Conservation Letters

WILEY

Conservation Letters
A journal of the Society for Conservation Biology
Open Access

LETTER OPEN ACCESS

Complex Measures of Habitat Fragmentation and Edge Can Complicate Biodiversity Conservation

Amanda E. Martin[1,2] | Carmen Galán-Acedo[2] | Víctor Arroyo-Rodríguez[3,4] | Lindsay Daly[5] | Simon G. English[6] | Andrew K. Habrich[2] | Aino Hämäläinen[7] | Federico Riva[8] | Lenore Fahrig[2]

[1]National Wildlife Research Centre, Environment and Climate Change Canada, Ottawa, Ontario, Canada | [2]Department of Biology, Carleton University, Ottawa, Ontario, Canada | [3]Escuela Nacional de Estudios Superiores, Universidad Nacional Autónoma de México, Mérida, Mexico | [4]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Mexico | [5]Canadian Wildlife Service, Environment and Climate Change Canada, Ottawa, Ontario, Canada | [6]Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC, Canada | [7]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden | [8]Institute for Environmental Studies, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

Correspondence: Amanda E. Martin (Amanda.Martin@ec.gc.ca)

Received: 14 May 2024 | **Revised:** 16 March 2025 | **Accepted:** 19 March 2025

Funding: This work was funded by a grant from the Natural Sciences and Engineering Research Council of Canada to Lenore Fahrig. Amanda E. Martin is supported by funding through Environment and Climate Change Canada.

Keywords: biodiversity | conservation policy | conservation practice | edge influence | habitat configuration | habitat fragmentation | habitat loss | wildlife

ABSTRACT

Understanding habitat fragmentation effects on wildlife is critical to promoting effective conservation practices. There are many metrics of habitat fragmentation, from simple (number of habitat patches) to complex metrics designed to summarize many aspects of landscape patterns. To make meaningful inferences, we must understand how complex metrics are related to landscape patterns, especially to habitat amount. Here, we examine the behavior of the Edge Influence index, a metric that has been used in several influential recent studies and is designed to assess fragmentation and edge effects. Contrary to expectation, this index does not primarily quantify fragmentation or edge but rather habitat amount. Therefore, researchers should take this into consideration when interpreting the results of studies based on the Edge Influence index. To guide meaningful conservation action in fragmented landscapes, we recommend using simple, direct measures of fragmentation and separating the effects of habitat configuration from the effects of habitat amount.

1 | Introduction

Continued biodiversity loss in human-modified landscapes has driven interest in understanding how landscape structure shapes biotic assemblages (Lindenmayer et al. 2008; Melo et al. 2013; Kremen and Merenlender 2018; Arroyo-Rodríguez et al. 2020). However, scientific research does not lead to effective conservation practice and/or policy if practitioners and policymakers are faced with conflicting findings and recommendations for action. A prominent case relates to the effects of habitat fragmentation on biodiversity, one of the most important themes in conservation biology since the late 1950s (Miller-Rushing et al. 2019). Some studies have concluded that habitat fragmentation harms biodiversity (e.g., Wilson et al. 2016; Fletcher et al. 2018). Yet, other studies suggest that habitat fragmentation effects are typically weak and usually positive when significant (e.g., Fahrig

Amanda E. Martin and Carmen Galán-Acedo should be considered co-first authors.

