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RESEARCH ARTICLE

The influence of matrix quality on species richness in remnant forest

Ian J. Reider · Maureen A. Donnelly · James I. Watling

Abstract

Context Habitat destruction is the leading threat to terrestrial biodiversity, isolating remnant habitat in a matrix of modified vegetation.

Objectives Our goal was to determine how species richness in several broad taxonomic groups from remnant forest was influenced by matrix quality, which we characterized by comparing plant biomass in forest and the surrounding matrix.

Methods We coupled data on species-area relationships (SARs) in forest remnants from 45 previously published studies with an index of matrix quality calculated using new estimates of plant biomass derived from satellite imagery.

Results The effect size of SARs was greatest in landscapes with low matrix quality and little forest cover. SARs were generally stronger for volant than for non-volant species. For the terrestrial taxa included in our analysis, matrix quality decreased as the proportion of water, ice, or urbanization in a landscape increased.

Conclusions We clearly demonstrate that matrix quality plays a major role in determining patterns of species richness in remnant forest. A key implication of our work is that activities that increase matrix quality, such as active and passive habitat restoration, may be important conservation measure for maintaining and restoring biodiversity in modified landscapes.

Keywords Connectivity · Dispersal · Habitat loss · Habitat modification · Isolation · Patch

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Introduction

Habitat loss is the primary threat to terrestrial biodiversity (Barnosky et al. 2012; Newbold et al. 2016). The link between habitat loss and biodiversity maintenance is rooted in the species-area relationship (SAR), which states that large areas of habitat harbor more species than small habitat areas. Large habitats are relatively species-rich because they are better buffered from stochastic extinction events (Gonzalez and Chaneton 2002), represent bigger targets for colonists (Jones et al. 2015), and contain more resources (Steinmann et al. 2011) than small areas. The benefits of large areas for biodiversity provide the key rationale for conserving large, continuous habitat patches (Paz Durán et al. 2016), a hallmark of global

conservation efforts (Edgar et al. 2014; Watson et al. 2014).

Although habitat loss is recognized as the major threat to biodiversity, removal of habitat is usually accompanied by fragmentation, a change in landscape configuration resulting from the breaking apart of habitat (Fahrig 2003). Whereas habitat loss is a process in which the total amount of habitat in a landscape decreases, and the mean distance among patches of remnant habitat increases, fragmentation is the pattern that frequently emerges in such landscapes, wherein the number of habitat remnants and total edge length increase, and mean remnant size decreases (Fahrig 2003). Much debate has focused on the relative importance of habitat loss and fragmentation for biodiversity maintenance (Fahrig 2013; Rybicki and Hanski 2013). However, the fact that habitat loss and fragmentation are often strongly correlated (Haila 2002) means that populations in highly modified landscapes are frequently confined to relatively small and geographically distant habitat remnants that experience little if any demographic and genetic rescue because of limited inter-patch immigration (Brown and Kodric-Brown 1977; Brook and Buettel 2016).

Forest remnants resulting from deforestation resemble oceanic islands, so the extinction and colonization processes unified in the equilibrium theory of island biogeography (MacArthur and Wilson 1967) are thought to explain species responses in deforested terrestrial landscapes (Haddad et al. 2015; Resasco et al. 2017). An important difference between oceanic and terrestrial landscapes is that oceanic islands are separated by a truly inhospitable aquatic barrier, whereas forest remnants are generally surrounded by a matrix of modified vegetation that may not be uniformly inhospitable. Many studies have found that the matrix plays an important role in determining patterns of species occurrence, abundance, and richness in forest remnants (Cook et al. 2002; Prevedello and Vieira 2010; Nowakowski et al. 2013a, b). For forest-dwelling species, low- and high-quality matrix may be differentiated by plant biomass (Marzluff and Ewing 2001; Kupfer et al. 2006; Biswas and Wagner 2012). Here we considered high quality matrix to have similar biomass to forest remnants (e.g., secondary regrowth around primary forest remnants), whereas low quality matrix had low plant biomass (e.g., clear cuts, savanna, or maintained grassland surrounding remnant forest).

