Functional Ecology
British Ecological Society

Functional Ecology 2016, **30**, 1558–1567 doi: 10.1111/1365-2435.12632

Reconciling contradictory relationships between mobility and extinction risk in human-altered landscapes

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Summary

1. Some empirical and theoretical studies suggest that more mobile species are less at risk in human-altered landscapes, while others suggest the opposite.

2. We propose three novel hypotheses to explain these contradictory findings: (i) extinction risk increases with increasing mobility when mobility is measured as emigration, but decreases with increasing mobility when mobility is measured as immigration; (ii) the most mobile species (whether measured by emigration or immigration) in unaltered landscapes are least mobile in human-altered landscapes, so the relationship between mobility and risk is opposite when mobility is measured in unaltered and altered landscapes; and (iii) the mobility–risk relationship is ∩-shaped; thus, the relationship is apparently positive when studied species have low-to-intermediate mobility, but negative when species have intermediate-to-high mobility. We also evaluate a fourth hypothesis that had been previously theorized: that some landscape structures drive evolution of dispersal characteristics that increase both mobility and risk, while others drive evolution of characteristics that increase mobility and decrease risk.

3. To evaluate these four hypotheses, we created an individual-based, spatially explicit simulation model to simulate population dynamics, evolution of dispersal characteristics and species response to habitat loss.

4. Our simulations supported the first and fourth hypotheses. Extinction risk increased with emigration rate but decreased with immigration rate. Species in landscapes with historically more abundant, less fragmented habitat and more frequent disturbance had increased risk and mobility during habitat loss, while species in landscapes with lower matrix quality had increased risk and decreased mobility.

5. *Synthesis*. This is the first study to investigate why some studies find that more mobile species are less at risk in human-altered landscapes, while others find the opposite. Our results suggest that these contradictory relationships occur because of differences in how mobility is measured and differences in the historic structure of species' landscapes. Understanding how mobility and the historic landscape influence extinction risk can help us identify species of conservation concern. Our results suggest that we should focus on species with high emigration rates but low immigration rates, and those that evolved in landscapes with non-fragmented habitat and high-risk matrix.

Key-words: dispersal, emigration, habitat fragmentation, habitat loss, immigration, land use, movement, population persistence

Introduction

If we could predict which species are most at risk in human-altered landscapes, we would be able to focus our limited resources for conservation on these species. Empirical studies suggest that large-bodied, specialist species with low fecundity and limited geographic ranges are most at risk of extinction in human-altered landscapes (e.g.Vance, Fahrig & Flather 2003; Kotiaho *et al.* 2005; Davidson *et al.* 2009). In addition, several studies suggest that extinction

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*Correspondence author. E-mail: Amanda.Martin@glel.carleton.ca risk is related to species mobility, where 'mobility' refers to the tendency to leave the current home range or territory (i.e. emigrate) and the likelihood of settling in a different habitat patch (i.e. immigrate). However, these studies report both greater extinction risk (Gibbs 1998; Shahabuddin & Ponte 2005; Van Houtan *et al.* 2007) and lower extinction risk (Kotiaho *et al.* 2005; Reinhardt *et al.* 2005; Jiguet *et al.* 2007) for more mobile species. The purpose of this study was to evaluate four hypotheses, described below, that might explain these contradictory findings: (i) the metric type hypothesis, (ii) the metric context hypothesis, (iii) the metric range hypothesis and (iv) the historic landscape hypothesis.

METRIC TYPE HYPOTHESIS

There is little consensus on how to measure mobility. Metrics include direct measurements of emigration rate, dispersal distance and immigration rate (Jiguet *et al.* 2007; Van Houtan *et al.* 2007; Öckinger *et al.* 2009), and indirect measures such as expert opinion and wing shape (Kotiaho *et al.* 2005; Shahabuddin & Ponte 2005). We hypothesize that whether a mobile species is more or less vulnerable to human landscape change than a sedentary species depends on whether the measure of mobility is essentially related to emigration or immigration (Fig. 1). Although individuals must emigrate before they immigrate, emigration does not equal immigration, because emigrants can settle in a new location within their home habitat patch, or die during dispersal (Fig. 1). This hypothesis predicts that mobility increases extinction risk when mobility is measured as emigration, and mobility decreases extinction risk when mobility is measured as immigration. This is because the emigration rate reflects the impact of dispersal mortality on population persistence, while the immigration rate reflects the population's ability to recolonize local extinctions and rescue small populations (Brown & Kodric-Brown 1977; Hanski 1998; Fahrig 2001).

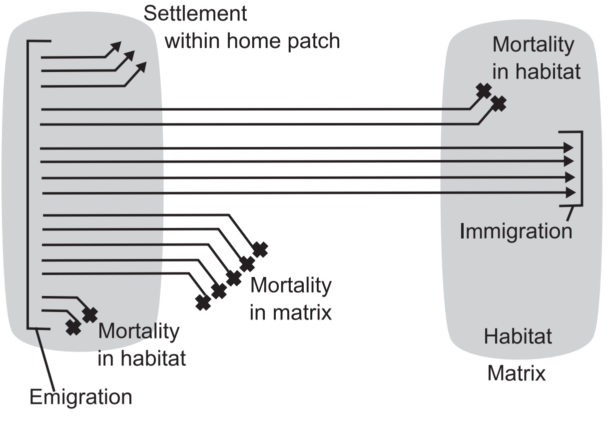

Fig. 1. Depiction of emigration, that is exit from the current home range or territory, and immigration, that is when the individual leaves its current home range or territory and settles in a different habitat patch. Emigration does not equal immigration, because emigrants can settle in a new location within their home habitat patch or die during dispersal. Mortality can occur while searching for a place to settle within habitat or during movement through matrix (non-habitat) areas of the landscape.