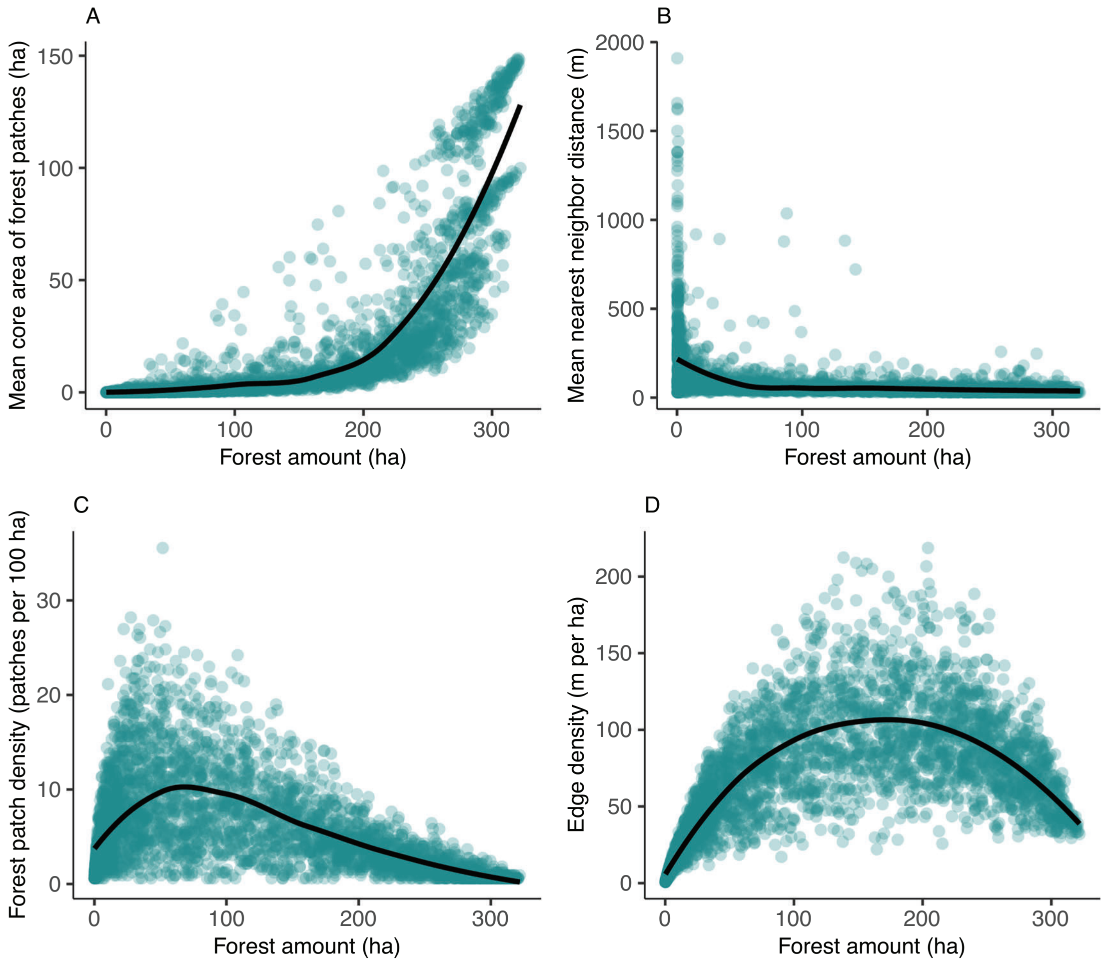

FIGURE 1 | Associations between forest amount and each of four common measures of forest fragmentation. For visualization purposes, we fit second-order local polynomial regression models (black lines). Points represent 5000 one-km-radius landscapes, randomly selected from a set of 69,758 landscapes (see Section 3 for details).

2017; Galán-Acedo et al. 2019). These contrasting findings and inferences are likely related to the use of different study designs, methods for analyses (Valente et al. 2023), and definitions of fragmentation (Fahrig 2003; Martin et al. 2021).

Contrasting findings and inferences about the effects of habitat fragmentation on biotic assemblages can also result from differences in the metrics used to index fragmentation (Valente et al. 2023). For example, Püttker et al. (2020) assessed the effects of two fragmentation metrics on the species richness of animals and plants and found the results depended on the fragmentation metric they used. Similarly, Semper-Pascual et al. (2021) found that the effects of fragmentation on birds and mammals depended on the metric used and whether they controlled for habitat amount. In fact, one of the most important distinctions between studies concluding that biodiversity tends to decrease with fragmentation and those concluding the opposite is whether they inherently combine habitat fragmentation and habitat amount or measure fragmentation independent of habitat amount (fragmentation per se, sensu Haila and Hanski 1984; Fahrig 2003; Valente et al. 2023).

Thus, it is important to understand what a landscape metric measures, particularly whether it is indexing habitat amount, the breaking apart of habitat (fragmentation), or both. This is because habitat loss and fragmentation can have different and often contrasting effects on biotic assemblages (Haila 2002; Fahrig 2017). Additionally, although habitat loss results in changes in the spatial pattern of remnant habitat, it does not necessarily result in increased fragmentation (Figure S1). This means that habitat amount and fragmentation are not always tightly coupled; many landscapes worldwide have both high amounts of forest and high fragmentation and vice versa (Riva et al. 2024). Furthermore, even when habitat amount is related to metrics of fragmentation (Figure 1), we can disentangle their effects by designing studies to minimize correlations between habitat amount and fragmentation and/or statistically controlling for their relationships (e.g., McGarigal and McComb 1995; Trzcinski et al. 1999; Wang et al. 2014).

