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Paths to extinction: mode of habitat loss structures extinction thresholds and debts

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Both authors conceived of the study and numerical approach. EJW created the simulation scripts and wrote the first draft of the manuscript. Both authors edited the manuscript.

All data and code are available through <https://github.com/EmmaJWalker/PathstoExtinction>.

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Abstract

Species are faced with global changes that can lead to decline and extinction through one of two routes: habitat destruction, such as occurs locally with land-use change, and habitat degradation, occurring through larger-scale changes such as nitrogen deposition or climate change. We develop theory showing, even for identical impacts on a species' total amount of habitat, these two processes have distinct consequences for species dynamics and extinction. Using metapopulation theory and simulations, we characterize these impacts through the rate of species decline with habitat reduction, extinction thresholds, and the duration of extinction debts. Habitat degradation proves particularly detrimental to rare species due to faster species declines when habitat reduction is low. While, 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 poorer dispersal steepening thresholds.

Main Text

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 (1–3). Although many species persist with no evidence of decline today, many have declined with global changes, and these declines may be the first step towards extinction as population dynamic lags and continued global changes are realized (3–6).

Habitat loss is considered the greatest cause of species extinction and decline (2, 7), but other global changes are increasingly important and may cause more cryptic loss of species (8, 9). In general, global changes act through two distinct types of impact. First, large-scale processes like climate change can create overall degradation resulting in relatively uniform reduction in population sizes across a landscape. Second, local processes (e.g., resource extraction, land-use change or point source pollution) can result in destruction of individual habitat patches (Fig. 1). Species can experience both impacts – entire landscapes that are degraded and destruction of individual habitat patches within landscapes. An important but unresolved question is whether these distinct types 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 (10, 11). Landscape heterogeneity, including host distributions for consumers and parasites, cause ubiquitous patchiness (12). Moreover, both degradation and habitat loss can force initially contiguous populations into smaller and more isolated units (13, 14). Poor understanding of how metapopulation declines may differ when habitat loss or degradation is the underlying cause poses a growing problem for conserving increasingly fragmented and declining populations.

Classic metapopulation theory suggests different consequences emerge in metapopulations that experience local habitat destruction versus those that are universally degraded (15). Numerous researchers have added ecological complexity to simple metapopulation models, trading-off realism in one ecological attribute of a model for another (16–18). For example, Casagrandi and Gatto examined relative impacts of degradation and habitat destruction for frequent versus infrequent dispersers, assuming patches are identical and dispersal redistributes individuals at random across all patches (19). However, other studies suggest the impacts of global changes likely differ when dispersal traits and habitat heterogeneity can interact as observed in nature (e.g., (17)). Ovaskainen and Hanski developed Spatially Realistic Metapopulation Models (SRMMs) that are ideally suited to understanding the role of spatial heterogeneity and global change. Their models maximise generality, spatial realism and tractability for metapopulations that have relatively fast local dynamics, where colonization occurs at a slower rate than it takes local populations to approach equilibrium (explained further in Methods) (4). Studies using SRMMs highlight the role of habitat heterogeneity on metapopulation persistence and use this to track extinction that results from habitat destruction (11, 20) or degradation (9). However, it remains unclear how the impacts of habitat destruction would compare to 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 (20, 21).

An important advance that arises from SRMMs is the derivation of two metrics that inform the long-term viability of a metapopulation, the persistence capacity (λ_m) and the invasion criterion (λ_i). The first metric translates to the stationary probability that patches of a metapopulation are occupied (P^* , the quasi-equilibrium occupancy; see ref (22)), and thus the metapopulation feasibility ($\exists P^* > 0$). Invasion capacity measures a metapopulation's rate of increase, in number of new patches colonized per patch, when it falls to very low densities (4), analogous to R_0 in models of disease spread. These metrics are extremely important for empiricists as well as theorists – extinction debts frequently arise in metapopulations, meaning that the last sub-

population to disappear does so hundreds of years after metapopulations begin deterministic extinction trajectories (9, 16, 20). As a result, understanding the response of these metrics to global change impacts is essential to predicting long-term viability of metapopulations.