Since these different components of mobility (i.e. emigration and immigration) may have different effects on species extinction risk, hereafter, we use 'emigration' or 'immigration' when referring to only one component of mobility, and we reserve use of the term 'mobility' for cases where we are referring to some combination of both emigration and immigration. Note that for most empirical studies, we do not differentiate between the components of mobility, because we do not know whether the measure the authors used (e.g. expert opinion, body size) is most related to emigration or immigration.

METRIC CONTEXT HYPOTHESIS

The metric context hypothesis proposes that the relationship between mobility (measured as either emigration or immigration) and extinction risk in human-altered landscapes depends on whether the measure of mobility was taken in a human-altered landscape or in an unaltered landscape that resembles the species' historic landscape. Altering the landscape, for example through habitat loss, changes the mobility of a species, and the degree of change in mobility may depend on how mobile the species is to start with. Species that emigrate more frequently in their historic landscape will be particularly vulnerable to dispersal mortality in the altered landscape, causing the emigration rates of these species to decline more than those of species that emigrate infrequently. Increases in immigration rates in response to habitat loss and fragmentation may be larger for species with historically lower immigration rates, because these species are more sensitive to declining patch sizes and need to increase dispersal among habitat fragments to avoid the negative effects of small patch sizes (Öckinger *et al.* 2009). If these effects are large, the most mobile species before landscape change might become the least mobile species after landscape change. This would mean that the relationship between mobility and extinction risk would be opposite if mobility is measured in an unaltered landscape vs. if mobility is measured in a human-altered landscape. In particular, extinction risk would (i) increase with emigration rate when emigration rate is measured in human-altered landscapes (see Metric type hypothesis, above), but decrease with emigration rate when measured in unaltered landscapes, and (ii) decrease with immigration rate when immigration rate is measured in human-altered landscapes, but increase with immigration rate when measured in unaltered landscapes.

METRIC RANGE HYPOTHESIS

The metric range hypothesis says that the direction of the cross-species mobility–risk relationship depends on the range of mobilities represented by the different species in a given study, because the true relationship between species mobility and extinction risk is nonlinear. Thomas (2000) found that butterfly species with intermediate mobility were at greater risk of extinction than either sedentary or highly mobile species. Species with intermediate emigration and immigration rates may be at greatest risk because they disperse enough to be at risk from increased dispersal mortality in the human-altered landscape, but not enough for the benefits of immigration (recolonization and rescue of small populations) to outweigh the cost of emigration (dispersal mortality). If species with intermediate mobility are at greatest risk of extinction, then the direction of the mobility–risk relationship should depend on the range of mobilities represented by the different species in the study. The mobility–risk relationship will be apparently positive when the study includes sedentary species to moderately mobile species, but the mobility–risk relationship will be negative when the study includes moderately mobile species to highly mobile species.

HISTORIC LANDSCAPE HYPOTHESIS

The historic landscape hypothesis argues that a species' dispersal characteristics depend on the landscape in which it evolved, that is its 'historic' landscape (Fahrig 2007b). Extinction risk in human-altered landscapes will then depend on these evolved dispersal characteristics. Differences in the mobility–extinction risk relationship will arise if some historic landscape attributes drive the evolution of dispersal characteristics that increase both mobility and extinction risk in human-altered landscapes, while others drive evolution of characteristics that increase mobility and decrease extinction risk in human-altered landscapes.

Materials and methods

To address our four hypotheses, proposed to explain the contradictory findings on the role of mobility in extinction risk, we created an individual-based, spatially explicit simulation model in the NetLogo programming language and modelling environment (Wilensky 1999). We simulated population dynamics and evolution of dispersal characteristics in different historic landscape types, varying in habitat amount, habitat fragmentation, matrix (i.e. non-habitat) quality and disturbance frequency. We then subjected each landscape (and its population with optimal, evolved dispersal characteristics) to habitat loss. For the metric type hypothesis, we measured mobility during habitat loss as both emigration and immigration, and related extinction risk to mobility measured in both ways. For the metric context hypothesis, we again related extinction risk to mobility measured as emigration and immigration, but this time we took measurements in landscapes both before habitat loss began and during habitat loss. For the metric range hypothesis, we related extinction risk to the emigration and immigration rates during habitat loss, using quadratic polynomial regression to allow for nonlinear relationships. For the historic landscape hypothesis, we compared the emigration–extinction risk and immigration–extinction risk relationships for different historic landscape types.

SIMULATION OF EVOLVED DISPERSAL CHARACTERISTICS IN HISTORIC LANDSCAPES

We simulated population dynamics and evolution of dispersal characteristics in artificial landscapes over 1000 generations. Four dispersal characteristics were modelled as independent, heritable traits: (i) dispersal probability, that is the probability that an individual leaves its current habitat location, (ii) path straightness in matrix, (iii) path straightness in habitat and (iv) probability of boundary crossing, that is the probability of crossing from habitat to matrix when a dispersing individual encountered a habitat–matrix boundary. See Fig. 2a and Appendix S1 in Supporting Information for flow charts and summary of model parameters.

