

Research article

The implications of metalandscape connectivity for population viability in migratory songbirds

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Abstract

Landscape connectivity is considered important for species persistence, but linkages among landscape populations (*metalandscape connectivity*) may be necessary to ensure the long-term viability of some migratory songbirds at a broader regional scale. Because of regional source-sink dynamics, these species can maintain steady populations within extensively fragmented landscapes (landscape sinks) owing to high levels of immigration from source landscapes. We undertook a modeling study to identify the conditions under which immigration, an index of metalandscape connectivity, could rescue declining populations of songbirds in heavily disturbed landscapes. In general, low to moderate levels of immigration ($m = 0\text{--}20\%$) were sufficient to rescue species with low edge-sensitivity in landscapes where $<70\%$ habitat had been destroyed. At the other extreme, moderate to high levels of immigration ($m = 11\text{--}40\%$) were usually required to rescue highly edge-sensitive species in these same landscapes. Very high levels of immigration ($m > 40\%$) were required to rescue highly edge-sensitive species in extensively fragmented landscapes that had lost $>50\%$ habitat, or when any landscape lost $\geq 50\%$ habitat gradually over a period of 100 or more years ($r = 0.5\%$ habitat lost/year). Paradoxically higher levels of immigration were thus necessary to offset population declines when habitat was lost gradually than when it was lost quickly, where population response lagged behind landscape change. This implies that the importance of metalandscape connectivity for population viability may not be fully appreciated in landscapes undergoing rapid rates of change. Natural immigration rates for migratory songbirds match the very high levels ($>40\%$) we found necessary to sustain populations in heavily disturbed landscapes, which underscores the importance of metalandscape connectivity for the continued persistence of many migratory songbirds in the face of widespread habitat loss and fragmentation.

Introduction

Connectivity is a central theme in landscape ecology (Taylor et al. 1993; With et al. 1997; Tischendorf and Fahrig 2000), and has important

implications for conservation owing to its effects on dispersal and metapopulation dynamics, and hence species persistence (With 2004). Connectivity links spatially subdivided populations. Although dispersal corridors may physically connect

habitat patches and thus populations (*structural connectivity*), populations may be connected more subtly by the exchange of individuals among populations, linking subpopulations into metapopulations (*functional connectivity*). The concepts of connected patches and metapopulations readily extend to broader landscape and regional scales.

Consider that even when the amount of habitat is not sufficient to support viable populations at the landscape scale (population sinks; Pulliam 1988; Pulliam and Danielson 1991), species may nevertheless persist owing to immigration from surrounding landscapes that produce a surplus of individuals (landscape sources, With and King 2001). Sufficient connectivity among landscape populations – *metalandcape connectivity* – may thus be necessary for the persistence of some species. Migratory songbirds, for example, exhibit such regional source-sink dynamics in the Midwestern United States, where agricultural conversion of forests and grasslands has created extensively fragmented landscapes throughout much of the region (Robinson et al. 1995; Donovan et al. 1995a; Brawn and Robinson 1996). Viability analyses for some migratory songbird populations within these fragmented landscapes, such as Ovenbirds (*Seiurus aurocapillus*) and Wood Thrushes (*Hylocichla mustelina*), have demonstrated that they are generally not self-sustaining (e.g., Donovan et al. 1995b; Trine 1998; Porneluzi and Faaborg 1999; Fauth 2000). Productivity is simply too low, owing to high rates of nest predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) in the remaining habitat fragments, to offset mortality and sustain populations (Robinson et al. 1995). Nevertheless, populations often remain relatively constant in these fragmented landscapes (Brawn and Robinson 1996), which implies that immigration from outlying landscape sources is sufficient to rescue sink populations from local extinction. In other words, metalandscape connectivity underlies the regional source-sink dynamics that may ultimately be responsible for the continued persistence of many migratory songbird populations in the Midwestern United States.