There are many metrics of habitat fragmentation (e.g., Wang et al. 2014), and new metrics continue to be proposed (e.g., Rivas et al. 2022). Different applications can require different methods, but care should be taken with complex metrics that aim to summarize many aspects of landscape patterns. If not, we risk perpetrating the confusion that has surrounded habitat fragmentation for decades (Valente et al. 2023). To make meaningful inferences from studies of the effects of such metrics on ecological responses, we first need to understand how they are

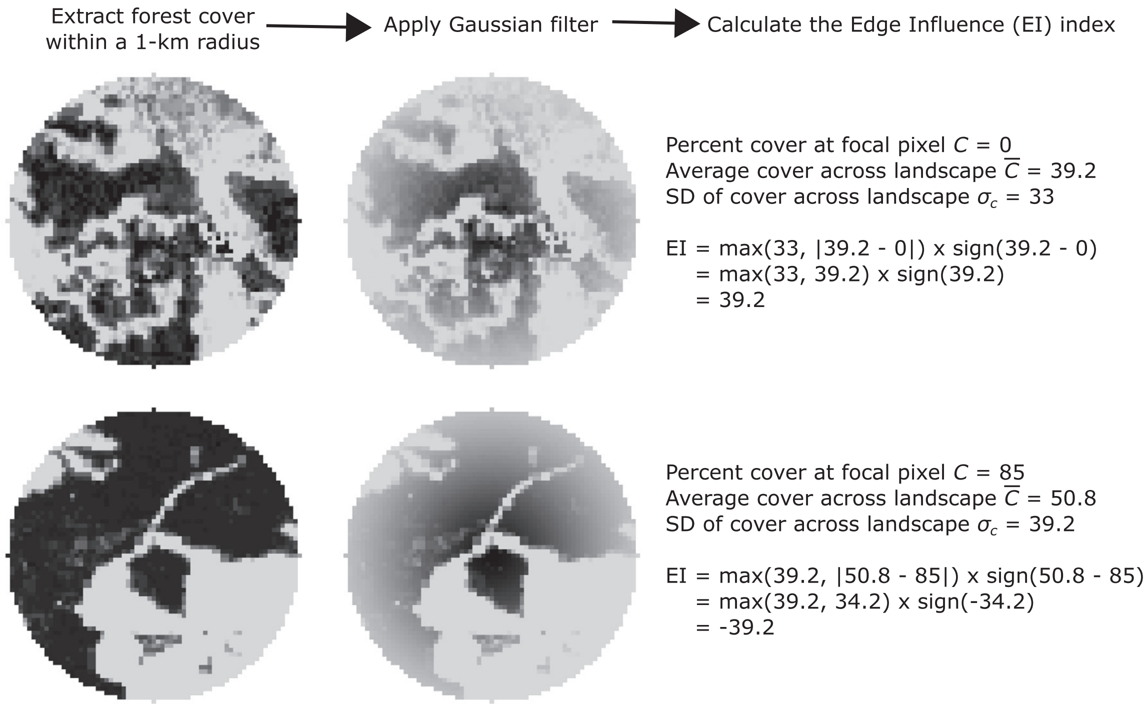

FIGURE 2 | Two example landscapes and associated Edge Influence index calculations, where light grey to black indicate percent forest covers of 0% to 100% (left panels). Gaussian filtering (central panels) results in a reduction in the percent cover values with increasing distance from the focal pixel.

related to various aspects of landscape patterns, including habitat amount.

Here, we assess what the Edge Influence (EI) index measures by analyzing its relationships with a suite of metrics to which researchers expect it to be related (see Additional Methods S1 in the Supporting Information). We focused on the EI index because it is a complex metric proposed to simultaneously quantify many aspects of fragmented habitat and habitat edge in a landscape (Lefebvre et al. 2016; Pfeifer et al. 2017). Furthermore, it has been at the core of several recent analyses leading to high-profile articles (Pfeifer et al. 2017; Betts et al. 2019; Weeks et al. 2023), which are highly cited in the habitat fragmentation literature (Riva et al. 2024).

