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THE INFLUENCE OF MATRIX CONTRAST ON SPECIES RICHNESS IN FRAGMENTED LANDSCAPES

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THE INFLUENCE OF
MATRIX CONTRAST ON
SPECIES RICHNESS IN
FRAGMENTED
LANDSCAPES

A Thesis Submitted to the
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Requirements for the Degree
of Master of Sciences

By
Ian J. Reider
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Abstract:

Habitat destruction is the leading threat to biodiversity worldwide, causing once continuous landscapes to become fragmented and isolated and harming the persistence of biodiversity. Our goal was to determine how species richness in fragmented forest landscapes is influenced by the vegetation density of the surrounding matrix. We gathered existing studies of fragmented landscapes with Species Area Relationship (SAR) data and analyzed the landscape vegetation in each study site using satellite imagery in ArcGIS. We investigated to see how contrast between vegetation density in matrix versus forested habitat areas correlated to the strength of the SAR for the 45 study landscapes included. We found that overall SAR was stronger in landscapes with high contrast matrices than low contrast matrices. This relationship was even stronger in landscapes with <15% habitat left and when considering only birds and flying invertebrate taxonomic groups. In general, we found that habitat remnant size is a good predictor of species richness when landscape contrast is high, suggesting that species move less frequently between fragments and that high contrast matrices are inhospitable to the majority of species analyzed in our analysis. Based on our findings as well as by example from other conservation efforts, we suggest both active and passive forest restoration in high contrast matrices as an initial measure to increase connectivity and restore biodiversity in fragmented landscapes.

Keywords:

Matrix contrast, Fragmentation, Remote sensing, Species richness

Introduction:

Habitat loss is the primary threat to terrestrial biodiversity (Tilman et al. 1994; Dirzo and Raven 2003; Murphy and Romanuk 2014). The link between habitat loss and the maintenance of biodiversity is rooted in the species-area relationship (SAR), which states that large areas of habitat harbor more species than small 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 (Blake and Karr 1984; Godefroid and Koedam 2003; Tabarelli and Gascon 2005; Le Roux et al. 2015), a hallmark of global conservation efforts (Diamond 1975; Lasky and Keitt 2013).

Although habitat loss is recognized as the main 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). Through this process, 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 1998; Rybicki and Hanski 2013). However, the fact that habitat loss and fragmentation are 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 (Brook and Buettel 2016).

Habitat remnants resulting from deforestation resemble oceanic islands, leading several authors to suggest that the extinction and colonization processes unified in the equilibrium theory of island biogeography may explain species responses in deforested terrestrial landscapes (MacArthur and Wilson 1967; Fahrig and Merriam 1994; Zschokke et al. 2000; Fernandez-Chacon 2014). However, an important difference between oceanic and terrestrial landscapes is that oceanic islands are separated by a truly inhospitable aquatic barrier, whereas terrestrial remnants are generally surrounded by a matrix of modified terrestrial cover types that may not be uniformly inhospitable. Many studies have found that the matrix plays an important role in determining patterns of species occurrence in remnant habitat (Cook et al. 2002; Perfecto and Vandermeer 2002; Prevedello and Vieira 2010; Fahrig 2013), in part because differences in matrix quality influence movement behavior and colonization success of dispersing individuals (Holderegger and Wagner 2008; Eycott et al. 2010; Martin and Fahrig 2012).

The fact that variation in matrix quality can influence colonization rates means that matrix permeability, the extent to which the matrix facilitates movement of individuals among patches (Collinge and Palmer 2002), may modify the influence of geographic distance on species occupancy, abundance, and richness. Several individual

studies have shown that differences in matrix quality can moderate the strength of isolation by distance effects in terrestrial landscapes. 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. The importance of the matrix is also apparent in synthetic studies across taxa and landscape types. For example, one meta-analysis found that although patch area generally was the primary driver of species occupancy in fragmented habitats, isolation was the best predictor of species occupancy for habitat patches embedded in a clear cut forest matrix (Prugh et al. 2008). Another study found that metrics of matrix permeability were more important for predicting species occupancy and abundance than distance-based isolation metrics (Watling et al. 2011).

The matrix has even been shown to influence the strength of the SAR in modified landscapes. A common metric of the strength of the SAR is the z -score, the slope of the regression line resulting from \log_{10} transformations of species richness and patch area. Generally, z -scores range between 0.1 - 0.5 (Lomolino 2000), with a typical, 'canonical' value of 0.262 (Preston 1962). It has been shown that z -scores are greater for oceanic islands than habitat remnants in primarily agricultural landscapes (Watling and Donnelly 2006) and greater in habitat remnants than in equivalent areas sampled in continuous forest (reviewed in Fahrig 2013). Weak SARs (e.g., those with low z -scores) are frequently interpreted as indicating low extirpation rates on small patches (Losos and Schluter 2000; Rivard et al. 2000; Gao and Perry 2016), which may result from

demographic and genetic rescue occurring on habitat patches embedded in a relatively permeable matrix.

One attribute of the matrix that has been linked to differential permeability is contrast, which describes differences in land cover or vegetation structure between habitat patches and the surrounding matrix (Kupfer et al. 2006; Marzluff and Ewing 2001; Collinge and Palmer 2002). For example, a high contrast landscape may include remnant primary forest surrounded by a clear-cut matrix dominated by grasses, whereas a low contrast landscape would consist of primary forest remnants surrounded by a matrix of secondary forest. Contrast presumably has its greatest impact by influencing species movement rates and behaviors, with high-contrast matrix impeding movement and encouraging directed, linear movements (Haynes and Cronin 2006) compared with low contrast matrix. For example, populations of hazel grouse in a relatively high contrast landscape (forest habitat surrounded by farmland) showed evidence of isolation over much shorter distances than populations in low contrast landscapes (mostly deciduous forest habitat within non-habitat coniferous forest; Åberg et al. 1995). In another study, the Angola black and white colobus, an arboreal primate, had a higher probability of being encountered in matrix with a greater proportion of tall vegetation and tree cover, which more closely resembled its forest habitat, than in matrix of shorter vegetation with lower canopy cover (Anderson et al. 2007).

Although landscape contrast may be a key variable influencing species distributions in modified landscapes, the effect of contrast may be influenced by additional factors such as landscape context and species identity. The fragmentation threshold hypothesis suggests that negative effects of decreasing patch size and

increasing isolation on species richness do not become distinct and apparent until 10-30% of original habitat remains in a landscape (Andrén 1996). Although, evidence for the fragmentation threshold hypothesis is inconclusive and there is no consensus on if a threshold exists. Also, species perceive landscape variation differently, and a species' gap-crossing ability (Lees and Perez 2009) or capacity for orienting through the matrix (Pettit et al. 2017) may influence whether a landscape is perceived as high or low contrast.