Variation in matrix quality can influence organisms in many ways (Kupfer et al. 2006), but movement dynamics are particularly important because they directly influence the colonization success of dispersing individuals (Holderegger and Wagner 2008; Eycott et al. 2010; Martin and Fahrig 2012) that permits demographic and genetic rescue of small populations. Specifically, high matrix quality increases permeability, the extent to which the matrix facilitates movement of individuals among habitat patches (Collinge and Palmer 2002; Haynes and Cronin 2006). For example, ant richness in Mexican coffee plantations (Perfecto and Vandermeer 2002) and squirrel occupancy in urban woodlands in Brussels (Verbeylen et al. 2003) both increased when patches were surrounded by high quality matrix, regardless of the distance to the nearest patch. Populations of Hazel Grouse on forest remnants in Sweden showed evidence of isolation over much shorter distances when surrounded by low-quality matrix (farmland) than high-quality matrix (coniferous forest; Åberg et al. 1995). Arboreal primates in Kenya were encountered more frequently in high-quality matrix (tall vegetation with some tree cover), than in low-quality matrix (short vegetation with little canopy cover; Anderson et al. 2007). The importance of matrix quality is also apparent in synthetic studies across taxa and landscape types. For example, one meta-analysis found that although patch area typically was the primary driver of species occupancy in fragmented habitats, isolation (distance to nearest patch) was most important when habitat patches were embedded in a low-quality, clear-cut matrix (Prugh et al. 2008). Another synthesis found that metrics describing matrix quality were more important for predicting species occupancy and abundance on habitat patches than distance-based isolation metrics (Watling et al. 2011).

Matrix quality has even been shown to influence the strength of the SAR via its relationship with z, the slope of the regression line resulting from $\log_{10}$ transformations of species richness and area of habitat remnants. Generally, z-scores range between 0.1 and 0.5 (Lomolino 2000), with a typical, 'canonical' value of 0.262 (Preston 1962). Mean z-scores are greater on oceanic islands than on habitat remnants in agricultural landscapes (Watling and Donnelly 2006), and

greater on forest remnants than in equivalent areas sampled in continuous forest (reviewed in Fahrig 2013). Low *z*-scores suggest that populations are experiencing low extirpation rates (Losos and Schluter 2000; Rivard et al. 2000; Gao and Perry 2016) at least in part because of demographic and genetic rescue as individuals move through relatively permeable matrix (Hovestadt and Poethke 2005; Kierepka et al. 2016).

Although matrix quality may be a key variable influencing species distributions in modified landscapes, its importance may be taxon-specific, and influenced by additional factors such as the extent of forest cover in a landscape. Species traits may mediate responses to matrix quality because gap-crossing ability (Lees and Peres 2009) or capacity for orienting through the matrix (Pettit et al. 2017) may influence how species perceive matrix quality. With respect to forest cover, the fragmentation threshold hypothesis suggests that negative effects of decreasing patch size and increasing isolation on species richness do not become apparent until 70–90% of habitat has been removed from a landscape (Andrén 1996). When forest cover is high, populations may not be functionally isolated from one another, and species richness may vary little among remnants (Rybicki and Hanski 2013). As forest cover decreases, populations become increasingly isolated, and small populations become vulnerable to extirpation.

It is clear that matrix quality can influence species richness in remnant forest, but the generality and magnitude of matrix effects are not well understood. In an effort to clarify the role of matrix quality in deforested landscapes, we used a meta-analytic approach to address the following research question: How does variation in matrix quality influence the strength of SARs in forest remnants? We predicted that the strength of SARs, measured using an effect size metric derived from the correlation coefficient between species richness and remnant area, would be strongest when matrix quality and forest cover were low. We also predicted the existence of strong SARs in landscapes with low matrix quality for terrestrial dispersers (non-flying invertebrates, amphibians, reptiles, and mammals) that experienced movement constraints and infrequent rescue when matrix quality was low, but weak effects for volant species. Finally, we predicted that matrix quality would be inversely related to the proportion of ice, water, and urban areas in study landscapes, because those land cover types are

thought to be particularly impermeable to movement for many terrestrial species (Forman 2000; Lees and Gilroy 2014). To test our predictions, we coupled SARs from previously published studies from around the world with a metric of matrix quality obtained from remotely sensed satellite data, yielding a synthetic, quantitative assessment of the influence of matrix quality on SARs in remnant forest.

