EFFECT OF HABITAT FRAGMENTATION ON THE EXTINCTION THRESHOLD: A SYNTHESIS

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Abstract. I reviewed and reconciled predictions of four models on the effect of habitat fragmentation on the population extinction threshold, and I compared these predictions to results from empirical studies. All four models predict that habitat fragmentation can, under some conditions, increase the extinction threshold such that, in more fragmented landscapes, more habitat is required for population persistence. However, empirical studies have shown both positive and negative effects of habitat fragmentation on population abundance and distribution with about equal frequency, suggesting that the models lack some important process(es). The two colonization–extinction (CE) models predict that fragmentation can increase the extinction threshold by up to 60–80%; i.e., the amount of habitat required for persistence can shift from <5% of the landscape to >80% of the landscape, with a shift from completely clumped to completely fragmented habitat. The other two models (birth–immigration–death–emigration, or BIDE models) predict much smaller potential effects of fragmentation on the extinction threshold, of no more than a 10–20% shift in the amount of habitat required for persistence. This difference has important implications for conservation. If fragmentation can have a large effect on the extinction threshold, then alteration of habitat pattern (independent of habitat amount) can be an effective tool for conservation. On the other hand, if the effects of fragmentation on the extinction threshold are small, then this is a limited option. I suggest that the difference in model predictions results from differences in the mechanisms by which the models produce the extinction threshold. In the CE models, the threshold occurs by an assumed reduction in colonization rate with decreasing habitat amount. In the BIDE models, loss of habitat is assumed to increase the proportion of the population that spends time in the matrix, where reproduction is not possible and the mortality rate is assumed to be higher (than in breeding habitat). Habitat loss therefore decreases the overall reproduction rate and increases the overall mortality rate on the landscape. I hypothesize that this imposes a constraint on the potential for habitat fragmentation to mitigate effects of habitat loss in BIDE models. To date, empirical studies of the independent effects of habitat loss and fragmentation suggest that habitat loss has a much larger effect than habitat fragmentation on the distribution and abundance of birds, supporting the BIDE model prediction, at least for this taxon.

Key words: colonization; dispersal mortality; extinction; habitat fragmentation; habitat loss; metapopulation; population persistence; spatial models; threshold, population extinction.

INTRODUCTION

Destruction of habitat in a landscape results in loss of populations of organisms that depend on that habitat. Different species disappear at different points on the habitat loss gradient (Lande 1993, Gibbs 1998, Hager 1998, Eriksson and Kiviniemi 1999), and the "extinction threshold" is the minimum amount of habitat required for a population of a particular species to persist in a landscape (Lande 1987, Lawton et al. 1994, Hanski et al. 1996). Modeling studies depict the extinction threshold in one of two ways, depending on whether the modeling approach is essentially deterministic or

stochastic (Fig. 1). In the former case, the threshold is depicted as the minimum amount of habitat below which the equilibrium population size is 0 (Fig. 1A), and in the latter case it is depicted as the minimum amount of habitat below which the probability of long-term population survival is <1 (Fig. 1B).

What causes the extinction threshold? Populations can only persist if long-term reproduction outweighs long-term mortality. As the amount of habitat in the landscape declines, models predict that the overall (landscape-scale) mortality rate increases relative to the overall reproduction rate. Exactly how habitat loss is assumed to affect these rates differs among modeling studies, as I will discuss (see *Cause of the extinction threshold*).

