Pardini et al., 2010) and to exhibit threshold levels for abundance (With and Crist, 1995). Specifically, we used individual-based simulations of specialist species with different dispersal capacities inhabiting landscapes with varying amount, fragmentation and carrying capacities of habitat. Using the simulations, we *a*) compare the relative sensitivity and consistency of responses in population abundance, genetic diversity and genetic differentiation to ongoing habitat loss and *b*) assess the trajectory of the different metrics after experiencing habitat loss.

2. Materials & methods

We simulated individuals living in landscapes that are continuously reduced in habitat amount. Specifically, we used the spatially-explicit, population genetic simulation model SimAdapt developed by Rebaudo et al. (2013) for NetLogo 5.0.3 (Wilenski, 1999), which has been validated in its consistency with classical population genetic models (Rebaudo et al., 2013). The model simulates dispersal, reproduction, birth and death of individuals living in landscapes that vary in the amount and fragmentation of habitat. We made slight changes in the SimAdapt code in order to adjust the model to our study goals, e.g. we replaced random dispersal with correlated random walks (see below). Detailed information on the individual-based simulations is provided as an ODD protocol (Grimm et al., 2010, 2006) in the supplementary material (see also Table A1 and Fig. A1).

2.1. Simulation experiments

2.1.1. Trait parameters

We created habitat specialists and varied parameters related to dispersal and population size. Specifically, we varied dispersal distance (*disp.dist*, five levels), movement probability (*disp.prob*, three levels) and carrying capacity of the habitat (*k*, three levels), resulting in different population densities and dispersal characteristics (Table 1). Note that these different parameter combinations (hereafter referred to as ‘traits’) represent a cross section of possible dispersal capacities and population densities, rather than particular species with specific dispersal behaviors. We simulated this variety of dispersal

Table 1

Landscape and species parameters of the simulation model.

Parameters	Values/description
<i>Landscape parameters</i>	10, 20, 30, 40, 50, 60, 70, 80, 90, 100%
Habitat amount (<i>A</i>)	
Habitat aggregation (<i>p</i>)	0.1, 0.2, 0.3, 0.4, 0.5
<i>Species parameters</i>	5, 10, 20
Carrying capacity per cell (<i>k</i>)	
Initial population size (<i>N</i>)	Maximal number of individuals depending on carrying capacity
Number of offspring	$\frac{N_t}{K}$
Dispersal distance (<i>disp.dist</i>)	$N_{t+1} = N_t e^{rK}$
Dispersal probability (<i>disp.prob</i>)	very low: 1–2 steps, low: 2–7 steps, intermediate: 3–12 steps, high: 4–17 steps, very high: 5–22 steps
	0.05, 0.1, 0.5

capacities and population densities to ensure that our results are valid for a range of specialist species rather than being limited to a single set of parameter values. Hence, including a combination of different dispersal and density characteristics increases the robustness of our inferences.

2.1.2. Landscape characteristics and habitat loss

We simulated binary (habitat vs. non-habitat) landscapes using the randomHabitat function of the *seccr* R package (Efford, 2018). Simulated landscapes always had the same extent (50 × 50 cells), but differed in habitat amount and fragmentation (see supplementary material for details on simulated landscape). The spatial configuration of habitat patches was controlled by the spatial autocorrelation parameter *p*, with smaller *p* values indicating more fragmented habitat (Gardner et al., 1987). We varied *p* across five levels (0.1–0.5 in 0.1 increments, Fig. A2) and modelled habitat loss through five scenarios differing in the maximum amount of habitat loss a landscape experienced (*rem.Hab*, five levels). Within each scenario, habitat amount (*A*) was reduced in 10%

increments every generation starting from landscapes completely covered with habitat (*A* = 100%), down to a *rem.Hab* value of either 50, 40, 30, 20 or 10% of remaining habitat. In order to analyze the development of response variables over time, simulations continued for 20 generations after the maximum value was reached, i.e. after habitat loss had stopped (Fig. A3). Overall, the total simulation period comprised 124 to 128 generations, depending on *rem.Hab*.

We replicated each combination of *p* and *A* ten times and each species scenario five times in order to account for the stochasticity in our simulations (i.e. random components of genetic and landscape simulations). In total, the combination of all parameters lead to 56,250 individual simulation runs (5 levels of *p* × 5 levels of *rem.Hab* × 45 trait combinations × 10 landscape replicates × 5 genetic replicates).

Our simulation of habitat loss mimicked a relatively fast reduction in habitat (10% loss in every time step) down to a final habitat amount value where habitat loss was no longer ongoing, for example due to habitat protection. Since we sampled only populations within a constant focal site (see below), habitat loss in the beginning proceeded in the surrounding landscape and thus, represents indirect effects of habitat loss. In contrast, direct loss of habitat only occurred when the landscape-wide habitat amount reduced the area of focal sites.

2.2. Population genetic simulation

Every simulation experiment started with a continuous landscape that was homogeneously inhabited by individuals. The total number of individuals depended on the carrying capacity (*k*) of each cell (Table 1). Thirty neutral genetic loci were simulated and alleles at each locus were assigned to individuals randomly. Alleles were chosen from a normal distribution, which corresponded to an expected heterozygosity around 70% and a number of possible alleles *z* around 10 (see SimAdapt documentation of Rebaudo et al., 2013, pp. 12). To reach a stable population before habitat loss started, each scenario was started with a burn-in period of 100 generations running on the continuous landscape (i.e. no habitat loss).