The spatially explicit version of Levins' classic metapopulation model (eqn. S1) arises in many systems described by continuous or discrete time dynamics and can be used to assess the long-term viability of metapopulations following global change. This model produces identical solutions for λ_m and λ_i , which are defined as the leading eigenvalue of the transition matrix. Although the transition matrix differs depending on the model specifics, it has a general form with diagonal elements equal to zero and non-diagonal elements:

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

Where E_i is the extinction rate of patch i , and C_{ij} is its colonization rate from donor patch j . The parameter d_{ij} is the distance between the donor patch j and the focal patch i , K denotes patch carrying capacity, and α and h are species-specific parameters that describe dispersal rates and composite traits relating to establishment and extinction probabilities (see Supplementary for model assumptions and precise parameter definitions). Importantly, eqn. 1 allows us to see that the transition matrix is sensitive to degradation through ubiquitous reductions in carrying capacity, causing metapopulations to respond to habitat degradation in a predictable way:

$$\lambda_{M_{degraded}} = \lambda_{M_{pristine}} * (1 - \omega)^2 \quad (2)$$

where ω is the proportion of patch carrying capacity lost through degradation (Supplementary) and the persistence capacity (λ_m) is the leading eigenvalue of the transition matrix. 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 (23, 24):

$$\lambda_{M_{destruction}} \approx \lambda_{M_{pristine}} * (1 - \omega) \quad (3)$$

But equation 3 only holds for globally dispersing species in highly uniform landscapes. In spatially heterogeneous landscapes, habitat destruction changes the spatial configuration of patches and interpatch distances, causing additional impacts through the exponentiated distance term (eqn. 1). Comparing eqns (2) and (3) illustrates that when an initially intact metapopulation experiences small amounts of destruction or degradation, the long-term impacts of degradation are expected to be far worse (Fig. 2). However, the impact of habitat destruction changes as metacommunities become more fragmented and, in the extreme case, no species can persist in a single patch even though some may persist in an equally degraded landscape (Supplementary eqn. S8). Indeed, unless species can disperse easily across a landscape, λ_m will be highly non-linear as habitat destruction progresses (Fig. 2).

The different long-term dynamics associated with habitat degradation and destruction may also generate important differences in transient dynamics following global change. Habitat destruction can lead to an extinction debt, or more generally a lag between when a change is imposed and when its long-term consequences are expected to occur (11, 16). Such lags can also occur with habitat degradation (9), but the transition probabilities that govern the lags differ. Habitat degradation causes network-wide changes to both colonization and extinction rates but these are compounded across all patches. In the case of habitat destruction, local extinction rates are unchanged, but colonization rates are necessarily changed for some patches and rates are compounded across fewer patches. The lags associated with these qualitatively different changes in transition probabilities are unclear, making it impossible to generalize about transient dynamics and extinction debts following global changes despite their clear importance for management and protection of species (25).

In this paper, we couple analytic methods (eqns. 1, 2) 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) Do the relative impacts of these two processes depend on species dispersal abilities and species' abundances prior to disturbance? 3) Do habitat destruction and degradation generate distinct transient dynamics and, if so, which process is expected to produce larger lags and extinction debts? We make use of a SRMM version of Levins model, using a discrete time formulation for stochastic simulations (4, 9), and test these models on simulated landscapes ranging in spatial heterogeneity (patch clustering; (17)). 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 initial metapopulation size. However, degradation often generates long-time lags, meaning that extinction debts are more likely with habitat degradation but may not be realised if species can adapt quickly.

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 lead us to these conclusions.

Metapopulation persistence capacity and invasion capacity (λ_M)

Our analytical predictions for persistence capacity (eqn. 3,4) were supported and showed far greater impact of habitat degradation than habitat destruction when the focal species dispersed equally to all patches (Fig. 3). Even when dispersal was more limited and habitats were heterogeneous, habitat degradation was always initially worse than destruction (Fig. 3A). However, habitat destruction had a more negative impact as spatial heterogeneity increased, with heterogeneity driven by both limited dispersal and patch clustering (compare panels and shading in Figs. 3A and S1). Habitat destruction caused a sigmoidal decline in λ_M , with destruction initially causing almost no change in λ_M , followed by a rapid drop (Fig. 3A). 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 this sigmoidal decline in λ_M , a metapopulation subjected to destruction often had a much greater persistence capacity just before the crossover at which its relative impact surpassed that of degradation, but a far lower persistence capacity just after the crossover (Fig. 3A).