It is clear that the matrix can influence species richness on habitat remnants in fragmented landscapes, although the generality and magnitude of matrix effects is not well understood. In an effort to clarify the importance of the matrix in mediating the strength of SARs in terrestrial habitat remnants, we focus on contrast as a key landscape attribute. We suggest that landscape contrast can be characterized using easily-calculable metrics obtained from remotely-sensed data, and applied to taxonomically diverse species assemblages. We hypothesize that the strength of the SAR will increase with landscape contrast, with particularly strong effects of contrast in landscapes with little remaining habitat and for dispersal-limited taxa (e.g., birds and small mammals). To test our hypotheses, we coupled SARs from previously-published studies of several taxonomic groups in study regions around the world with a metric of matrix contrast obtained from remotely-sensed satellite data, yielding a synthetic, quantitative assessment of the influence of matrix structure on SARs in terrestrial fragmented forest landscapes.

Materials and methods:

We searched the primary literature for studies on species richness on habitat remnants in modified terrestrial landscapes. In order to be included in our analysis, we required that studies 1) reported a z -score for the SAR or raw data on remnant area and species richness from which we could calculate a z -score; 2) included sufficient information for identification of study fragments in satellite imagery, either by description, geographic coordinates, or a map of the study area; 3) surveyed habitat fragments that could be differentiated from the surrounding landscape in satellite images. In practice, this meant that habitat patches consisted of forest and were distinguishable from the surrounding matrix. If any of the three criteria were not met, the study was excluded from our analysis. Two studies investigated different clusters of habitat remnants in a single region. The two clusters did not overlap, so were included as separate landscapes, with individual z -scores and landscape variables calculated for each case.

Our literature review began by reviewing papers from a previous meta-analysis by one of the authors (Watling and Donnelly 2006), which included 148 studies published through April 2005. Although all studies from that dataset included sufficient data to calculate z -scores, only 24 studies (~ 16%) met inclusion criteria two and three and could be 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 385 articles, of which 21 (~ 5%) met our inclusion criteria. Therefore, our analyses are based on a total of 45 studies conducted in modified landscapes around the world.

We extracted the following data from each study: z -score, regional species richness across all remnants, number of remnants, taxonomic group (birds, reptiles and amphibians, mammals, plants, or invertebrates), and matrix type (human-dominated grassland, natural savanna, agriculture, plantation, urban, clearcut, pasture, and sand). In cases where several matrix types were present in a single study, the dominant matrix type listed in each publication was used. Taxa were categorized as volant (birds and flying invertebrates) or non-volant (all other groups) for subsequent analysis.

We downloaded satellite images of each study landscape from the Landsat 4-5 mission archive, which includes data obtained between 1984 and 2013. The cloud-free image closest to the date in which fieldwork was completed was used, with all satellite images obtained within five years of the sampling period. We converted the raw Landsat data to reflectance values in each of the six spectral bands using standard calibration coefficients (Chandler et al. 2009), and projected images into the equal area Eckert IV projection. We created a minimum bounding polygon circumscribing each study site by manually selecting points around all remnants surveyed. To ensure that contrast estimates were obtained within a biologically-relevant landscape in each study, we buffered each study area polygon by the maximum dispersal distance for each taxon using data on body mass – dispersal relationships from a previous study (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 meters for large mammals.

Before assessing landscape contrast, it was first necessary to differentiate habitat remnants from the surrounding matrix. To do this, we used a supervised classification of

each study landscape (Churches et al. 2014) in which random forest (Breiman 2001) and generalized boosting model (Friedman 2001) algorithms were used to differentiate habitat and matrix areas. We superimposed random points over each landscape area and visually assessed whether the points intersected habitat or matrix area using true- and false-color renderings of the Landsat images. Reflectance values were extracted for 100 forest and 100 matrix points and were used as predictor variables in a classification of study landscapes into forest (habitat) and non-forest (matrix). 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 create the model and the predictions from the model were evaluated by using 25 points from the testing set. We did this five times, each time with a unique, random 75-25 training-testing split of the data. Models were evaluated based on the true skill statistic (TSS), a metric of model accuracy ranging from 0-1, with higher values indicating greater ability to discriminate forest from non-forest (Allouche et al. 2006). Models were used to estimate the probability of each pixel in the landscape being either habitat or matrix and TSS scores that were higher than 0.70 were used. The mean prediction for both algorithms was found and the resulting probabilities were converted to binary prediction maps differentiating habitat remnants from the surrounding matrix.

We used the Enhanced Vegetation Index (EVI) as the basis for our landscape contrast metric. The EVI gives accurate readings in high biomass landscapes and is less prone to atmospheric interference than other indices such as the normalized difference vegetation index. The EVI yields values between -1 and 1, with higher values representing greater vegetation density (Huete and Justice 1999). To calculate landscape

contrast, we extracted EVI values for forest and matrix separately using the binary prediction maps for each landscape. The values of all pixels from the habitat only raster were averaged and then divided by the average pixel value of the matrix only raster file. Higher values of this contrast index represent higher levels of contrast between habitat remnants and matrix vegetation.

We used a meta-analytic framework to determine whether z -scores were greater in high contrast landscapes compared with low contrast landscapes. We extracted Pearson's r describing the correlation between z -score and landscape contrast in each study. Pearson's r was converted to an estimate of effect size using Fisher's z transformation: $z = 0.5 * \ln((1+r)/(1-r))$ with variance $v_z = 1/(n-3)$. We divided the full dataset into two groups based on the landscape contrast metric, with half the studies ($N = 22$) being categorized as 'high contrast' and remaining studies ($N = 23$) as 'low contrast'. We analyzed the effect of contrast on Fisher's z using weighted means analysis of variance (ANOVA), with each study being weighted by $1/v_z$. The sum of squares value for the contrast factor from the weighted means ANOVA is reported as Cochran's Q heterogeneity statistic and tested against a chi-square distribution with 1 degree of freedom (Konstantopoulos and Hedges 2009). We followed up the categorical analysis with a weighted regression to assess the linear relationship between z -score and landscape contrast. Weights were calculated using the number of habitat remnants in each study. We conducted separate regressions for the complete dataset, studies in which habitat was less than 15% of the total area of each landscape, studies where habitat area was $> 15\%$, studies of volant organisms, and studies of non-volant species. Finally, to understand how landscape contrast was influenced by land cover, we used linear

regression to assess the relationship between contrast and the proportion of 3 land cover categories that are commonly reported as inhospitable and impermeable in the literature (Lees and Gilroy 2013; Forman 2000) in each study landscape. Land cover data were acquired from the European Space Agency Climate Change Initiative (ESA CCI) from years 2000, 2005, 2010, and the layer that corresponded most closely to the year that field work was completed for each study was used for analysis. Satellite images were processed for analysis using ArcMap version 10.3 and all other analyses were completed in R (R core team 2016).