Individual dispersal was modelled as a correlated random walk (CRW) (Kareiva and Shigesada, 1983) where movement direction depends on the direction of the previous step. This approach simulates moving animals that exhibit directional persistence while dispersing, as is commonly the case in reality (Fagan and Calabrese, 2014; Schtickzelle et al., 2007), especially when habitat becomes fragmented (Van Dyck and Baguette, 2005). The dispersal distance was influenced by the landscape, i.e. by different resistance values of habitat (= 1) and matrix cells (= 5) (see ODD protocol in supplemental material). Since a hostile matrix causes higher mortality rates (Fahrig, 2002), individuals that were located in the landscape matrix at the end of the dispersal movements did not reproduce and died. This approach was chosen to create model species that are characterized by limited tolerance towards matrix habitat, i.e., specialist species. Dispersal behavior partly followed an informed dispersal strategy. In the last steps, the individual was given a perceptual range of a two-cell radius. If there was habitat within that radius, the individual moved to this cell instead of passing nearby habitat and terminating movement in the matrix.

Reproduction was sexual with non-overlapping generations, and the number of offspring was determined by a density-dependent logistic growth function (Ricker, 1954) (Table 1). This, together with the probability to disperse (*disp.prob*)

creates density-dependent dispersal, as more individuals are available to emigrate out of high density patches. For each reproduction, two parents were randomly drawn among the different individuals inhabiting a cell, and offspring genotypes were generated from parental genotypes using Mendelian inheritance.

2.3. Sampling

It is usually not feasible to sample all individuals of a species within an entire study landscape, and, thus, empirical studies are often conducted in pre-defined sampling areas (i.e., remaining habitat patches) within a fragmented landscape. Hence, to track the development of the different population responses as habitat loss increased, we sampled individuals in sampling areas that varied between simulation scenarios, but remained constant over time within each scenario (Fig. 1). This sampling approach allowed us to track changes in abundance and genetic variation as landscape-wide habitat loss increased without any bias caused by varying sampling schemes across time. Furthermore, the use of constant sampling areas cross time ensures that focal populations within these sites are affected by both indirect effects of landscape-wide loss (i.e., habitat loss increases isolation of focal populations; Fig. 1B and C), as well as by direct local habitat loss (Fig. 1D). Finally, this sampling approach also mimics empirical monitoring schemes, where the same sites are repeatedly sampled over time to detect changes in response variables (see also discussion).

Since the fragmentation parameter p (see above) determines the clustering of habitat, the focal sites differed between simulation experiments but remained constant within one simulation run of habitat loss. Depending on the simulation experiment, the number of sampled sites ranged between 5 and 42. Individuals within a site were considered to belong to the same focal population. For all scenarios, we counted the number of individuals in the focal populations (population size N_i) and recorded individual genotypes and spatial coordinates of all individuals within focal populations.

2.4. Quantifying genetic variation

We used the R package *fpga* (Signer, 2015) for population genetic analyses. Genetic diversity was calculated as allelic richness (A_R) for each focal population using rarefaction (Kalinowski, 2004), and we averaged A_R over all populations to compare genetic diversity among landscapes with different amounts of habitat. We chose Jost' D (Jost, 2008) to measure genetic differentiation, as it correctly accounts for within-population diversity and is hence suitable to compare genetic differentiation among multiple landscapes (Balkenhol et al., 2013). To compare genetic differentiation between landscapes, we averaged pair-wise Jost' D for each population compared to all other populations to describe its overall genetic differentiation.

2.5. Statistical analysis

2.5.1. Critical thresholds in population abundance and genetic variation

We used piecewise regression models to detect potential non-linear responses of population abundance, genetic diversity and genetic differentiation to decreasing habitat amount using the R package *segmented* (Muggeo, 2008). Basically this approach uses an iterative process where multiple possible values of breakpoints (ψ) and slopes (β) are fitted repeatedly until parameters converge at the maximum likelihood estimate (Muggeo, 2003). Piecewise regression requires a starting estimate for ψ . Initial estimates for breakpoints were based on the examination of scatterplots. We systematically tested for different breakpoints and also tested for multiple thresholds when suggested by exploratory plots. To test whether habitat loss led to linear responses, rather than thresholds, we also calculated linear regressions and compared linear and threshold models based on their Akaike's information criterion (ΔAIC ; Burnham and Anderson, 2002).

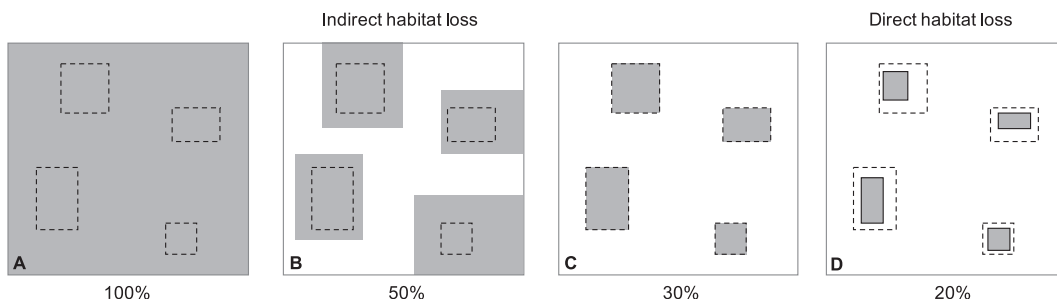


Fig. 1. Schematic illustration of sampling scheme within one landscape simulation. Pre-defined focal sites (dotted lines) were chosen within a continuous landscape **A**, where the relative amount of landscape-wide habitat (grey color) was 100%. During habitat loss (**B**, **C**, **D**), these sampling sites remained constant. Population abundance, genetic diversity and differentiation were estimated for populations inhabiting these sites ("focal populations") to track the dynamics of each of these responses over time as habitat loss continued (10% reduction every generation). Note that in **B** and **C**, focal populations are affected indirectly by habitat loss via increased population isolation. In **D**, focal populations are also affected directly by habitat loss.