The crossover point at which the negative impacts of habitat destruction surpassed those of habitat degradation varied from 35 – 99%, with the crossover happening at the lowest levels in clustered landscapes when average dispersal distances were less than the mean minimum interpatch distance (Fig. 3A). Increasingly uniform distributions of patches further shift the crossover such that degradation has larger impact at almost all levels of loss (Supplementary).

Overall, the predicted decline of the metapopulation persistence capacity with degradation (eqn. 3) held for all levels of degradation. Similarly, the decline in persistence capacity followed a near 1:1 linear decline for species' with extremely high dispersal abilities in more uniform landscapes (eqn. 4; Fig S1 lightest shaded line). This linear decline with habitat destruction became increasingly sigmoidal with greater spatial heterogeneity.

Rarity and Extinction

The stationary occupancy of patches (P^*) can also be used to understand how occupancy in pristine landscapes informs extinction thresholds. Since patch occupancy will be zero where $\lambda_{M_{final}}/\lambda_{M_{pristine}}$ crosses the extinction threshold, the minimum scaling of $\lambda_{M_{pristine}}$ (eqn. 2) and subsequent effect on P^* (eqns. 5, 6) can be calculated (Fig. 3 B). The value of this approach is that it links the initial abundance (occupancy) of a metapopulation to its extinction threshold, giving a concrete measure of how rare and abundant species respond differently to habitat destruction versus degradation. Here P^* represents a spatially weighted patch occupancy as opposed to an average patch occupancy (Fig. 3 B), but these measures are monotonically related for a given landscape. We found that P^* must initially be very high for species to persist beyond even small amounts of habitat loss by either process. This is because destruction's nonlinear impacts cause species with initially low or moderate P^* to fail to persist beyond ~35 – 45% loss, even with high dispersal.

Average proportion of patches occupied at equilibrium (\bar{P}^*)

The expected occupancy of patches, \bar{P}^* , followed a concave curve for both degradation and destruction (Fig. 4 A and 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 $\lambda_M = 1$ (Figs. 3 A, 4 A and 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 (see Supplementary 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. 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. Habitat degradation 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}^* (Fig. 4 B). Interestingly, these long time-lags (measured by $t_{\bar{P}^*}$) were found to be especially long near the extinction threshold when dispersal was high (Fig. 4 D) taking up to 1000 or more generations before reaching the predicted equilibrium patch occupancy. In contrast, destruction revealed 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 (Fig. 4 A and C).

For species dispersing at the average minimum interpatch distance or smaller, demographic stochasticity more commonly caused sudden and earlier extinctions than expected by \bar{P}^* for both destruction and degradation (Fig. 4 E and F). Thus, degradation and destruction produce surprisingly similar patterns of stochastic extinction when dispersal is low, but diverge 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 scaling of $\lambda_{Mpristine}$. There was little qualitative difference across a twenty-fold difference in the number of patches within landscape networks and across a five-fold difference in scaling of $\lambda_{Mpristine}$ (Fig. S5-S6), suggesting our results are generally applicable. We note also that SRMMs assume 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 reveals 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, while habitat degradation threatens others. These results lead 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 shows 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 the relative impact of habitat destruction and degradation changes as global change becomes more severe (Fig. 3). 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., (20, 28)). We used simple mathematical arguments to predict that a transition in the relative impact of habitat loss and degradation must occur (eqns. 3, 4, 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 mitigating responses 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 (27). Here we show 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 (12). Large scale changes decreasing habitat quality are more detrimental early on, but the heightened potential for threshold drops in viability through local processes 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 non-intuitive consequences for rare species. While we expect 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 causes rare species to be lost at low levels of degradation first. In our study, this is always true for species initially occupying <50% of habitable patches. Indeed, only common species are predicted to remain viable beyond modest habitat reduction by either local or large-scale processes (Fig. 3). This prediction agrees with the empirical findings of Betts et al. (28), that biodiversity should be most heavily eroded early on in habitat loss, albeit with lags that may obscure this early erosion for some time (11, 29). The reported reductions in population sizes or habitat in many regions of the world are likely approaching or within reach of our suggested thresholds (28).