Results:

We acquired species and landscape data for 45 landscapes in 24 countries, representing 695 patches ranging in size from 0.1- 23,300 hectares.

Species-area relationships were significantly weaker in low contrast landscapes compared with high contrast landscapes, with a mean effect size in low contrast landscapes ($x = 0.61 \pm 0.05$) 62% lower than the mean effect size from high contrast landscapes (1.09 ± 0.052 ; $Q = 23.98$, $P < 0.001$; Fig. 1). Across all studies, there was a significant, positive relationship between z -score and matrix contrast ($F_{1,43} = 10.50$, $P = 0.002$; Fig. 2). This relationship was particularly strong for studies taking place in landscapes with less than 15% habitat ($F_{1,20} = 21.56$, $P < 0.001$; Fig. 3). In landscapes in which habitat amount exceeded 15%, there was no significant effect of matrix contrast on z -score ($F_{1,21} = 0.52$, $P = 0.478$). There was a significant, positive relationship between z -score and matrix contrast for volant species (birds and flying invertebrates; $F_{1,17} = 9.41$, $P = 0.007$; Fig. 4), whereas non-volant organisms did not show a significant relationship

between matrix contrast and z -score ($F_{1,24} = 1.43$, $P = 0.243$). We found that when >15% of the matrix was made up of urban area, water, or snow/ice that there was a positive trend showing that the greater the extent of these three land cover types in the matrix, the higher contrast of that landscape ($F_{1,10} = 4.43$, $P = 0.06$; Fig. 5).

Discussion:

Our study provides quantitative evidence suggesting that matrix vegetation structure in fragmented landscapes plays a major role in determining species richness patterns in habitat remnants. Mean effect size of patch area was over 50% greater in high contrast landscapes compared with low contrast landscapes. Species-area relationships were particularly strong in high-contrast matrices when total habitat amount in the landscape was less than 15%, and for relatively vagile species such as birds and flying invertebrates. Our results indicate that remotely-sensed contrast metrics may provide a tractable means of assessing landscape effects for multi-species assemblages when detailed ecological data are unavailable. We provide clear support for the importance of conservation actions that focus on reducing the effective isolation of the matrix, such as actively or passively promoting vegetation regrowth in the matrix.

The matrix matters for biodiversity on habitat fragments in part because it influences the rate and success of movement among remnants (Prugh et al. 2008; Prevedello and Vieira 2010; Ruffell et al. 2017). When major differences in vegetation structure between habitat and matrix in high-contrast landscapes prevent inter-patch movement and decrease functional connectivity (Tischendorf and Fahrig 2000; Smith and

Hellman 2002; Filgueiras et al. 2015; Vasudev et al. 2015), remnants may experience infrequent demographic or genetic rescue (Brown and Kodrick-Brown 1977). For example, voles in Indiana meadows and beetles in California prairies have been found to completely avoid or have difficulty traversing shorter more contrasting vegetation than taller grasses that more closely resemble forest habitat patches (Collinge and Palmer 2002; Russell et al. 2007). In another study, understory forest birds avoided corn fields and preferred to enter low contrast *Eucalyptus* matrix, possibly due to decreased predation risk or increased resource availability (Biz et al. 2017). The end result of reduced connectivity may be an increase in extirpation, particularly for small populations on the smallest patches, resulting in the high z-scores we observed in high-contrast landscapes (Fig. 6).

We found that the positive relationship between the SAR and matrix contrast was particularly strong in landscapes where 15% or less of the total landscape area was comprised of habitat. This implies that in landscapes where habitat amount is especially low, high contrast may exacerbate the negative effects of habitat loss on species persistence. There has been some support in the literature that declines in species richness with decreasing patch area should not become apparent until suitable habitat comprises less than about 30% of a landscape (Andr n 1994; Fahrig 1998). This hypothesis of a threshold has found some support in the literature (Betts et al. 2007; Ochoa-Quintero et al. 2015) however, the notion is not universally accepted (Fahrig 2003). One way to resolve apparent discrepancies between studies that report fragmentation threshold effects and those that do not may be to focus on landscape contrast. Our results suggest that threshold effects may be particularly apparent in high-contrast landscapes, whereas

threshold effects may be obscured in low-contrast landscapes where demographic rescue and/or landscape supplementation buffer negative impacts. Landscapes with <15% habitat are severely isolated by definition, and by considering the potential for high contrast matrix to disrupt species movement, we are able to identify and quantify a factor that is potentially exacerbating biodiversity losses in hyper-fragmented landscapes.

Another result to emerge from our study was a particularly strong positive relationship between the strength of the SAR and matrix contrast for relatively vagile taxonomic groups (birds and flying invertebrates), implying that vagile species move infrequently from patch to patch when matrix contrast is high. Although initially we had expected that z-scores would be greater in high-contrast landscapes for taxa perceived to be dispersal limited (small mammals, reptiles and amphibians), previous studies have shown both birds and flying invertebrates often limit travel time spent in the matrix (Desrochers and Hannon 1997; Castellon and Sieving 2006). Some species of understory birds (Sekercioglu et al. 2001; Harris and Reed 2002) even avoid crossing the matrix entirely. If a species is able to sample the high matrix contrast and perceive it as inhospitable, inter-patch movements may be deterred (Clobert et al. 2009), whereas species not able to sample and perceive the matrix as inhospitable may not avoid the matrix as often. Birds and butterflies respond relatively quickly to subtle structural changes in the matrix, suggesting that they are able to experience and perceive the matrix and discriminate whether or not it is hospitable (Ries and Debinski 2001; Ricketts 2001; Martin and Possingham 2005). Some species specific-data exists on how species may perceive the matrix (Goheen et al. 2003; Uezu et al. 2005), but we are relatively data

deficient for the majority of species in need of conservation effort and need to further study how species perceive and navigate the matrix.

Our analysis found that high contrast between habitat remnants and the surrounding matrix results in sharp gradients in species richness as species are lost in small habitat remnants. Minimizing species losses in fragmented landscapes can be achieved by minimizing the extent of 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 also suggest that mitigating species losses in fragmented landscapes can be achieved by increasing connectivity through reduced landscape contrast. Increasing landscape connectivity can be achieved using corridors (Gilbert-Norton et al. 2010; Haddad et al. 2017) or small stepping stone fragments to reduce effective isolation in fragmented landscapes (Baum et al. 2004; Saura et al. 2014). Another approach to increasing landscape connectivity is to increase matrix permeability through passive or active regeneration (Smallbone et al. 2014; 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 reducing landscape contrast is the Atlantic Forest Restoration Pact (AFRP), 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 2006). Under this program, landscape contrast decreased as forest cover increased from 20% to 50% between 1980 and 2001 (Morse et al. 2009). The benefit of conservation plans such as these are multi-faceted, enhancing the delivery of ecosystem services while increase landscape connectivity, with collateral benefits for biodiversity by facilitating movement between forest fragments.