Methods

Literature survey

We searched the primary literature for studies on species richness on forest remnants in modified terrestrial landscapes. To be included in our analysis, we required that studies (1) reported either the correlation coefficient (Pearson's *r*) between log_{10}-transformed species richness and remnant area, or raw data from which we could calculate *r*; (2) included sufficient information for identification of forest remnants in satellite imagery, either by description, geographic coordinates, or a map of the study area; (3) surveyed forest remnants that could be differentiated from the surrounding landscape in satellite images. If any of the three criteria were not met, the study was excluded from our analysis (Table S1). Two studies investigated different clusters of forest remnants in a single region. The two clusters did not overlap, so were included as separate landscapes, with individual SARs and landscape variables calculated in each case. We focused on remnant forest because of difficulty differentiating non-forest habitat from modified cover in satellite images, and because most studies of habitat modification center on forest.

We first reviewed papers from a previous meta-analysis (Watling and Donnelly 2006), which included 148 studies published through April 2005. Although all of those studies included data on the SAR, only 24 (∼ 16%) met inclusion criteria two and three and were added to our database. We then searched Web of Science with the search terms '*species richness* and *habitat fragmentation* and *isolation*' to update the database with studies from April 2005 to June 2016. Searching these keywords resulted in a total of 339 articles, of which 21 (∼ 6%) met the inclusion criteria. Therefore, our analyses are based on 45 studies conducted in modified landscapes around the

world (Figure S1, Table S2). We extracted the following data from each study: the r value of the correlation between $\log_{10}$-transformed species richness and remnant area, number of remnants, and taxonomic group (birds, reptiles and amphibians, mammals, plants, or invertebrates).

Describing matrix quality

We downloaded satellite images of each study landscape from the Landsat 4–5 mission archive, which includes data obtained between 1984 and 2013, and used the cloud-free image closest to the date in which fieldwork was completed. All satellite images were obtained within five years of the sampling period. We used standard calibration coefficients (Chandler et al. 2009) to convert the raw data to reflectance values in each of six spectral bands, and projected images into the equal-area Eckert IV projection. We created a minimum bounding polygon circumscribing each study landscape by connecting points superimposed on the satellite images at the outer edges of the most outlying remnants surveyed. To ensure that matrix quality estimates were obtained within a biologically relevant landscape in each study, we buffered each study area polygon by the mean maximum dispersal distance for the study taxon using previously-published data on body mass-dispersal relationships (Jenkins et al. 2007). Buffer radii for each taxonomic group were 32 m for vascular plants, 794 m for inverts, 3.1 km for small rodents, 3.1 km for reptiles and amphibians, 6.3 km for birds, and 63 km for large mammals.

Before assessing matrix quality, it was necessary to differentiate forest remnants from the surrounding matrix. To do this, we created a supervised classification of each study landscape (Churches et al. 2014), using random forest (Breiman 2001) and generalized boosting (Friedman 2001) algorithms to differentiate forest from the surrounding matrix. To create our classification, we first superimposed 1000 points at random throughout each landscape, and visually assessed whether the points intersected forest or non-forest using true- and false-color renderings of the Landsat images. From this pool of classified points, we extracted reflectance values in each of the six spectral bands for 100 randomly selected points in forest and non-forest, respectively. The 200 points were then split randomly into two groups of 100 points each for

model training and testing. A random 75 points from the training set were used to calibrate a model, which was then evaluated using 25 points from the testing set. We repeated this process five times, each time using a unique, random 75–25 training–testing split of the data. Models were evaluated using the true skill statistic (TSS), a metric of model accuracy that ranges from 0 to 1, with higher values indicating greater ability to discriminate forest from non–forest (Allouche et al. 2006). All models has TSS values ≥ 0.70 (Table S2), indicating good classification ability. We therefore used all 200 points to create a prediction map for each landscape. We converted continuous prediction maps indicating the probability that individual cells were forested to binary forest/non-forest maps using a unique threshold for each of the 45 landscapes, determined as the value at which TSS was maximized in the test data.