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 (16) or degradation (9). Here we show 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 predicts that degradation will have a large impact on rare species regardless of dispersal ability. These differing predictions suggest that trait-based studies on poor versus good dispersers would provide a clear test of the contrasting impacts of different global changes and possible synergistic effects between them (30, 31). Increasingly available data on species distributions and their traits are making empirical tests of these hypotheses possible, although we note that even long-term studies have shown lagged effects that make definitive tests based on sampling data difficult (29, 32).

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 reveals 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 focussed on habitat destruction (e.g., see refs (16, 20)), 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 (33). 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 (12). 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 empirical assessment of habitat reduction thresholds and extinction risk. Extensive lags in metapopulation decline following habitat degradation creates 'apparent thresholds' (Fig. 4). These apparent thresholds manifest as declines that are not predictable from symptomatic sampling, 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) (9), and lags are particularly pronounced and important in extinction debt conditions (Fig. 3F) (11).

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 (4). 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 (Figs. 3,4). A second simplifying assumption is that the impacts of global changes can be represented by a reduction in population carrying capacity, be it distributed locally (habitat destruction) or at large scales (habitat degradation). Reduction of carrying capacity at different scales appears to be general to many organisms facing global changes (6, 9, 34), 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. The distinct consequences allow a general understanding of the types of global changes that disproportionately impact rare species and poor dispersers, that cause symptomatic sampling to be an unreliable predictor of future 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.

Materials and Methods

Landscape Creation

Landscapes with more uniform, random and clustered patch distributions were created with lognormally distributed patch areas with a log(mean) of 2 and standard deviation of 1. Clustering was implemented using 500 iterations of a clustering algorithm akin to Adler and Nuernberger's, which we briefly outline (17).

To randomly distribute patches, x and y coordinates within a 100 by 100 grid were randomly chosen. Connectivity in terms of distance between patches was defined as

$$D_i = \sum e^{-d_{ij}}$$

Where d_{ij} is the distance between patches i and j . More clustered landscapes were created by subsequently picking up and moving randomly selected patches to a new randomly selected location if this connectivity to other patches was found to increase. For more uniform (evenly spaced) landscapes, the same process was carried out if this connectivity to other patches in terms of distance was found to decrease. This procedure was run for a set number of iterations (500) until the desired degree of clumping/de-clumping was achieved as measured by the skew and kurtosis of the distribution of minimum interpatch distances (Fig. S2). We also ensured that no patches overlapped throughout this process.

Varying dispersal (α)

100 test landscapes of 50 and 500 patches were initially created, and from these test landscapes α values (1/the average dispersal distance) were chosen 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 8x, 4x, 2x, 1x, 1/2x, 1/4x, 1/8x 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 results in more uniform landscapes exhibiting longer nearest neighbour distances than more clustered landscapes. This is because the clustering algorithm we chose moves patches closer together to increase clustering and moves patches further apart to increase uniformity. By varying α appropriately, we account for this difference in nearest neighbour distances across landscape types to test purely for how differences in heterogeneity of interpatch distances alter the impact of habitat destruction and degradation.

Calculating metapopulation metrics: λ_m , λ_i and P^*

For the Spatially Realistic Levin's Model, a metapopulation's persistence capacity, λ_m , is equal to its invasion capacity, λ_i , thus both are denoted here by the persistence capacity λ_m . These metrics are obtained by calculating the leading eigenvalue of the transition matrix with non-diagonal elements given in eqn. (2) and diagonal elements of zero, since patches do not colonize themselves (Supplementary Information).

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 simply iterating

$$p^{n+1} = f(p^n) \quad (5)$$

Where f is given by

$$fi(P) = \frac{c_i(P)}{c_i(P) + E_i(P)} \quad (6)$$

This approach (see ref. 4) allows us to use the mean P^* to determine the expected mean occupancy of the metapopulation (\bar{P}^*).