2.5.2. Temporal change in population abundance and genetic variation

In order to investigate the rate of change in population abundance, A_R and Jost'D over time within the last 20 generations following habitat loss, we calculated the relative difference between the first generation and each subsequent generation and compared the magnitude of changes between the three response variables.

All statistical analyses were performed in R software (R Developmental Core Team, 2011).

3. Results

Across scenarios, Jost'D and allelic richness were strongly negatively correlated ($r = -0.995$), while abundance was positively correlated with allelic richness ($r = 0.596$) and negatively correlated with Jost'D ($r = -0.519$). Despite these correlations among the three measured population responses, we found differences in their reaction to increasing habitat loss, especially with respect to the location and consistency of non-linear thresholds. Since the general patterns within response variables were very similar across simulation parameters, we first summarize our results across all simulated traits and habitat loss scenarios, before discussing effects of individual simulation parameters.

3.1. Threshold effects of habitat loss

Overall, there was a clear relationship between the amount of remaining habitat and the three calculated metrics. Specifically, population abundance and genetic diversity declined with increasing habitat loss, while genetic differentiation increased (Fig. 2A–C, solid horizontal lines). In all three metrics, these responses were not linear, but instead indicated the existence of critical thresholds of habitat loss with stable values before the threshold and a rapid change in slope at the threshold. Hence, the response variables were best predicted by threshold models compared to linear models (Table 2) across the 45 modelled traits. The location of these thresholds differed strongly in population abundance versus genetic variation. Specifically, the detected breakpoints were more consistent across traits for the two genetic metrics (allelic richness and genetic differentiation) than for abundance. For the latter, we found a strong decline at 32.6% (CI 29.3–35.9%) of remaining habitat (Fig. 2A, vertical lines). At this point, population abundance in the focal sites had on average dropped by about 10.0% (CI 5.3–16.6%) compared to its initial value in the continuous landscape (Table A2). However, in 18 out of 45 trait combinations, breakpoint models with two breakpoint estimates ($\psi_1 = 30$, $\psi_2 = 60$) performed better than models with only one estimate ($\psi_1 = 30$) (Table 2). For these traits, piecewise regression modeling indicated a first threshold at on average 59.0% (CI 54.5–63.4%) of habitat (Fig. 2A). However, in 12 of these 18 traits, population abundance first dropped slightly until on average 48% habitat remained, but then increased again until the actual threshold at 30%. Thus, this first threshold detected in 27% of simulations indicates the transition from a negative to a positive change in the slope of population abundance whereas in only 13% of simulations an actual, slight decrease was detected.

In 662 simulation scenarios (i.e., 1.2% of simulations), individuals went extinct before simulations were complete. These scenarios were distributed over five parameter settings, but population went extinct more often under low population densities and high dispersal abilities (i.e., high dispersal distance and high dispersal probability). Extinction occurred more often when habitat was reduced heavily to a remaining value of 10% ($A = 10$, extinction probability of 55%), but also occurred at other values (i.e., with $A = 20, 30, 40$ and 50%, where extinction occurred in 28, 8, 4, and 1% of simulations, respectively).

Thresholds detected for genetic variation were more consistent and occurred at lower levels of habitat loss. Specifically, piecewise regression performed best when selecting two breakpoints ($\psi_1 = 30$, $\psi_2 = 60$) in all scenarios for both A_R and Jost'D (Table 2). A_R first significantly decreased at habitat amounts of 59.7% (CI 58.5–60.9%) and Jost'D increased at 58.8% (CI 57.6–60.0%) of remaining habitat (Fig. 2B and C, solid horizontal lines). At this first threshold, populations lost on average 0.3% (CI 0.2–0.4%) of genetic diversity and genetic differentiation increased by 9% (CI 6.4–11.9%) (Table A2). This change in the two genetic metrics was followed by a second pronounced decrease in A_R at 22.8% (CI 22.6–23.0%) and a strong increase in Jost'D at 22.5% (CI 22.3–22.8%) of remaining habitat. At this second threshold, A_R decreased on average by 1.8% (CI 1.3–2.2%) and Jost'D increased by 67.0% (CI 44.8–88.9%) (Table A2).

For A_R and Jost'D, breakpoint detection was consistent over scenarios as indicated by narrow confidence intervals at the first breakpoint and even more narrow confidence intervals for the second threshold (Fig. 2B and C, dotted vertical lines).

3.2. Temporal metric behavior after habitat loss stopped

In the 20 generations after habitat loss had stopped, the effects of habitat loss generally continued over time, i.e., population abundance and genetic diversity continued to decline and genetic differentiation continued to increase. The magnitude of responses varied between habitat loss scenarios. Landscapes that had experienced extensive habitat loss ($rem.Hab = 10\%$) exhibited highest changes in population abundance and A_R (Fig. 3A and B). Jost'D showed similar patterns within the first five generations, but decreased afterwards to lower values compared to scenarios where habitat was reduced to 20 and 30% (Fig. 3C).

Generally, the further habitat loss had proceeded, the larger was the change between generations for A_R and Jost'D. Relative changes in genetic diversity and differentiation were still increasing after 20 generations. In contrast, relative changes in population abundance first increased exponentially, but then became asymptotic after about 15 generation post habitat loss.