We used the Enhanced Vegetation Index (EVI) as the basis for our matrix quality metric. The EVI yields values between -1 and 1, with large values representing high plant biomass (Huete and Justice 1999). The EVI provides accurate estimates of plant biomass even in high-biomass landscapes, and is less prone to atmospheric interference than other indices such as the normalized difference vegetation index (Huete et al. 2002). We calculated a standardized matrix quality metric as

$$1 - \left(\frac{\overline{EVI}_{forest} - \overline{EVI}_{non-forest}}{\overline{EVI}_{total}} \right)$$

by differentiating mean EVI from pixels intersecting forest or non-forest portions of each landscape. The metric describes the difference in plant biomass between forest and matrix as a proportion of the mean EVI in each landscape. Small values of the metric indicate low-quality matrix, where plant biomass was much lower than in forest (Fig S2).

Data analysis

To measure the strength of the SAR in each of the 45 studies, we converted Pearson's r to an estimate of effect size using Fisher's z transformation: $z = 0.5 \times \ln\left(\frac{1+r}{1-r}\right)$ with variance $v_z = \frac{1}{n-3}$. Our first two predictions were evaluated using weighted means analysis of variance (ANOVA), with each study weighted by $\frac{1}{v_z}$. The sum of squares value for each predictor from

weighted means ANOVAs were reported as Cochran's
Q heterogeneity statistic, and tested against a Chi
square distribution with 1 degree of freedom (Kon-
stantopoulos and Hedges 2009).

We first tested the prediction that the strength of the
SAR decreased as matrix quality increased in land-
scapes with little forest cover. For this test we included
matrix quality, forest cover, and their interaction as
predictor variables, and Fisher's z as the response
variable. We expected this analysis to reveal a
significant interaction between matrix quality and
forest cover, with particularly strong and negative
relationships between effect size and matrix quality in
landscapes with low forest cover. Before conducting
regressions, we confirmed that matrix quality and
forest cover were not highly correlated (Pearson's
$r = 0.39$). To test the prediction that the strength of the
SAR decreased as matrix quality increased for terres-
trial dispersers but not volant taxa, we first categorized
the dispersal mode for species in each study as
primarily volant (birds and flying invertebrates) or
non-volant (all other taxa). We included dispersal
mode, matrix quality, and their interaction as predictor
variables, and Fisher's z as the response, with the
expectation of a significant interaction between matrix
quality and dispersal mode. Prior to analysis, we
confirmed that the observed number of studies of
volant ($N = 19$) and non-volant species ($N = 26$) did
not differ significantly from expected counts
($\chi^2 = 1.09$, df = 1, P = 0.297). Finally, we used
simple linear regression to test the prediction that
matrix quality decreased with increasing cover of ice,
water, and urban areas. Land cover data were acquired
from the European Space Agency Climate Change
Initiative (ESA 2017) for years 2000, 2005, and 2010,
and the layer that corresponded most closely to the
year that fieldwork was conducted for each study was
used for analysis. Satellite images were processed for
analysis using ArcMap version 10.3 (Environmental
Systems Research Institute 2012) and all other anal-
yses were completed in R (R core team 2016).

Results

We acquired species and landscape data for 45
landscapes in 24 countries, including 695 patches
ranging in size from 0.1 to 23,300 hectares. The 45
studies included in our database were predominately

of invertebrates (16 studies, 36%) and birds (13
studies, 29%), with fewer studies of mammals (nine
studies, 20%), amphibians and reptiles (four studies,
9%), and plants (three studies, 7%).

