

ARTICLE

Extinction dynamics: The interplay of species traits and the spatial scales of metapopulation declines

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Handling Editor: Tom Miller**Abstract**

Global changes can lead to species declines and extinctions through their impacts on species habitats at two distinct spatial scales: habitat destruction, in which individual habitat patches are destroyed by land-use change or natural disasters, and habitat degradation, in which larger scale changes, such as nitrogen deposition or climate change, lower mean population abundances across landscapes. We developed a theory showing that, even when these two forms of global change have an identical impact on a species' total amount of habitat, they have qualitatively different consequences for species dynamics and extinction. Using metapopulation theory and simulations, we found distinct impacts of these global changes characterized through several responses: the rate at which populations are lost from the remaining patches, extinction thresholds, and the duration of extinction debts. Habitat degradation causes a faster decline in species populations when habitat reduction is low, making it particularly detrimental for rare species. Habitat destruction has smaller impacts for low habitat reduction, but shows clear thresholds beyond which it surpasses degradation's negative impact; the location and steepness of the threshold depends on species dispersal, with poor dispersers having steeper thresholds. These results highlight the challenge of using population monitoring to assess the consequences of global changes and predict consequences of further change: extinction trajectories cannot be predicted due to thresholds (habitat destruction) and lagged dynamics that lead to extinction debts (habitat degradation). Our research clarifies why the impacts of one type of global change may poorly predict the impacts of the other and suggests general rules for predicting the long-term impacts of global changes based on species traits.

KEYWORDS

conservation, extinction debts, global change, habitat loss, metapopulation, population decline

INTRODUCTION

Human-induced global changes have caused a 1000-fold increase in extinction rates, entering us into one of the

largest mass extinctions on Earth (Dirzo et al., 2014; Pimm et al., 1995; Vitousek, 1994). Although some species may benefit from such changes and others show no evidence of decline today, many have declined with

global changes (Dirzo et al., 2014; Rosenberg et al., 2019; Seibold et al., 2019). Even minor declines may be the first step toward extinction, as population dynamics lag and continued global changes are realized (Dirzo et al., 2014; Hanski & Ovaskainen, 2002).

Habitat loss is considered the greatest cause of species extinction and decline (Pimm et al., 1995; Wilcove et al., 1998), but other global changes are increasingly important and may cause more cryptic loss of species (Dullinger et al., 2012; Gilbert & Levine, 2013). In general, global changes range from having widespread distributed impact across populations to impacts concentrated more locally on individual populations. In the extreme cases, this occurs through two characteristic forms. First, large-scale processes such as climate change and widespread invasion can create overall degradation, resulting in a relatively uniform reduction in population sizes across a landscape. Second, local processes (e.g., resource extraction, land-use change, natural disasters, or point source pollution) can result in the destruction of individual habitat patches (Figure 1). Species can experience both impacts—entire landscapes that are degraded and destruction of individual habitat patches within landscapes—or any blend of the two. But an important

and unresolved question is whether these distinct scales of impact have different consequences for species persistence.

Habitats are patchy for most species, which may cause populations to decline in fundamentally different ways than is expected in continuous landscapes (Hanski & Ovaskainen, 2002; Schnell et al., 2013). Landscape heterogeneity, including host distributions for consumers and parasites, cause ubiquitous patchiness (Gilbert & O'Connor, 2013). Moreover, both degradation and habitat loss can force initially contiguous populations into smaller and more isolated units (Fahrig, 2003; Hanski, 2005). The poor understanding of how metapopulation declines may differ when habitat loss or degradation is the underlying cause that poses a growing problem for conserving these increasingly fragmented and declining populations.

Classic metapopulation theory suggests that different consequences emerge in metapopulations that experience local habitat destruction versus those that are universally degraded (Levins, 1969). Numerous researchers have added ecological complexity to simple metapopulation models, often adding realism in one ecological attribute of a model at the expense of another (Adler & Nuernberger, 1994; Hanski & Ovaskainen, 2003; Tilman et al., 1994). For example, Casagrandi and Gatto examined the relative