Regional source-sink dynamics imply that there is spatial variability in population growth rates among subregions (i.e., landscapes) within the

region. The dynamics of (relatively closed) populations within individual landscapes are known to be influenced by the structure and dynamics of those landscapes (i.e., through spatially-dependent demography; With and King 2001; Schrott et al. 2005). These landscape populations are linked through source-sink dynamics into a regional metapopulation, and the various landscapes occupied by these populations (subpopulations of the regional metapopulation) are connected by immigration into a metalandscape. The term ‘metalandscape connectivity’ draws attention to the fact that populations in the regional metapopulation are influenced by landscape-scale processes and pattern. The degree to which these landscape populations interact through immigration, however, ultimately affects the regional persistence of the species, and which therefore cannot be inferred from the dynamics of a single landscape population. Thus, the region is a spatially structured collection of landscapes linked by immigration (a metalandscape), and landscape-scale structure affects the degree to which immigration influences populations within the metalandscape.

Metalandcape connectivity is dependent upon the rate of immigration among landscapes. Intuitively, immigration rates should reflect the relative isolation of landscape populations; high immigration rates equate to high metalandscape connectivity and minimal isolation, whereas low immigration rates may indicate that landscapes have become isolated. This is an extension of the metapopulation concept of population or patch connectivity to a broader regional scale. In metapopulation theory, colonization (immigration) rate is strongly correlated with patch connectivity (Ims and Yoccoz 1997; Hanski 1999; Moilanen and Nieminen 2002). Isolated patches have low immigration rates; alternatively, patch isolation can be assessed by the rate of immigration into the patch (patches with low rates of immigration are considered to be isolated; Tischendorf and Fahrig 2000).

Landscape immigration rates, as an index of metalandscape connectivity, thus indicate the extent to which declining populations within a given landscape may be rescued by immigration from other landscape populations in the region. On the other hand, if the rate and magnitude of habitat destruction within a given landscape are

extreme, then immigration may be insufficient to offset population declines (i.e., even maximum metaland-
scape connectivity would not be sufficient to halt or reverse population declines). We therefore undertook a modeling study to identify the rate and magnitude of habitat destruction as well as the immigration rates where metaland-
scape connectivity would not be sufficient to rescue declining populations of hypothetical songbirds.

Methods

Our approach was to couple a spatially structured model of avian demography with a dynamic landscape model that simulated ongoing habitat destruction at different rates and intensities of fragmentation. This dynamic, spatially structured avian demographic model (dSSAD), discussed in detail in Schrott et al. (2005), is an extension of the spatially structured avian demographic (SSAD) model applied to static landscapes that was presented by With and King (2001). Schrott et al. (2005) assumed a closed landscape. Here we relax that assumption to allow for immigration. We provide only an overview of the essential features of the model to demonstrate how immigration was incorporated; further description of the model can be found in Schrott et al. (2005).

Model overview

dSSAD integrates conventional avian demographic modeling with a landscape perspective on how habitat structure influences demographic rates, namely fecundity (b). In most avian demographic models, the age-specific birth rate (b_x , the expected number of female produced per female at age x) or the equivalent maternity function (m_x) is typically a free parameter estimated from nest success, which is assumed to be constant across all patches. In Neotropical songbirds, however, nest success has been shown to be lower in small habitat fragments owing to negative edge effects (such as increased nest predation and brood parasitism) than in large patches or in landscapes with more contiguous habitat (Robinson et al. 1995; Flashpohler et al. 2001). In dSSAD, we have made nest success (the probability that a nest will pro-

duce at least one fledgling), and consequently fecundity b (number of female fledglings produced), an explicit function of patch geometry (specifically the edge:area ratio of the patch), which is a largely novel feature of our model (With and King 2001; Schrott et al. 2005). For this study, we modeled three different species-types that varied in their sensitivity to edge effects (*edge-sensitivity*) based on how quickly nest success declined as a function of patch size (low, intermediate and high edge-sensitivity; see Figure 1 in Schrott et al. 2005).