Meta-analysis revealed that the effect of patch area
on species richness was influenced by the interaction
between matrix quality and forest cover ($Q = 10.75$,
P = 0.001). Inspection of the interaction plot con-
firmed that the strength of SARs decreased with
increasing matrix quality in low forest cover land-
scapes, with weaker effects in landscapes with rela-
tively high forest cover (Fig. 1). However, our
prediction that matrix quality would interact with
dispersal mode to influence the strength of SARs was
not supported ($Q = 1.01$, P = 0.315). There was a
significant main effect of dispersal mode on the
strength of SARs ($Q = 18.26$, P < 0.001), with overall
stronger SARs reported for volant compared with non-
volant species (Fig. 2). As expected from our third
prediction, matrix quality decreased as landscapes
became increasingly dominated by impermeable land
cover types (water, ice, and urban areas; $F_{1,43} = 17.94$,
P < 0.001; Fig. 3).

Discussion

Here we provide clear, quantitative evidence to
suggest that matrix quality plays a major role in
determining patterns of species richness in remnant
forest. Species-area relationships were particularly
strong in landscapes with low matrix quality and little
remaining forest. We found that SARs were stronger
for volant species such as birds and flying inverte-
brates that for terrestrial dispersers, but no differences
in the response to matrix quality by dispersal mode.
Our data underscore the importance of conservation
actions that focus on increasing matrix quality, such as
actively or passively promoting vegetation regrowth
in deforested landscapes.

We found that the strength of the SAR decreased
with increasing matrix quality in landscapes with less
than about 20% forest cover (Fig. 1). The relationship
implies that low matrix quality may exacerbate the
negative effects of habitat loss in severely deforested
landscapes. The matrix matters for biodiversity in part
because it influences the rate and success of movement
among habitat remnants (Prugh et al. 2008; Prevedello
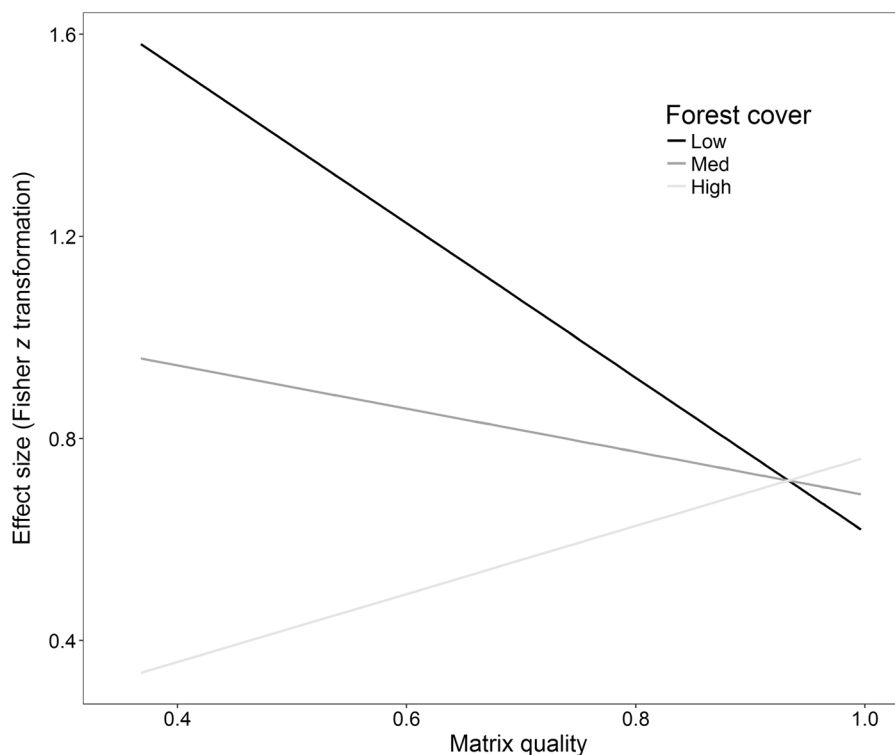and Vieira 2010; Ruffell et al. 2017). For example,