Our study utilized satellite imagery and remote sensing techniques to provide a metric of landscape contrast to help explain trends in species responses. A drawback to using just this single metric is that it may not adequately describe landscape contrast for all species. For example, some species may not respond to vegetation structure, but to other keystone species (Delibes-Mateos et al. 2007). Also, resource specialists such as monarch butterflies may not use the matrix the same way as generalist butterflies due to specific breeding needs (Flockhart et al. 2017). Our study is no substitute for detailed species specific plans. However, because it is impractical to generate species-specific data for all in need, this approach is easily applicable to many species at once. Data generalizing species responses to matrix vegetation can be used to suggest preliminary conservation strategies for many, rather than few species where immediate conservation practices are needed (Lambeck 1977). An example of an area in need of immediate conservation is Peninsular Malaysia. Here 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 if immediate conservation action is not taken. Being a crisis discipline in which immediate action is often needed, the field of conservation would benefit from generalized far reaching initial solutions to mitigate biodiversity loss while further data can be collected to reveal more system specific conservation needs.

By documenting and quantifying the role of matrix vegetation structure on species in fragmented landscapes, our research contributes a quantitative result in which the vegetation structure of the matrix may be influencing species richness within habitat fragments. We found the greater the difference between density of matrix vegetation and habitat vegetation, the stronger the effect of patch area alone on species richness. Our data may have important conservation value where species specific data do not exist, and our analysis suggests an explanation to how the matrix influences biodiversity in fragmented landscapes. Our analysis also provides support for using remote sensing and satellite imagery to help determine general relationships between species and landscapes at a global scale in an efficient and cost effective way. Although there are limitations and drawbacks of our analysis, we provide a potential starting point for identifying fragmented landscapes likely to experience greater effective isolation in habitat fragments that would benefit from conservation techniques within the matrix. Future research is needed so that we can better understand how species are navigating and using the matrix and field experiments are needed so we may further understand our results and the

mechanisms behind them. Future studies should focus on taxonomic groups that are not as well represented in the literature such as reptiles, amphibians, mammals, and plants to determine if the relationship we found in this analysis is supported with a more balanced taxonomic representation. Although more work needs to be done to validate and further understand how the structure of matrix vegetation influences species dynamics, our findings suggest that there may be conservation value in managing the matrix in a way that minimizes the difference between the vegetation density of habitat fragments and the matrix.

Literature Cited:

- Åberg J, Jansson G, Swenson JE, Angelstam P (1995). The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. *Oecologia* 103:265–269
- Allouche O, Tsoar A, Kadmon R (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* 43:1223-1232
- Anderson J, Rowcliffe JM, Cowlishaw G (2007). Does the matrix matter? A forest primate in a complex agricultural landscape. *Biological Conservation* 135:212–222
- Andrén H (1994). Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: a Review. *Oikos* 71:355–366
- Andrén H (1996). Population Responses to Habitat Fragmentation : Statistical Power and the Random Sample Hypothesis. *Oikos* 76: 235–242.
- Belaire JA, Whelan CJ, Minor ES (2017). Having our yards and sharing them too: the collective effects of yards on native bird species in an urban landscape. *Ecological Applications* 24:2132–2143
- Betts MG, Fahrig L, Hadley AS, Halstead KE, Bowman J, Robinson WD, Wiens JA, Lindenmayer DB (2014). A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography* 37:517–527

- Biz M, Cornelius C, Paul J, Metzger W (2017). Matrix type affects movement behavior of a Neotropical understory forest bird. *Perspectives in Ecology and Conservation* 15:10–17
- Blake JG, Karr JR (1984). Species composition of bird communities and the conservation benefit of large versus small forests. *Biological Conservation* 30:173–187
- Brancalion PHS, Schweizer D, Gaudare U, Manguiera JR, Lamonato F, Farah FT et al. (2016). Balancing economic costs and ecological outcomes of passive and active restoration in agricultural landscapes : the case of Brazil. *Biotropica* 48:856–867
- Breiman L (2001). Random Forests. *Machine Learning* 45:5-32
- Brook BW, Buettel JC (2016). Emigration is costly, but immigration has benefits in human-altered landscapes. *Functional Ecology* 30:1478–1479
- Brown JH, Kodric-Brown A (1977). Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology* 58:445-449
- Bullock JM, Aronson J, Newton AC, Pywell RF, Rey-benayas JM (2011). Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends in Ecology and Evolution* 26:541–549
- Castellón TD, Sieving KE (2006). An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation Biology* 20:135-145
- Chandler G, Markham BL, Helder DL (2009). Summary of Current Radiometric Calibration Coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI Sensors. *Remote Sensing of Environment* 1-24

- Churches CE, Wampler, PJ, Sun, W, Smith, AJ (2014). International Journal of Applied Earth Observation and Geoinformation Evaluation of forest cover estimates for Haiti using supervised classification of Landsat data. *International Journal of Applied Earth Observations and Geoinformation* 30:203–216
- Clobert J, Le Galliard JF, Cote J, Meylan S, Massot M (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* 12:197-209
- Collinge SK, Palmer TM (2002). The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. *Landscape Ecology* 17:647–656
- Cook WM, Lane KT, Foster BL, Holt RD (2002). Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters* 5:619–623
- Delibes-Mateos M, Redpath SM, Angulo E, Ferreras P, Villafuerte R (2007). Rabbits as a keystone species in southern Europe. *Biological Conservation* 137:149-156
- Desrochers A, Hannon SJ (1997). Gap Crossing Decisions by Forest Songbirds during the Post-Fledging Period. *Conservation Biology* 11:1204–1210.
- Diamond JM (1975) The Island Dilemma: Lessons of Modern Biogeographic Studies for the Design of Natural Reserves. *Biological Conservation* 7:129-146
- Dirzo R, Raven PH (2003). Global State of Biodiversity and Loss. *Annual Review of Environment and Resources* 28:137–167

Environmental Systems Research Institute (ESRI). 2012. ArcGIS Release 10.3. Redlands, CA

Eycott A, Watts K, Brandt G, Buyung-Ali L, Bowler D, Stewart G, Pullin A (2010). Collaboration for Environmental Evidence 1-120