Annual changes in the population are described by an age-structured matrix population model parameterized from a demographic life table. Females begin breeding at 1 year, can produce 4–5 eggs/clutch (species are assumed to be single-brooded, with successful broods producing an equal fledgling sex ratio), and may survive up to 8 years. Annual survival probabilities are defined for two age classes: juveniles (< 1 year; $s_0 = 0.3$) and adults ($s = 0.6$). These values are typical for Neotropical migrants (Karr et al. 1990; Anders et al. 1997). A model run began with a landscape consisting entirely of suitable breeding habitat ($h = 100\%$). Given the specified survival probabilities, the model initialization and parameter calibration procedure (see Schrott et al. 2005) calculates the initial steady-state b at time $t = 0$ (b_0), as well as the initial steady-state female population N_0 and stable age-class distribution consistent with that value of b_0 . In dSSAD, the offspring production term in the maternity function b is a function of patch geometry that is changing over time (i.e., the landscape is dynamic); thus, b is a time-dependent parameter b_t . At each time step $t \geq 1$, the landscape and population at time t are used to calculate b_t . This value is used to update the life table and age-structured projection matrix accordingly, and the number of females in the population is projected forward one year. This cycle is repeated for the duration of the simulation until all habitat has been destroyed (see *Simulation of landscape dynamics*).

Simulation of metaland- scape connectivity via immigration rates

We simulated metaland-
scape connectivity with different rates of immigration into the focal landscape. Immigration was modeled as the annual

addition of a fixed number of individuals to the population, with that number defined as a percentage (m) of the initial population size (N_0). Thus, if $m = 1\%$ and $N_0 = 1000$, the number of immigrants (N_m) each year is 10. Immigrants were assumed to be first-year adults and were added to that age class of the population at each time step. Immigration rate was a constant for each landscape trial, reflecting the assumption that meta-landscape connectivity did not change over the time period simulated, even though habitat loss and fragmentation was occurring within the focal landscape. This could occur, for example, if disturbances are restricted to a particular part of the region (i.e., the focal landscape), or if the strength of source landscapes is unaffected by habitat destruction occurring elsewhere throughout the region (e.g., if the source landscape is a protected reserve). It should be possible to ‘couple’ local and regional landscape dynamics if desired, by making immigration rate (m) a dependent function of landscape pattern, such that m declines through time as the landscape (and region) became progressively disturbed ($h \rightarrow 0$). For the purposes of this study, however, we opted to keep m constant throughout a model run, which helped to isolate the effects of metalandscape connectivity (immigration rate) from local landscape effects due to habitat loss and fragmentation.

Simulation of landscape dynamics

Landscape dynamics were simulated as a time-series of landscape maps depicting different scenarios of habitat destruction, in which disturbance (habitat loss and fragmentation) was modeled as a fractal distribution using RULE (fractal neutral landscape models, With 1997; multifractal landscape maps, Gardner 1999). Landscapes were generated as 128×128 -cell grids; we set the cell resolution at 30×30 m, which produced a spatial extent of 1452 ha (~ 14.5 km²). We needed to assign physical dimensions to these landscapes in order to calculate the amount of suitable breeding habitat available on the landscape that met the territory and minimum area requirements of these generic songbirds (see With and King 2001; Schrott et al. 2005). The actual dimensions of the landscape are ultimately unimportant, however, because population dynamics were normalized for

landscape size as part of the model initialization and calibration procedure (see Schrott et al. 2005) and were thus not scale-dependent (i.e., the use of larger or smaller landscapes would not have affected model results).

As noted above, landscapes were initialized at 100% habitat ($h = 100$). Because the rate and duration of landscape disturbance (landscape history) can have different implications for population dynamics and extinction risk (Schrott et al. 2005), we subjected landscapes to three different rates of habitat loss that encompassed those reported for real landscapes ($r = 0.5, 1.0$, and 5.0% of the initial habitat lost/year; Spies et al. 1994; Moreira et al. 2001). Habitat was destroyed at a constant rate (r) until all habitat had been destroyed ($h = 0$). The time required to lose all habitat thus depended on the rate of habitat loss (r), and involved a longer time-series when habitat destruction occurred gradually (200 years at $r = 0.5$) than when it took place rapidly (20 years at $r = 5.0$). Disturbances were either correlated ($H = 1.0$, where H controls the spatial contagion of disturbance in the fractal generator, Gardner 1999), uncorrelated ($H = 0.5$), or negatively correlated ($H = 0.0$) in space. This produced three levels of landscape fragmentation, from highly fragmented ($H = 0.0$) to highly clumped ($H = 1.0$) habitat distributions (see With and King 2001 for examples of fragmented and clumped fractal landscape patterns). Ten replicate time-series were generated for each scenario of landscape change ($r \times H$ combination). Thus, the experimental design of our dynamic landscapes scenarios was a 3×3 factorial with $n = 10$ replicates (a total of 90 time-series). The spatially structured avian demographic model was then run on each of these replicated time-series of landscape change.