Simulating metapopulation dynamics to obtain metrics: \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 (see Supplementary for details), to obtain the average patch occupancy for the last 50 of 1000 generations (\bar{P}_{1000}) following each level of habitat degradation and destruction. We also quantified the generational time until the expected \bar{P}^* was reached ($t_{\bar{P}^*}$), and time to extinction ($t_{extinct}$), if it occurred within this timeframe. 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. Thus, we have a measure of how the long-term metapopulation size after ~1000 years (\bar{P}_{1000}) responded, and how long it took for equilibrium dynamics and extinction to be reached ($t_{\bar{P}^*}$ and $t_{extinct}$ respectively), for greater and greater perturbations of habitat loss from an initial pristine landscape.

Landscape destruction and degradation

An iterative procedure was developed in R 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 were generated. Initially, for each pristine landscape, λ_M was scaled by an appropriate ratio of species-specific extinction to colonization parameters (e/c ; Eqn. S7) to achieve the same initial value of λ_M for all landscapes. This allowed us to compare changes from this initial $\lambda_{Mpristine}$ across landscapes. For our simulations, $\lambda_{Mpristine}$ was scaled to 20, and results for landscapes of 50 patches were recalculated, with $\lambda_{Mpristine}$ scaled to 100 to ensure that this arbitrary choice of $\lambda_{Mpristine}$ 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 patch area in the pristine metapopulation, the second landscape had all carrying capacities decrease by 3%. Metapopulation metrics were calculated, and then the habitat loss and degradation process was repeated 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 (Fig. S5).

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

All simulations were analysed using median change in $\lambda_{Mfinal}/\lambda_{Mpristine}$, \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 (Fig. S3), and our interest was whether the majority of each metrics' results were higher or lower for destruction than degradation (aka which is worse for each landscapes case) more so than the average magnitude of difference (since this is likely highly dependent on individual landscapes). Because patch areas and thus exact percent habitat loss differed amongst simulations, we binned results to calculate the median value of each metric for a given percent loss. Confidence intervals of the median were calculated by bootstrapping.

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Figures and Tables

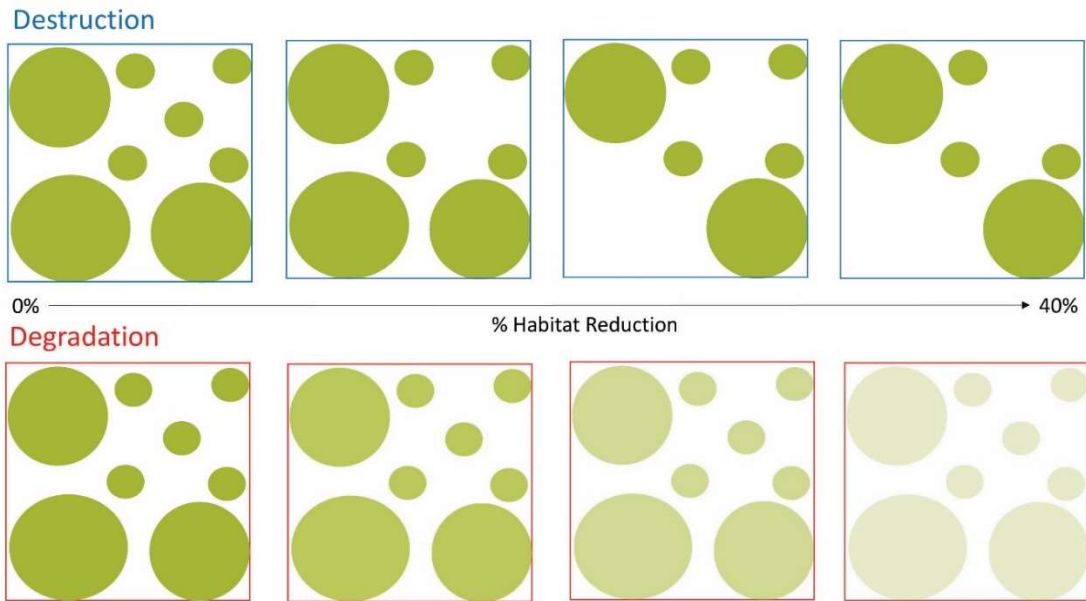


Figure 1. An illustration of the two extreme scales on which global changes act: local destruction (e.g. resource extraction, land-use change or point source pollution) resulting in a loss of individual habitat patches versus overall degradation (eg. climate change) reducing habitat quality (or carrying capacity) across a landscape.