The extinction threshold occurs at the amount of habitat at which mortality balances reproduction over
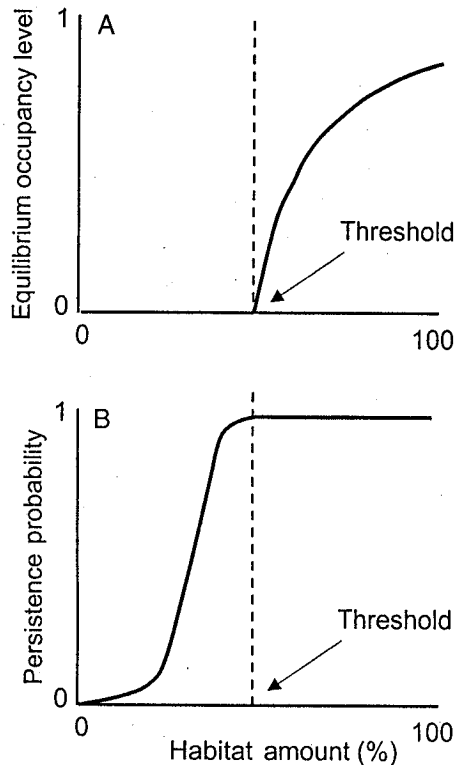
FIG. 1. Depiction of the extinction threshold. (A) The threshold is shown as the minimum amount of habitat below which the equilibrium population size (or proportion of the landscape occupied) is 0. (B) The threshold is shown as the minimum amount of habitat below which the probability of long-term population survival is less than 1.

the landscape. Any factor that affects how habitat amount influences this balance will affect the extinction threshold. Habitat fragmentation has been suggested as one such factor. Models predict that habitat fragmentation can increase the extinction threshold such that more habitat is needed for population persistence in more fragmented landscapes (Burkey 1995, Hill and Caswell 1999, With and King 1999). Here, habitat "fragmentation" is literally the "breaking apart" of habitat. As such, it is an element of the pattern of habitat that is independent of the amount of habitat (see Fahrig 1997: Fig. 1, Fahrig 1998: Fig. 6).

One approach to the question, "does habitat fragmentation affect the extinction threshold?", has been to compare the predictions of spatially implicit vs. spatially explicit models (Adler and Nürnberger 1994, Bascompte and Solé 1996, Hill and Caswell 1999, With and King 1999). In spatially implicit models, all habitat is assumed to be equally accessible to all dispersers, whereas in spatially explicit models, dispersal is assumed to be limited to within some neighborhood of the disperser's origin. These comparisons usually predict a higher extinction threshold for the spatially explicit model, suggesting that when dispersal is spatially

constrained, more habitat is required for population persistence. However, this approach cannot tell us how or how much fragmentation affects the extinction threshold, because only the species response to the habitat pattern is altered, not the pattern itself.

A direct analysis of the effect of habitat fragmentation on the extinction threshold requires a comparison of model landscapes having different levels of habitat amount (from near 0% to near 100% of the landscape) and different levels of fragmentation (from completely random to completely clumped), in a spatially explicit context. In this paper, I compare predictions of the four such modeling studies of which I am aware (Fahrig 1997, 1998, 2001, Bevers and Flather 1999, Hill and Caswell 1999, With and King 1999; Flather and Bevers 2001), and I compare the model predictions to relevant empirical studies.

The spatially explicit versions or components of all four models are grid based; the spatial unit is the grid cell. A grid cell can be designated as either habitat or nonhabitat. Note that some authors refer to grid cells as "patches." To ease comparison, I reserve the term "patch" for its more usual definition, i.e., a group of contiguous habitat cells. Although grid cells are of constant size, habitat patches can be of any size, within the limits of the grain and extent of the landscape model (Wiens 1989). Apart from their common grid structure, the four models vary widely in structure. I do not describe them in detail here, as this information is available in the original papers. However, in the following sections, I do describe the components of the models that I believe account for the similarities and differences in their predictions regarding the effect of habitat fragmentation on the extinction threshold. These comparisons are summarized in Table 1.

OCCURRENCE OF THE EXTINCTION THRESHOLD

All four models predict the occurrence of an extinction threshold for at least some parameter combinations. Testing empirically for extinction thresholds is extremely difficult and perhaps impossible. By definition, the threshold occurs at the habitat amount at which the equilibrium population size is 0 or, equivalently, where the long-term persistence probability is <1 (Fig. 1). In practice, human-caused habitat loss has occurred over only a short time span relative to the response times of most affected organisms (Eriksson and Kiviniemi 1999, Robinson 1999), so we do not have empirical information on equilibrium or long-term responses. It might be possible to compare populations across natural landscapes with different amounts of available habitat, but extrapolation to human-modified landscapes would be somewhat tenuous.