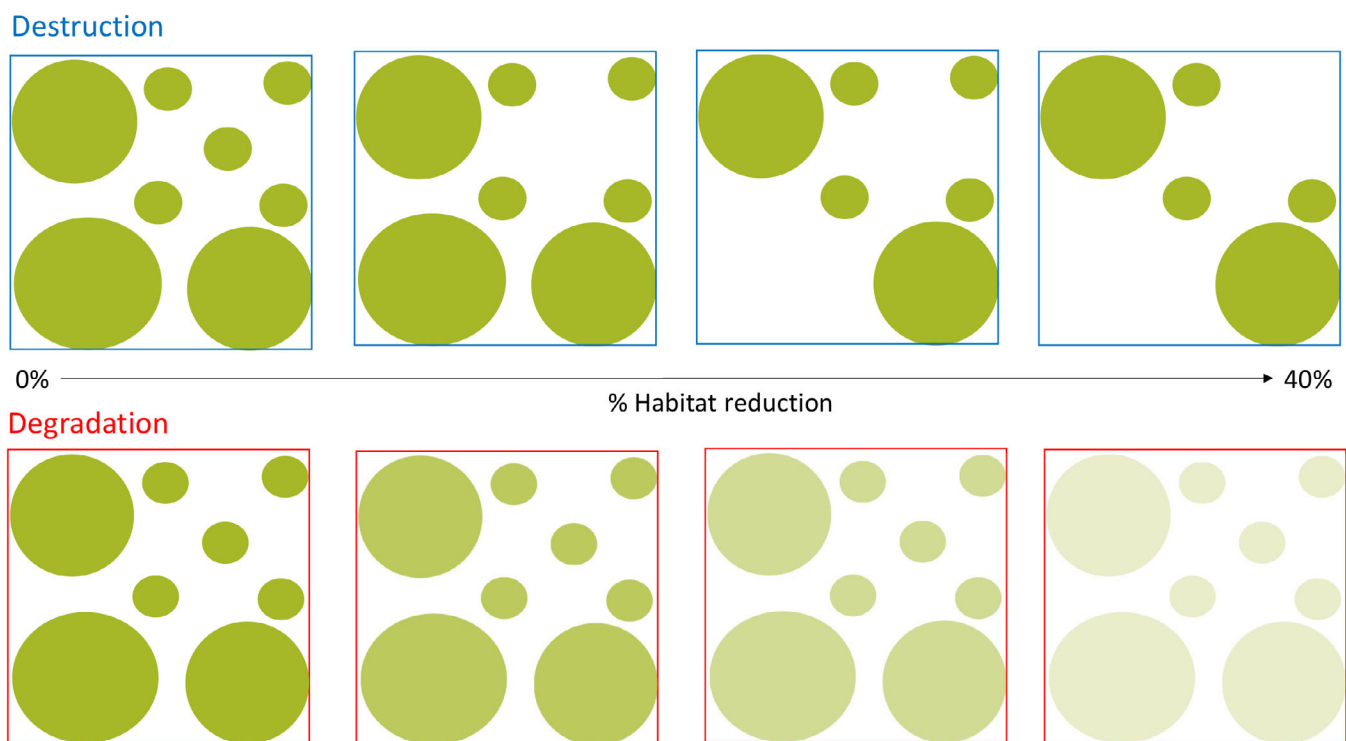


FIGURE 1 An illustration of the two extreme scales on which global changes act: local destruction (e.g., resource extraction, land-use change, or point source pollution) resulting in a loss of individual habitat patches versus overall degradation (e.g., climate change), reducing habitat quality (or carrying capacity) across a landscape. The scenarios shown represent our modeling approach: the total remaining carrying capacity in a landscape is equal for a given level of habitat reduction (the sum of K is equal in top versus bottom panels), allowing direct comparison of the impact of degradation and destruction.

impacts of degradation and habitat destruction for frequent versus infrequent dispersers, assuming that patches are identical and that dispersal redistributes individuals at random across all patches (Casagrandi & Gatto, 2002). However, other studies have suggested that the impacts of global changes are likely to differ when dispersal traits and habitat heterogeneity can interact, as observed in nature (e.g., Adler & Nuernberger, 1994). Ovaskainen and Hanski (2001) developed Spatially Realistic Metapopulation Models (SRMMs) that are ideally suited to understanding the role of spatial heterogeneity and global change. Studies using SRMMs have highlighted the role of habitat heterogeneity on metapopulation persistence and have used this to track extinction that results from habitat destruction (Hanski & Ovaskainen, 2000, 2002) or degradation (Gilbert & Levine, 2013). However, it remains unclear how the impacts of habitat destruction would compare with those that arise from habitat degradation, if both were measured on a common species and landscape, although degradation is often hypothesized to be more detrimental (Fahrig, 2013; Hanski & Ovaskainen, 2000).

The spatially explicit version of Levins' classic metapopulation model (Appendix S1: Equation S1) can be used to assess the long-term viability of metapopulations following global change. As with classic metapopulation models (Levins, 1969), the dynamics of the spatially explicit model are governed by colonization (C) and extinction (E) dynamics, but these vary among sites in ways that depend on site quality (K; carrying capacity) and connectivity. Mathematically, dynamics are modeled with a site-by-site "transition matrix" that captures these dynamics, and the long-term viability of a metapopulation (λ_M) is defined as the leading eigenvalue of the metapopulation's transition matrix. The general form of the metapopulation transition matrix has diagonal elements equal to zero (indicating no self-colonization of patches) and nondiagonal elements:

$$\frac{C_{ij}}{E_i} = hK_iK_j e^{-\alpha d_{ij}} \quad (1)$$

where C_{ij} is the colonization rate of the focal patch i from donor patch j and E_i is the focal patch's extinction rate. The exponentiated term defines spatial connectivity, where d_{ij} is the distance between patches and α is a specific dispersal parameter. The parameter h captures composite traits relating to per-capita establishment and extinction probabilities (please refer to Appendix S1: Sections S1–S4 for model assumptions and precise parameter definitions). Intuitively, the transition matrix captures rates of colonization relative to extinction for each patch and its eigenvalue, λ_M , characterizes the persistence (or eventual extinction) of the metapopulation.

For the Spatially Explicit Levin's Model, λ_M translates to the stationary probability that patches of a metapopulation are occupied (p^* , the quasiequilibrium occupancy; Ovaskainen & Hanski, 2001), as the metapopulation feasibility ($\exists p^* > 0$) (Appendix S1: Section S5). In addition, λ_M measures a metapopulation's rate of increase, in number of new patches colonized per patch, when the metapopulation falls to very low densities of occupancy (Ovaskainen & Hanski, 2001), similar to R_0 in models of disease spread. Therefore this metapopulation feasibility metric is extremely important for empiricists as well as theorists: extinction debts frequently arise in metapopulations, meaning that the last subpopulation to disappear may do so hundreds of years after metapopulations begin deterministic extinction trajectories (Gilbert & Levine, 2013; Hanski & Ovaskainen, 2000; Tilman et al., 1994). As a result, understanding the response of this metric to global change impacts is essential for predicting the long-term viability of metapopulations.

The dependence of λ_M on the transition matrix (Equation 1) suggests that the consequences of large-scale degradation and local patch destruction may have distinct dynamical properties. Habitat destruction reduces the carrying capacity of some sites to zero and, in doing so, changes the average connectivity of the entire matrix. As a result, local population extinction rates are unchanged in untouched patches, but total colonization rates are necessarily changed for some patches, and rates are compounded across fewer patches. In contrast, habitat degradation causes reductions in habitat quality (K) across all sites. Previous research has shown that each of these changes has important dynamical consequences, from surprising and sometimes rapid changes in λ_M , to long lags between when a change is imposed and when its long-term consequences are expected to occur (Hanski & Ovaskainen, 2002; Tilman et al., 1994). However, because habitat degradation and destruction affect the transition matrix differently, it is likely that both their long-term consequences (λ_M , governing metapopulation extinction) and the rates at which these are realized (i.e., lags and extinction debts) differ (Hanski & Ovaskainen, 2000). As a result, it is likely that some well known characteristics of species, such as dispersal ability and occupancy rates within a metapopulation (i.e., rarity), that influence persistence following habitat destruction may have different consequences following degradation. Nonetheless, we lack a formal comparison of habitat degradation and destruction, making it impossible to generalize about equilibrium dynamics and extinction debts following global changes, despite their clear importance for management and protection of species (Kuussaari et al., 2009).