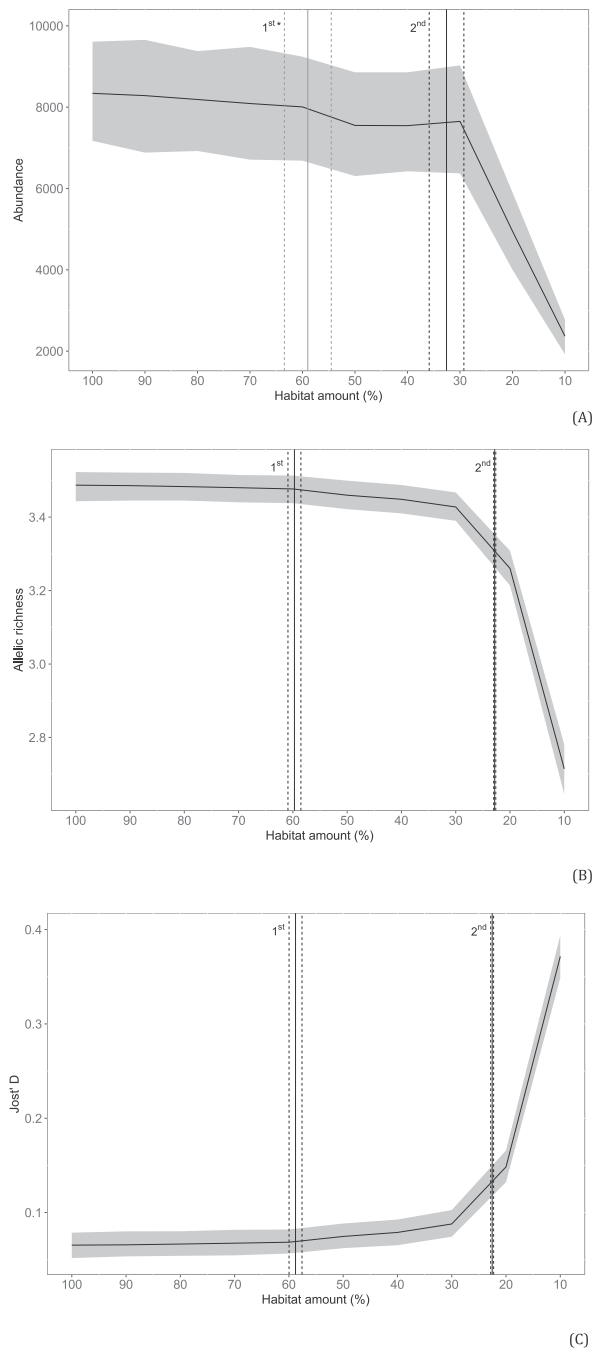


Fig. 2. Relationship of mean abundance (A), allelic richness (B), and Jost'D (C) values (horizontal solid lines) with habitat loss for all 45 simulated species scenarios with 95% confidence intervals (grey ribbon). Solid vertical lines indicate first and second breakpoints suggested by piecewise regression and dashed lines indicate their confidence intervals. (*) A first breakpoint for population abundance was selected in only 18 species.

In comparison to population abundance and allelic richness, the magnitude of change in Jost'D was much more pronounced. Four generations after habitat loss proceeded to 30, 20 or 10%, differentiation values had increased by about 50% compared to the first generation. In contrast, A_R and population abundance had changed by 7% and 13%, respectively, when habitat loss proceeded to a maximum of 10% remaining habitat (Table A.3).

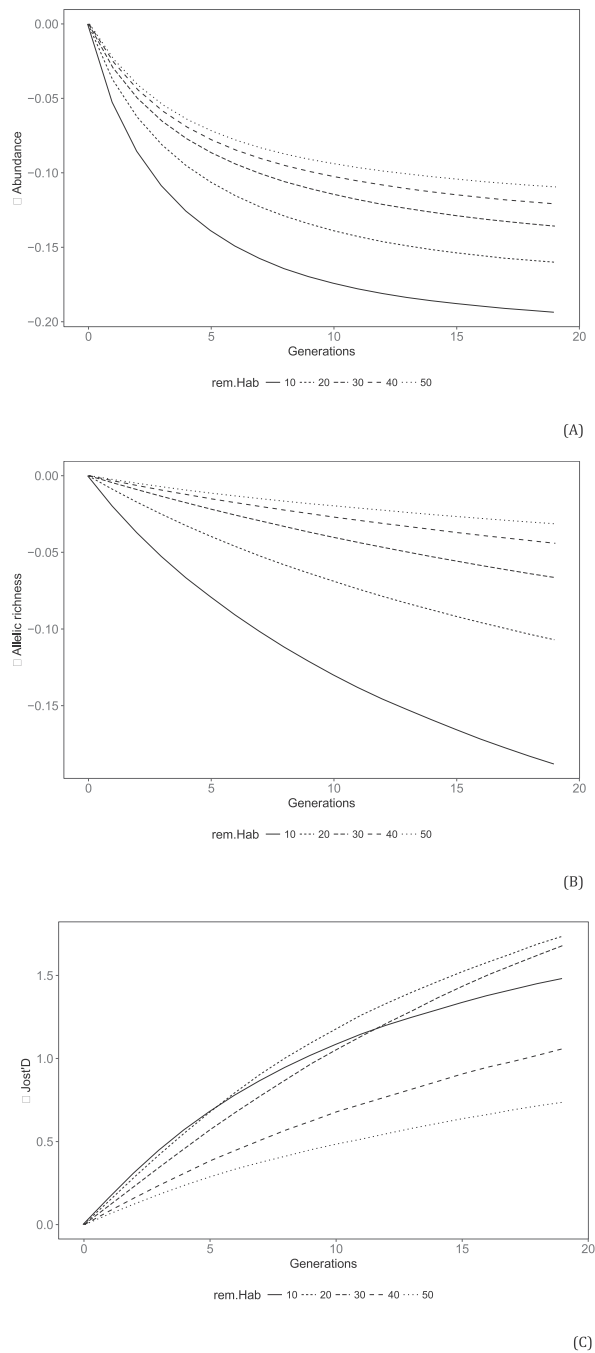


Fig. 3. Temporal development of mean population abundance (A), allelic richness (B), and Jost' D (C) over the last 20 generations following habitat loss. The relative difference corresponds to the difference between each generation in comparison to the first generation (generation 0) after habitat loss was terminated. Different line types represent the different habitat loss scenarios, where habitat was reduced either to 50, 40, 30, 20, or 10% habitat (*rem.Hab*).