Fahrig L (1998). When does fragmentation of breeding habitat affect population survival? *Ecological Modeling* 105:273–292

Fahrig L (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution and Systematics* 34:487–515

Fahrig L (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography* 40:1649–1663

Fahrig L, Merriam G (1994). Conservation of Fragmented Populations. *Conservation Biology* 8:50–59

Fernández-Chacón A, Stefanescu C, Genovart M, Nichols JD, Hines JE, Páramo F, Oro D (2014). Determinants of extinction-colonization dynamics in Mediterranean butterflies: The role of landscape, climate and local habitat features. *Journal of Animal Ecology* 83:276–285

Filgueiras BKC, Tabarelli M, Leal IR, Vaz-de-mello FZ, Iannuzzi L (2015). Dung beetle persistence in human-modified landscapes : Combining indicator species with anthropogenic land use and fragmentation-related effects. *Ecological Indicators* 55:65–73

Flockhart DTT, Brower LP, Ramirez MI, Hobson KA, Wassenaar LI et al. (2017). Regional climate on the breeding grounds predicts variation in the natal origin of

monarch butterflies overwintering in Mexico over 38 years. *Global Change Biology* 23:2565-2576

Forman, RTT (2000). Estimate of the Area Affected Ecologically by the Road System in the United States. *Conservation Biology* 14:31–35.

Friedman JH (2001). Greedy Function Approximation: A Gradient Boosting Machine. *The Annals of Statistics* 29:1189-1232

Gao D, and Perry G (2016). Species – area relationships and additive partitioning of diversity of native and nonnative herpetofauna of the West Indies. *Ecology and Evolution* 6:7742–7762

Garibaldi LA, Gemmill-Herren B, D’Annolfo R, Graeub BE et al. (2017). Farming Approaches for Greater Biodiversity, Livelihoods, and Food Security. *Trends in Ecology & Evolution* 32:68-80

Gilbert-Norton L, Wilson R, Stevens JR, Beard KH (2010). A Meta-Analytic Review of Corridor Effectiveness. *Conservation Biology* 24:660–668

Godefroid S, Koedam N (2003). How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? *Global Ecology and Biogeography* 12: 287–298

Goheen JR, Swihart RK, Gehring TM, Miller MS (2003). Forces structuring tree squirrel communities in landscapes fragmented by agriculture : species differences in perceptions of forest connectivity and carrying capacity. *Oikos* 102:95–103

- Gonzalez A, Chaneton EJ (2002). Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *Journal of Animal Ecology* 71:594–602.
- Grismer JL, Schulte II JA, Alexander A, Wagner P, Travers SL, Buehler MD, Welton LJ, Brown RM (2016). The Eurasian invasion: phylogenomic data reveal multiple Southeast Asian origins for Indian Dragon Lizards. *BMC Evolutionary Biology* 16:43
- Haddad NM, Gonzalez A, Brudvig LA, Burt MA, Levey DJ, Damschen EI (2017). Experimental evidence does not support the Habitat Amount Hypothesis. *Ecography* 40:48–55
- Haila Y (2002). A Conceptual Genealogy of Fragmentation Research : From Island Biogeography to Landscape Ecology. *Ecological Applications* 12:321–334
- Harris RJ, Reed JM (2002). Behavioral barriers to non-migratory movements of birds. *Annales Zoologici Fennici* 39:275-290
- Haynes KJ, Cronin JT (2006). Interpatch movement and edge effects : the role of behavioral responses to the landscape matrix. *Oikos* 113:43–54.
- Holderegger R, Wagner HH (2008). Landscape Genetics. *BioScience* 58:199–207
- Huete AR, Justice C. MODIS vegetation index (MOD13) algorithm theoretical basis document. Ver. 3, 1999.
- Jenkins DG, Brescacin CR, Duxbury CV, Elliott JA, Evans JA, Grablow KR, Williams SE et al. (2007). Does size matter for dispersal distance? *Global Ecology and Biogeography* 16:415–425

- Joly CA, Metzger JP, Tabarelli M (2014). Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. *New Phytologist* 204:459-473
- Jones NT, Germain RM, Grainger TN, Hall AM, Baldwin L, Gilbert B (2015). Dispersal mode mediates the effect of patch size and patch connectivity on metacommunity diversity. *Journal of Ecology* 103:935–944
- Kay GM, Driscoll DA, Lindenmayer DB, Pulsford SA (2016). Agriculture, Ecosystems and Environment Pasture height and crop direction influence reptile movement in an agricultural matrix. *Agriculture, Ecosystems and Environment* 235:164–171
- Konstantopoulos S, Hedges LV (2009) Analyzing effect sizes: fixed-effects models. In: H Cooper, LV Hedges and JC Valentine, Russell Sage Foundation, New York, pp. 279-293
- Kupfer JA, Malanson GP, Franklin SB (2006). Not seeing the ocean for the islands: The mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography* 15:8–20
- Lambeck RJ (1997). Focal Species : A Multi-Species Umbrella for Nature Conservation. *Conservation Biology* 11:849–856
- Lasky JR and Keitt TH (2013). Reserve Size and Fragmentation Alter Community Assembly, Diversity, and Dynamics. *The American Naturalist* 182:143–160
- Lees AC, Gilroy, JJ (2014). Vagrancy fails to predict colonization of oceanic islands. *Global Ecology and Biogeography* 23:405–413
- Lees AC, Peres CA (2009). Gap-Crossing Movements Predict Species Occupancy in Amazonian Forest Fragments. *Oikos* 118:280–290.

- Le Roux DS, Ikin K, Lindenmayer DB, Manning, AD, Gibbons P (2015). Single large or several small? Applying biogeographic principles to tree-level conservation and biodiversity offsets. *Biological Conservation* 191:558–566
- Lomolino MV (2000). Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography* 27:17-26
- Losos BJ, Schluter D (2000). Analysis of an evolutionary species-area relationship. *Nature* 408:847-850
- MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press, New Jersey
- Martin AE, and Fahrig L (2012). Measuring and selecting scales of effect for landscape predictors in species-habitat models. *Ecological Applications* 22:2277–2292
- Martin TG, Possingham HP (2005). Predicting the impact of livestock grazing on birds using foraging height data. *Journal of Applied Ecology* 42:400-408
- Marzluff JM, Ewing K (2001). Restoration of Fragmented Landscapes for the Conservation of Birds : A General Framework and Specific Recommendations for Urbanizing Landscapes. *Restoration Ecology* 9:280–292
- Morse WC, Schedlbauer JL, Sesnie SE, Finegan B, Harvey C A, Hollenhorst SJ et al. (2009). Consequences of Environmental Service Payments for Forest Retention and Recruitment in a Costa Rican Biological Corridor. *Ecology and Society* 14: 23