In this paper, we couple analytic methods with simulations to test the transient and long-term dynamical

consequences of habitat degradation and destruction. By equally reducing the total carrying capacity of identical landscapes, either through random patch destruction or whole-landscape degradation, we test three questions: (1) How do the relative impacts of habitat destruction and degradation on metapopulation viability change as habitat is reduced? (2) How do the relative impacts of these two processes depend on a species' dispersal ability and its rarity prior to disturbance? (3) Do habitat destruction and degradation generate distinct transient dynamics and, if so, which process is expected to produce longer lags and extinction debts? We make use of an SRMM version of Levins model, using a discrete time formulation for stochastic simulations (Gilbert & Levine, 2013; Ovaskainen & Hanski, 2001), and test these models on simulated landscapes that range in their spatial heterogeneity (patch clustering; [Adler & Nuernberger, 1994]). We show that habitat degradation has a larger impact on metapopulations, up to a switching point at which local destruction has a greater impact than degradation. This switching point depends critically on average dispersal distance, patch clustering, and a species rarity prior to disturbance. However, lags between disturbance and a species reaching its new equilibrium are often long following habitat degradation, meaning that extinction debts are more likely with habitat degradation.

METHODS

Our model assumes that colonization and extinction dynamics are sufficiently slow that a patch can be characterized as occupied or unoccupied, as once successfully colonized it quickly reaches its realized carrying capacity (K) (Ovaskainen & Hanski, 2001). This simplification of within-patch dynamics allows us to generalize to heterogeneous patches within a metapopulation (please refer to "Discussion" for the limitations of this assumption). We assumed and tested varying levels of heterogeneity as follows. First, carrying capacity varies across the landscape unless K values are equal for all patches (Equation 1). We assumed that carrying capacity was log-normally distributed across landscapes, in keeping with previous models and many natural systems (e.g., Gilbert & Levine, 2013). The consequences for heterogeneous K are important, as both the number of emigrants and the probability of extinction depend on patch-carrying capacity (Equation 1; Appendix S1: Equations S3–S6). Second, heterogeneity in connectivity among patches varies with dispersal (α) and the distribution of patch distances (d) from one another (Equation 1). We varied the dispersal distance parameter, α , while maintaining an exponential dispersal curve. We created random, clumped, and uniform distributions of d ,

with results from random and more uniform distributions presented in the Appendix S1. Varying K , α , and d in metapopulations that are otherwise comparable is not trivial, and we detail our methods in the following paragraphs. We also note that d characterizes the distances that species travel, which may correspond to Euclidean distance (e.g., wind dispersed plants), but could equally capture dispersal networks (e.g., riverine systems).

Landscape creation

Landscapes with more uniform, random, and clustered patch distributions were created (e.g., Appendix S1: Figure S2). In all landscapes, patch-carrying capacities were log-normally distributed with a log mean of 2 and log standard deviation (SD) of 1. Clustering was implemented using 500 iterations of a clustering algorithm akin to Adler and Nuernberger's algorithm, which we will briefly outline (Adler & Nuernberger, 1994).

To randomly distribute patches, x and y coordinates within a 100×100 grid were randomly chosen. We chose to simulate over a landscape realistic of most landscapes in nature where edge effects do come into play at large spatial extents, however we found negligible differences from what would be mathematically expected otherwise (Appendix S1: Section S4). We first created random landscapes by randomly placing patches on a landscape, with the centroid drawn from uniform distributions for x and y coordinates. Clustered landscapes were initiated in the same way, and patches were then randomly moved to increase connectivity. Connectivity was defined as $D_i = \sum e^{-d_{ij}}$, where d_{ij} is the distance between patches i and j . Note that, unlike Adler and Nuernberger, we did not include a dispersal term in our clustering algorithm, as we manipulated dispersal ability independently of landscape configuration (described in subsequent paragraphs). To increase clustering, a patch was chosen at random and moved to a new random location if the new location resulted in a higher D for that patch. For more uniform (evenly spaced) landscapes, the same process was carried out, with the decision to move a patch dependent on decreasing D . This procedure was run for 500 iterations that, based on initial simulations, produced distinctively more clustered/more uniform landscapes both visually and as exhibited by the skew and kurtosis of the distribution of minimum interpatch distances (Appendix S1: Figure S4).

Varying dispersal (α)

Here, 100 test landscapes of 50 and 500 patches were initially created, and α values (1/the average dispersal distance)

were chosen from these test landscapes based on the distribution of the mean minimum interpatch distances within each landscape type. Specifically, α was varied from values pertaining to an average dispersal distance of the entire landscape (global dispersal) to $8\times$, $4\times$, $2\times$, $1\times$, $1/2\times$, $1/4\times$, $1/8\times$ the mean minimum interpatch distance.

We chose to vary α based on the distribution of minimum interpatch distances within each landscape type to account for the fact that our clustering algorithm resulted in more uniform landscapes that exhibited larger -nearest-neighbor distances than more clustered landscapes. This was because our chosen clustering algorithm moved patches closer together to increase clustering and moved patches further apart to increase uniformity. Therefore, any given species would be inherently more dispersal limited in our more uniform versus more clustered landscapes. By varying α appropriately, we accounted for this difference in nearest-neighbor distances across landscape types to test purely for how differences in heterogeneity of interpatch distances altered the impact of habitat destruction and degradation. We noted that this choice of scaling α relative to the average minimum interpatch distance introduced a built-in assumption that landscape clustering did not affect metapopulation capacity prior to destruction or degradation. Biologically, this means that we compared equally well adapted metapopulations in their pristine landscapes, with species in more uniform environments having greater absolute dispersal distances to allow them to be equally well adapted. This equalization of metapopulation capacity in pristine landscapes is key to allowing a comparison of the two processes.

Calculating metapopulation metrics: λ_M , P^* and O^*

λ_M is given by the leading eigenvalue of the transition matrix with nondiagonal elements given in Equation (1) and diagonal elements of zero, as patches do not colonize themselves (Appendix S1: Section S4). The structure of the transition matrix allowed us to see, through linear algebra, a way to (1) impose comparable impacts across metapopulations in different landscapes and (2) make analytical predictions of how both habitat degradation and destruction should impact the metapopulation feasibility denoted by λ_M .