Each simulation started with the creation of an artificial, historic landscape and an initial population. Each historic landscape was defined by its habitat amount, habitat fragmentation, matrix quality and disturbance frequency. The landscape was a square 127 × 127 (16 129) grid of habitat and matrix cells. The differences between habitat and matrix were that reproduction could only occur in habitat cells, and dispersal mortality was lower in habitat than matrix. All habitat cells were of equal quality, that is each habitat cell was able to support the same number of individuals and had the same probability of dispersal mortality. We used a fractal surface, generated through midpoint displacement, to assign cells as habitat or matrix (Fig. 3; Saupe 1988). We did this by superimposing the fractal surface on the landscape and assigning the required proportion of cells (as defined by the habitat amount parameter) with the highest fractal values as habitat. All remaining cells were matrix. Habitat fragmentation was controlled by the Hurst exponent (H), where H determines the autocorrelation in the fractal surface. Matrix quality was assigned as the probability of mortality in matrix cells. We then identified habitat patches as groups of contiguous habitat cells, based on a Moore neighbourhood rule, and assigned each patch a disturbance interval, that is number of generations until disturbance. Each disturbance interval was randomly drawn from a Poisson distribution, with a mean equal to the disturbance frequency. For each simulation run, we seeded the landscape with one individual per habitat cell. Each individual was assigned a random value for each of its

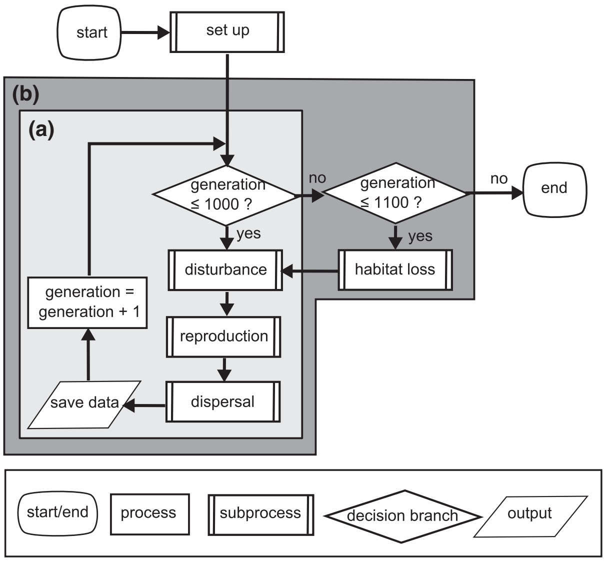

Fig. 2. The sequence of events for the simulation model, simulating (a) evolution of dispersal characteristics in historic landscapes, and (b) population persistence in response to habitat loss. See Appendix S1 for flow charts for each of the five subprocesses.

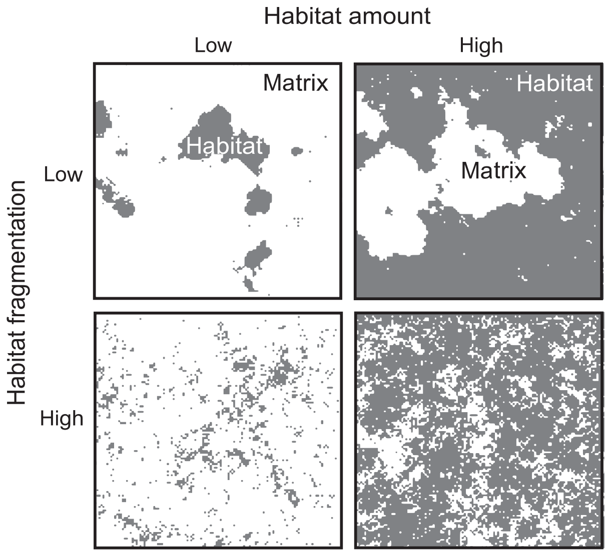

Fig. 3. Examples of the simulated historic landscapes, varying in habitat amount, that is the proportion of the landscape in habitat, and habitat fragmentation, that is how clumped or distributed habitat is, for a given habitat amount. Cells in a 127 × 127 grid landscape were assigned as either habitat or matrix (non-habitat), based on values of a fractal surface, generated through midpoint displacement (Saupe 1988). The fractal surface was superimposed on the landscape, and the proportion of cells with the highest fractal values were assigned as habitat (i.e. the habitat amount). All remaining cells were matrix. Habitat fragmentation was controlled by the Hurst exponent (H) for the fractal surface, where lower H result in more fragmented habitat.

four genetically determined dispersal characteristics. The starting habitat cell for each individual was selected at random.

Each generation involved (i) habitat disturbance, (ii) reproduction, including transfer and mutation of dispersal genotypes and (iii) dispersal, that is movement of individuals from their birth place, resulting in either dispersal mortality or settlement in a new location.

Disturbance caused death of all individuals in a habitat patch. When a habitat patch reached its disturbance interval, it was disturbed, after which a new disturbance interval was selected from the Poisson distribution.

After disturbance, adults in habitat reproduced, assuming an asexual, haploid species. The number of offspring produced by each adult was randomly drawn from a Poisson distribution, where the mean for cell *i* in generation *t* was

$$\mu_{i,t} = \lambda/(1 + a \times N_{i,t}),$$

where $a = (\lambda - 1)/k$, λ = intrinsic growth rate, k = cell carrying capacity and $N_{i,t}$ = number of adults in cell i at generation t (Hassell 1975). Offspring inherited the parental genotype for the four dispersal characteristics. Genes could mutate during reproduction. A mutation randomly increased or decreased the value of the dispersal characteristic by 0·01. All adults died after reproducing.

Each juvenile dispersed or not, depending on its genetically determined dispersal probability. There was no time- or distance-limit imposed on dispersing individuals, that is a dispersing individual kept moving until it either settled in a new habitat cell or died. Dispersal could be within or between habitat patches, but was limited to movements within the bounds of the landscape; if a movement step would take an individual outside the landscape, a new direction was randomly selected such that it would remain within the landscape. Use of a bounded landscape can potentially cause differences in dispersal patterns and habitat occupancy at the edge of the grid compared to the central cells (i.e. mid-domain effects). However, we found no evidence to suggest there were consistent differences in habitat occupancy or abundance between edges of the landscape and the central cells (see Appendix S2). Additionally, there was no evidence that the strength of mid-domain effects depended on the landscape structure (see Appendix S2). Therefore, it is unlikely that our conclusions are influenced by use of a bounded landscape.