Fig. 1 The strength of the species-area relationship (measured as the effect size of the correlation between $\log_{10}$ (patch area) and $\log_{10}$ (species richness)) decreased with matrix quality in landscapes with low forest cover, but was less affected by matrix quality in landscapes with high forest cover. Here we describe matrix quality in terms of plant biomass, such that high-quality matrix has greater plant biomass than low-quality matrix. To illustrate the interaction between forest cover and matrix quality on the effect size of the species-area relationship, we modeled the relationship between Fisher's z and matrix quality at three levels of forest cover: 10, 20, and 30%. Only four of 45 studies included in the analysis occurred in landscapes where forest cover exceeded 30%

voles in Indiana meadows (Russell et al. 2007) and beetles in California prairies (Collinge and Palmer 2002) have been found to avoid or make reduced use of portions of the matrix comprised of low-quality, short-statured vegetation compared with tall grasses that more closely resemble their forest habitat. In another study, understory forest birds avoided corn fields, preferring to move among forest remnants via relatively high-quality *Eucalyptus* stands, possibly because of decreased predation risk or increased resource availability (Biz et al. 2017). When large differences in plant biomass between forest and matrix in low-quality landscapes prevent inter-patch movement and decrease functional connectivity (Tischendorf and Fahrig 2000; Smith and Hellmann 2002; Vasudev et al. 2015), remnants may experience infrequent demographic or genetic rescue (Brown and Kodric-Brown 1977), a process that is likely to be

particularly important in the most severely deforested landscapes (Fig. 1).

We observed stronger overall SARs for volant compared with non-volant taxa, but no indication that responses to matrix quality differed significantly by dispersal mode. Although we were initially surprised that SARs were strongest for volant species, previous research has demonstrated that both birds and flying invertebrates may limit travel through the matrix (Desrochers and Hannon 1997; Castellón and Sieving 2006). Some species of understory birds even avoid entirely crossing the matrix (Harris and Reed 2002; Şekercioḡlu et al. 2002). Furthermore, birds and butterflies often respond relatively quickly to even subtle structural changes in the matrix, suggesting that they have great ability to perceive matrix quality (Ricketts 2001; Ries and Debinski 2001; Martin and Possingham 2005). Inter-patch movements may be