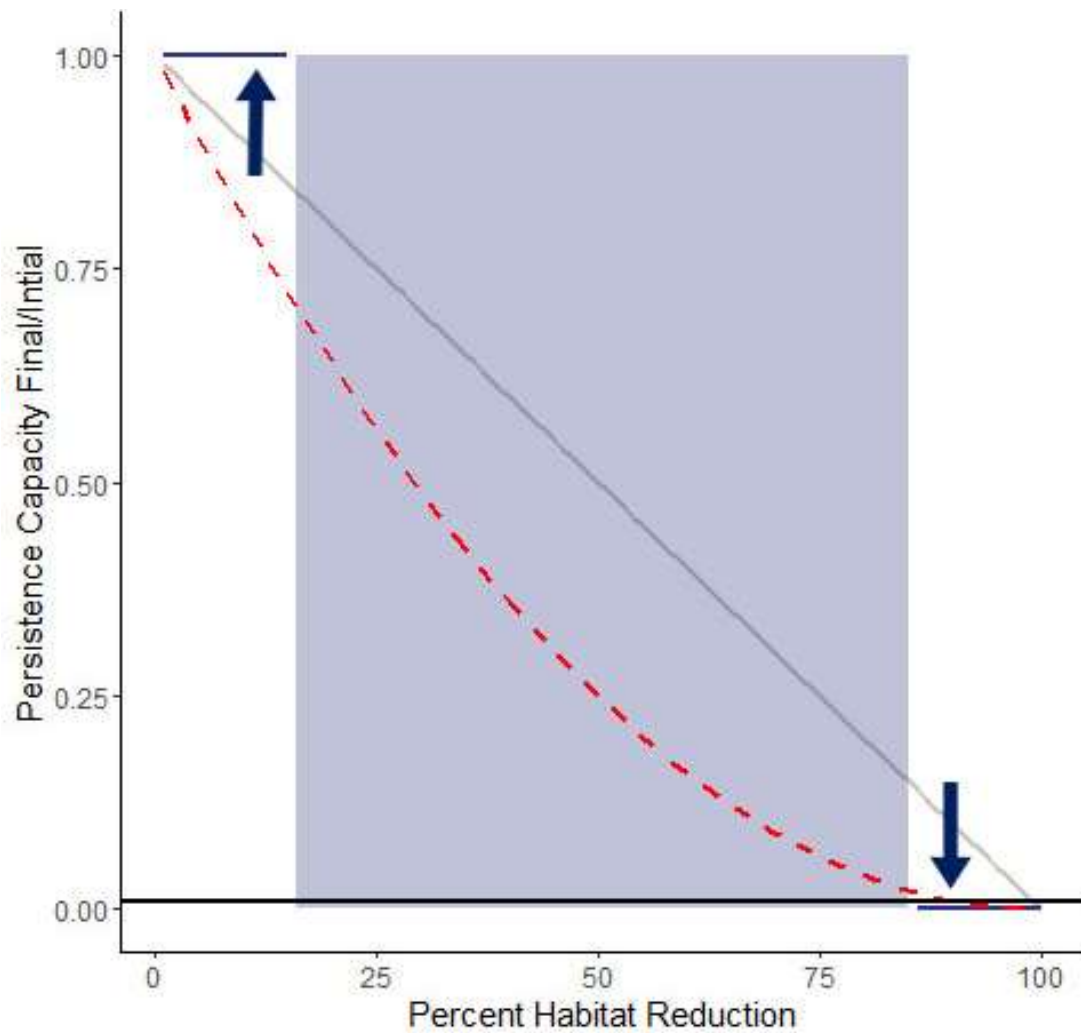


Figure 2. Illustration of the predicted decline of the metapopulation persistence capacity, $\lambda_{M_{final}}/\lambda_{M_{initial}}$, as habitat is degraded (red dashed line) versus individual habitat patches are destroyed from a completely uniform landscape with global dispersal (grey solid line) versus destroyed from a highly heterogenous landscape (solid blue line, indicated by blue arrows, broken by the solid blue region in which relative impacts are unknown).