Dispersal was modelled as a series of movement steps of one cell-length each. The change in direction between consecutive steps was randomly drawn from a wrapped Cauchy distribution with a mean of zero and a concentration parameter (ρ), where ρ was genetically determined for each individual, with different values for habitat and matrix. If a movement step would cause the individual to cross from habitat to matrix, whether it actually crossed or not depended on its genetically determined boundary-crossing response. If the individual decided not to cross, it would move in a randomly selected direction within habitat or, if no such option existed, it remained in its current location. Dispersal mortality was applied after each movement step. If the individual moved between a habitat cell and a matrix cell, the probability of mortality was the average of the probabilities in habitat and matrix. After each movement step, if the individual landed in a habitat cell with fewer than *k* individuals, it settled there; otherwise it took another movement step.

This initial simulation phase lasted for 1000 generations. At the end of the initial phase, the population's dispersal characteristics had evolved to the optimal levels for the given historic landscape type (A.E. Martin and L. Fahrig, unpublished data).

SIMULATION OF POPULATION PERSISTENCE IN RESPONSE TO HABITAT LOSS

Following the initial simulation phase, we subjected each landscape, and its population with optimally evolved dispersal characteristics, to habitat loss for 100 generations or until the population went extinct (Fig. 2b). Habitat disturbance, reproduction and dispersal were simulated as described above. In each generation prior to reproduction, a proportion of the remaining habitat cells were converted to matrix. This habitat loss was simulated as encroachment of matrix into habitat; cells converted from habitat to matrix were on the edges of habitat patches, that is they had at least one neighbouring matrix cell.

TESTING THE HYPOTHESES

We simulated population dynamics, evolution of dispersal characteristics and population response to habitat loss in 1000 different historic landscapes. For each simulation, we measured mobility in the historic landscape and in the human-altered landscape, measuring mobility as the (i) emigration rate, that is proportion of the population that left their initial habitat cell and did not return, per generation, and (ii) immigration rate, that is proportion of the population that settled in a different habitat patch, per generation. To measure mobility in the historic landscape, we used the mean emigration rate and mean immigration rate, averaging each over the final 50 generations before habitat loss. To measure mobility in the human-altered landscape, we averaged each of the two mobility metrics over the 100 generations during habitat loss, or over all generations until the population went extinct.

We repeated simulations with slow, moderate and fast rates of habitat loss, selected based on the percentage of populations that went extinct within 100 generations in preliminary simulation runs. For slow loss, 0·03 of remaining habitat cells were replaced by matrix per generation, and 18·0% of populations went extinct.

For moderate loss, 0·05 of remaining habitat cells were replaced by matrix per generation, and 58·9% of populations went extinct. For fast loss, 0·07 of remaining habitat cells were replaced by matrix per generation, and 92·4% of populations went extinct. We evaluated the hypotheses for each rate of habitat loss.

To evaluate the metric type hypothesis, we compared the relationship between the extinction risk (i.e. probability of extinction during habitat loss) and emigration rate to the relationship between extinction risk and immigration rate. The hypothesis would be supported if the former relationship was positive and the latter was negative.

For the metric context hypothesis, we compared the mobility–extinction risk relationships for emigration and immigration rates measured in the historic landscapes, that is during the 50 generations before habitat loss began, to the mobility–extinction risk relationships for emigration and immigration rates measured during habitat loss. The hypothesis would be supported if (i) extinction risk increased with emigration rate when emigration rate was measured during habitat loss, but decreased with emigration rate when measured before habitat loss, and (ii) extinction risk decreased with immigration rate when immigration rate was measured during habitat loss, but increased with immigration rate when measured before habitat loss.

To evaluate the metric range hypothesis, we modelled quadratic relationships between extinction risk and the emigration and immigration rates. The hypothesis would be supported if there was a ∩-shaped relationship, such that extinction risk was greatest for species with intermediate emigration and immigration rates.

For the landscape type hypothesis, we compared the relationship between extinction risk and a landscape attribute to the relationship between mobility and the landscape attribute, repeated for each of the four attributes of the historic landscapes (habitat amount, habitat fragmentation, matrix quality and disturbance frequency), using each of the two mobility metrics. The hypothesis would be supported if some historic landscape attributes increased both risk and mobility, while other historic landscape attributes increased risk and decreased mobility in the altered landscape.

Results

Extinction risk increased with emigration rate but decreased with immigration rate, supporting our metric type hypothesis (Fig. 4). The direction of the relationship between the extinction risk and mobility was consistent for all rates of habitat loss, but the strength of the relationship changed. The emigration rate–extinction risk relationship was stronger with faster habitat loss, while the immigration rate–extinction risk relationship was weaker with faster habitat loss (Fig. 4).

We found no support for our metric context hypothesis. The direction of the relationship between the extinction risk and a given measure of species mobility was the same when mobility was measured prior to habitat loss as when mobility was measured during habitat loss (Fig. 4).

We also found no support for the metric range hypothesis. Extinction risk was not highest in species with intermediate mobility; instead, extinction risk increased with the emigration rate and decreased with the immigration rate (Fig. 5).

Some historic landscape attributes increased both extinction risk and mobility in human-altered landscapes, while others increased risk but decreased mobility, supporting our landscape context hypothesis (Fig. 6). Specifically, we found higher probability of extinction and higher emigration rates for species with historically more abundant and less fragmented habitat. Disturbance frequency also drove a positive mobility–risk relationship, with higher extinction risk, and higher emigration and immigration rates, for species in landscapes with more frequent habitat disturbance. In contrast, the historic matrix quality drove a negative mobility–risk relationship, with higher extinction risk but lower emigration and immigration rates for species in landscapes with historically lower matrix quality.

