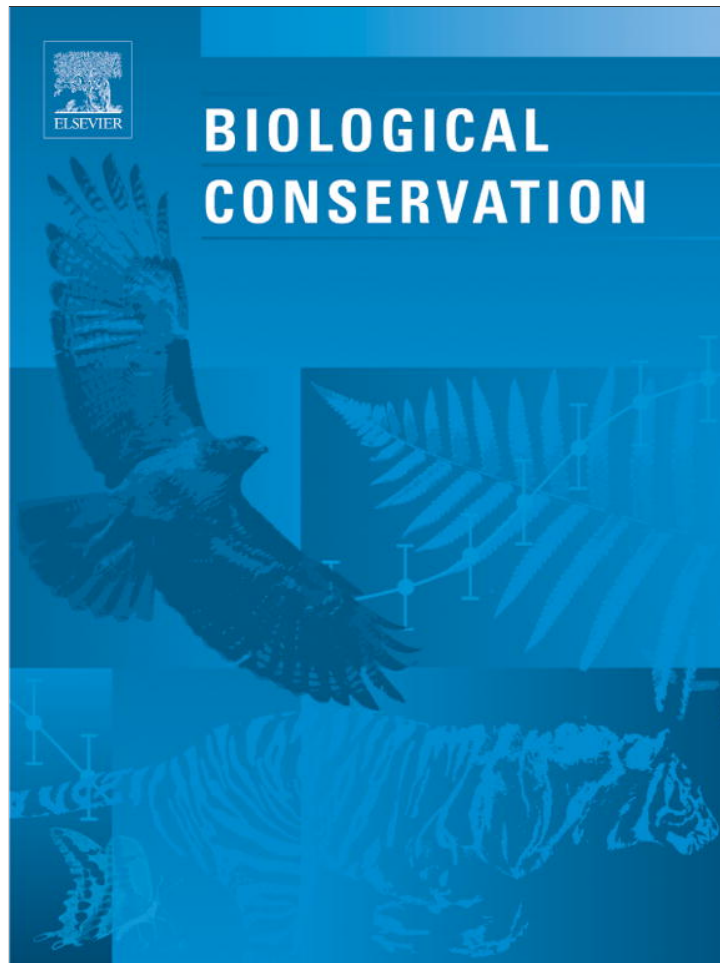


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## Conifer plantations consistently act as barriers to movement in a deciduous forest songbird: A translocation experiment

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### ABSTRACT

Many authors have concluded that habitat loss has a greater influence on biodiversity than habitat fragmentation *per se*. Yet, several animal species have been shown to be reluctant to move across inhospitable landscape matrices, a phenomenon that would be expected to exacerbate fragmentation effects. In this study, we tested the ability of a forest songbird (Ovenbird, *Seiurus aurocapilla*) to move across two contrasting landscapes whose matrix (intensively managed forest) would be expected to be relatively permeable compared to agricultural or urban matrices. We hypothesized that males would be less likely to return to their territory in a landscape dominated by forest generally unsuitable for breeding (spruce plantations) than in another dominated by potential breeding habitat (deciduous forest). The probability of resighting translocated males ( $n = 48$ ) on their territory was significantly lower in the plantation landscape and this relationship was consistent over two successive years. Neither translocation time nor body mass, time of capture, or structural size were significant predictors of probability of resighting. Although this species is sufficiently vagile to return quickly to its territory (e.g. one male returning in less than 2 h), these results indicate that even a forested matrix may impose a resistance to the movements of a forest bird species when its structure or composition differs from that of breeding habitat. Matrix resistance to movements potentially restricts the ability of individuals to detect and colonize suitable habitat fragments. Less vagile species would be even more affected and, therefore, we submit that a more inclusive perspective on effects of landscape change is warranted.

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### 1. Introduction

Across the world, the increasing human footprint associated with land use intensification (Gibson et al., 2011) has rekindled the debate on the relative influence of habitat loss and fragmentation (Didham et al., 2012). In a review, Fahrig (2003) concluded that “empirical studies to date suggest that habitat loss has large, consistently negative effects on biodiversity” and added that “habitat fragmentation *per se* has much weaker effects”. Few authors would challenge the contention that habitat loss (e.g. Zitske et al., 2011) or habitat degradation (Harrison and Bruna, 1999) are serious threats to biodiversity. However, past studies may not have properly disentangled effects of habitat loss and fragmentation owing to the statistical pitfalls involved in this process (Smith et al., 2009). There is also empirical evidence suggesting that fragmentation *sensu strictu* may affect the demography of certain species through matrix resistance to movements (Castellón and Sieving, 2006; Epps et al., 2007; Sheperd et al., 2008) or through

a disruption of predator–prey (Whittington et al., 2011) or host–parasite dynamics (e.g. Roland, 1993).