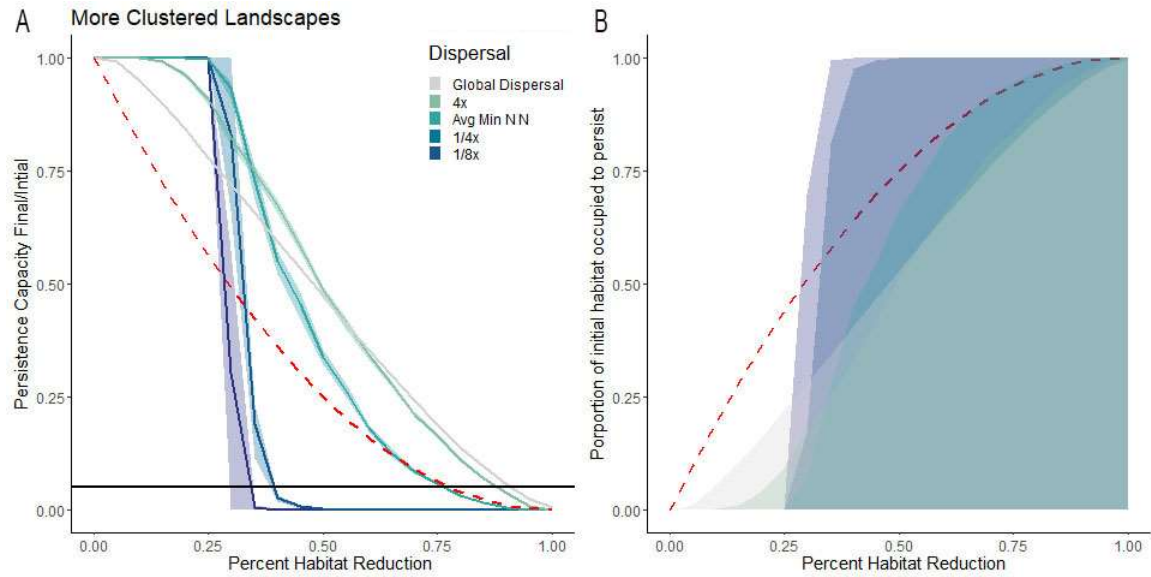


Figure 3. Impact of degradation and destruction on persistence capacity and initial occupancy necessary for persistence for a given level of habitat reduction in landscapes of 50 patches ($N=2000$, $\lambda_{M_{pristine}}=20$). A) Decline in metapopulation capacity for degraded (red dotted line) and destroyed (solid blue lines) landscapes. Lines show the median ratio in eigenvalues for each scenario ($\lambda_{M_{degraded}}/\lambda_{M_{pristine}}$ and median $\lambda_{M_{destroyed}}/\lambda_{M_{pristine}}$) and bands show bootstrapped 95% confidence intervals. B) Initial patch occupancy allowing persistence for a given amount of habitat degradation (P^* , shown by the area beneath red dotted line) and destruction (shown by the blue shaded regions.). Data was binned over intervals of 0.05% habitat reduction.