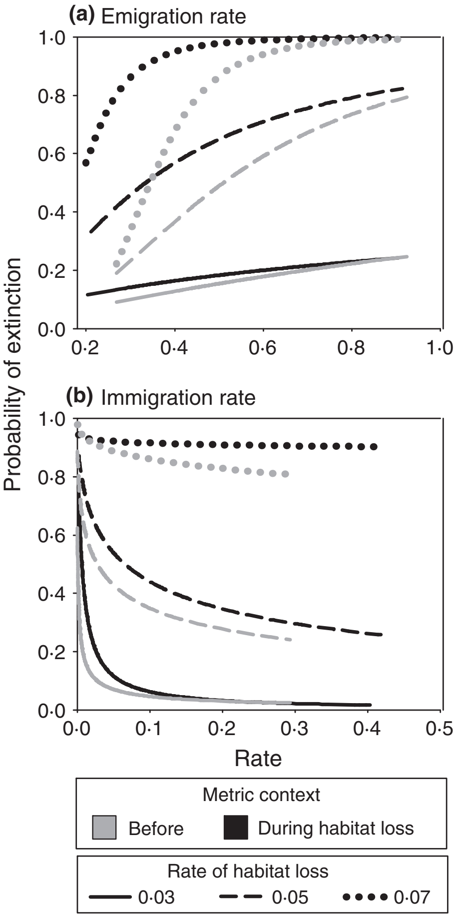

Fig. 4. Comparison of the relationships between the probability of extinction within 100 generations and species mobility when mobility was measured before habitat loss, to the relationships when mobility was measured during habitat loss. Mobility was measured as the (a) emigration rate and (b) immigration rate. Relationships were modelled by logistic regression in R (R Core Team 2014), using ln-transformed emigration and immigration rates (back-transformed prior to plotting), for the 1000 simulated populations at each of three rates of habitat loss: 0·03, 0·05 and 0·07 of remaining habitat cells replaced by matrix per generation.

Discussion

METRIC TYPE HYPOTHESIS

Our simulations support the metric type hypothesis, suggesting that extinction risk in human-altered landscapes

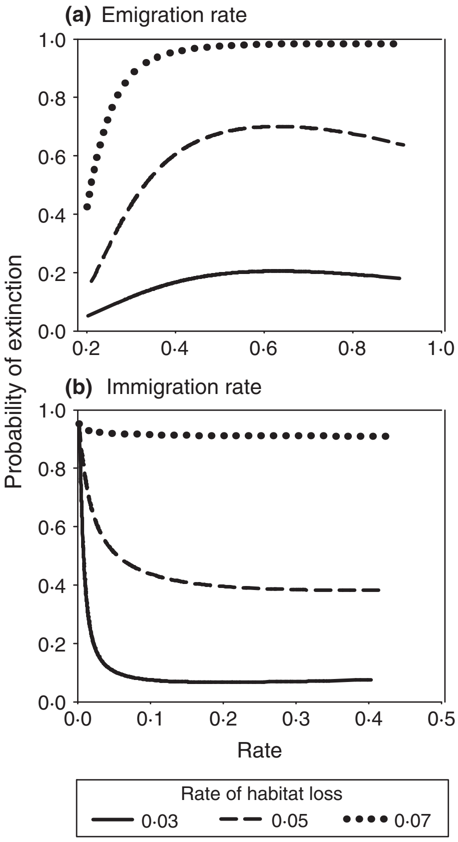

Fig. 5. Nonlinear relationships between the probability of extinction within 100 generations and species mobility, when mobility was measured as the (a) emigration rate and (b) immigration rate during habitat loss. Relationships were modelled by quadratic polynomial logistic regression in R (R Core Team 2014), using ln-transformed emigration and immigration rates (back-transformed prior to plotting), for the 1000 simulated populations at each of three rates of habitat loss: 0·03, 0·05 and 0·07 of remaining habitat cells replaced by matrix per generation.

increases with increasing mobility when mobility is measured as emigration, but decreases with increasing mobility when mobility is measured as immigration. Although individuals must emigrate before they can immigrate, emigration does not equal immigration; most emigrants in our simulations settled in a new location within their home habitat patch or died during dispersal (see Fig. S1). We infer that emigration puts populations at risk because dispersers are more likely to die in a human-altered landscape than sedentary individuals, thus higher emigration results in higher mortality rates. However, successful movement among habitat patches (immigration) allows rescue of small populations and recolonization after local extinction, reducing extinction risk. Therefore, species that emigrate frequently, but rarely move successfully between habitat patches, may be most at risk in human-altered landscapes.

Other theoretical studies also showed greater risk for more mobile species when mobility was measured as emigration (Casagrandi & Gatto 1999; Fahrig 2001; Heino & Hanski 2001), and less risk for more mobile species either when mobility was measured as immigration or when there was no dispersal mortality (Hill, Hastings & Botsford 2002; Grimm *et al.* 2004; Reed 2004). However, comparisons to empirical studies are limited, because few studies directly measured mobility. One empirical study of French birds supported our findings: species with longer dispersal distances and, presumably, more movement among habitat patches were at less risk in human-altered landscapes (Jiguet *et al.* 2007). A study on tropical birds found species with higher immigration rates were at greater extinction risk, in contrast to our model predictions (Van Houtan *et al.* 2007). However, in that study mobility was confounded with foraging strategy, that is more mobile species were more likely to be group foragers than less mobile species (Van Houtan *et al.* 2006, 2007). Group foragers may be at greater risk than solitary foragers, because of their larger area requirements or feeding behaviour (e.g. ant-following), and thus these species may have been more at risk because of their foraging strategy.