To allow us to compare impacts across landscapes, we used the species-specific composite parameter (h , Equation 1). Because this parameter is a scalar that influences all patches equally, it causes an identical change to the leading eigenvalue, so that doubling h doubles the eigenvalue, all else being equal. This allowed us to rescale the initial λ_M (prior to any patch destruction or

degradation) to a common $\lambda_{M,pristine}$ across landscapes and for species of differing dispersal abilities. Although we used the composite parameter h to accomplish this rescaling, we noted that this parameter captured a combination of per-capita colonization and extinction rates, meaning that it is a biologically measurable parameter (Appendix S1: Sections S2–S4). The long-term metapopulation feasibility is defined as $\lambda_M > 1$, and scaling all landscapes and species to an equal λ_M prior to habitat loss means that all scenarios must undergo the same loss in λ_M to no longer be viable. Essentially, this means that we assumed species would be equally well adapted to their initial pristine landscape, regardless of how clustered habitats within that landscape may be, and the species' ability to disperse between them. We note that some authors defined feasibility as $\lambda_M > e/c$ due to a factoring out of parameters in the transition matrix (Ovaskainen & Hanski, 2001), but we opted to analyze the full matrix, so that λ_M is more easily interpretable for species with different traits.

Related to λ_M is the weighted fraction of patches that is occupied at equilibrium. Following previous research, we defined $O^* = 1 - \lambda_{post}/\lambda_{pre}$ as an estimate of the minimum occupancy prior to habitat loss required for long-term persistence (Equation 5 of Gilbert & Levine, 2013). More specifically, O^* is the minimum spatially weighted fraction of patches occupied at equilibrium prior to habitat loss that is required to ensure that λ_M is ≥ 1 after habitat loss (λ_{post}), given its viability prior to loss (λ_{pre}). We noted that other authors used p_λ^* or p^* to refer to the spatially weighted fraction of patches (Gilbert & Levine, 2013; Hanski & Ovaskainen, 2000; Ovaskainen & Hanski, 2001), but we avoided this notation to avoid confusion with the vector of occupied patches (p^*) described below.

To determine the stationary probability of patch occupancy, we calculated the vector of occupancy probabilities for each patch, p^* . For the Spatially Realistic Metapopulation Model, p^* can be obtained by iterating:

$$P_{n+1} = f(P_n) \tag{2}$$

where f is given by

$$f_i(P) = \frac{C_i(P)}{C_i(P) + E_i(P)} \tag{3}$$

The functions describing patch-specific colonization (C_i) and extinction (E_i) are given in Appendix S1 for discrete and continuous time models. Equations (2) and (3) allow us to use the mean p^* across patches to determine the equilibrium fraction of occupied patches (\bar{P}^* ; Ovaskainen & Hanski, 2001).

Simulating metapopulation dynamics: \bar{P}_{1000} , $t_{\bar{P}^*}$ and t_{extinct}

We simulated dynamics within each metapopulation using a discrete time version of the Spatially Realistic Levin's Model. We started simulated metapopulations at the p^* associated with the pristine landscape, and simulated the metapopulation's dynamics for 1000 generations following each increment of habitat loss from the initial pristine landscape. Transition probabilities for each patch at each time step were generated from our model (Appendix S1: Equations S2, S5, S6) and colonization and extinction events were drawn from a binomial distribution (please refer to Appendix S1: Section S3 for model details). For each simulation, we obtained the average patch occupancy throughout the last 50 of 1000 generations (\bar{P}_{1000}) following each level of habitat degradation and destruction. We also quantified the generational time until \bar{P}^* , the fraction of patches occupied at equilibrium, was reached ($t_{\bar{P}^*}$), and time to extinction (t_{extinct}), if it occurred within this timeframe.

Landscape destruction and degradation

An iterative procedure was developed to obtain the metrics λ_M , \bar{P}^* , \bar{P}_{1000} , $t_{\bar{P}^*}$, and t_{extinct} for both degradation and destruction scenarios applied to multiple landscapes of each type. To do this for each value of α , landscapes of each type (more clustered, random, or more uniform) were generated. Initially, for each pristine landscape, λ_M was scaled by an appropriate ratio of species-specific extinction to colonization parameters ($h \equiv e/c$; Appendix S1: Equation S7) to achieve the same initial value of λ_M for all landscapes. This allowed us to compare changes from this initial $\lambda_{M_{\text{pristine}}}$ across landscapes. For our simulations, $\lambda_{M_{\text{pristine}}}$ was scaled to 20, and results for landscapes of 50 patches were recalculated, with $\lambda_{M_{\text{pristine}}}$ scaled to 100 to ensure that this arbitrary choice of $\lambda_{M_{\text{pristine}}}$ did not influence our results.

Two copies of the original landscape were made. In one, a patch was randomly selected and removed (destroyed) from the landscape. Simultaneously, in the other landscape, all patch-carrying capacities were decreased by an equivalent percentage to the habitat loss in the first copy. For example, if the randomly selected patch made up 3% of the total carrying capacity in the pristine metapopulation, the second landscape had all carrying capacities decreased by 3% (Figure 1). All metapopulation metrics were then calculated for that level of destruction and degradation. We continued this process with randomly selected patches and adjusting K ,

so that the total K across the landscape was always equal in the destruction and degradation scenarios, until no habitat remained. This procedure was repeated 2000 times for each α value and for landscapes of 50 patches and 100 times for landscapes of 500 patches (due to simulation time constraints with increasing numbers of patches). The 500 patch simulations were used to compare changes in λ_M between simulations with differing patch numbers to ensure that changing patch numbers did not alter our results (Appendix S1: Figure S7).

To avoid rounding errors in R that cause nonzero, small values were rounded to zero, we assigned an extremely small minimum probability so that patches could be colonized at any distance. This was necessary to ensure that no patch was completely isolated from all others due to rounding errors, and that it was justified biologically, because there was always some probability of colonization, even over great distances within such landscapes.

All simulations were analyzed using median change in $\lambda_{M_{\text{post-disturbance}}}/\lambda_{M_{\text{pristine}}}$, \bar{P}^* , \bar{P}_{1000} , $t_{\bar{P}^*}$, and t_{extinct} . The median value across simulations was used rather than the mean because the distribution shifted from a heavy right skew to a heavy left skew as habitat was lost by random destruction (Appendix S1: Figure S5), and because our interest was whether the majority of each metrics' results was higher or lower for destruction than degradation (i.e. which was worse for each landscape case) more so than the average magnitude of difference (as this was likely to be highly dependent on individual landscapes). Because patch-carrying capacities and therefore exact percent habitat loss differed among simulations, we binned results to calculate the median value of each metric for a given percentage loss.

RESULTS

Overall, the long-term effects of habitat degradation were far worse than those of habitat destruction when metapopulations were close to their pristine conditions. These trends reversed for dispersal limited species, especially in clustered habitats, whether persistence capacity or patch occupancy were used to measure impact. The crossover point at which habitat destruction had a larger impact than degradation varied with dispersal rate, and also determined when rare versus common species would be more strongly impacted by one process than the other. Transient dynamics frequently showed trends that differed from long-term expectations, with good dispersers showing large lags that masked the impact of degradation. Below we detail the results that led us to these conclusions.