In forest birds, including some highly vagile migratory species, translocation experiments and telemetry studies have shown that movements can be significantly impeded by the creation of an inhospitable matrix, e.g. agricultural fields, clearcuts, periurban areas, or areas disturbed by mining (Bayne and Hobson, 2001a; Gobeil and Villard, 2002; Kennedy and Marra, 2010; Desrochers et al., 2011; Tremblay and St. Clair, 2011). Forest specialists have also been shown to be more sensitive to matrix type (Gobeil and Villard, 2002; Kennedy and Marra, 2010; Ibarra-Macias et al., 2011) or the presence of riparian corridors (Gillies and St. Clair, 2008) than forest generalists. Matrix resistance to movements would be expected to exacerbate fragmentation effects in the strict sense, i.e. the breaking apart of habitat irrespective of habitat loss in the landscape.

Based on such evidence, a more inclusive perspective on the ecological implications of landscape alterations is required because the erosion of biodiversity associated with habitat loss and degradation can be compounded by a gradual disruption of functional connectivity and by negative matrix effects on reproduction in habitat fragments (Andrén, 1992; Poulin and Villard, 2011; Falk

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et al., 2011; Rodewald et al., 2011). This is even more important when considering that functional connectivity will be critical as climate change causes significant shifts in species distributions (Clobert et al., 2009; Rodenhouse et al., 2009). However, it could be argued that habitat fragmentation is mainly relevant to highly contrasted landscape mosaics, where individuals have to move across highly inhospitable matrices.

In this study, we subjected a focal species of passerine bird (Ovenbird, *Seiurus aurocapilla*) to what we deemed a moderately challenging situation over two successive years through experimental translocations. The Ovenbird reaches its highest breeding densities in mature and old unmanaged deciduous or mixedwood forest stands (Pérot and Villard, 2009; Porneluzi et al., 2011), where it nests and forages on the ground. We moved individuals in two different landscapes: one whose matrix was dominated by spruce plantations and the other whose matrix was dominated by partially-harvested deciduous stands. We reasoned that these matrices would be relatively permeable to movements of a forest bird. This particular experiment was performed (1) to assess the variability in the responses of each group of individuals to the same challenge, (2) to determine whether this species responds differently to two types of forest matrices, and if so (3) to determine whether this response is robust through time.

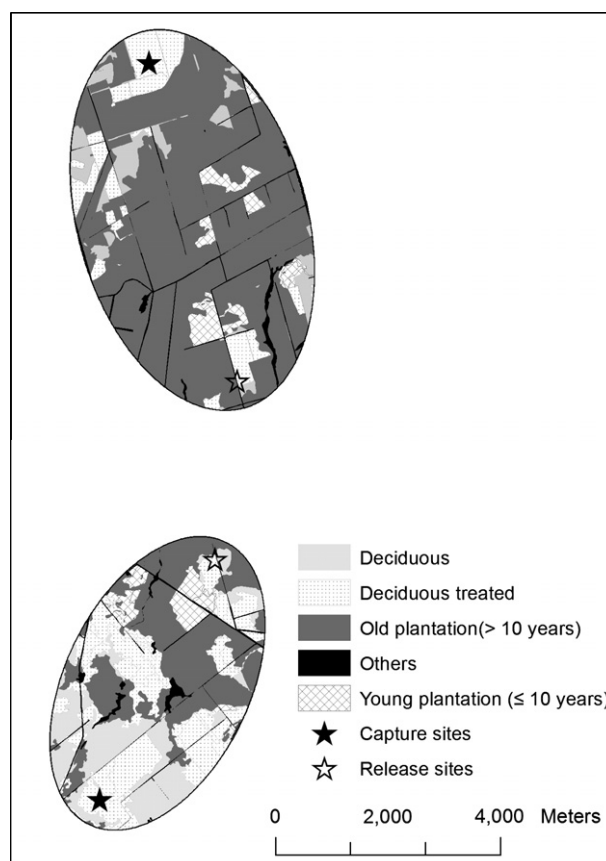
On the basis of the Ovenbird's habitat use, both matrix types would be expected to be relatively permeable to its movements relative to large clearcuts, agricultural fields, or residential areas (Bélisle et al., 2001; Gobeil and Villard, 2002). Nonetheless, we hypothesized that males would be more likely to return in the "deciduous landscape" because the matrix is more similar to the breeding habitat of the species than in the "plantation landscape". We also hypothesized that older (experienced) males would be more likely to return than first-time breeders, owing to their greater familiarity and thus, attachment, to their territory (Pärt, 1995; Piper, 2011).