Quantifying the impact of metalandscape connectivity

The importance of metalandscape connectivity for the persistence of local landscape populations was assessed in terms of the extent to which immigration was sufficient to offset population declines resulting from habitat loss and fragmentation within these landscapes. We defined a rescue index as $RI = N_t/N_0$, where N_t is the size of the

population at time t . In the absence of immigration ($m = 0$) and with the scenarios of habitat loss used here, all populations modeled by dSSAD will decline (Schrott et al. 2005, with $N_t < N_o$ for $t > 0$ and $RI < 1$). A certain balanced level of immigration is thus necessary to maintain initial population sizes ($RI = 1$), and high levels of immigration may contribute to larger than initial populations ($N_t > N_o$ or $RI > 1$), at least for a time. Because habitat loss is ongoing in these landscapes, even populations sustained early on by immigration eventually cross the rescue index threshold ($RI = 1.0$). The RI threshold is thus useful for identifying the minimum level of immigration necessary to sustain declining populations for a given scenario of landscape change.

Design and analysis of simulation experiment

The factorial design for this simulation experiment consisted of three species-types that varied in their sensitivity to fragmentation (low, intermediate and high edge-sensitivity); nine landscape disturbance scenarios ($r = 0.5, 1.0, 5.0$; $H = 0.0, 0.5, 1.0$), each of which was replicated 10 times ($9 \times 10 = 90$ time-series; see *Simulation of Landscape Dynamics*); and, 13 levels of immigration ($m = 0, 1, 2, 5, 10, 20, 30, \dots, 80\%$). Model trials consisted of 100 runs of the stochastic, spatially structured avian demographic model (see *Overview of Model*) on

each time-series of dynamic landscape change for each level of species and immigration ($90 \times 3 \times 13 = 3510$ trials). Model results were averaged across runs ($n = 100$ runs of demographic model) for each trial, and these means were averaged across trials ($n = 10$ time-series maps) for each species-landscape-immigration scenario ($n = 351$ scenarios; $351 \times 10 = 3510$ trials).

Results

With sufficient immigration, simulated songbird populations initially increased ($N_t > N_o$, $RI > 1.0$) despite the loss and fragmentation of their breeding habitat. Because populations in isolated landscapes ($m = 0\%$) began declining almost immediately following the onset of habitat destruction, this population increase was due entirely to the rescue effect of immigration. As an example, consider a species with intermediate edge-sensitivity in landscapes subjected to moderate habitat fragmentation ($H = 0.5$) at a rate of 1%/year (Figure 1). An immigration rate of 2%/year is sufficient to maintain initial population sizes ($N_t = N_o$, $RI = 1.0$) for at least the first decade of habitat destruction (which equates to a 10% total loss of habitat given $r = 1\%/year$). Higher rates of immigration ($m > 2\%$) thus increase the rescue effect, more than doubling the initial