3.3. Effects of simulation parameters

As stated above, our reason for varying dispersal and density parameters of the simulated species was to ensure that results are robust, and not limited to a specific parameter set. Hence, our simulated data are not suitable to directly quantify the exact influence of different parameter values on obtained results, and a detailed discussion of these effects is out of the scope of this study. Nevertheless, it is informative and important to discuss several obvious patterns in the simulated data.

Overall, a similar trend (i.e., threshold response) could be observed across most simulation parameters for genetic variation and abundance. Simulated species traits mostly affected the initial values of genetic variation (i.e., the values observed at generation 100, after the burn-in without habitat loss). In contrast, the location of the breakpoint, i.e. the value of habitat amount at which the slope rapidly changed, varied across species traits for population abundances.

Initial values of genetic diversity were higher and genetic differentiation weaker for simulated species with higher dispersal distances (simulation parameter *disp.dist*), and higher probability to disperse (*disp.prob*). However, with higher dispersal probability, the increase in genetic differentiation and decrease in genetic diversity after the threshold around 60% was more pronounced. Furthermore, initial values of genetic diversity were higher and genetic differentiation lower in scenarios with higher habitat capacity (*k*) and lower levels of fragmentation (*p*).

Relative to carrying capacity (*k*) settings, initial values for abundance were slightly higher in scenarios with lowest dispersal distances and probability. In these scenarios, individuals were not able to move very far and thus, have a higher probability of remaining in the focal sites. As mentioned above, response curves and thresholds detected for population abundance were not consistent across simulation parameters. In some species scenarios, intermediate dispersal abilities led to a slight increase in population abundance between 50% and 40% remaining habitat. In six scenarios, high dispersal ability (i.e., *disp.dist* = 20, 25; *disp.prob* = 0.5, *k* = 5, 15, 20) led to a sharp and pronounced decline in population abundance between 60 and 50% remaining habitat, but in most scenarios, the first drop in abundance was not observed until 30% remaining habitat. Finally, the reduction in population abundance after a threshold was generally steeper for scenarios with higher habitat capacity (*k*).

4. Discussion

Before discussing results and their potential implications in detail, we need to acknowledge several limitations of our simulation approach. Generally, simulations and their underlying models are supposed to simplify complex reality, by representing only those key characteristics or behaviors of a system that are considered most relevant for a specific research question. This means that we need to identify the key variables and processes of interest that should be included in our simulations, and to make simplifying assumptions about which parameters to exclude or hold constant (Grimm and Railsback, 2005). In our simulations, a first simplification was our focus on habitat-specialist species. While other, less specialized species might show different responses to habitat loss, we chose specialist species because they are most sensitive to habitat destruction, making them particularly suitable indicator species for conservation. We also only modelled binary landscapes consisting of habitat and non-habitat, as this is the way that specialist species will most likely perceive landscapes experiencing habitat loss, and because conservation applications of habitat thresholds typically distinguish only between habitat and non-habitat areas. Nevertheless, a heterogeneous landscape matrix with varying resistances to movement will potentially impact when and how populations respond to increasing habitat loss, and we encourage future studies to evaluate how varying matrix qualities alter demographic and genetic responses of populations to landscape-wide habitat loss.

Concerning demography, we only considered a logistic, density-dependent model of reproduction (see Table 1 and the ODD protocol). Many other options for modeling population dynamics exist, but a logistic, density-dependent growth has been reported in many different terrestrial vertebrate species (Bonenfant et al., 2009; Chavel et al., 2017; Fowler, 1987). Importantly, since population size was determined by density-dependent growth, and because dispersers were chosen as a certain proportion of the total population (determined by the parameter *disp.prob*), our simulations also include density-dependent dispersal, as more emigrants are sent out from high-density populations. Since we varied initial population size N_t and carrying capacity *k*, our simulations actually lead to a variety of different population trajectories and density-dependent dispersal patterns, thus increasing the robustness of our inferences. Finally, we modelled non-overlapping generations, which is obviously not realistic for most vertebrate species. Overlapping generations can be simulated in only a few simulation tools (Hoban et al., 2012), and these are typically not individual-based and cannot directly include landscape data in the simulations (Landguth et al., 2015). For example, the software CDMetaPOP (Landguth et al., 2017), can simulate overlapping generations and landscape-dependent dispersal probabilities, but cannot incorporate mortality of individual dispersers in the matrix, which is vital for capturing the effects of habitat loss on population persistence (Fahrig, 2002). Also, CDMetaPop uses age-dependent survival and reproductive rates, which would have required us to make additional assumptions. Moreover, both population abundances and genetic variation were created under the same simulation framework involving non-overlapping generations, so comparing their relative response to increasing landscape-wide habitat loss should still be valid.

Overall, our simulation-based study clearly involves several simplifications that call for a careful interpretation of our results, and for future studies that address some of the limitations of our study. Nevertheless, our results were remarkable clear across a large range of simulation scenarios (i.e., traits and landscapes), and they thus provide a first indication for the general existence of non-linear genetic responses to landscape-wide habitat loss in specialist species.

4.1. Non-linear responses

Both abundance and genetic variation showed non-linear responses to habitat loss. In the early stages of habitat loss, focal populations were stable in size, had high genetic diversity and low genetic structure. However, when a certain value of habitat

amount within the surrounding landscape was reached, all metrics responded in a sudden and non-linear way. The value of habitat amount at which the slope rapidly changed differed between abundance and genetic variation, and this difference is most likely due to indirect vs. direct effects of habitat loss.