Fig. 2 The mean effect of patch area on species richness was greater for volant species than for non-volant taxa. Individual effects for each study are superimposed over the boxplots
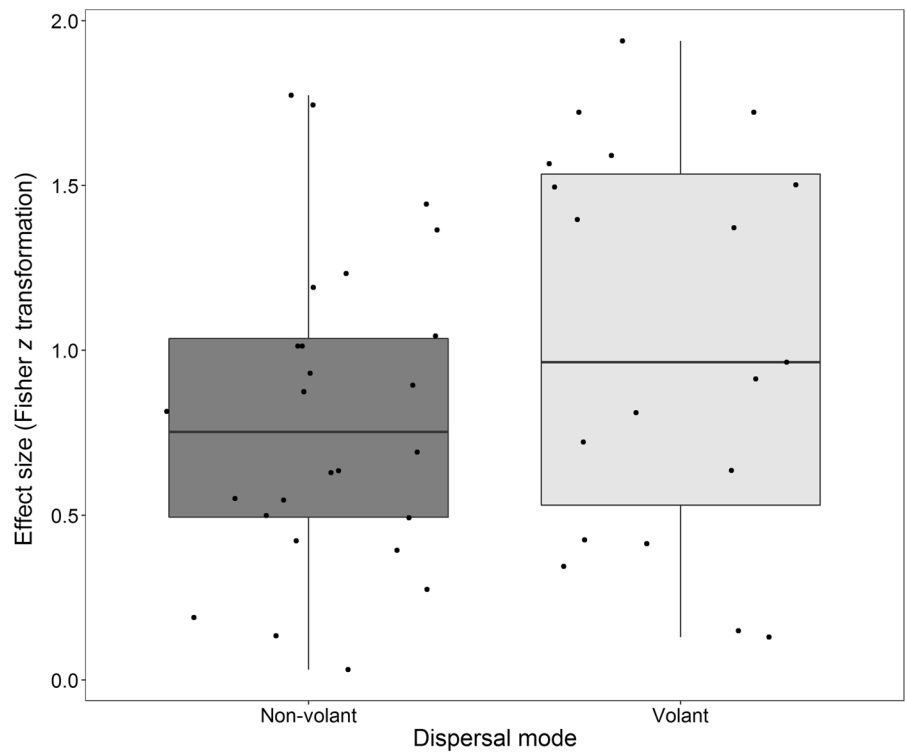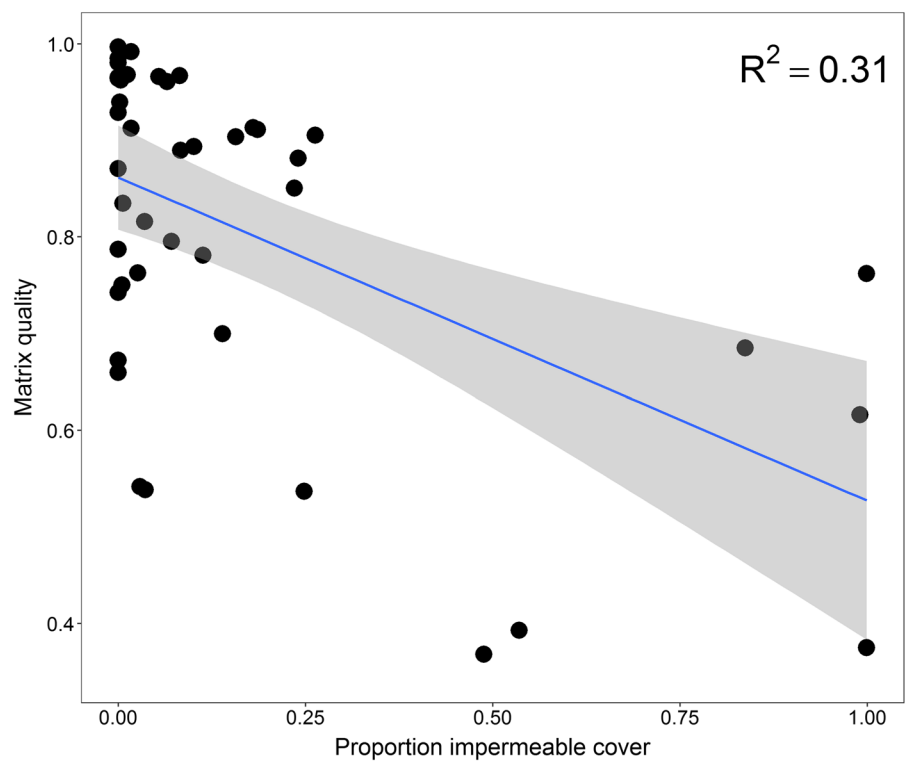

Fig. 3 Matrix quality decreases as the proportion of impermeable terrestrial cover types (ice, water, and urban areas) increases

severely or entirely inhibited for species able to sample and perceive low-quality matrix as inhospitable (Clobert et al. 2009), whereas species with limited perceptual ability may not avoid the matrix as frequently. Although decades of research have revealed few taxon-based differences in SARs that can be interpreted clearly in terms of dispersal ability (Öckinger et al. 2010; Aranda et al. 2013; Matthews et al. 2016; Fattorini et al. 2017), most of that work has focused on z-scores, rather than the effect size metric we analyzed here. We suggest that the strong effect of patch size on species richness that we observed for volant species may be a consequence of greater perceptual abilities for flying organisms compared with passive or terrestrial dispersers, but emphasize that more data are needed to evaluate this possibility.