## 2. Methods

### 2.1. Study area and experimental design

The study area (Black Brook District) is located in northwestern New Brunswick, Canada (47°23'N; 67°40'W). It is characterized by rolling hills with broadleaf deciduous forests (northern hardwood forest, dominated by sugar maple, *Acer saccharum*; American beech, *Fagus grandifolia*; and yellow birch, *Betula alleghaniensis*) on hilltops (ca. 25% of land base), conifer-dominated stands (spruces, *Picea* spp.; balsam fir, *Abies balsamea*) at lower elevations (20%), and scattered mixedwood stands (18%). Under private ownership (J.D. Irving Ltd.), the land base is intensively managed for timber production, with ca. 37% cover of spruce plantations (mainly white and black spruces, *Picea glauca* and *Picea mariana*) (Etheridge et al., 2006).

Within the study area, we performed experimental translocations in two contrasting landscapes (Fig. 1): one whose matrix was dominated by deciduous forest, and the other whose matrix was dominated by ≥10 years old spruce plantations (Table 1). In each landscape, we used a single capture and a single release site, both located in broadleaf deciduous forest stands (all >17 ha). In the "plantation landscape", the capture and release sites had been treated through shelterwood harvesting in 1992 and 1993, respectively. In the "deciduous landscape", the capture site was treated through selection harvesting in 2005 and the release site was partially harvested in 2000. Capture sites covered ca. 25 ha whereas all releases were performed at a specific point along the edge of a deciduous fragment. Ovenbird males could be heard singing when we released translocated individuals in either landscape, suggesting that these sites represented suitable breeding habitat. In spite



**Fig. 1.** Map of the main land cover types in the two landscapes (ellipses; eccentricity = 0.70) where experimental translocations were performed. Treatments in deciduous forest stands include shelterwood and selection harvesting. "Others" represents, wetlands, fields, or roads.

**Table 1**

Percent cover of selected land cover types in the two landscapes used to perform translocations (see also Fig. 1). See Section 2 for silvicultural treatments applied to deciduous forest stands.

Land cover type	Deciduous landscape	Plantation landscape
Deciduous forest, untreated	22.7	8.8
Deciduous forest, treated	31.5	9.5
Plantations ≥ 10 year old	36.8	71.6
Plantations <10 year old	5.4	6.0
Other land cover types	3.6	4.1

of the differences in treatment intensity and timing between study sites in the two landscapes, stand structures were very similar at the time of the experiment, since shelterwood harvest treatments are more intensive than selection/partial cutting but they were applied several years earlier.

Owing to the particular configuration of Ovenbird habitat, the distance between release and capture sites in the deciduous landscape was slightly shorter (4.5 km) than that in the plantation landscape (5.6 km). The landscape is characterized by gently rolling hills but topography differed slightly between the two landscapes: both capture sites had a flat topography but that of the plantation landscape was located on a hilltop, whereas the capture site of the deciduous landscape was located at a similar altitude as its surroundings.

### 2.2. Translocation protocol

All translocations were performed from 19–24 May 2010 ( $n = 28$ ) and from 21–23 May 2011 ( $n = 20$ ), ca. 10 days after the first observation of males settling in the study area (Thériault et al., in

press). This was done to ensure that males, including recruits (individuals breeding for the first time in the site), would be established on their territory. We also wanted to ensure that the translocation period would be as short as possible to control for the potential influence of translocation date. Individuals were caught between 550 and 1345 h by attracting them into a mist-net using a playback of conspecific vocalisations and carried in an opaque cotton bag to the research vehicle. Upon arrival at the release site, the male was banded using a numbered metal band from the Canadian Wildlife Service, and given a unique color band combination (Hughes celluloid bands). It was then weighed and we measured its (unflattened) wing chord and tarsus length to determine whether body mass or structural size could influence homing probability. Male age was determined according to the angle of the third rectrix to distinguish first-time breeders (SY: second-year males) from older (ASY: after second-year) males (Bayne and Hobson, 2001b). We recorded the time elapsed between capture and release ( $70.7 \pm 26.4$  min [mean  $\pm$  SD]) to determine whether the translocation delay influenced homing probability.