Empirical evidence is therefore limited to a few, recent studies in which the definition of threshold is somewhat different from that used in the modeling studies. Jansson and Angelstam (1999) found thresh-

TABLE 1. Comparison of four spatial models that predict the landscape-scale effect of habitat fragmentation on the population extinction threshold.

Predictions and characteristics of models	Hill and Caswell (1999)†	With and King (1999)†	Flather and Bevers (2001)‡	Fahrig (2001)‡
A) Model predictions				
1) Extinction threshold	yes	yes	yes	yes
2) At least some effect of fragmentation on the extinction threshold	yes	yes	yes	yes
3) Fragmentation effect on population size/persistence increases with decreasing habitat	yes	yes	yes	yes
4) Maximum change in extinction threshold between highly clumped and highly fragmented landscapes	65%	82%	10%	17%
B) Model characteristics responsible for CE vs. BIDE difference in magnitude of fragmentation effect (prediction 4)				
1) Local (within-cell) population dynamics included in modeling framework	no	no	yes	yes
2) Patch emigration affects local persistence	no	no	yes	yes
3) Habitat loss causes	reduced colonization	reduced colonization	increased proportion of population in matrix, causing reduced reproduction and increased mortality	increased proportion of population in matrix, causing reduced reproduction and increased mortality

† Extinction–colonization (CE) model.
‡ Birth–immigration–death–emigration (BIDE) model.

olds in local patch occupancy by the Long-tailed Tit (*Aegithalos caudatus*) as a function of habitat amount in the surrounding landscape. Flather et al. (C. H. Flather, M. Bevers, E. Cam, J. Nichols, and J. Sauer, *unpublished manuscript*) plotted the probability of occupancy by forest-breeding birds of landscapes defined by breeding bird survey routes in the eastern United States, vs. the amount of forest in the landscapes. For several species, they found a significant change in slope of the relationship at a "threshold" habitat amount. Above the threshold, the probability of occupancy was fairly constant whereas below the threshold, the probability of occupancy declined precipitously with decreasing habitat amount.

CAUSE OF THE EXTINCTION THRESHOLD

The cause of the extinction threshold differs among the four models. Two of the models (Hill and Caswell 1999, With and King 1999) can be loosely categorized as metapopulation-based or colonization–extinction (CE) models, in which the occupancy of a habitat cell is determined by colonization and extinction. In these models, landscape-scale population persistence is determined by the overall rates of colonization and extinction in the landscape.

The other two models (Fahrig 1997, 1998, 2001; Flather and Bevers 2001) include local population dynamics within each cell in the modeled landscape (see also Lande 1998). Population size in a cell is determined by births, immigration, deaths, and emigration

(BIDE models). In these models, landscape-scale population persistence is determined by the overall rates of birth and death in the landscape.

All four models predict that, as habitat is lost, the relative rates of landscape-scale mortality (extinction in CE models) and landscape-scale reproduction (colonization in CE models) shift in favor of mortality. This results in a minimum amount of habitat below which mortality outweighs reproduction and the population cannot persist on the landscape. However, the mechanisms causing the extinction threshold differ qualitatively between the two pairs of models. In the CE models, the extinction threshold is caused by a decrease in cell colonization rate with decreasing habitat amount. Loss of habitat results in loss of source cells, which reduces the rate of colonization. However, because colonization of an empty habitat cell is a function of the number of occupied cells within some neighborhood of that cell, cells can maintain high levels of colonization if they occur in neighborhoods in the landscape that maintain large amounts of habitat following habitat loss. In these models, cell extinction rate is independent of habitat loss.