For genetic differentiation and diversity, and across all modelled parameters, a negative effect of habitat loss could be detected around 60% remaining habitat. This level of remaining habitat coincides with the level of habitat fragmentation where interpatch distances begin to suddenly increase exponentially, so that habitat patches become effectively isolated (Fig. A4, Fahrig, 2003; Gardner et al., 1987). The growing spatial isolation leads to a severe reduction in successful dispersal, and genetic exchange cannot counterbalance the loss of genetic variation due to genetic drift any more. This indirect effect of habitat loss in the landscape surrounding focal populations leads to a strong differentiation among them, as well as to a loss of within-population diversity over few generations.

In contrast, population abundance in focal sites was stable in most scenarios until only 30% habitat remained and then decreased rapidly to low numbers or even to extinction when habitat loss proceeded. At this high level of landscape-wide habitat loss, the effects are no longer just indirect, but directly affect the sampled focal populations (see Fig. 1D). Specifically, any further habitat loss directly reduces the number of individuals within the focal sites, thus substantially decreasing population sizes. This reduction in population size also leads to a large change in allele frequencies, thus increasing genetic differentiation and decreasing genetic diversity in the next generation. Here, genetic variation follows demographic changes with a time-lag, a pattern also found in real systems and other simulation studies (Holzhauer et al., 2006; Landguth et al., 2010; Spear and Storfer, 2008).

In sum, we detected a first non-linear threshold response for genetic variation at around 60% of remaining habitat. This threshold can be explained by indirect effects of landscape-wide habitat loss on successful dispersal among remaining patches. We next detected a threshold for abundance at ca. 33% of habitat, which is when direct habitat loss effects become apparent. The resulting decline in local population sizes is followed by another, strong threshold response in genetic variation at 22% habitat. These results show that population size, genetic diversity and genetic differentiation are not independent, but that their temporal response to ongoing habitat loss differs.

Previous empirical work supports our finding that genetic variation responds more quickly to habitat loss than population abundance or species richness within remaining habitat patches. For example, Pardini et al. (2010) could only detect negative effects of habitat loss on the total number of Amazonian small non-volant mammal species in a landscape with 10% remaining habitat, while species compositions in study landscapes with 30 and 50% remaining habitat were still similar to the composition in a continuous landscape. Changes in species composition were caused by the extinction of habitat specialist species in the landscape with only 10% habitat remaining. In contrast to these results for the species pool, the genetic variation of one of its members, i.e. the habitat specialist Grey Slender Opossum (*Marmosops incanus*), was already detectable at lower levels of habitat loss (Balkenhol et al., 2013).

Clearly, local population size (i.e., abundance) impacts genetic variation, because the size of a local population governs genetic drift, which is counteracted by gene flow. Thus, small populations experience particularly strong drift when they are isolated from other populations, which increases genetic differentiation while reducing genetic diversity. Nevertheless, our results suggest that the response of abundance and of genetic variation to landscape-wide habitat loss should be considered separately, as they do not show the same trajectories in our simulations. Indeed, population abundance only explained about 30% of the genetic metrics (see correlations reported in the results section), indicating that looking at abundance alone will not provide sufficient insight on potential genetic habitat loss effects.

Obviously, landscape-wide habitat loss also directly affects the overall size of the population in the entire landscape. Thus, had we not analyzed data from the focal populations, but instead from the entire study landscapes, we would have detected a response of abundance to increasing habitat loss at much higher levels of remaining habitat. However, we do not believe that such a complete landscape-wide sampling is realistic in most practical settings. Instead, population responses to increasing habitat loss are usually assessed and monitored in defined focal areas (i.e., remaining habitat patches; e.g., Pardini et al., 2010; Ochoa-Quintero et al., 2015) and our goal here was to assess the response of these focal areas to landscape-wide habitat loss over time. Thus, our results suggest that abundance and genetic variation of specialist species in remaining habitat fragments will often show non-linear responses to increasing landscape-wide habitat loss, that thresholds are caused by direct and indirect effects, and that the location of thresholds differs for the three metrics we evaluated.

4.2. Consistency of abundance vs. genetic variation

When dispersal distance and dispersal rate were high (i.e., 50% of individuals disperse), populations declined earlier than under more sedentary conditions. These negative effects of higher dispersal capabilities on abundance might seem counterintuitive, but (Ewers and Didham, 2006) showed that the species most sensitive to increasing fragmentation are the ones that either are highly sedentary, or those with high dispersal ability. While the former loose connectivity among sub-populations due to a lack of movement and eventually face inbreeding depression, the latter face high mortality in the matrix. None of our trait combinations led to a completely sedentary behavior (i.e., zero movement out of focal populations), but since we simulated mortality of dispersers located in the matrix after they reached their maximum dispersal distance, our simulations likely represent the case where high dispersal is actually more detrimental under increasing habitat loss. Our simulation scenarios with high dispersal abilities of habitat specialists represent rather extreme cases and are possibly not often found in real life, where species might also adapt their dispersal behavior to fragmentation (Schtickzelle et al., 2006;

Turlure et al., 2011). Nevertheless, our results are congruent with empirical studies that confirm that longer travels in the matrix increase mortality of dispersers (Bonelli et al., 2013; Mennechez et al., 2003; Waser et al., 1994) while a reduction in dispersal can have a positive effect on the population especially when habitat is highly fragmented (e.g. Schtickzelle et al., 2006). Overall, the response of population abundance appears to be dependent on specific trait characteristics, which agrees with the highly variable results of empirical evaluations of habitat thresholds (e.g. Radford et al., 2005; Ochoa-Quintero et al., 2015).