Analytic results

Habitat degradation causes a ubiquitous loss in carrying capacity, which enters into the each element of the transition matrix twice through its effect on the focal patch and the donor patch (Equation 1). This causes metapopulations to respond to habitat degradation in a predictable way:

$$\lambda_{M_{\text{degraded}}} = \lambda_{M_{\text{pristine}}} \times (1 - \omega_{\text{deg}})^2 \quad (4)$$

where ω_{deg} is the proportion of patch-carrying capacity lost through degradation (Appendix S1: Section S4) and the persistence capacity (λ_M) is the leading eigenvalue of the transition matrix. This result for habitat degradation arises from the multiplicative importance of patch-carrying capacities and has large consequences despite its simplicity. First, because this analytic solution does not depend on dispersal or habitat heterogeneity, it allows us to determine the amount of habitat degradation that occurs before a metapopulation is lost, such that $\sqrt{\lambda_{M_{\text{pristine}}}} > \frac{1}{(1 - \omega_{\text{deg}})}$ for persistence. Second, because degradation causes loss of λ_M without being influenced by dispersal and landscape characteristics, Equation (4) can be used to understand the impact of degradation when it occurs in conjunction with habitat destruction by multiplying the impact of destruction by $(1 - \omega_{\text{deg}})^2$.

In contrast, if a similar amount of carrying capacity is lost by losing a single patch from an otherwise fully connected and large network, the expected change in metapopulation capacity is (Grilli et al., 2015; Hanski et al., 1996):

$$\lambda_{M_{\text{destruction}}} \approx \lambda_{M_{\text{pristine}}} \times (1 - \omega_{\text{des}}) \quad (5)$$

where ω_{des} is the proportion of the landscape's total carrying capacity lost through destruction. But the approximation given by Equation (5) only holds for globally dispersing species in highly uniform landscapes (when all patches equally support the metapopulation). In spatially heterogeneous landscapes, habitat destruction changes the spatial configuration of patches and interpatch distances, causing additional impacts through the exponentiated distance term (Equation 1). Comparing Equations (4) and (5) illustrates that when an initially intact metapopulation experiences small amounts of destruction or degradation, the impacts of degradation are expected to be far worse. However, the impact of habitat destruction changes as metapopulations become more fragmented and, in extreme cases, no species can persist in a single patch even though some may persist in an equally degraded landscape (Appendix S1: Equation S8). Indeed, unless species can disperse easily across a landscape, λ_M will be highly nonlinear as habitat destruction progresses.

Simulation results

Metapopulation feasibility (λ_M)

Our simulation results reflect our analytical results for declines in metapopulation feasibility λ_M (Equations 4 and 5) showing a far greater impact of habitat degradation than habitat destruction when the focal species dispersed equally to all patches (Figure 2; lines showing degradation versus destruction with global dispersal). Even when dispersal was more limited and habitats were heterogeneous, habitat degradation was always initially worse than destruction (Figure 2a). However, habitat destruction had a more negative impact as spatial heterogeneity increased, with heterogeneity driven by both limited dispersal and patch clustering (compare panels in Figures 2a and Appendix S1: Figure S3). Habitat destruction caused a sigmoidal decline in λ_M by initially causing almost no change in λ_M , followed by a rapid drop (Figure 2a). The initial lack of response of λ_M , and the steepness of its decline beyond a threshold, were both greater with higher spatial heterogeneity (greater patch clustering and lower dispersal). Due to the sigmoidal decline in λ_M , a metapopulation subjected to destruction often had a much greater λ_M just before the crossover at which its relative impact surpassed that of degradation, but a far lower λ_M just after the crossover (Figure 2a).

The crossover point at which the negative impacts of habitat destruction surpassed those of habitat degradation varied from 35%–99% habitat loss, with the crossover happening at the lowest levels in clustered landscapes when average dispersal distances were less than the mean minimum interpatch distance (Figure 2a). Increasingly uniform distributions of patches further shifted the crossover such that degradation had a larger impact at almost all levels of loss (Appendix S1: Figure S3).

Overall, the predicted decline in metapopulation feasibility with degradation (Equation 4) held for all levels of degradation. Similarly, as predicted for destruction, the decline in metapopulation feasibility followed a near 1:1 linear decline for species' with extremely high dispersal abilities in more uniform landscapes (Equation 5; Appendix S1: Figure S3 lightest shaded line). This linear decline with habitat destruction became increasingly sigmoidal with greater spatial heterogeneity.

Rarity and extinction

As patch occupancy will be zero when $\lambda_{M_{\text{post-disturbance}}} / \lambda_{M_{\text{pristine}}}$ crosses the extinction threshold, the minimum scaling of $\lambda_{M_{\text{pristine}}}$ and subsequent effect on the stationary occupancy of patches p^* (Equations 2 and 3) can be calculated to obtain a minimum spatially