In the BIDE models, loss of habitat increases the probability that individuals enter and spend time in nonbreeding habitat (or "matrix") areas, where reproduction is not possible and mortality rate is assumed to be higher. This decreases the overall reproduction rate and increases the overall mortality rate on the landscape. This reduces the overall population size, which

indirectly causes a decrease in the rate of cell immigration. Reduced immigration reduces the rescue effect and the colonization rate. The local extinction rate is also higher due to an increased emigration rate (caused by higher edge:interior ratios; see Bevers and Flather 1999), and the lack of a rescue effect. Habitat loss therefore causes both an increase in the local extinction rate and a decrease in the colonization rate. These differences in model structure lead to quantitative differences in the predicted effects of fragmentation on the extinction threshold, as discussed in the section *Effect of habitat fragmentation on the extinction threshold: model divergence.*

EFFECT OF HABITAT FRAGMENTATION ON THE EXTINCTION THRESHOLD: MODEL CONGRUENCE

To examine the effect of fragmentation on the extinction threshold, in each of the four modeling studies habitat pattern was varied from completely random (fragmented) to highly clumped, and the amount of habitat was independently varied from nearly 0% to nearly 100% of the landscape. All four models show at least some effect of fragmentation on the extinction threshold, and in all cases, the predicted effect of fragmentation is an increase in the extinction threshold; i.e., the models predict that populations in more fragmented landscapes require more habitat for persistence. This prediction results from the model assumptions as follows. The CE models assume that the colonization rate decreases with decreasing proximity of potential donor cells. If the habitat on a landscape is dispersed (fragmented), the overall colonization rate will go down. In the BIDE models, increasing habitat fragmentation increases the amount of edge on the landscape. This increases the probability of individuals leaving habitat and entering the hostile matrix, where the death rate is higher. This increases the overall mortality rate of the population, which increases the cell extinction rate and decreases the immigration rate.

The fact that the four models predict negative effects of fragmentation on population persistence (and therefore positive effects on the extinction threshold) does not imply that fragmentation effects in nature must be negative. In fact, it is easy to imagine situations in which fragmentation might decrease the extinction threshold. Positive edge effects or higher survival of individuals in matrix than in breeding habitat could result in a decrease in the extinction threshold with increasing fragmentation. Positive effects of fragmentation on abundance or distribution have, in fact, been found for several species of forest breeding birds (see the review of literature in section *Empirical studies of habitat loss vs. fragmentation*).

A second area of congruence among the four models is that they predict an increasing effect of fragmentation on population size (Flather and Bevers 2001), cell occupancy (Hill and Caswell 1999, With and King

1999), or population persistence time (Fahrig 1997, 1998, 2001), with decreasing habitat amount. Because cell occupancy and population persistence time are correlated with population size (Venier and Fahrig 1996, Fahrig 1998), these results are congruent. This prediction is supported by an empirically based simulation study of chipmunk (*Tamias striatus*, a forest-dwelling small mammal) population dynamics (Henein et al. 1998). In their simulations, Henein et al. varied the amount of forest from 10% to 30% to 50% and the number of forest patches from two to four to eight. They found that the effect of patch number on chipmunk population persistence was largest in simulated landscapes containing 10% habitat. This prediction is also supported empirically by Flather et al. (C. H. Flather, M. Bevers, E. Cam, J. Nichols, and J. Sauer, *unpublished manuscript*), who found for several bird species that the proportion of variation in abundance that was explained by fragmentation increased with decreasing amount of habitat. This effect was, however, not found by Trzcinski et al. (1999), perhaps due to lower statistical power. Andrén (1994, 1999) reviewed studies of patch size and isolation vs. population density and found that the effects were stronger with decreasing habitat amount in the landscape. This seems to support the prediction that fragmentation effects increase with decreasing habitat amount. However, because patch size and isolation are typically correlated with habitat amount in the landscape, the effect of habitat amount must be statistically controlled in order for these metrics to represent true measures of fragmentation per se (Fahrig 1997). This result could more conservatively be interpreted as an increasing effect of habitat loss with decreasing habitat amount, rather than an increasing effect of habitat fragmentation with decreasing habitat amount. The evidence for this model prediction is therefore rather weak at present; more empirical work is needed.