2 | The EI index

First introduced in 2016, in tandem with the BioFrag software (Lefebvre et al. 2016), the authors of the EI index state that it incorporates multiple attributes of a landscape's structure in one metric, including "distance to multiple edges and edge shape, fragment contrast and habitat quality … fragment size, fragment isolation and local configuration … it encompasses edge effects, local habitat amount, local contrast, shape and local connectivity" (Lefebvre et al. 2016). Yet, they also state that the index "does not correlate closely with any single traditional landscape fragmentation metric, such as distance to the nearest edge, edge structure, fragment shape or fragment size, but rather aims to represent all of these previous metrics in a single metric" (Pfeifer et al. 2017). Thus, its creators and users acknowledge that relationships between the EI index and other individual measures of fragmentation and edge may be weak. However, for the EI index to represent the suite of metrics above, it ought to show consistent and predictable relationships with these metrics. This is particularly important for edge and fragmentation metrics, given the name of the EI index ("*edge* influence") and the history of controversy in habitat fragmentation research.

A notable feature is that the formula of the EI index does not explicitly include measures of fragmentation and edge. Specifically, the EI index is measured in the landscape surrounding a focal pixel on a raster land cover map, where land cover is represented by a continuous variable, such as the percent habitat cover in each pixel (Pfeifer et al. 2017). Thus, the EI index measures the landscape context of a site (i.e., focal pixel), with the site located at the center of the landscape and the landscape extent defined as the radius of a circular buffer. This radius is also referred to as the "depth of influence" (DEI; see Lefebvre et al. 2016, User Manual).

The formula for the EI index is:

$$\max(\sigma_C, \left|\bar{C} - C\right|) \times sign\left(\bar{C} - C\right),$$

where C is the percent habitat cover in the focal pixel; $\bar{C}$ is the percent habitat cover per pixel, averaged across all pixels in the landscape; and σ_C is the standard deviation (SD) of the per-pixel percent habitat cover in the landscape. The percent habitat cover in the landscape is Gaussian filtered prior to calculations of $\bar{C}$ and σ_C, which reduces the influence of the landscape context with distance from the focal pixel. See Figure 2 for example landscapes and calculations. Thus, the EI index returns a value for the focal pixel, which is the larger of (i) the SD of the Gaussian-filtered percent habitat cover across the landscape, or (ii) the absolute value of the difference between the Gaussian-filtered average percent habitat cover in the landscape and the percent habitat cover in the focal pixel. In either case, the result is multiplied by the sign (−1 or 1) of the difference between the average percent habitat cover in the landscape and the percent habitat cover in the pixel.

It is clear from the formulation of the EI index described above that this metric differs from the common definition of "edge influence," which usually refers to differences in environmental conditions (e.g., temperature, canopy cover) at the edge versus the interior of a habitat patch (Harper et al. 2005). Although the authors expect it to be representative of the distance to the nearest edge, the EI index also does not explicitly include the distance from the forest edge to the interior in its formula.

The relationships between the EI index and landscape-scale measures of fragmentation and edge are also nonintuitive. This can be seen in simplified, illustrative examples (Figure 3). Thus, there is a need to empirically quantify how the EI index relates to measures of fragmentation and edge that authors expect it to represent (Pfeifer et al. 2017; Betts et al. 2019; Weeks et al. 2023) and that are typically used in landscape ecology research. How the EI index relates to other local or landscape attributes is a question for future study.