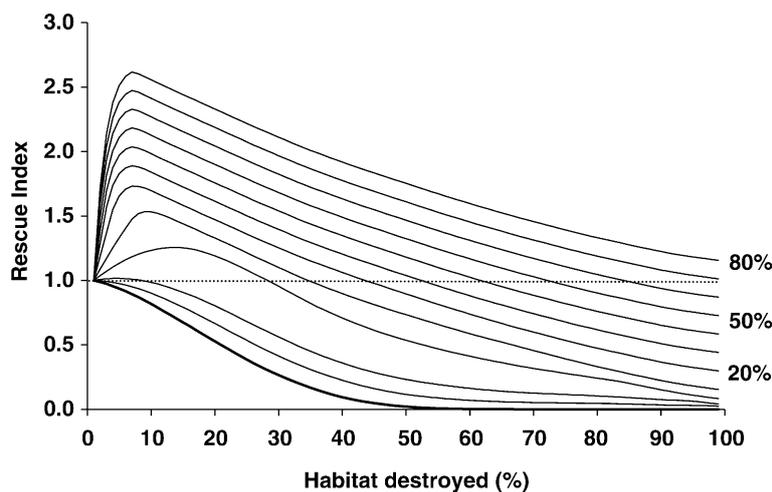


Figure 1. Effect of metalandscape connectivity, as indexed by immigration rate, on the rescue index (N_t/N_o) for a species with intermediate edge-sensitivity on landscapes subjected to moderate fragmentation ($H = 0.5$) at a rate (r) of 1%/year. Immigration rates (m) for 0% (no immigration, heavy line), 1%, 2%, 5%, 10%, 20%...80% are shown. The RI threshold is defined as the level of habitat loss at which immigration is no longer sufficient to rescue declining populations ($RI < 1.0$; where the curves cross the horizontal line).

population size ($RI > 2.0$) when $m > 50\%$ (Figure 1). The rescue effect ($RI \geq 1$) can persist for many years in spite of ongoing habitat loss (Figure 1), but generally undergoes a slow decay until immigration is no longer sufficient to offset population declines ($RI < 1.0$). The value of habitat loss at which this threshold is crossed (the RI threshold) depends upon the immigration rate (Figure 1). When $m = 10\%$, the RI threshold for this particular species and landscape scenario occurs after 30% habitat has been destroyed (> 30 years), but high levels of immigration ($m > 70\%$) can sustain populations almost indefinitely until virtually all habitat has been destroyed on the landscape (Figure 1). Results for other species and landscape scenarios were qualitatively similar, but differed with respect to the minimum level of immigration required to offset population declines and the critical level of habitat loss at which populations crossed the RI threshold (Figures 2 and 3).

The minimum level of immigration (degree of metalandscape connectivity) required to rescue declining populations also depended on the extent to which the focal landscape was being fragmented (H) (Figure 2). The effect of habitat fragmentation on the RI threshold was actually greatest for species with an intermediate degree of edge-sensitivity (Figures 2 and 3). This was due to an

‘all-or-nothing’ response of the other species to habitat loss. The species with low edge-sensitivity was so insensitive to edge (given the function we used), that the level of fragmentation (H) had little effect on population responses to landscape change (Schrott et al. 2005). At the other extreme, the species with high edge-sensitivity was so sensitive, that even a little fragmentation had a significant impact on populations (Schrott et al. 2005). For species with intermediate edge-sensitivity, higher rates of immigration were required to rescue populations subjected to a given amount of habitat loss in extensively fragmented landscapes ($H = 0.0$, Figure 2). For example, if 70% of the habitat had been destroyed, an immigration rate of 62% was required to maintain initial population sizes in extensively fragmented landscapes, but an immigration rate of only 36% was required in less-fragmented landscapes ($H = 1.0$) (Figure 2).

In general, low to moderate levels of immigration ($m = 0-20\%$) were sufficient to rescue species with low edge-sensitivity in landscapes where $< 70\%$ habitat had been destroyed, regardless of the extent of fragmentation (H) or rate at which habitat was destroyed (r) (Figure 3). At the other extreme, moderate to high levels of immigration ($m = 11-40\%$) were usually required to rescue highly edge-sensitive species in these same landscapes (Figure 3). However, very high levels of