EFFECT OF HABITAT FRAGMENTATION ON THE EXTINCTION THRESHOLD: MODEL DIVERGENCE

Although the models all make similar qualitative predictions regarding the effect of habitat fragmentation on the extinction threshold, they differ greatly in their quantitative predictions. The two CE models predict much larger potential effects of fragmentation on the extinction threshold than do the two BIDE models (Table 1). Hill and Caswell (1999) and With and King (1999) predict that reducing habitat fragmentation could reduce the extinction threshold by up to 82% and 65%, respectively; i.e., the amount of habitat required for persistence can shift from <5% of the landscape to >80% of the landscape, with a shift from completely clumped to completely fragmented habitat. On the other hand, Flather and Bevers (2001) and Fahrig (1997, 1998, 2001) predict much smaller maximum potential effects of fragmentation on the extinction threshold, of

up to 10% and 17%, respectively. Note that these numbers represent the maximum predicted effect of fragmentation. All of the models predict situations in which the fragmentation effect is much smaller and even zero.

From a conservation perspective, it is important to understand the reason for this difference between the two pairs of models. If fragmentation has a large effect on the extinction threshold, then alteration of habitat pattern (independent of habitat amount) is an effective tool for species conservation, as suggested by Kareiva and Wennergren (1995). This is particularly important in forestry, where some hope that judicious planning of the spatial pattern of harvests can compensate for loss of forest (Bennett 1999, Rochelle et al. 1999). On the other hand, if the effects of fragmentation on the extinction threshold are small, then this is a limited option. In addition, by understanding the reason for the different predictions between the two pairs of models, we should be able to predict circumstances in which there is a large potential for altering population persistence by reducing habitat fragmentation (independent of habitat amount).

As stated previously, the four models are very different in structure. However, the fact that the predicted magnitude of the fragmentation effect is similar within CE and BIDE model pairs and differs greatly between them suggests that this difference results from model assumptions that are common within, but different between, the model pairs. Note that the difference is not due to different assumptions about dispersal directionality; all four models either implicitly or explicitly assume random dispersal direction.

Implicit in the structure of the CE models is the assumption that colonization of an empty habitat cell is a function of the number of occupied cells within some neighborhood of that cell. The size of the neighborhood is determined by the dispersal range of the organism. Habitat fragmentation increases the extinction threshold (i.e., increases the amount of habitat required for population persistence) by decreasing the number of occupied cells within the neighborhood of a typical (unoccupied) cell. Clumping habitat together means that most habitat cells are surrounded by other habitat, which greatly increases overall colonization rate. Therefore, even if there is only a small amount of habitat left in the landscape, as long as it is clumped together, these models predict high cell colonization and therefore high persistence.

In the BIDE models, habitat fragmentation affects the extinction threshold by increasing the amount of edge in the landscape, which increases the probability of individuals leaving habitat cells and moving into matrix cells, where the mortality rate is assumed to be higher. This increases overall mortality and local extinction rates, and indirectly reduces the rate of cell immigration by reducing the number of potential immigrants.

How does this difference in model structure lead to the different predictions of the effect of fragmentation on the extinction threshold? I hypothesize that in the BIDE models, the effect of habitat loss on reproduction and mortality rates in the landscape may impose a limit on the potential effect of habitat fragmentation (or reduced fragmentation) on the extinction threshold. As habitat is lost in the landscape, the overall reproduction rate goes down and the overall mortality rate goes up, because more and more individuals end up in the matrix for longer, where reproduction is not possible and the mortality rate is higher. Clumping of habitat can reduce this to some extent, in some circumstances (Fahrig 1998). However, the potential effect of this is limited. The decrease in reproduction and increase in mortality due to increasing amount of matrix cannot be effectively countered by altering the habitat pattern. This constraint is not present in the CE models; in these models, cell extinction probability is independent of habitat amount.