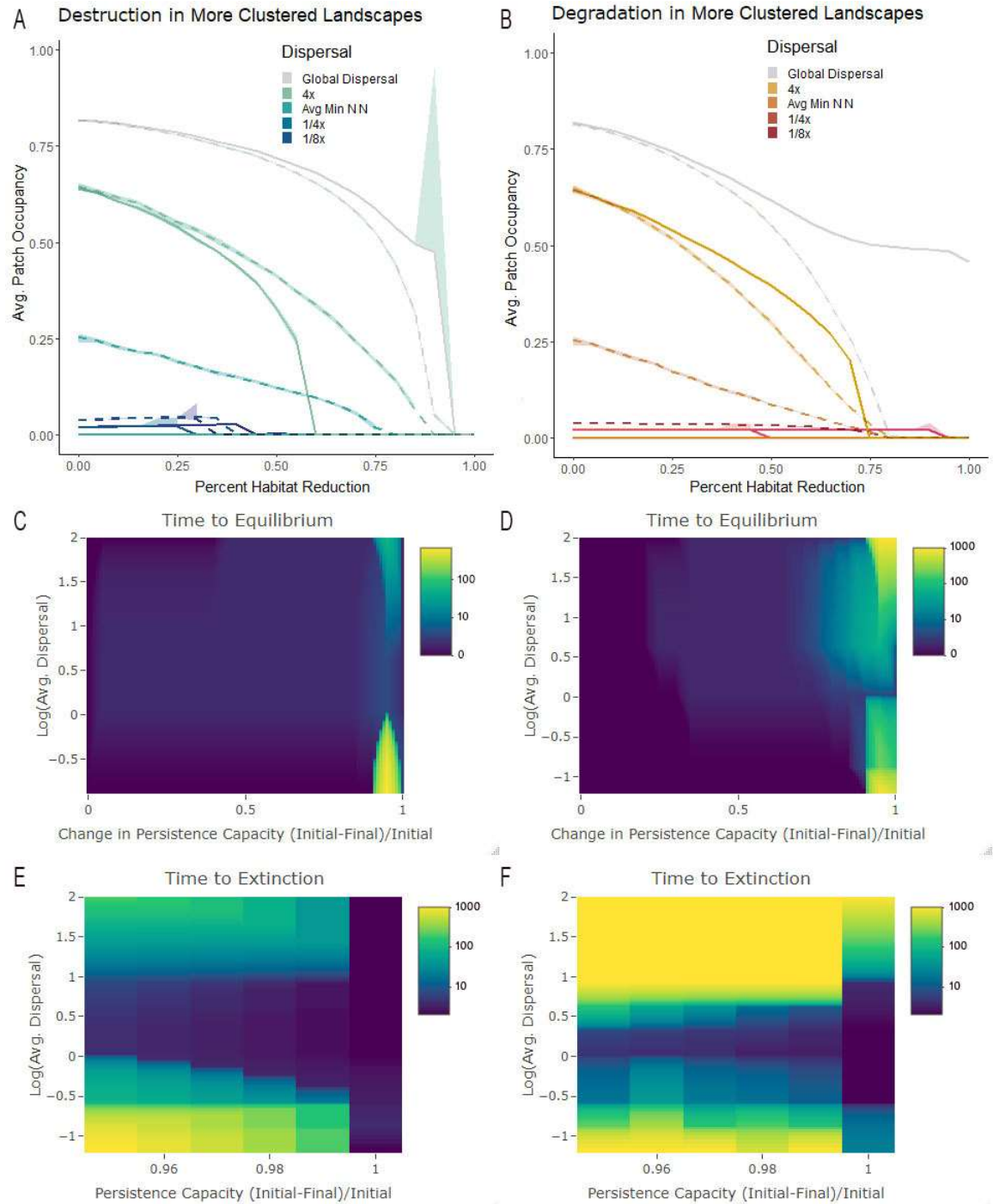


Figure 4. Transient metapopulation response to patch destruction (A,C,D) and degradation of the landscape (B,D,F). A) Destruction's impact on the median average expected probability patches occupied at equilibrium (expected \bar{P}^* , shown by the blue dotted lines) and average occupancy for the last 50 of 1000 simulated generations (\bar{P}_{1000} , shown by the blue solid lines). B) Degradation's impact on the median average expected probability patches occupied at equilibrium (average P^* , shown by the blue dotted lines) and average occupancy for the last 50 of 1000 simulated generations (average \bar{P}_{1000} , shown by the blue solid lines). C) Mean time (eg. years for an annual plant) for expected \bar{P}^* to be reached under destruction (t_{P^*}). D) Mean time for expected \bar{P}^* to be reached under degradation. E) Mean time till extinction (t_{extinct}) under destruction. F) Mean time till

extinction (t_{extinct}) under degradation. All across 50 patch landscapes (N=2000). $\lambda_{M_{\text{pristine}}}$ was scaled to 20. Data was binned over intervals of 0.05% habitat loss.