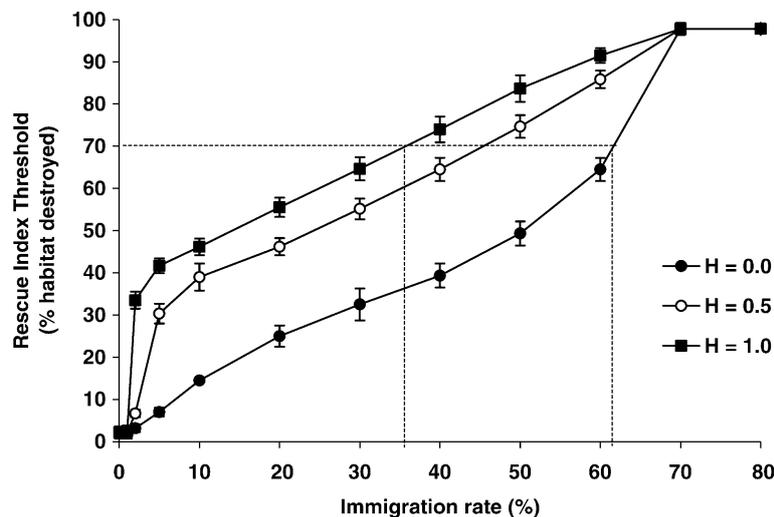


Figure 2. Effect of habitat fragmentation (H) on the minimum immigration rate (m) required to rescue declining populations ($N_t/N_0 < 1.0$) of a bird with intermediate edge-sensitivity (averaged over all levels of r). The rescue index threshold (RI threshold) is the level of habitat loss at which immigration is no longer sufficient to rescue declining populations ($RI < 1.0$; cf. Figure 1). Error bars are the standard error of the mean across trials of different habitat loss rates for a given level of habitat fragmentation (H).

(a)

Edge-sensitivity	H	Total habitat destroyed (%)			
		10	30	50	70
Low	0.0	0.5	0.5	12	39
	0.5	0.5	0.5	10	33
	1.0	0.5	0.5	9	31
Intermediate	0.0	6	26	49	61
	0.5	2	6	23	45
	1.0	1.5	2	13	35
High	0.0	22	32	47	62
	0.5	16	22	37	51
	1.0	14	18	30	47

(b)

Edge-sensitivity	r	Total habitat destroyed (%)			
		10	30	50	70
Low	0.5	0.5	0.5	15	38
	1.0	0.5	0.5	14	38
	5.0	1	0.5	3	28
Intermediate	0.5	3	14	32	51
	1.0	3	13	32	49
	5.0	4	7	21	42
High	0.5	17	26	41	55
	1.0	16	26	40	54
	5.0	17	20	33	48

Figure 3. Effect of habitat fragmentation (H ; shown in a) and habitat loss rate (r ; shown in b) on the minimum immigration rate (m) required to rescue declining populations ($N_t/N_o = 1.0$) for hypothetical songbirds (defined by edge-sensitivity) at different levels of habitat loss. Cell shading denotes the following levels of immigration: low = < 10% (white), moderate = 11–20% (light gray), high = 21–40% (dark gray), and very high = > 40% (black). For example, the minimum level of immigration required to rescue a declining species with intermediate edge-sensitivity in a highly fragmented landscape ($H = 0.0$) that has experienced a 70% loss of habitat (Figure 3a) is $m = 61\%$ (cf. Figure 2).

immigration ($m > 40\%$) were required to rescue highly edge-sensitive species in extensively fragmented ($H = 0.0$) landscapes that had lost > 50% habitat (Figure 3a), or when any landscape lost $\geq 50\%$ habitat gradually, over a period of 100 or more years ($r = 0.5\%/year$, Figure 3b). The latter result, where higher immigration rates are necessary to sustain populations when habitat loss is slow rather than fast, may at first seem counter-intuitive. In this scenario, however, habitat loss has

occurred over a long time interval (100 years) and encompassed more than 40 generations of these hypothetical songbirds (generation time = 2.3 years), compared to about 20 generations when habitat is lost twice as fast (1%/year). Thus, a gradual but persistent erosion of habitat can result in a slow demographic hemorrhaging, where fecundity is not sufficient to sustain the population. A higher level of immigration is thus required to maintain the initial population size.

Discussion

Connectivity is a central theme in landscape ecology (Wiens 2002). Although landscape ecology has traditionally focused on the importance of connectivity *within* landscapes (Taylor et al. 1993; With et al. 1997; Tischendorf and Fahrig 2000; With 2002), the current study emphasizes the importance of connectivity *between* landscapes (*metalandscapes connectivity*) for certain ecological processes, such as source-sink population dynamics that may contribute to the regional persistence of many migratory songbirds (Donovan et al. 1995a, b; Robinson et al. 1995; Brawn and Robinson 1996). Connectivity can be defined at multiple spatial scales (Noss 1991), from the distribution of foraging patches within a bird's territory to the dispersion of territories within a habitat patch to the distribution of suitable breeding habitat within a landscape (Ims 1995; With 2002). Incorporating metalandscape connectivity within this hierarchical framework thus permits the extension of metapopulation concepts from a landscape to regional scale (With 2004), akin to the notion of the 'megapopulation' proposed by Ricklefs (1992), which involved the demographic coupling of resident and migratory bird populations between regions. 'Migratory connectivity' has also been used to describe the linkage between breeding and wintering populations of migratory species, which may encompass continent-wide or even global scales (Webster et al. 2002).