After the release of a translocated male, the capture site and its vicinity were revisited two times: once within 24–48 h and once within 2–3 weeks after the capture date (at which time most females were incubating). Searches for returning males took place between sunrise and 1400. Each time, the observer (M.A.V. or S.H.) returned to the capture site and closely watched nearby males to identify their color band combination. When no banded male was detected nearby, we played a recording of a conspecific song within 50–75 m of the capture location for a 10–15 min period and searched for color banded males among those showing a territorial response.

### 2.3. Statistical analyses

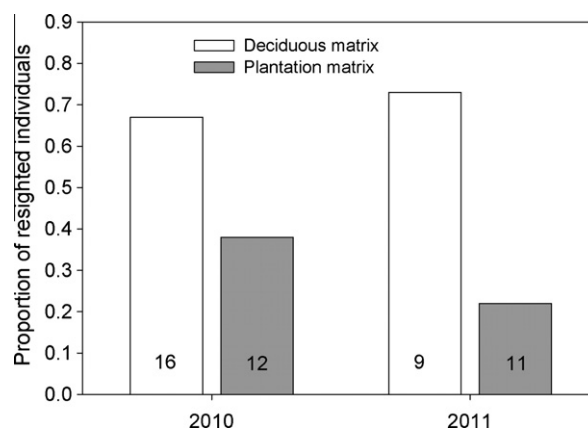
We evaluated the influence of several potential predictors of the probability of resighting males on their territory after translocation using a generalized linear model (logit link function). The predictors we tested were matrix type (plantation or deciduous), male age (ASY or SY), and year, as well as matrix  $\times$  age, matrix  $\times$  year, and age  $\times$  year interactions. We used the same generalized linear models to examine the effects of potential confounding variables, namely translocation time, body mass, and structural size (as estimated from tarsus and wing lengths, and interactions (body mass  $\times$  wing length, body mass  $\times$  tarsus length, and wing  $\times$  tarsus length). Because body mass varies during the day, even in males (Meijer et al., 1994), we tested a separate model using time of capture instead of body mass. We reasoned that time of capture might reflect the bioenergetic status of males and, thus, their ability to complete the return flight to their territory.

We did not model effects of landscape type, male age and other independent variables on return time because we did not quantify this parameter precisely enough. However, with respect to the probability of return, resighted males were either observed at the capture site or within ca. 50 m thereof, which suggests that resighting probability was very high.

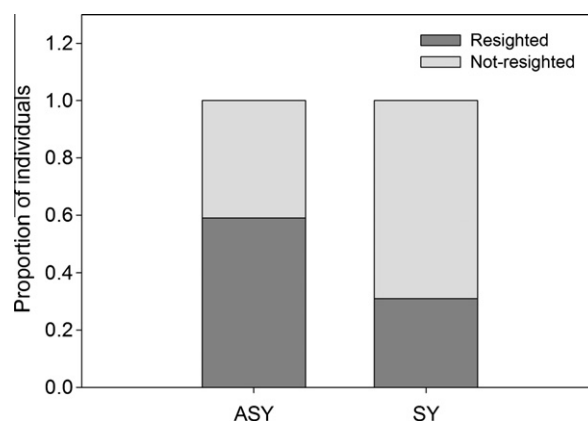
## 3. Results

We translocated a total of 48 males over the 2 years, roughly half of which were captured in each landscape type (plantation:  $n = 25$ ; deciduous:  $n = 23$ ). Of these, 32 (66.7%) were older (ASY) males and 16 were second-year (SY) males. The SY:ASY ratio did not differ between the two landscape types ( $G = 1.052$ ;  $P = 0.305$ ). Of the 48 males translocated, exactly half (24) returned to their territory, and three were observed in the release sites.