Unexpectedly, we found that the emigration–extinction risk relationship was stronger, and the immigration–extinction risk relationship weaker, with faster habitat loss. We suggest this is because (i) emigration increases local extinction while immigration determines recolonization (see Fig. S2), and (ii) the rate of local extinction is more important than the recolonization rate when habitat loss is very rapid. Under most circumstances, recolonization events are critical for population persistence (Fahrig & Merriam 1994); however, when recolonization is rare, the local extinction rate drives extinction risk, because following local extinction that habitat is essentially lost to the population. Recolonizations become rarer with faster habitat loss because, in any given generation, there are fewer dispersers, fewer and smaller habitat patches, and larger distances among patches than in a landscape with slower habitat loss (Fahrig 2007a).

METRIC CONTEXT HYPOTHESIS

Our results did not support the hypothesis that the relationship between mobility and extinction risk in human-altered landscapes depends on whether the measure of mobility was taken in a human-altered landscape or in an unaltered landscape that resembles the species' historic landscape. The direction of the relationship between extinction risk and species mobility was the same whether mobility was measured prior to habitat loss or during habitat loss. This was because a species' emigration rate was generally lower, and its immigration rate higher, during habitat loss than before habitat loss, regardless of its historic mobility (see Fig. S3). The increased risk of dispersal mortality in the altered landscape favoured lower emigration rates (Bonte *et al.* 2006), while habitat loss increased immigration rates because a dispersing individual was more likely to disperse to a site in a different patch than to a site in the same patch, when patch size declined (Baguette *et al.* 2003).