Degradation and destruction in more clustered landscapes

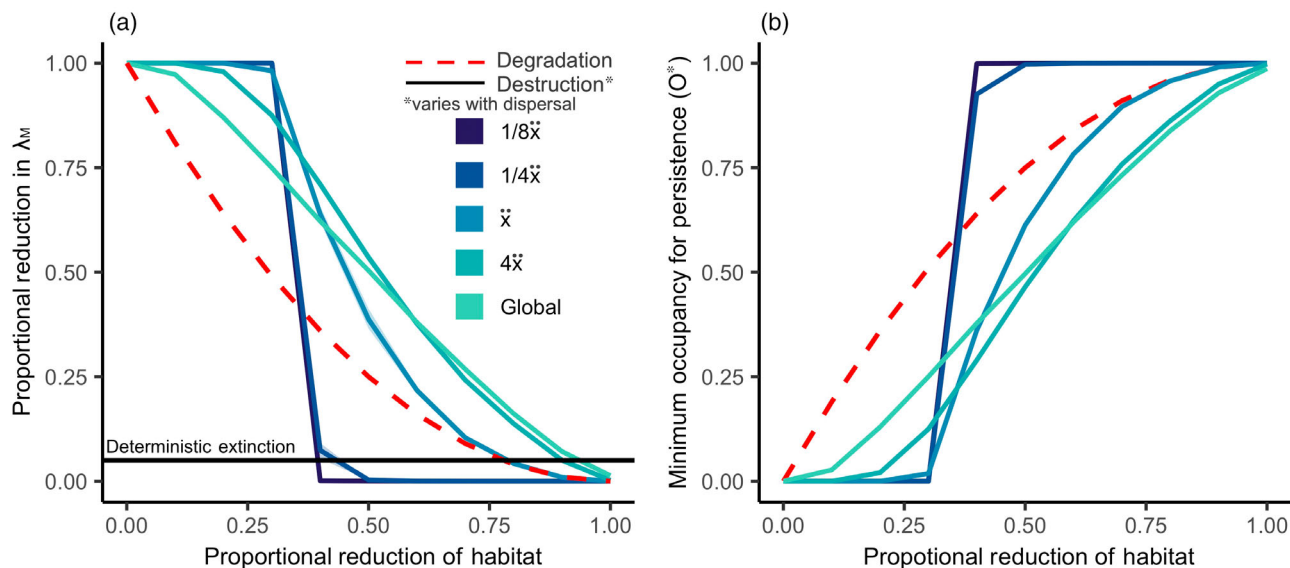


FIGURE 2 Impact of degradation and destruction on persistence capacity and minimum initial occupancy necessary for persistence for a given proportional decrease in habitat by either process (i.e., $K_{\text{total,degraded or destroyed}}/K_{\text{total,pristine}}$) in landscapes of 50 patches ($N = 2000$, $\lambda_{M,\text{pristine}} = 20$). (a) Decline in metapopulation capacity for degraded (red dotted line) and destroyed (solid blue lines) landscapes. Lines show the median proportional decrease in metapopulation feasibility λ_M (i.e., the ratio in eigenvalues for each scenario, $\lambda_{M,\text{degraded}}/\lambda_{M,\text{pristine}}$ and median $\lambda_{M,\text{destroyed}}/\lambda_{M,\text{pristine}}$) and bands show bootstrapped 95% confidence intervals. As metapopulations are only viable if $\lambda_M > 1$, whereas metapopulations with a postdisturbance $\lambda_M < 1$ will eventually become extinct, we denoted this switching point for the proportional decrease in λ_M with a horizontal black line. (b) Minimum weighted patch occupancy of a metapopulation prior to any habitat loss for which it is required to persist following habitat degradation (O^* , shown by the red dotted line) and destruction (shown by the blue solid lines). \bar{x} in the dispersal legend denotes the average minimum nearest-neighbor interpatch distance. Data were binned over intervals of 5% habitat reduction.

weighted occupancy for persistence O^* to understand how occupancy in pristine landscapes informs extinction thresholds (Figure 2b). The value of this approach is that it links the initial equilibrium occupancy of a metapopulation to its extinction threshold, giving a concrete measure of how rare and abundant species (i.e., with initially low or high occupancy) respond differently to habitat destruction versus degradation. We found that O^* must initially be very high for species to persist beyond even a small amount of habitat loss by either process. This is because destruction's nonlinear impacts cause species with initially low or moderate O^* to fail to persist beyond ~35%–45% loss, even when they have high dispersal.

Patch occupancy (\bar{P}^*)

The equilibrium fraction of occupied patches, \bar{P}^* , followed a concave curve for both degradation and destruction (Figure 3a,b). The shape of this curve caused \bar{P}^* to initially decrease gradually but then drop off steeply, especially for habitat destruction. Although the extinction points where \bar{P}^* reached zero had to occur at $\lambda_M = 1$ (Figures 2a and, 3a,b), the change in \bar{P}^* with habitat

destruction and degradation was otherwise distinct from the change in λ_M . For example, decreased dispersal and increased clustering resulted in lower \bar{P}^* in pristine landscapes with identical λ_M (please refer to Appendix S1: Figure S6 for details), but was also accompanied by flattening the decline in \bar{P}^* with habitat loss. With habitat degradation, the point at which \bar{P}^* reached zero was ~78% given an initial $\lambda_M = 20$. In contrast, habitat destruction caused deterministic extinction to occur much earlier with decreased dispersal and increased clustering, as low as ~63% in random landscapes, and ~35% in more clustered landscapes for lower dispersal capabilities. In addition, the more spatial heterogeneity (limited dispersal and patch clustering), the flatter \bar{P}^* with habitat reduction, causing changes in occupancy (\bar{P}^*) alone to be an extremely poor predictor of the effects of further reducing habitat.

Transient metapopulation dynamics

Transient dynamics also differed between habitat degradation and destruction scenarios, but in opposite ways to long-term dynamics. In particular, habitat degradation