As predicted, the homing probability of translocated males was higher (approximately twice as high) across a matrix dominated by



**Fig. 2.** Proportion of translocated male Ovenbirds that were resighted on their territory by matrix type and year. Sample sizes are indicated at the base of each bar. There was a significant effect of matrix type, but no year effect on the probability to resight males in the capture site. See Section 3 for further details.



**Fig. 3.** Proportion of translocated male Ovenbirds that were resighted on their territory according to their age. SY (second year) designates first-time breeders ( $n = 16$ ) and ASY (after second-year) represents older males ( $n = 32$ ). The trend was not statistically significant.

deciduous forest than it was across a matrix dominated by spruce plantations ( $F_{1,41} = 5.69$ ;  $P = 0.022$ ; Fig. 2) and there was no year effect. Homing probability was not related to male age ( $F_{1,41} = 1.79$ ;  $P = 0.188$ ), although the trend was in the direction predicted (Fig. 3). Neither translocation time between capture and release nor body mass, time of capture, or parameters of structural size (wing chord and tarsus length) had a significant influence on homing probability.

Of the three translocated males resighted in release sites the same year they were translocated, two behaved as if they were caring for nestlings or recently-fledged young (carrying food or walking on the ground, fluttering wings) whereas the third responded strongly to a conspecific playback, indicating that he was territorial. One male (ASY) was relocated at the release site in the deciduous landscape whereas the other two (SY) were resighted in the plantation landscape. Unfortunately, the exact number of translocated individuals that settled in release sites is unknown because we did not perform standardized searches.

## 4. Discussion

Forest management has been shown to have moderate effects on forest bird assemblages relative to those of agriculture or

urbanization (Andrén, 1992; Drapeau et al., 2000; Rodewald and Yahner, 2001; Vitz and Rodewald, 2006). Yet, our results indicate that habitat fragmentation is not only relevant to highly contrasted landscape mosaics. In our managed forest landscape, translocated Ovenbird males were less likely to be resighted on their territory when the matrix was dominated by spruce plantations than when it was dominated by deciduous forest. Because birds were not radio-tracked following their release, we could not confirm that they moved preferentially through deciduous stands in the deciduous landscape. In the plantation landscape, birds had no choice but to move across large expanses of spruce plantations (Fig. 1). Although Ovenbirds have been detected during the breeding season in 40–55 year old spruce plantations elsewhere in the study area, this species typically does not occur in plantations unless they are adjacent to deciduous stands or include scattered deciduous trees contributing to the leaf litter (MacKay and Villard, unpublished results).

The Ovenbird definitely has the vagility and navigational ability required to return quickly to its territory over the distance range used in this study. For example, a second-year male (first-time breeder) translocated as part of this study was detected 1:55 h after its release in the deciduous landscape. Hence, matrix resistance to movements seems to reflect a behavioral response rather than an actual physical barrier. The fact that some of the translocated males settled in the release sites is also consistent with the notion of a behavioral reluctance of some individuals to move across the landscape, although we cannot rule out subtle differences in habitat quality between capture and release sites. The lower homing probability in the plantation landscape could also be attributed in part to the greater distance (5.6 vs. 4.5 km) over which the birds were displaced, as shown by Desrochers et al. (2011). However, these authors compared local (ca. 2 km) and landscape level (ca. 25 km) translocations. Bélisle et al. (2001) did not find a significant effect of translocation distance on homing time or probability (range: 842–4286 m). Hence, it seems unlikely that the difference we observed in homing probability between our two landscapes could be attributed to the ca. 1 km difference in translocation distance (exact distances varied slightly). The perceptual range may also have differed between the two landscapes under study, but the bias should have favoured individuals translocated in the plantation landscape, because the capture site would have been more visible to birds flying above the canopy than was the case in the deciduous landscape. Our results do not suggest that perceptual range played a significant role, here.

Experimental translocations were performed ca. 10–15 days after male arrival from spring migration in our study area (Thériault et al., *in press*). Hence, they were probably firmly established on their territory, as suggested by their strong response to conspecific playbacks. To reduce the potential influence of pairing status on their tendency to return to their territory, we performed all translocations over a short period each year, at a time when females had just arrived to the study area. The capture sites in each landscape had similar basal areas of trees (15.9 vs. 17.2 m<sup>2</sup>/ha in the deciduous and plantation landscapes, respectively). However, forest stand structure was heterogeneous, making it difficult to control for variability among territories within and between the two landscapes. Thus, we cannot rule out an effect of territory quality on propensity to return to capture sites in either landscape.