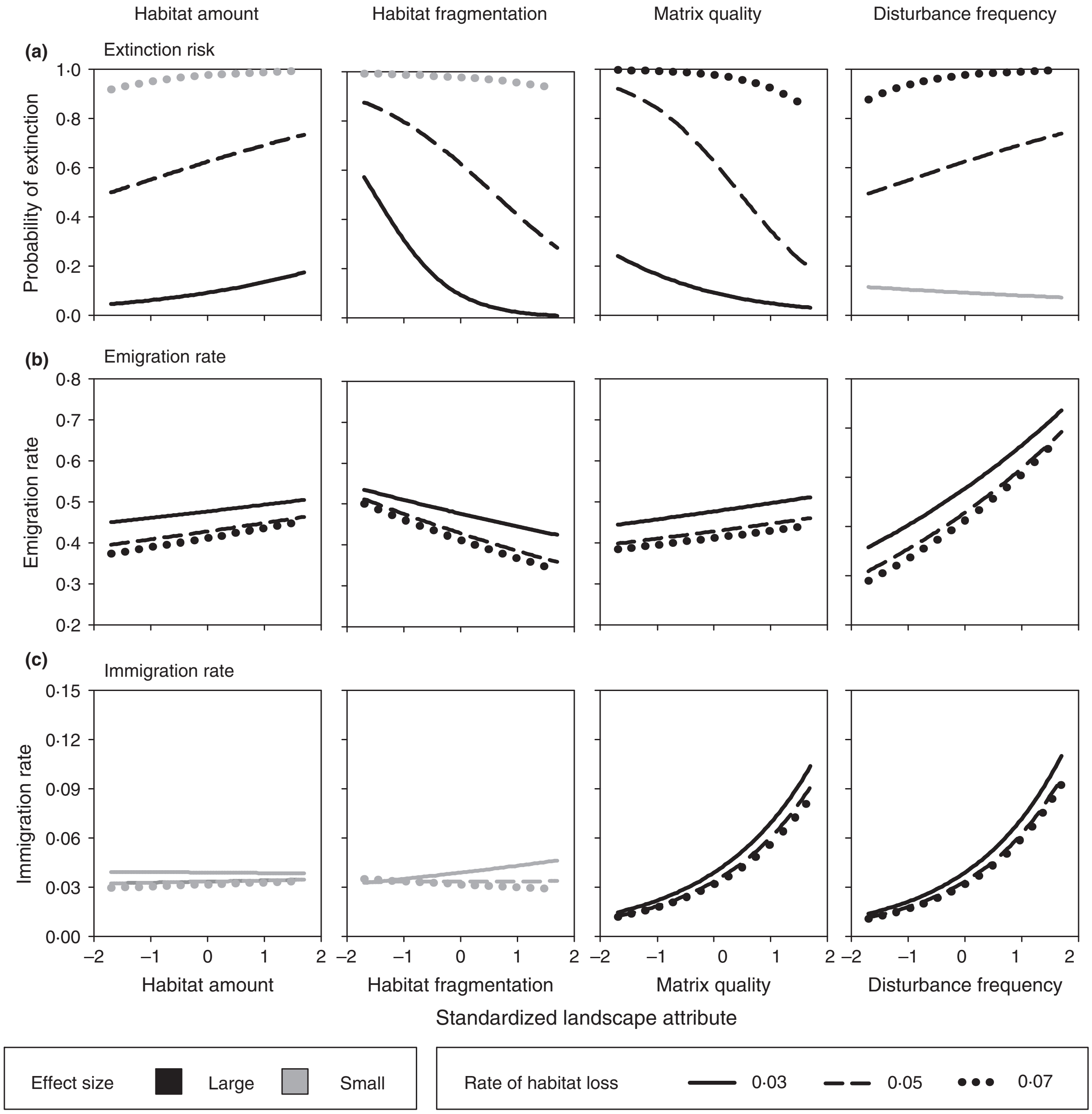

Fig. 6. Relationships between the (a) probability of extinction during 100 generations of habitat loss, (b) emigration rate and (c) immigration rate, and each of four historic landscape attributes, when holding all other landscape attributes at their mean values. Standardized landscape attribute values were scaled such that larger values indicate more habitat, more fragmented habitat, higher matrix quality and more frequent disturbance. Relationships between the probability of extinction and the standardized landscape attributes were modelled by multiple logistic regression in R (R Core Team 2014). Relationships between each measure of mobility and the standardized landscape attributes were modelled by multiple linear regression, using ln-transformed emigration and immigration rates (back-transformed prior to plotting). These analyses were repeated three times, using the 1000 simulated populations at each of three rates of habitat loss: 0·03, 0·05 and 0·07 of remaining habitat cells replaced by matrix per generation. To simplify, we focus on relationships with moderate-to-large effects, that is those where the estimated probability of extinction changed by more than 0·1 across the range of modelled landscape attribute values or where the estimated mobility changed by more than 0·05 across the range of modelled landscape values.

METRIC RANGE HYPOTHESIS

Our results did not support the hypothesis that the relationship between mobility and extinction risk in human-altered landscapes depends on the range of mobilities represented by the different study species. Although Thomas (2000) reported greatest risk for species with intermediate mobility, such relationships have not been detected in other empirical studies (Reinhardt *et al.* 2005; Öckinger *et al.* 2009; Garrard *et al.* 2012). Our simulations do not support the idea that studies do not detect nonlinear cross-species mobility–risk relationships because the range of mobilities represented by their study species was not wide enough. This is because our modelled species had a wide range of mobilities, similar to that in Thomas (2000), which included sedentary species (with emigration rates <20%) to highly mobile species (up to 100% emigration). Emigration rates in our simulations ranged from 20 to 91%.

LANDSCAPE CONTEXT HYPOTHESIS

Our results support the hypothesis that the relationship between mobility and extinction risk in human-altered landscapes depends on the historic landscape structure in which the species dispersal characteristics evolved (Fahrig 2007b). Species in landscapes with historically more abundant habitat, less fragmented habitat, and more frequent disturbance had increased extinction risk and mobility in human-altered landscapes, while species in landscapes with lower matrix quality had increased extinction risk and decreased mobility in human-altered landscapes.

The historic landscape structure likely causes conflicting mobility–risk relationships, at least in part, because the historic landscape drives evolution of dispersal characteristics (see Fig. S4), and these characteristics influence the species' dispersal success in the human-altered landscape. For example, species from landscapes with historically un-fragmented habitat were more mobile in the human-altered landscape than those from landscapes with fragmented habitat because un-fragmented habitat drove evolution of higher dispersal probabilities and probabilities of boundary crossing (see Fig. S4). However, species with historically un-fragmented habitat were poorly adapted to dispersal through matrix; more tortuous movement paths in the matrix resulted in higher mortality rates, putting the species at risk of extinction (see Fig. S4).

However, it is also possible that mobility is associated with extinction risk, not just because mobility *per se* affects extinction risk, but because species mobility evolves in response to historic landscape conditions that influence species' susceptibility to habitat loss. This may occur if favourable historic conditions that result in large population sizes drive evolution of mobility, and large population sizes when habitat loss begins make these species more likely to persist in a human-altered landscape than species that started under poor historic conditions. However, our simulation results do not support this explanation. If this were the case, we would expect species with historically abundant and less fragmented habitat to be at less risk from habitat loss than species from landscapes with rare, fragmented habitat, because the former conditions are more favourable than the latter. Instead, we found higher extinction risk for species with historically more abundant, less fragmented habitat.

The historic landscape conditions may also influence species' susceptibility to habitat loss if historic landscape attributes that drive evolution of mobility persist in the human-altered landscape, and these attributes exacerbate the risk from habitat loss. For example, in our simulations (as expected in real landscapes), an altered landscape with historically frequent disturbance was more frequently disturbed than an altered landscape with historically infrequent disturbance. Frequent disturbance may put species at risk, regardless of their mobility, because frequent disturbance causes portions of the remaining habitat to become temporarily unavailable to species, exacerbating the effects of habitat loss on extinction risk. Because mobility and the historic landscape structure are intrinsically linked by evolutionary processes in our simulations, we are unable to quantify the independent contributions of mobility *per se* and the historic landscape structure to the extinction risk. However, previous simulations have observed an effect of mobility on extinction risk, independent of the landscape attributes (e.g. Fahrig 2001), and an effect of landscape attributes on extinction risk, independent of mobility (e.g. Boughton & Malvadkar 2002). This suggests that both mobility *per se* and historic landscape attributes that persist in the human-altered landscape can influence extinction risk.

Species in landscapes with higher rates of habitat loss, and thus less remaining habitat in the human-altered landscapes, were more likely to go extinct than species in landscapes with lower rates of habitat loss. However, our finding of greater extinction risk for species with historically more abundant habitat suggests that extinction risk does not depend solely on habitat availability in the human-altered landscape. If extinction risk was determined by how much suitable habitat there was during habitat loss, species with historically rare habitat should have been more at risk than species with abundant habitat in our simulations. This is because species with historically abundant habitat always had more remaining habitat than a species with historically rare habitat. This is opposite to what we observed. Thus our simulations suggest that extinction risk does not depend solely on habitat availability.