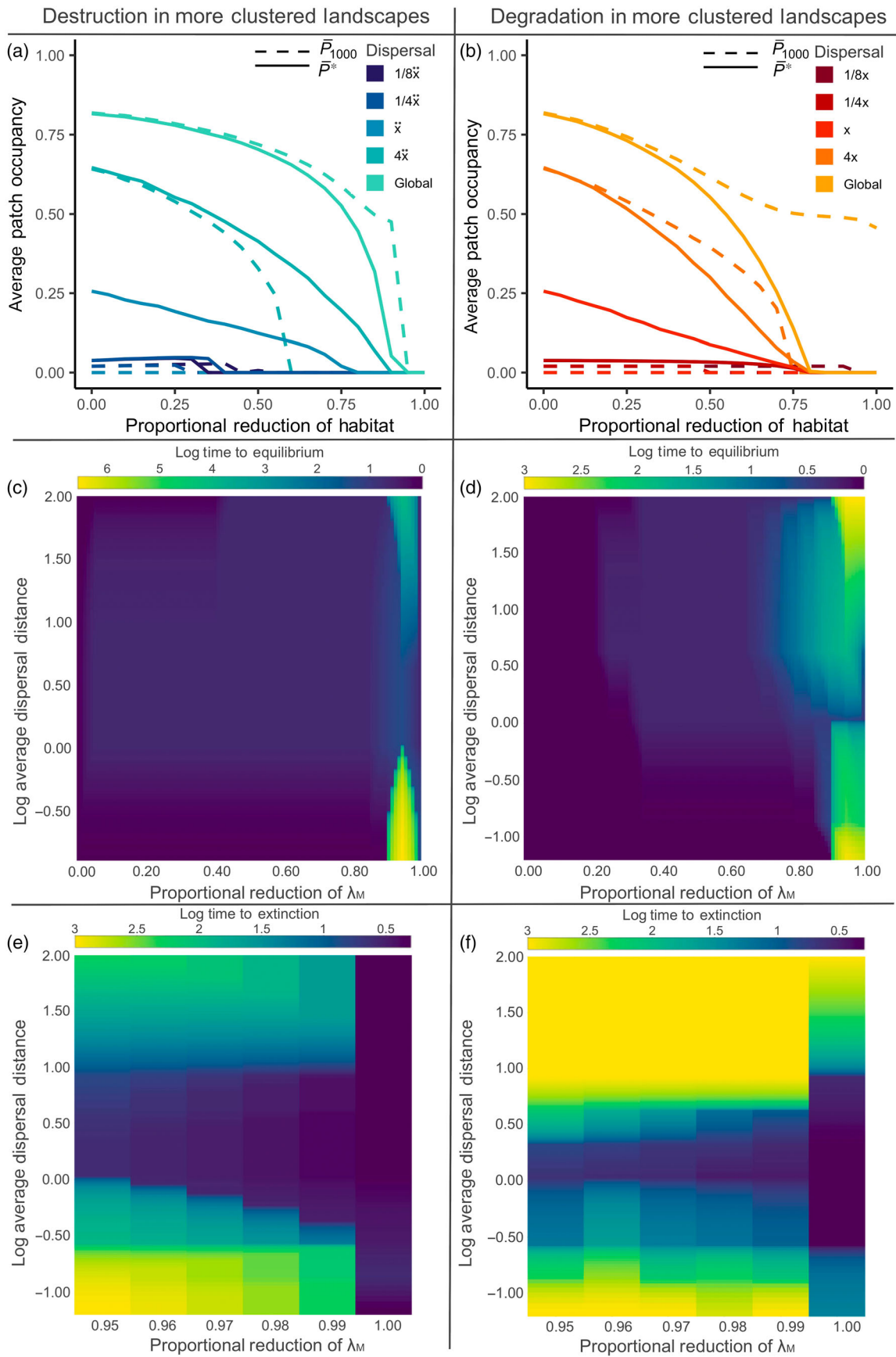


FIGURE 3 Legend on next page.

and high dispersal caused long lags in metapopulation dynamics, such that the short-term consequences of degradation appeared less severe than they were.

Simulations of degradation within landscapes revealed slow tracking of \bar{P}^* , with the average number of patches occupied 1000 generations after degradation (\bar{P}_{1000}), frequently at values well above \bar{P}^* (Figure 3b). Interestingly, these long time lags (measured by $t_{\bar{P}^*}$) were found to be especially long near the extinction threshold when dispersal was high (Figure 3d), taking 1000 or more generations before reaching the predicted equilibrium patch occupancy. In contrast, destruction caused more rapid and closer tracking of \bar{P}^* with the average number of patches occupied ~ 1000 generations after the loss of a patch falling close to \bar{P}^* , with only slight time lags to reach the predicted equilibrium patch occupancy when dispersal was high (Figure 3a,c).

For species that typically disperse the average minimum interpatch distance or less, demographic stochasticity more commonly caused extinctions more sudden and earlier than expected by \bar{P}^* for both destruction and degradation (Figure 3e,f). Therefore, degradation and destruction produced surprisingly similar patterns of stochastic extinction when dispersal was low, but diverged with degradation causing greater lags when dispersal was high.

Sensitivity to model constraints

We assessed the sensitivity of our model to the number of patches simulated and our choice of scaling $\lambda_{M_{\text{pristine}}}$. There was little qualitative difference across a 20-fold difference in the number of patches within a landscape network and across a five-fold difference in the scaling of $\lambda_{M_{\text{pristine}}}$ (Appendix S1: Figures S7 and S8), suggesting that our results were generally applicable. We noted also that SRMMs assumed that internal patch dynamics are fast relative to colonization and extinction dynamics. Rather than assess the impacts of this assumption directly, we discuss below the range of dispersal distances simulated and those results that are most robust to SRMM assumptions.

DISCUSSION

Our study revealed that habitat degradation has vastly different transient and long-term consequences than habitat destruction. Impacts of one type of global change may poorly predict the other, even if the two changes produce an equivalent loss in carrying capacity across a landscape. Species traits further moderate the effect of each global change so that habitat destruction is more detrimental for some species, whereas habitat degradation threatens others. These results led to new insights for conservation planning, monitoring changes in populations to predict the consequences of future habitat loss, the role of species traits in moderating the consequences of habitat loss, and how transient dynamics alter the potential role of evolutionary rescue. Indeed, our research showed that these distinct types of global change differentially alter two properties of metapopulation dynamics, lag times, and threshold conditions, each of which can lead to faulty management decisions.

One of the most striking predictions that emerges from our study is that the relative impact of habitat destruction and degradation changes as global change becomes more severe (Figure 2). Previous research on metapopulations has tracked the impact of progressive habitat destruction or degradation on extinction, with the explicit goal of understanding the consequences of a single type of global change (e.g., Casagrandi & Gatto, 2002; Hanski & Ovaskainen, 2000). We used simple mathematical arguments to predict that a transition in the relative impact of habitat loss and degradation must occur (Equations 3 and 4, Appendix S1: Equation S8), yet, to our knowledge, this shift in importance has not been suggested previously nor has its dependence on species traits and landscapes been explored.

Shifts in the relative importance of different global changes as habitat reduction progresses poses a clear challenge for prioritizing conservation and mitigation in response to ongoing global change. Uncertainty in the contribution of the wide range mechanisms which could put species at risk of extinction, and their synergistic effects, has led to heavy reliance on symptomatic population monitoring over mechanistic understanding (Mace et al., 2008).

FIGURE 3 Transient metapopulation response to patch destruction (a,c,e) and degradation of the landscape (b,d,f). (a) Destruction's impact on the fraction of patches occupied at equilibrium (\bar{P}^* , median shown by the blue solid lines) and average occupancy for the last 50 of 1000 simulated generations (\bar{P}_{1000} , median shown by the blue dotted lines). (b) Degradation's impact on the fraction of patches occupied at equilibrium (\bar{P}^* , median shown by the red solid dotted lines) and average occupancy for the last 50 of 1000 simulated generations (\bar{P}_{1000} , median shown by the red solid lines). (c) Mean time (e.g., years for an annual plant) for \bar{P}^* to be reached under destruction ($t_{\bar{P}^*}$). (d) Mean time for \bar{P}^* to be reached under degradation. (e) Mean time to extinction (t_{extinct}) under destruction. (f) Mean time to extinction (t_{extinct}) under degradation. All simulations used 50 patch landscapes ($N = 2000$) with $\lambda_{M_{\text{pristine}}}$ scaled to 20. \bar{x} in the dispersal legend denotes the average minimum nearest-neighbor interpatch distance. Data were binned over intervals of 5% habitat loss.