- Murphy GEP, Romanuk TN (2014). A meta-analysis of declines in local species richness from human disturbances. *Ecology and Evolution* 4:91–103
- Ochoa-quintero JM, Gardner TA, Rosa I, Frosini S, Ferraz DB, Sutherland WJ (2015). Thresholds of species loss in Amazonian deforestation frontier landscapes. *Conservation Biology* 29:440–451
- Pagiola S (2008). Payments for environmental services in Costa Rica. *Ecological Economics* 65:712–724
- Perfecto I, Vandermeer J (2002). Quality of agroecological matrix in a tropical montane landscape: Ants in coffee plantations in Southern Mexico. *Conservation Biology* 16:174–182
- Pettit L, Greenlees M, Shine, R (2017). The impact of transportation and translocation on dispersal behaviour in the invasive cane toad. *Oecologia* 184:411–422
- Pinto SR, Melo F, Tabarelli M, Padovesi A, Carrascosa H et al.. (2014). Governing and Delivering a Biome-Wide Restoration Initiative: The Case of Atlantic Forest Restoration Pact in Brazil. *Forests* 5:2212–2229
- Preston FW (1962). The Canonical Distribution of Commonness and Rarity: Part I. *Ecology* 43:187–215
- Prevedello JA, Vieira MV (2010). Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation*, 19:1205–1223
- Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008). Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America* 105:20770–20775

- R Core Team (2016). R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Reed JM, Harris RJ (2002). Behavioral barriers to non-migratory movements of birds. *Annals Zoologici Fennici* 39:275–290
- Rezende CL de, Uezu A, Scarano FR, Araujo DSD (2015). Atlantic Forest spontaneous regeneration at landscape scale. *Biodiversity and Conservation* 24:2255–2272
- Ricketts TH (2001). The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158:87–99
- Ries L, Debinski DM (2001). Butterfly Responses to Habitat Edges in the Highly Fragmented Praries of Central Iowa. *The Journal of Animal Ecology* 70:840-852
- Rivard DH, Poitevin J, Plasse D, Carleton M, Currie DJ (2000). Changing Species Richness and Composition in Canadian National Parks. *Conservation Biology* 14:1099-1109
- Ruffell J, Clout MN, Didham RK (2017). The matrix matters, but how should we manage it? Estimating the amount of high-quality matrix required to maintain biodiversity in fragmented landscapes. *Ecography* 40:171–178
- Russell RE, Swihart RK, Craig BA (2007). The Effects of Matrix Structure on Movement Decisions of Meadow Voles (*Microtus pennsylvanicus*). *Journal of Mammalogy* 88:573-579

- Rybicki J, Hanski I (2013). Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecology Letters* 16:27–38
- Saura S (2014). Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Applied Ecology* 51:171–182
- Schoener TW (1976). Alternatives to Lotka-Volterra competition: Models of intermediate complexity. *Theoretical Population Biology* 10:309–333
- Şekercioğlu CH, Ehrlich PR, Daily GC, Aygen D, Goehring D, Sandi R (2002). Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences of the United States of America* 99:263-267
- Smallbone LT, Matthews A, Lunt ID (2014). Landscape and Urban Planning regrowth provides complementary habitat for woodland birds of conservation concern in a regenerating agricultural landscape. *Landscape and Urban Planning* 124:43–52
- Smith JNM, Hellmann JJ, Brooker M (2002). Population persistence in fragmented landscapes. *Trends in Ecology and Evolution* 17:397–399
- Steinmann K, Eggenberg S, Wohlgemuth T, Linder, HP, Zimmermann NE (2011). Niches and noise — Disentangling habitat diversity and area effect on species diversity. *Ecological Complexity* 8:313–319
- Tabarelli M, Gascon C (2005). Lessons from Fragmentation Research: Improving Management and Policy Guidelines for Biodiversity Conservation. *Conservation Biology* 19:1–6
- Taylor JJ, Lepczyk CA, Brown DG (2016). Patch and matrix level influences on forest birds at the rural-urban interface. *Landscape Ecology* 31:1005–1020

- Tilman D (1994). Competition and Biodiversity in Spatially Structured Habitats. *Ecology* 75:2–16.
- Tischendorf L, Fahrig L. (2000). On the usage and measurement of landscape connectivity. *Oikos* 90:7–19.
- Turlure C, Baguette M, Stevens VM, Maes D (2011). Species- and sex- specific adjustments of movement behavior to landscape heterogeneity in butterflies. *Behavior Ecology* 22:967-975
- Uezu A, Metzger JP, Vielliard JME (2005). Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biological Conservation* 123:507–519
- Vasudev D, Jr RJF, Goswami VR, Krishnadas M (2015). From dispersal constraints to landscape connectivity : lessons from species distribution modeling. *Ecography* 38:967–978
- Verbeylen G, De Bruyn L, Adriaensen F, Matthysen E (2003). Does matrix resistance influence Red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape? *Landscape Ecology* 18:791-805
- Watling, JI, Donnelly MA (2006). Fragments as islands: A synthesis of faunal responses to habitat patchiness. *Conservation Biology* 20:1016–1025
- Watling JI, Nowakowski AJ, Donnelly MA, Orrock JL (2011). Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Global Ecology and Biogeography* 20:209–217

Zschokke S, Dolt C, Rusterholz HP, Oggier P, Braschler B, Thommen GH, Baur B (2000). Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. *Oecologia* 125:559–572

Figures:

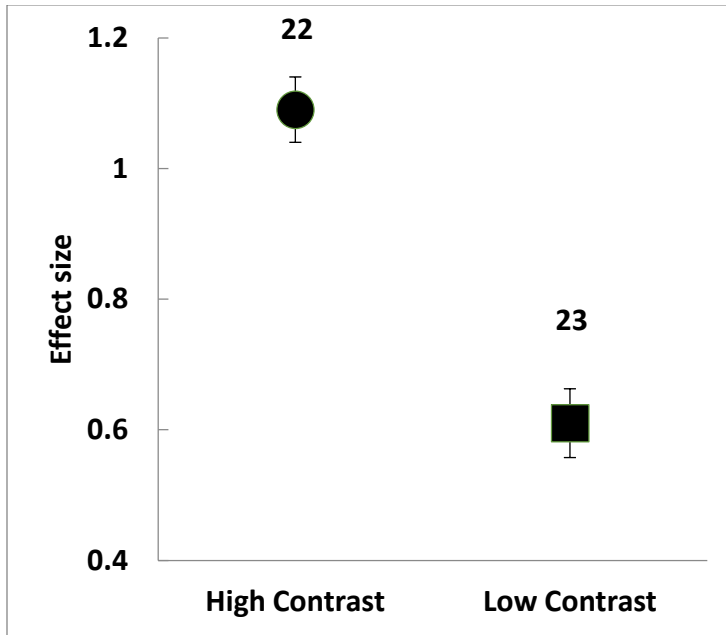


Fig. 1 Plot of mean effects of patch area on species richness in high and low contrast landscapes. Means are weighted by number of habitat fragments sampled in each study with variances. The number of studies included in each group for calculation is indicated above the mean effect sizes.