This leads to the question: under what conditions in nature might we expect a large potential effect of habitat fragmentation on the extinction threshold? This should occur when habitat removal does not result in an increase in the rate of dispersal into the matrix. This is clearly the case for any species that will not move into the matrix at all (e.g., Bascompte and Solé 1996). If an organism is constrained strictly to one type of habitat in the landscape, then as habitat is lost and fragmented, the patches of habitat become smaller, patch populations become smaller, and local (patch) extinction probabilities increase. Because there is no between-patch movement, the overall extinction probability depends simply on the size of the largest patch in the landscape. Reducing habitat fragmentation will increase the size of the largest patch, thus increasing persistence time (and decreasing the extinction threshold). By not assuming any increase in extinction rate with increasing amount of matrix in the landscape, the CE models function in a way that is similar to this sort of habitat-constrained movement.

EMPIRICAL STUDIES OF HABITAT LOSS VS. FRAGMENTATION

To date there are no empirical studies that test for the effect of fragmentation on the extinction threshold. However, there is one empirically based simulation study and there are several empirical studies that compare the relative *independent* effects of habitat amount and habitat fragmentation (pattern) on species abundance, distribution, or richness. These studies are relevant to the threshold issue: if the effect of habitat fragmentation is very small compared to the effect of habitat loss, then alteration of habitat pattern (reduced fragmentation) is unlikely to have a large effect on the extinction threshold. Conversely, if the effect of fragmentation is large, alteration of habitat pattern has at

least the potential to significantly shift the extinction threshold.

To date, most of the studies suggest that the effects of habitat amount far outweigh the effects of habitat fragmentation. An empirically based simulation study (Henein et al. 1998) of chipmunk population dynamics predicts that forest amount explains 29–49% of variation in chipmunk population size, whereas forest fragmentation explains only 3–15%. This is perhaps not surprising, however, because the chipmunk model is a BIDE-type model.

McGarigal and McComb (1995) quantified the independent effects of forest area and configuration (fragmentation) on the abundance of 15 bird species associated with late-seral forest in 30 landscapes in the northwestern United States that contained late-seral forest in a matrix of 0–40 yr old conifer plantations. Overall, they found that habitat area had a much greater effect than habitat fragmentation. In addition, most significant fragmentation effects were positive; that is, species abundances increased with increasing fragmentation. Only Winter Wrens (*Troglodytes troglodytes*) showed an association with the least fragmented landscapes.

Meyer et al. (1998) compared the amount and configuration of old-growth forest in 50 landscapes centered on known Northern Spotted Owl (*Strix occidentalis caurina*) sites vs. 50 random landscapes in the same region of western Oregon, USA. They found that the main influences of landscape structure were related to the amount of habitat, not habitat configuration. They also looked at the duration of occupancy and reproduction in the 50 owl sites and found that, again, the amount of forest had a much greater effect than its configuration.

Trzcinski et al. (1999) quantified the independent effects of forest amount and fragmentation on the distribution (presence/absence) of 31 species of forest-breeding birds in 94 landscapes in southern Ontario, Canada. They found that the effects of forest amount far outweighed the effects of forest fragmentation. All 31 coefficients for habitat amount were positive (26 statistically significant), whereas the coefficients for fragmentation were about equally divided between negative and positive, and only six were statistically significant (four negative, two positive).

Villard et al. (1999) found the largest effect of fragmentation relative to amount of habitat of the empirical studies to date. They compared the relative effects of forest amount and fragmentation on the presence/absence of 15 forest bird species in 33 landscapes in eastern Ontario, Canada. The same number of species appeared to respond ($P < 0.1$) to forest amount as to forest fragmentation (six species each) over the two years of the study. The relative importance of amount and fragmentation is somewhat difficult to interpret here, however, because the analyses included a single measure of habitat amount (forest cover) but three measures of habitat fragmentation. The separate measures of fragmentation were included because different species were expected to respond to different aspects of habitat configuration. However, this inflates the relative likelihood of detecting a significant fragmentation effect. Interestingly, several of the fragmentation effects found by Villard et al. were positive (as also found by McGarigal and McComb [1995] and Trzcinski et al. [1999]). All three responses to the number of forest fragments (after controlling for total forest amount) were positive, and one of the four species responding to edge showed a positive response. However, Villard et al. (1999) suggest that the positive responses to fragmentation may reflect a bias caused by increased sampling effort in more fragmented landscapes.