Such a hierarchical approach to the conservation of Neotropical migratory songbirds has been proposed (Freemark et al. 2002). The problem is how to extrapolate information gained at the finer patch- or landscape-scale to broader regional scales. Just as information on population dynamics within an individual habitat patch (e.g., woodlot, pasture or field) is not sufficient for evaluating persistence of the entire metapopulation at a broader landscape scale (Brawn and Robinson 1996; Donovan et al. 1997), so too is information on metapopulation viability within a particular landscape insufficient for evaluating the status and viability of regional populations of migratory songbirds. For example, a species may be declining in numbers and have other indications of poor population performance (low pairing success, low nesting success, low juvenile survival)

within a given patch or landscape (Donovan et al. 1995b; Porneluzi and Faaborg 1999; Fauth 2000), but may nevertheless exhibit stable or even increasing numbers at the broader regional scale owing to coupled source-sink dynamics among landscape populations (Brawn and Robinson 1996). Thus, a species may persist at a regional scale if metalandscape connectivity is sufficient, in spite of a disruption of connectivity at a local landscape scale (i.e., landscapes have become fragmented). This decoupling of landscape and regional dynamics has important implications for conservation. Habitat connectivity within landscapes (landscape connectivity) is assumed to be important for population persistence, but unless the landscape is isolated, it may be difficult to make inferences regarding the long-term viability of a species within landscapes based solely on measures of landscape connectivity or landscape structure more generally (e.g., Flather and Sauer 1996; Fauth et al. 2000).

Landscape context may thus be important for evaluating species' responses to landscape change, which requires that such studies of landscape effects on populations be placed within a broader regional context. This is especially true where there exists strong regional variation in fragmentation effects on productivity. For example, the effects of forest fragmentation on Wood Thrush population dynamics are much more severe in the agricultural context of Midwestern landscapes, than in the eastern United States where levels of cowbird parasitism and nest predation are much lower (Trine 1998). Large tracts of forest (>1000 ha) in some regions of the Midwest (Illinois) can function as landscape sinks in most years (Trine 1998), whereas forest fragments much smaller than this (>100 ha) were capable of supporting viable populations in eastern landscapes (Hoover et al. 1995). Even in similarly fragmented landscapes elsewhere in the Midwest (Indiana), small forest patches may act as population sources for Wood Thrushes, at least in some years when conditions for breeding are particularly good (Fauth 2000, 2001). The importance of immigration among landscapes (metalandscapes connectivity) for species persistence means that local-scale dynamics can only be understood within a larger regional context.

Just as landscape connectivity is a species-dependent construct (With 2002), the importance

of metalandscapes connectivity for population persistence will likewise vary among species. Our study has shown that metalandscapes connectivity is expected to be less important for species with low edge-sensitivity, at least until <30% habitat remained on the landscape (>70% habitat has been destroyed), at which point high metalandscapes connectivity was necessary to sustain the local landscape population. Metalandscapes connectivity was most important for species with high edge-sensitivity, particularly if the local landscape was also extensively fragmented or when > 30% of the habitat in the landscape had been destroyed. This species-type is particularly sensitive to habitat loss and fragmentation, and landscape populations are easily pushed past the persistence threshold into the sink domain (With and King 2001). Because of demographic lags, however, the relationship between the rate of landscape change and the degree of metalandscapes connectivity necessary to sustain such populations is nevertheless counter-intuitive. If the landscape changes faster than the demographic response time of the population, population declines will lag behind the change in landscape structure (Schrott et al. 2005). For example, consider two landscapes in which 50% of the habitat has been destroyed. Populations on landscapes subjected to a gradual loss of habitat (0.5%/year) would have been subjected to disturbance for a longer period of time (100 years) vs. populations on landscapes in which habitat loss occurred rapidly (5%/year, in which case it would have taken only 10 years to lose 50% of the habitat on the landscape). Thus, populations on landscapes subjected to low-level chronic disturbance over long time periods are expected to suffer greater demographic erosion (in terms of fewer reproductive females producing fewer offspring) than populations that experience an intense bout of disturbance over a period of a few years (again, for the same total amount of habitat lost). In the latter case, females are still present on the landscape, but they are not breeding successfully owing to reduced numbers of territories available and greater edge effects. It takes awhile before these demographic consequences of landscape change are reflected in population growth rates or overall population size, however. This is the 'demographic response time' to landscape change that ultimately results in a demographic lag for populations in rapidly changing landscapes. Paradoxically higher