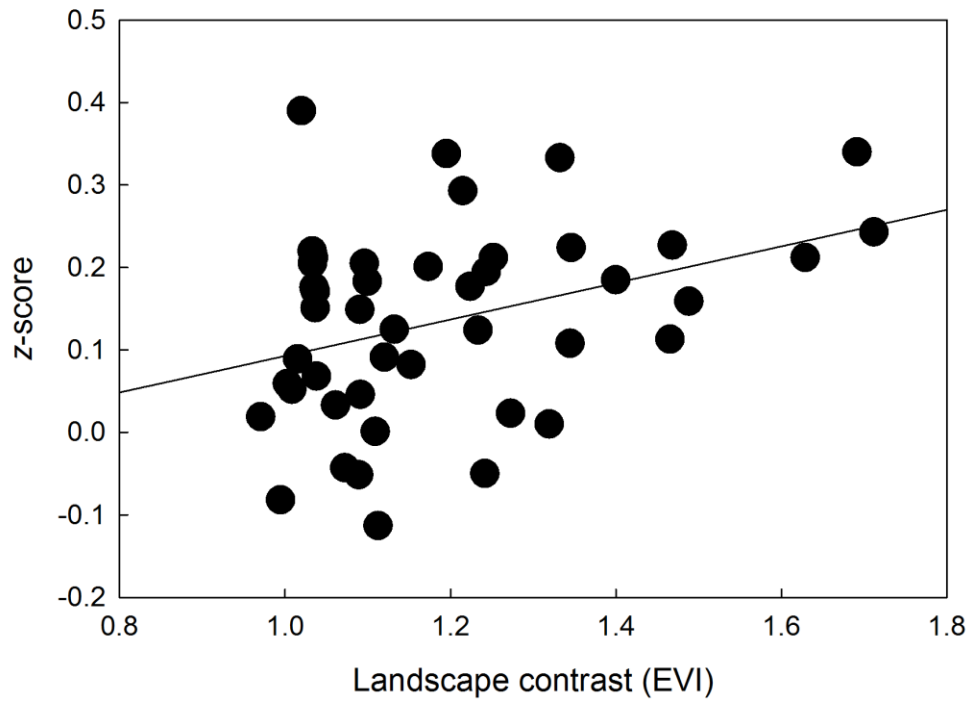


Fig. 2 Relationship between the z -score of species-area-relationship and landscape contrast between habitat area and matrix for all studies in analysis ($R^2 = 0.149$, $P = 0.002$), $n = 45$. Landscape contrast is weighted by the number of fragments where data were collected in each study.

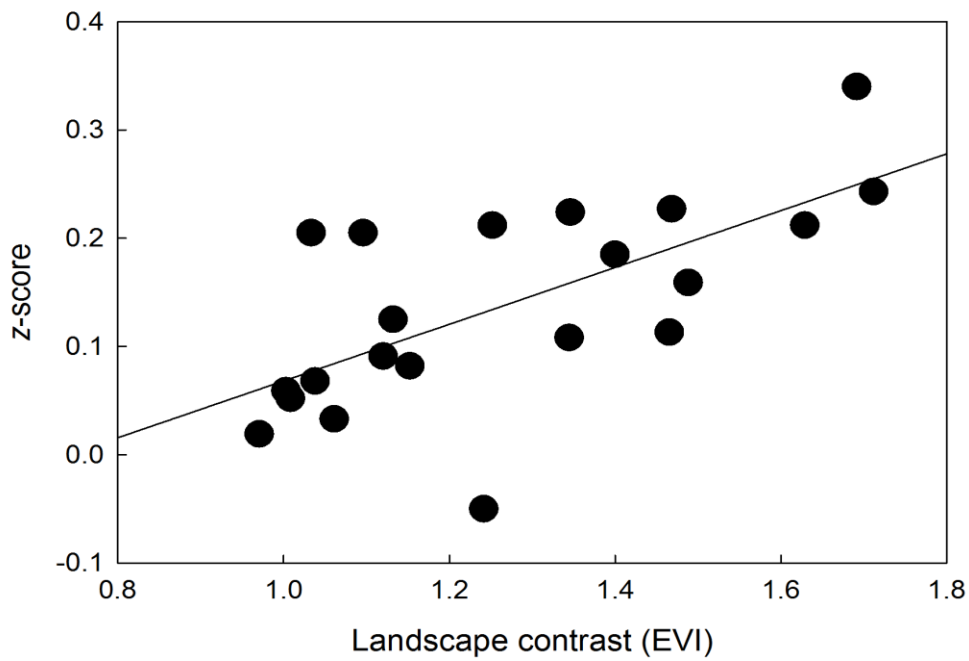


Fig. 3 Relationship between the z-score of species-area-relationship and landscape contrast between habitat area and matrix for all studies with landscapes that had <15% forest habitat remaining ($R^2 = 0.441$, $P = 0.002$), $n = 45$. Landscape contrast is weighted by the number of fragments where data were collected in each study.