Greater extinction risk for species with historically more abundant, less fragmented habitat is consistent with empirical observations. Although quantitative data on species' landscape structure prior to human alteration are rare, making comparisons to empirical study difficult, our simulations are consistent with the observed greater sensitivity of tropical species to forest loss and fragmentation relative to temperate species (Bregman, Sekercioglu & Tobias 2014). Temperate forest species should be better able to disperse in a human-altered landscape than tropical forest species, because tropical species evolved in forests that were historically larger and less fragmented than temperate forests (Baldi 1996). Our results may also help explain why habitat fragmentation frequently has positive effects on species occurrence and abundance (Fahrig 2003). Positive fragmentation effects may reflect our finding that species with historically more fragmented habitat were better adapted to dispersal in the human-altered landscape than species with historically less fragmented habitat. However, this assumes that landscapes with historically more fragmented habitat also tend to have more fragmented habitat after human landscape alteration (relative to landscapes with historically less fragmented habitat).

Species whose historic landscapes were more frequently disturbed were more at risk from habitat loss than species from less frequently disturbed landscapes. This was somewhat unexpected, because disturbance-tolerant species are typically thought to be more resilient to human landscape change. However, these species are generally considered disturbance-tolerant because they are able to colonize human-dominated areas of the landscape and are thus likely experiencing habitat gains rather than habitat losses (Davis, Debinski & Danielson 2007). The costs of higher emigration rates for species from landscapes with historically frequent disturbance are likely greater than the benefits of higher immigration for these same species when habitat loss is fast (as discussed above), thus increasing their risk relative to the less mobile species from landscapes with infrequent disturbance. Additionally, more frequent disturbances may increase species extinction risk from habitat loss because species in landscapes with more frequent disturbance require more habitat than species in landscapes with less frequent disturbance.

Species that evolved in landscapes with lower matrix quality had increased risk and decreased mobility in human-altered landscapes relative to species from landscapes with higher quality matrix. Historic matrix quality had stronger effects on immigration rates in the human-altered landscape than on emigration rates, with greater increases in immigration than emigration with increasing matrix quality. Thus more mobile species from landscapes with higher quality matrix were likely at less risk in human-altered landscapes because their dispersal characteristics, in combination with the lower mortality risk for movement through matrix, allowed them to maintain high immigration rates during habitat loss. This is consistent with empirical observations of greater rates of inter-patch movement and longer dispersal distances in landscapes with higher quality matrix (Haynes & Cronin 2003; Schooley & Wiens 2004).

MAJOR FINDINGS

Our simulations reconcile contradictory findings on the mobility–extinction risk relationship in human-altered landscapes. First, our simulations suggest that the relationship between mobility and extinction risk depends on how you measure mobility. If mobility is measured as emigration, extinction risk increases with increasing mobility, but if mobility is measured as immigration, extinction risk increases with decreasing mobility. Secondly, the relationship between mobility and extinction risk in human-altered landscapes depends on the species' historic landscape, because some historic landscape attributes increased both risk and mobility, while other historic landscape attributes increased risk and decreased mobility in the altered landscape.

We suggest two main mechanisms to explain mobility–risk relationships. First, a species' mobility may directly influence its susceptibility to habitat loss. In particular, species with frequent emigration but infrequent movement between habitat patches (immigration) will be most at risk, because of the combined effects of high dispersal mortality and low recolonization rates. However, it is also possible that mobility is indirectly associated with extinction risk, because species mobility evolves in response to (and is thus correlated with) historic landscape attributes that persist in the altered landscape and influence species' susceptibility to habitat loss. These mechanisms have different implications for how managers and ecologists think about mobility and species conservation. If species mobility directly influences its extinction risk, we should focus on decreasing dispersal mortality and increasing inter-patch dispersal, for example, by constructing road underpasses or overpasses to reduce road mortality and allow movements between populations separated by roads. However, if mobility is only correlated with the landscape attributes that are driving extinction risk, then we should focus on managing the attributes that influence extinction risk. For example, if frequent habitat disturbance exacerbates risk from habitat loss, regardless of how mobile the species is, conservation should focus on reducing the frequency of local extinction events. Future work is needed to determine the relative importance of these mechanisms for extinction risk, to inform species management and conservation.

Although our simulations do not predict which conservation actions are most likely to mitigate the effects of habitat loss on species extinction risk, they do suggest that species mobility and an understanding of the historic landscape structure can help identify species most at risk in human-altered landscapes. They suggest that species with frequent emigration but infrequent immigration will be most at risk. They also suggest that species that evolved in landscapes with abundant, un-fragmented, dynamic habitat and low quality matrix should be most at risk. If the model predictions are valid, conservation efforts should focus on these species.

Acknowledgements

This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) scholarships to A. E. M. and a NSERC Discovery Grant to L. F. We thank the members of the Carleton University Geomatics and Landscape Ecology Laboratory and the two anonymous reviewers for their helpful comments on this project.

Data accessibility

Simulation data uploaded as Supporting Information. Simulation model code uploaded as Supporting Information, and archived with the NetLogo User Community Models (https://ccl.northwestern.edu/netlogo/models/community/index.cgi).

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Received 2 June 2015; accepted 4 January 2016
Handling Editor: Jennifer Watling

Supporting Information

Additional Supporting information may be found in the online version of this article:

Fig. S1. Mean proportion of emigrants that settle in a new location within their initial habitat patch, die during dispersal through habitat, die during dispersal through matrix or settle in a new habitat patch (immigrate).

Fig. S2. Spearman rank correlations between the local extinction rate and emigration rate, and between the recolonization rate and immigration rate during habitat loss.

Fig. S3. Differences between emigration rates measured before and during habitat loss, and differences between immigration rates measured before and during habitat loss, as a function of these rates before habitat loss.

Fig. S4. Effects of the historic habitat amount, habitat fragmentation, matrix quality and disturbance frequency on the evolved dispersal characteristics.

Appendix S1. Supplementary methods.

Appendix S2. Habitat occupancy and population density in landscape edges and interior.

Appendix S3. Simulation data set.

Appendix S4. Code for the NetLogo simulation model.