In contrast, genetic variation showed very consistent responses to habitat loss regardless of simulated traits. However, it is important to highlight that our 45 simulated trait combinations do not resemble completely different species, but were rather supposed to capture variation in dispersal and density characteristics, which are not only species-dependent, but also vary with individual behavior, local habitat qualities, population densities, and degrees of habitat fragmentation (e.g., Schtickzelle et al., 2006; Turlure et al., 2011). Using different combinations of dispersal and density parameters makes our results somewhat robust to variation in these traits, but under very different simulation scenarios, we might have found genetic variation to respond less consistently to landscape-wide habitat loss, even in specialist species. Nevertheless, previous empirical work shows that genetic diversity in a large number of different terrestrial animals is affected by habitat loss, especially when it is very substantial (Lino et al., 2018; Rivera-Ortíz et al., 2015). Thus, even though our results only apply to our specific simulation settings, similar non-linear genetic responses to habitat loss might exist in a variety of species.

4.3. Genetic diversity vs. differentiation

Allelic richness and Jost'D were highly correlated, but since both indices are commonly reported in empirical studies, both are reported here. While the shape of the response to increasing habitat loss was very similar for both metrics (i.e., thresholds were detected at similar values of remaining habitat), the magnitude of their response differed substantially. Specifically, we found that the distribution of genetic variation (i.e., genetic differentiation) showed a more pronounced response to habitat loss than the amount of genetic variation (i.e., genetic diversity), expressed by larger relative changes in Jost'D during habitat loss. These findings are in congruence with previous studies. For example, Keyghobadi et al. (2005) demonstrated that habitat fragmentation impacts genetic diversity and differentiation at different temporal scales. While diversity in the butterfly *Parnassius smintheus* was best explained by past habitat patterns, genetic differentiation was best explained by recent habitat changes, suggesting that differentiation reacts more quickly to environmental changes. Extending this to multiple landscapes, Balkenhol et al. (2013) found that genetic differentiation of the studied small marsupial was already significantly higher in a landscape with 49% native forest, compared to a continuous landscape, while significantly lower levels of genetic diversity were only found when comparing the contiguous landscape to a landscape with 31% forest remaining. These studies and our findings based on multiple simulated species traits strongly suggest that different response trajectories can be expected for population abundance, genetic diversity and genetic differentiation in landscapes experiencing habitat loss.

4.4. Legacy effect after stopping habitat loss

An interesting finding of our simulations is the fact that changes in genetic metrics still continued for up to 20 generations after habitat loss was stopped, while changes in population abundance often reached stable values after five generations following habitat loss (Fig. 3A–C). For instance, even when half of the original habitat remained (*rem.Hab* = 50%), the loss of genetic diversity and increase in genetic differentiation continued over the entire 20 generations post habitat loss. This is again supported by two meta-analyses of empirical studies, which observed stronger habitat loss effects on genetic variation of populations that were longer subjected to these effects (Rivera-Ortíz et al., 2015; Schlaepfer et al., 2018). Our results suggest that just stopping habitat loss might be effective for stabilizing population abundances in the short term, but might not be enough to prevent genetic depletion and associated population declines in the long run (e.g., due to inbreeding depression or insufficient evolutionary potential). These results seem particularly important in the context of extinction debts, which cause species to go extinct due to events in the past (Kuussaari et al., 2009).

These results are also highly relevant for understanding landscape-genetic relationships in fragmented habitats. Researchers are increasingly aware of 'legacy effects' in landscape genetics, which occur when contemporary genetic patterns can be attributed to past landscape characteristics (Cushman et al., 2011; Epps and Keyghobadi, 2015). For example, Landguth et al. (2010) showed that under certain conditions, genetic effects of dispersal barriers can still be detected for more than 100 generations after barrier removal. However, while empirical studies investigating genetic legacy effects consider that the landscape is dynamic (i.e., the past landscape is considered in analyses), these studies still assume that the genetic pattern they measured is stable and representative of current or past landscape influences. Our results suggest that even in now stable landscapes, past habitat loss can still cause diversity to decline and differentiation to increase, which means that truly understanding genetic effects of landscape-wide habitat loss will require temporal monitoring schemes in which landscape-genetic relationships are assessed across multiple generations.

4.5. Potential conservation application

While our results are based on simulations with all their simplifications and limitations (see above), they nevertheless point towards an interesting potential of genetic data in practical conservation. Habitat thresholds, i.e., the maximum value of

habitat loss that a species can tolerate before it is threatened by extinction, are often used to define habitat conservation targets (McAlpine et al., 2007; Rompré et al., 2010; van der Hoek et al., 2015). Simple habitat thresholds are appealing, because they do not require actual field data to be collected and because the amount of habitat within a landscape can easily be derived from digital maps or remote sensing data. However, these threshold values can be inaccurate and misleading, and they also do not provide any actual evidence of habitat loss effects, which is often needed to convince stakeholders and policy-makers to invest in conservation actions. On the other hand, sophisticated early-warning indicators of imminent species decline (e.g., Dakos et al., 2012; Scheffer et al., 2009) could theoretically be used as an alternative to simple habitat threshold rules, but they require long-term demographic monitoring data that is difficult and expensive to obtain in most applied settings.