levels of immigration were thus necessary to offset population declines when habitat was lost gradually than when it was lost quickly. This means that the importance of metalandscapes connectivity for population viability may not be fully appreciated in landscapes undergoing rapid rates of change.

Alternatively, high metalandscapes connectivity could obscure the adverse effects of habitat loss and fragmentation on local populations. This is particularly true if population responses to habitat loss and fragmentation are assayed only in terms of population size or density. High levels of immigration could sustain or even increase population numbers, giving the impression that birds are unaffected by landscape-wide habitat loss and fragmentation. The importance of metalandscapes connectivity for local population persistence can be inferred from demographic analyses, which demonstrate that reproductive success, and ideally survival rates, are not sufficient to maintain stable populations (e.g., Donovan et al. 1995b; Anders et al. 1997; Proneluzi and Faaborg 1999; Fauth 2000, 2001; Murphy 2001). This approach does not give an idea of the magnitude of immigration necessary to offset population declines, however. Direct quantification of immigration rates for migratory birds is admittedly much harder to obtain. Band returns are often too low to permit reliable estimates of immigration in migratory songbird populations, especially because banded individuals may settle many kilometers from natal territories where they are unlikely to be re-sighted, and thus data on natal dispersal are biased toward shorter distances and sex-biased toward males (the philopatric sex in most songbirds; Greenwood 1980). Nevertheless, the evidence points to high rates of immigration, even for resident populations. For example, in a seven-year study of Eastern Bluebirds (*Sialis sialis*) in the southeastern United States, immigration accounted for 66% of the males and 76% of the females in this resident population (Plissner and Gowaty 1996). Nearly identical levels of immigration were found during a nine-year study of resident willow tits (*Parus montanus*) in northern Finland, with 63% of male and 76% of female breeders originating from outside the area (Orell et al. 1999). In the case of the migratory Pied Flycatcher (*Ficedula hypoleuca*), immigration accounted for about 71% of the population within a 25-ha oak woodland, with the annual immigration rate averaging 44% during an

11-year study in the UK (Stenning et al. 1988). During a 10-year study of a migratory population of White-crowned Sparrows (*Zonotrichia leucophrys*) in the Sierra Nevada mountains of California, 60% of the males and 64% of the females that returned to breed as yearling adults were immigrants (Morton et al. 1991). Immigration rates during a 16-year study of Wood Thrushes, a Neotropical migrant, in a 15-ha woodlot in Delaware averaged about 36% for males and 51% for females, although there was considerable variation among years (Roth and Johnson 1993). For males, immigration rates varied between 11 and 59%, whereas for females, immigration rates ranged from 25 to 71% across years. Collectively, these studies confirm that metalandscape connectivity is high for many songbirds, owing to their great mobility and ability to switch between breeding sites among years (e.g., Holmes et al. 1996; Murphy 2001).

Natural rates of immigration thus match the very high levels (> 40%) we found necessary to maintain populations in landscapes where significant habitat loss (> 70%) had occurred (i.e., landscape sinks, Figure 3). Because many contemporary landscapes contain < 30% suitable breeding habitat, as is the case in the Midwestern United States (e.g., Robinson et al. 1995), this again underscores the importance of regional source-sink dynamics for the persistence of many migratory songbirds. This does not mean, however, that the effects of habitat loss and fragmentation on species persistence can be entirely mitigated by metalandscape connectivity, at least not indefinitely. If habitat destruction is widespread across a region, then many landscape populations will be simultaneously impacted, resulting in the erosion of source strength of landscapes, if not a complete conversion of landscape sources into landscape sinks. Eventually, a threshold in region-wide habitat availability will be crossed that will make it impossible to sustain the species. Metalandscape connectivity may thus be necessary, but not sufficient, for the regional persistence of many Neotropical migrants.

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