The extent to which translocation experiments reflect the actual propensity for movement exhibited by dispersers remains unknown. We submit that experimental translocations, or homing experiments, represent an index of the resistance of the landscape matrix to animal movements under controlled conditions. Indeed, translocation experiments allow researchers to pre-select distances and landscape configurations into which they release individuals, thus permitting to test specific hypotheses about factors

potentially influencing movement patterns. When translocations are conducted beyond the neighborhoods where individuals may have acquired prior knowledge through off-territory forays (Norris and Stutchbury, 2001), they can thus be considered as providing an index of landscape resistance to movement until technological progress will allow monitoring the dispersal movements of small, territorial organisms (Desrochers et al., 2011). In the Hooded Warbler (*Wilsonia citrina*), Norris and Stutchbury (2001) observed extra-territorial movements by males extending up to 2.5 km away from their territory. Scarlet Tanager (*Piranga olivacea*) and Wood Thrush (*Hylocichla mustelina*) have also been shown to perform such movements (Fraser and Stutchbury, 2004; MacIntosh et al., 2011), the latter species being shown to move up to 400 m away from its territory. In this study, we translocated birds approximately 2–11 times farther.

The protocol we used to relocate translocated individuals was much less intensive than that used in some other studies (e.g. Bélisle et al., 2001; Gobeil and Villard, 2002; Kennedy and Marra, 2010). However, our focus was on the effect of predictors of homing probability rather than on homing time. Results were highly consistent between years and, thus, the influence of matrix type appears to be a robust result. Male age, however, was not a significant predictor of homing probability.

Many human activities create contrasting matrices from the perspective of animal taxa, and forest specialists appear to be especially reluctant to cross them (Gobeil and Villard, 2002; Gillies and St. Clair, 2008; Ibarra-Macias et al., 2011; Awade et al., 2012). The fact that organisms as vagile as migratory songbirds responded to relatively subtle variations in matrix type such as those investigated in this study suggests that habitat fragmentation in the strict sense, and the nature of the matrix, should be given serious attention in conservation planning. Gobeil and Villard (2002) found that Ovenbirds had a higher probability of return and shorter return time in a naturally-fragmented landscape than in landscapes fragmented by forestry, with agricultural landscapes being the least permeable. When controlling for amount of remnant habitat, Brady et al. (2011) found that matrix habitat attributes tended to be better predictors of mammal species richness than distance to the nearest patch, suggesting that in some cases, matrix composition can be more influential than fragmentation *sensu strictu*. Matrix habitats may also impact species inhabiting fragments by providing resources to nest predators or brood parasites, either in agricultural landscapes (Andrén, 1992; Falk et al., 2011) or in intensively managed forest landscapes (Poulin and Villard, 2011).

In this study, the permeability of the matrix to Ovenbird movements appeared to reflect its similarity to breeding habitat. Males released in the plantation landscape had to cross deciduous/spruce plantation edges whereas those released in the deciduous landscape could, at least initially, cross a softer edge until they reached relatively narrow gaps in deciduous cover. However, telemetry would be required to confirm that individuals respond to edge contrast. Other translocation experiments have shown species-specific responses to matrix type or landscape structure (Gobeil and Villard, 2002; Kennedy and Marra, 2010; Gillies and St. Clair, 2010; Ibarra-Macias et al., 2011), which is consistent with the notion that different species or species guilds perceive the landscape differently (Betts et al., 2007; Lloyd and Marsden, 2011). This is a critical consideration when developing strategies to restore functional connectivity (e.g. Lloyd and Marsden, 2011) and translocation experiments are an efficient tool to analyze species' perception of the landscape, to identify species most likely to exhibit disruptions in functional connectivity, and to help parameterize spatially-explicit models (e.g. Palmer et al., 2010; Pe'er et al., 2011).

The recent suggestion by Didham et al. (2012) that habitat loss and fragmentation represent a “false dichotomy” and that species responses to landscape change are interdependent runs counter to

the substantial evidence for species-specific responses to landscape structure reported through experimental translocations. “Habitat” and “matrix” actually are species-specific concepts and we should embrace this variability when developing conservation strategies.

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