Given the sharp, very consistent and early genetic responses to landscape-wide habitat loss found in our simulation study, we believe that genetic approaches might offer an avenue towards developing useful early-warning indicators for applied conservation management. Specifically, genetic indices could be used within a monitoring program, where the same landscape is continuously monitored as habitat loss is ongoing. Ideally, genetic data from before habitat loss started, e.g. from museum species, should be available for this temporal approach, as this data serves as a baseline for comparison of different points in time. If genetic differentiation is found to be significantly increased compared to the original, continuous landscape, habitat loss needs to be stopped to prevent species extinctions. If genetic diversity is significantly reduced, such conservation actions are urgently required. In reality, it will often be difficult to apply this temporal monitoring approach, because habitat alterations have already occurred in most unprotected areas across the globe, and because an actual monitoring requires long-term data collection, which is logistically and financially challenging. We therefore suggest that genetic early-warning indicators have greatest merit within a spatial framework that compares multiple landscapes at a single point of time to identify those areas that require most urgent conservation attention and where conservation efforts have the greatest potential to be effective (Fig. 4). This framework requires a control area (e.g., protected landscape) where genetic metrics of differentiation and diversity are estimated for one or several appropriate indicator (i.e., habitat-specialist) species. Landscapes showing significantly higher levels of genetic differentiation and lower levels of genetic diversity compared to the control area should receive highest priority for conservation, as they are likely close to severe declines in population abundance, resulting in high extinction risk and potentially irreversible regime shifts due to landscape-wide habitat loss (see also Pardini et al., 2010). We

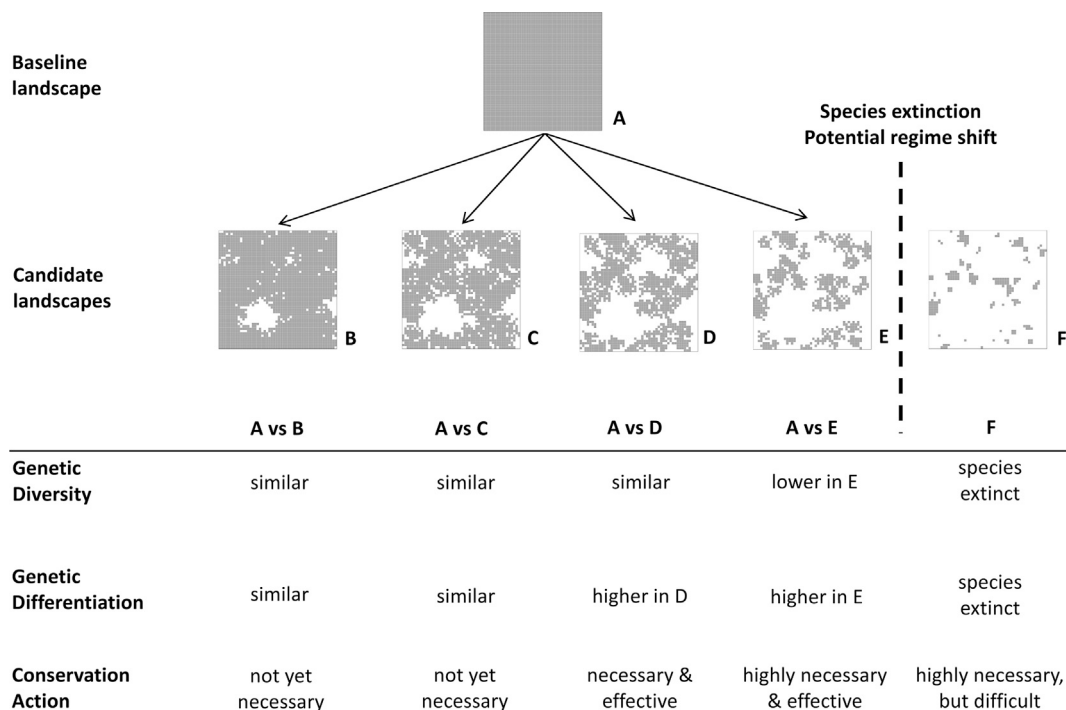


Fig. 4. Conceptual outline of genetic early warning indicators of landscape-wide habitat loss. Genetic diversity and genetic differentiation in a landscape showing continuous habitat (landscape A) are used as a baseline for comparison with several candidate landscapes where conservation actions are considered. In landscape B and C, no conservation action is needed, because genetic variation is essentially the same as in the continuous habitat. In landscapes D and E, conservation action (e.g., habitat restoration) is required and has the potential to be effective, because habitat loss has already impacted genetic variation, but has not yet caused species extinctions. In contrast, effective conservation is very difficult to achieve in landscape F, where habitat loss has already caused species extinctions and a potential regime shift. Shown example landscapes were simulated with a spatial autocorrelation parameter p of 0.3 and habitat amount A of 1 (landscape A), 0.9 (landscape B), 0.7 (landscape C), 0.5 (landscape D), 0.3 (landscape E), 0.1 (landscape F), respectively.

encourage future studies to further evaluate the usefulness and reliability of genetic early-warning indicators for detecting negative effects of habitat loss in both simulated and empirical species.

5. Conclusions

In sum, sudden non-linear responses to habitat loss and fragmentation can not only be detected in abundance, but also in genetic variation of habitat specialists under a variety of trait characteristics and landscape scenarios. Importantly, even relatively low levels of landscape-wide habitat loss can indirectly impact genetic variation, while abundances of local populations in our simulations were most strongly affected by direct habitat loss. This emphasizes that the current risk of population collapses and extinctions of habitat specialists might be higher than predicted from abundance data alone. Indirect habitat loss, i.e., loss of functional connectivity, is the likely driver for an earlier signal in genetic variation compared to local abundances, which suggests that genetic data may indicate negative habitat loss effects before irreversible tipping points have been reached and species go extinct. Since the loss of genetic variation decreases population viability, we suggest that an improved understanding of non-linear genetic effects is crucial to anticipate and ultimately prevent negative habitat loss effects.

We encourage others to further assess the generality of genetic habitat threshold effects, their relevance for understanding landscape effects on gene flow and population persistence, and their potential use in applied conservation using empirical and simulation studies.

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Appendix A. Supplementary data

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