Here we show how the spatial scale at which a simple mechanism (reduction in carrying capacity) operates drives a shift in how it contributes to extinction and decline as global change progresses (Gilbert & O'Connor, 2013). Large-scale changes that decrease habitat quality are more detrimental early on, but the heightened potential for threshold drops in viability through local processes that make it increasingly difficult to measure and project future impacts.

These predictions about the change in the relative importance of habitat destruction and degradation with more severe global change has nonintuitive consequences for rare species, meaning those species that are present in a low fraction of patches even prior to any habitat reduction. Although we expected species to be most heavily impacted by global changes operating on local scales as habitat reduction progresses, the initially rapid drop in metapopulation capacity with habitat degradation caused rare species to be lost at low levels of degradation first. Indeed, only common species were predicted to remain viable beyond modest habitat reduction by either local or large-scale processes (Figure 2). This prediction agrees with empirical findings that biodiversity should be most heavily eroded early on in habitat loss (Betts et al., 2017), albeit with lags that may obscure this early erosion for some time (Hanski & Ovaskainen, 2002; Vellend et al., 2006). The reported reductions in population sizes or habitat in many regions of the world are likely to be approaching or within reach of our suggested thresholds (Betts et al., 2017).

Just as traits that determine rarity are important for predicting the impact of global changes, dispersal plays a key role in determining their relative importance. Previous research has frequently focused on the consequences of limited dispersal in scenarios of habitat destruction (Tilman et al., 1994) or degradation (Gilbert & Levine, 2013). Here we show that habitat destruction is particularly harmful for poor dispersers, whereas the impacts of degradation do not depend on dispersal ability except when dispersal is linked to rarity. As a result, our model predicted that degradation will have a large impact on rare species, regardless of dispersal ability. These differing predictions suggested that trait-based studies on poor versus good dispersers would provide a clear test of the contrasting impacts of different global changes and the possible synergistic effects between them (De Bie et al., 2012; Jones et al., 2015). Increasingly available data on species distributions and their traits are making empirical tests of these hypotheses possible, although we noted that even long-term studies have shown lagged effects that made definitive tests based on sampling data difficult (Pagel et al., 2020; Vellend et al., 2006).

Ecologists and conservation biologists are increasingly concerned about extinction debts, an extreme form of time lag that occurs when extinction is deterministic but populations show little decline for some time. Our work revealed two novel aspects of extinction debts and time lags more generally. First, habitat destruction and habitat degradation produce distinct lag dynamics, with degraded metapopulations typically showing much larger lags. This increased lag causes extinction debts following habitat degradation to persist much longer than those following habitat destruction. Most of the research on extinction debt has focused on habitat destruction (e.g., Hanski & Ovaskainen, 2000; Tilman et al., 1994), suggesting that much of the scientific literature underestimates the importance of lags and extinction debts following large-scale global change. Long extinction debts raise the possibility that evolution may rescue the metapopulation through novel mutations or new genetic combinations when extinction is driven by habitat degradation (Bell & Gonzalez, 2011). Although possible, it is important to note that degradation also leads to smaller local populations with reduced gene flow, meaning that, just as evolution becomes important for rescuing populations, genetic drift is also expected to become more important and increase the potential for loss of adaptive genotypes (Gilbert & O'Connor, 2013). In other words, habitat degradation causes conditions that both favor and limit evolutionary rescue such that its net evolutionary effect is unclear.

The pronounced time lag in metapopulation decline following habitat degradation also limits the empirical assessment of habitat reduction thresholds and extinction risk. Extensive lags in metapopulation decline following habitat degradation creates “apparent thresholds” (Figure 3). These apparent thresholds manifest as declines that are not predictable from simply monitoring populations, but are due solely to the lag between the occurrence of the event and the dynamics reflecting that change. The staggering timescales over which little change may occur in our models is consistent with estimates from field-parameterized models of extinction debt (>1000 generations) (Gilbert & Levine, 2013), and lags are particularly pronounced and important in extinction debt conditions (Figure 3f) (Hanski & Ovaskainen, 2002).

Ecological models make simplifying assumptions to predict species dynamics, and it is important to evaluate the benefits and shortcomings of those simplifications. One key assumption of the class of models we use is that local (within-patch) dynamics are fast relative to among-patch dynamics, allowing local populations to reach carrying capacity quickly, relative to colonization of new patches (Ovaskainen & Hanski, 2001). These

conditions are most clearly met when dispersal among habitat patches is limited or carrying capacities are low, meaning that the models are increasingly relevant as habitat reduction progresses and for species that are predicted to be most heavily impacted (Figures 2 and 3). Nonetheless, when local dynamics are slow relative to colonization or extinction processes, the scale at which habitats experience stressors still has important, albeit different, consequences for metacommunity dynamics (Zhang et al., 2020). A second simplifying assumption is that the impacts of global changes can be represented by a reduction in population-carrying capacity, whether it is distributed locally (habitat destruction) or on a large scale (habitat degradation). Reduction of carrying capacity at different scales appears to be general to many organisms facing global changes (Gilbert & Levine, 2013; Rosenberg et al., 2019; Stepanian et al., 2020) and offers surprisingly deep insights into the dynamical consequences of the spatial scale at which global changes function. Indeed, the generality of our approach suggests that a coarser classification of global changes may benefit global change biology in much the same way that understanding species dynamics through the lenses of their functional traits has benefited ecology.

In summary, our model predicts that different global changes have distinct dynamical and long-term consequences for populations that depend on the scale at which they reduce population abundances. These distinct consequences allow a general understanding of the types of global changes that disproportionately impact rare species and poor dispersers, and that cause sampling data to reflect past, but not current, population viability, and that may allow sufficiently long lags for evolution to alter population trajectories. Our approach highlights the necessity and promise of using attributes of global changes to develop theory, and demonstrates a need for theoretical predictions to be paired with empirical tests rather than relying on symptomatic diagnoses for conservation.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Open Research: Data and code (Walker, 2022) are available in Zenodo at <https://doi.org/10.5281/zenodo.6915287>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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