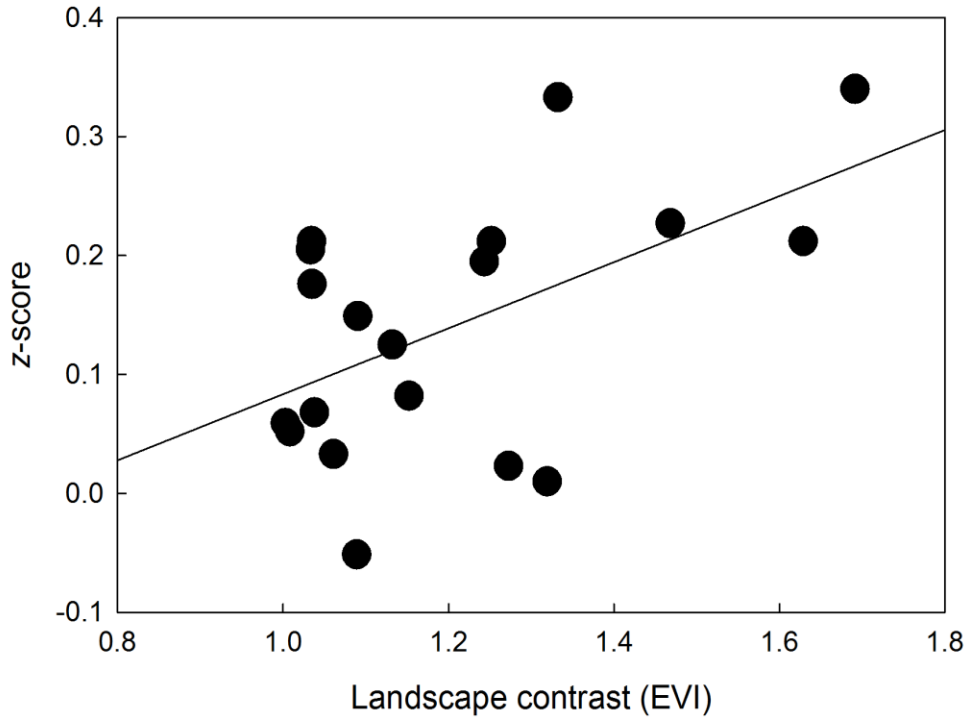


Fig. 4 Relationship between the z -score of species-area-relationship and landscape contrast between habitat area and matrix for all studies with volant taxonomic groups ($R^2= 0.283$, $P= 0.002$), $n= 45$. Landscape contrast is weighted by the number of fragments where data were collected in each study.

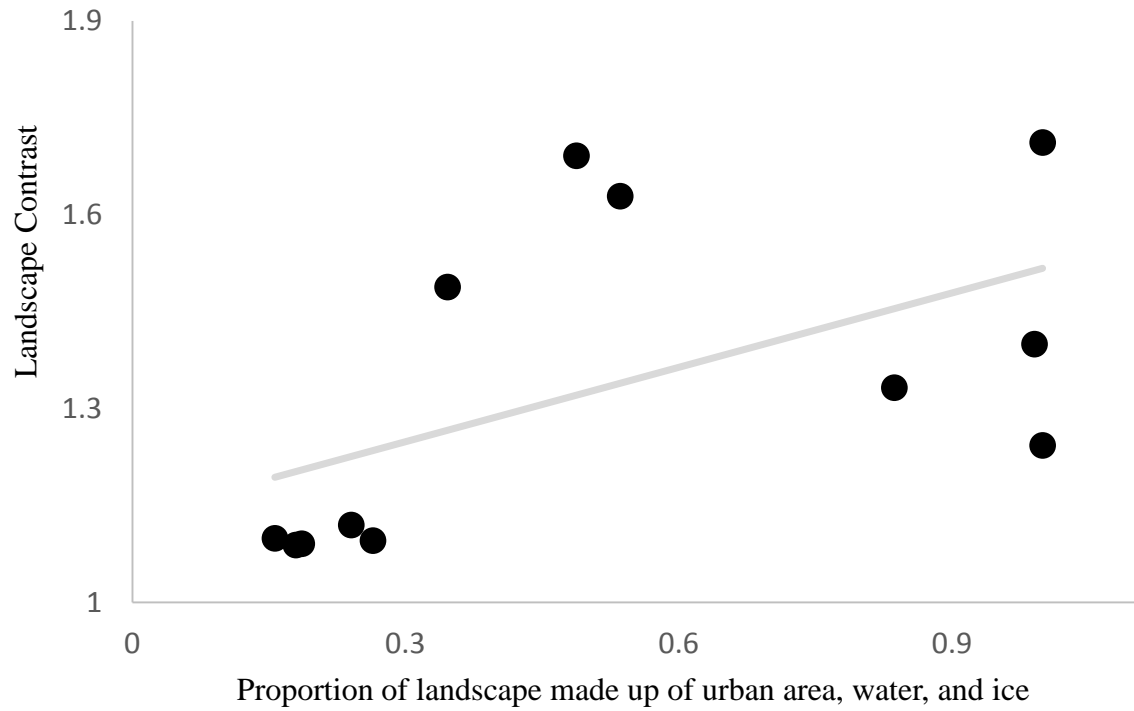


Fig. 5 Scatter plot of relationship between the magnitude of landscape contrast and the proportion of the landscape made up of vegetation-free matrices ($R^2= 0.33$, $P= 0.06$), $n= 12$. Each black dot is a study where at least 15% of the landscape consists of urban area, water bodies, or ice.

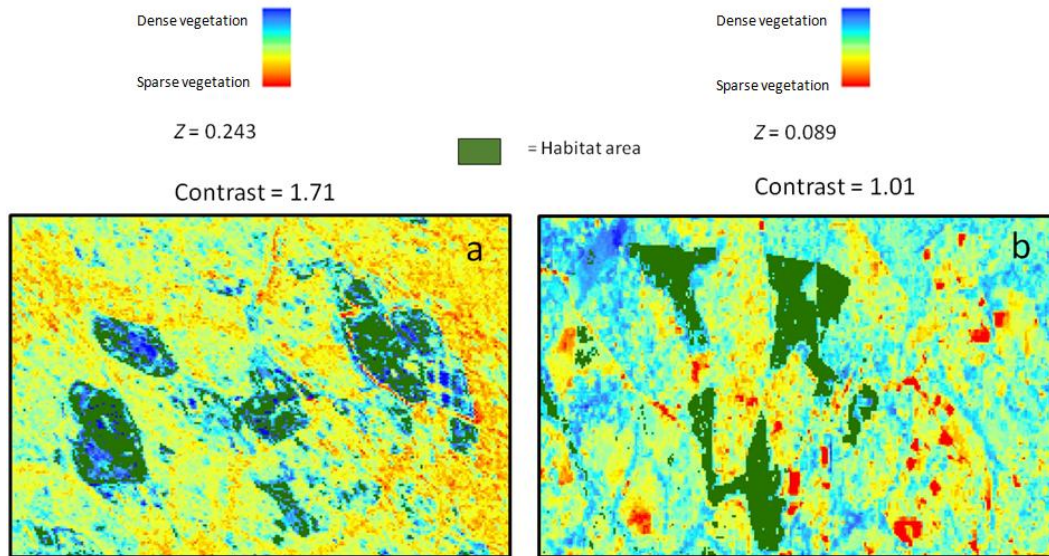


Fig. 6 Comparison of z -score and landscape contrast between two studies included in our analysis. Forest is indicated in dark green, and all other colors represent the matrix. Pixels in the images were each assigned a value of vegetation density based on the EVI and the average pixel value in habitat area was compared to the average pixel value in the matrix area. Panel a is on spider species in forest fragments in Tokyo and panel b is a study on dung beetle species in Uganda