Our analysis found particularly strong gradients in species richness in landscapes where forest remnants were surrounded by low-quality matrix. The most important way to mitigate species losses in modified landscapes is to minimize deforestation, although alleviating the pace of deforestation is complex, especially in the face of a growing human population and the possibility of future food insecurity (Garibaldi et al. 2017). However, our results imply that minimizing species losses in deforested landscapes may also be achieved by enhancing matrix quality to increase landscape connectivity. Several features have been suggested to increase landscape connectivity, including corridors (Gilbert-Norton et al. 2010; Haddad et al. 2017) and small stepping stone fragments that reduce effective isolation in fragmented landscapes (Baum et al. 2004; Saura 2014). Another way to increasing landscape connectivity is to increase matrix permeability via passive or active regeneration (Smallbone et al. 2014; de Rezende et al. 2015). Although active regeneration of the matrix may be more expensive than passive regeneration (Brancalion et al. 2016), it may increase the value of ecosystem services in managed landscapes, partially compensating for production losses tied to livestock, agriculture, and timber harvest (Bullock et al. 2011).

Managing the matrix to avert species losses in modified landscapes has become an increasingly important conservation strategy. One of the best examples of a large-scale conservation strategy focused on enhancing matrix quality is the Atlantic Forest Restoration Pact, in which more than 260 groups have organized to actively restore 15 million hectares of deforested and degraded lands by the year 2050 with the goal of conserving biodiversity (Pinto et al. 2014). In Costa Rica, the Payment for Environmental Services Program reimburses landowners for the ecosystem services their property provides through biodiversity, water, and carbon payments, as long as landowners protect existing vegetation or plant tree plantations on their property (Pagiola 2008). The benefit of conservation plans such as these are multifaceted, enhancing the delivery of ecosystem services while increase landscape connectivity, with collateral benefits for biodiversity by facilitating movement between forest remnants.

We used satellite imagery and remote sensing techniques to provide a metric of matrix quality that helps explain trends in species responses to landscape modification. A drawback to using a single metric is that it may not adequately describe matrix quality for all species. For example, distributions of some species are limited by the presence of keystone species rather than habitat quality (e.g., presence of predators determined by prey; Delibes-Mateos et al. 2007). Also, resource-limited habitat specialists such as monarch butterflies may not use the matrix the same way as generalist butterflies (Flockhart et al. 2017). Our approach does not provide a substitute for detailed species management plans. However, because it is impractical to generate species-specific data for all species of conservation concern, our approach to assessing matrix quality may be applied as an initial assessment for many species at once. Data generalizing species responses to matrix quality can be used to suggest preliminary conservation strategies for many, rather than few species where immediate conservation practices are needed (Lambeck 1997). For example, in Peninsular Malaysia, 558 isolated karst forests are at risk of destruction, and in just twelve forests, sixteen endemic and seven karst forest-adapted reptile species have been discovered in a seven-year period (Grismer et al. 2016). It is likely that these Malaysian species, as well as many others, are at risk of extinction without immediate conservation action. Our data suggest that efforts to increase matrix quality should reduce the threat of extirpation of vulnerable populations on small forest remnants.

In conclusion, we found that the effect of patch area on species richness is greatest in severely deforested landscapes where matrix quality is low (i.e., there is a large difference in plant biomass between forest

remnants and the surrounding matrix). Our analysis of global land cover confirmed that matrix quality was lowest in areas dominated by three relatively impermeable cover types: ice, water, and urban land. The impact of matrix quality on species-area relationships was particularly strong for volant species. Although the remotely sensed matrix quality metric we used here is not a perfect substitute for field data describing how plant biomass influences organism movement and population persistence, it does provide an approach that can be used to generalize one type of matrix effect on populations in remnant forest. A key implication of our work is that conservation strategies that incentivize active or passive restoration of the matrix should help maintain populations on forest remnants.

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