Finally, Flather et al. (C. H. Flather, M. Bevers, E. Cam, J. Nichols, and J. Sauer, *unpublished manuscript*) compared the independent effects of forest amount and fragmentation on the composite abundance of all "area-sensitive" species in 864 landscapes centered on breeding bird survey routes in eastern United States. They found that the amount of forest explained 44.3% of the variation in abundance, whereas the pattern of forest (controlled for amount) explained only 0.5%.

The empirical studies therefore appear mainly to support the notion that alterations in habitat configuration are likely to have only a small effect on the extinction threshold (i.e., the prediction from the BIDE models). However, there are two caveats to this conclusion. First, based on the three empirical studies to date that have found fragmentation effects (independent of habitat loss), it appears that fragmentation effects are at least as likely to be positive as negative. None of the modeling studies to date predicts positive effects of fragmentation on population persistence, indicating that an important component of species response to habitat pattern may be missing from the modeling work. It seems likely that positive edge effects are a factor. In a literature review, Kremsater and Bunnell (1999) found that many species do show positive edge effects. Because fragmentation increases the amount of edge in the landscape, positive edge effects could be responsible for positive effects of fragmentation on abundance or distribution. Frequent positive effects of fragmentation are also suggested by a meta-analysis of studies relating patch size to population density (Bender et al. 1998). Bender et al. (1998) found about equal numbers of species showing positive and negative effects of patch size on population density, resulting in only a very small overall effect size across all species combined. Negative effects of patch size on population density are opposite to the predictions of the BIDE models (Bevers and Flather 1999; note that CE models do not include density, so do not make predictions on this), again indicating that some important process(es) is missing from the models. Both positive edge effects

and negative effects of patch size on population density support the suggestion that landscape heterogeneity is an important component for the persistence and abundance of many species (McGarigal and McComb 1995, Jonsen and Fahrig 1997, Saab 1999).

The second caveat is that all of the empirical studies of which I am aware that quantify the independent effects of amount and fragmentation of habitat have been conducted on birds. Perhaps birds, in general, are more likely to meet the assumptions of the BIDE models than those of the CE models. If my interpretation of the models is correct, this would indicate that, for birds, habitat removal causes an increase in the rate of dispersal into matrix, which results in a decrease in reproduction or increase in mortality rate of the population at the landscape scale. In landscapes with less habitat, first-time breeders may spend more time searching for suitable habitat and therefore may have lower reproductive success and be more subject to mortality. This has been suggested by Matthysen (1999) for Nuthatches (*Sitta europaea*).

OTHER FACTORS AFFECTING THE EXTINCTION THRESHOLD

This review is focused primarily on the effect of habitat fragmentation on the extinction threshold. However, the modeling work to date predicts that factors other than fragmentation affect the extinction threshold. With and King (1999) and Fahrig (2001) found that reproductive output has the largest effect on the extinction threshold. This is obvious: if reproduction is too low relative to mortality, then no amount of habitat will be sufficient for population persistence and the extinction threshold will be >1 (i.e., $>100\%$ habitat needed for persistence). If the reproduction rate is extremely high, then a landscape containing only a tiny amount of habitat will be sufficient to maintain the population. This result suggests that conservation approaches that focus on improving population performance through improvements during the most critical life history stages for reproductive success and mortality have the potential to decrease the extinction threshold (see also Pulliam et al. 1992).

In addition, my simulations (Fahrig 2001) suggest that improvements in matrix quality can have a substantial effect on the extinction threshold. If matrix mortality is decreased from near 1 to near 0, by removing sources of very high mortality such as roads or pesticides, the model suggests that the extinction threshold can shift down by up to ~60%. This implies that conservation efforts should include consideration of the quality of the whole landscape. This is supported by a reanalysis of the Andrén (1994) data sets by Mönkkönen and Reunanen (1999), who found that landscape type had a large effect on the relationship between patch size and population density. The role of matrix quality in population declines will go undetected if only the quality and pattern of the preferred habitat are considered.

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