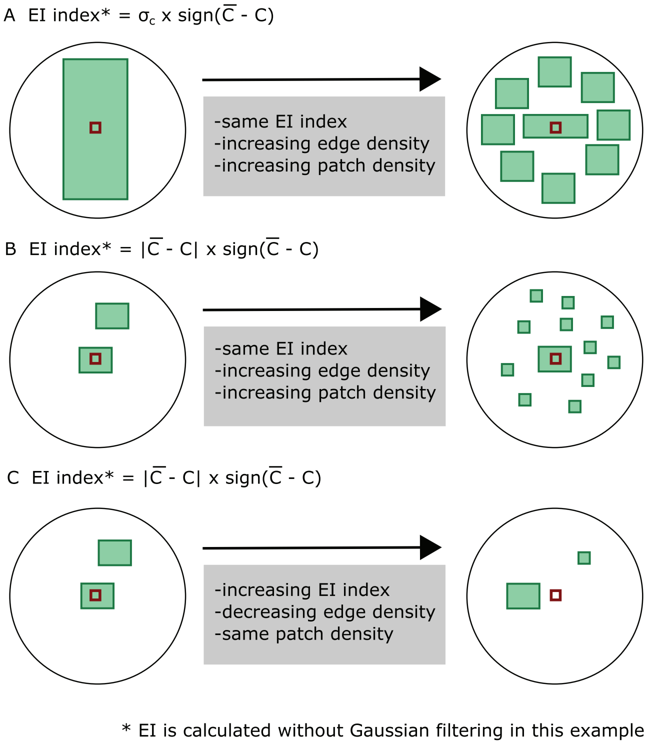

FIGURE 3 | Hypothetical landscape comparisons illustrate that the Edge Influence (EI) index is not necessarily related to edge density or to patch density (a common measure of habitat fragmentation). Landscapes are circles, red squares are the focal pixels where a biotic response is measured, all pixels in green areas are 100% habitat, all pixels in white areas are 0% habitat, and dark green is the habitat edge. For simplicity, the EI index is calculated without Gaussian filtering in these hypothetical landscapes. Note that the magnitude of the EI index is either the standard deviation of the percent habitat cover across the landscape (σ_C), or the absolute value of the difference between the average percent habitat cover in the landscape ($\bar{C}$) and the percent habitat cover in the central pixel C, whichever is larger. These examples suggest that two landscapes with the same habitat amount can have the same EI index value, irrespective of the degree of fragmentation of that habitat (Panels A and B). It is also possible to simultaneously have an increase in the EI index and a decrease in edge density (Panel C).

3 | What Does the EI Index Measure?

To empirically determine what the EI index measures in real landscapes, we randomly selected 100,000 points across all forested biomes (Figure S2). From each point, we calculated the EI index as described above, including the Gaussian filtering, using a continuous global tree cover dataset of the percent tree cover per pixel at a 30-m resolution (Hansen et al. 2013a, 2013b) and a landscape radius (DEI) of 1 km. Each landscape required at least one pixel with forest cover greater than 0%; any completely unforested landscape was replaced by another randomly selected landscape.

We selected 18 metrics for comparison to the EI index, based on descriptions of what the EI index is purported to measure from its creators and the papers that have used it (see Additional Methods S1 in the Supporting Information and Table S1). These 18 metrics represent different aspects of landscape structure and include measures made at both patch and landscape scales (e.g., distance to the nearest forest edge, edge density). We also extracted the percent forest cover at each focal pixel, given its central role in the EI index formula (above). All selected metrics (except for the EI index) required a binary (forest, non-forest) map. We, therefore, created a binary map by applying the biome-specific thresholds for defining forest in Dinerstein et al. (2017) to the global tree cover dataset (Additional Methods S2 in the Supporting Information). We then calculated the metrics for each landscape containing at least some forest and non-forest in the binary landscape, using either the "landscapemetrics" R package (Hesselbarth et al. 2019) or custom R code. We could not calculate all metrics in all landscapes. For example, some metrics require at least two habitat patches (e.g., mean distance to nearest neighbor). Thus, the number of landscapes with values varied among metrics from 26,038 to 85,050 landscapes.

Due to high correlations among metrics (Figures S3–S5), we reduced the metrics from 18 to 12 plus the percent forest cover in the focal pixel. To estimate the relative strengths of association between the EI index and each metric when controlling for the relationships of the EI index to all other metrics, we modeled the EI index simultaneously as a function of the 12 metrics plus cover in the focal pixel, where all metrics were standardized to mean = 0 and SD = 1, using nonparametric median regression. Since the inclusion of correlated predictor variables does not bias the direction or magnitude of regression coefficients (Smith et al. 2009; Morrissey and Ruxton 2018), this approach allows us to assess the independent contribution of each metric to the EI index. We separately assessed the 69,758 landscapes for which we could calculate values for all metrics (including landscapes with both positive and negative EI index values; Figure 4) and the

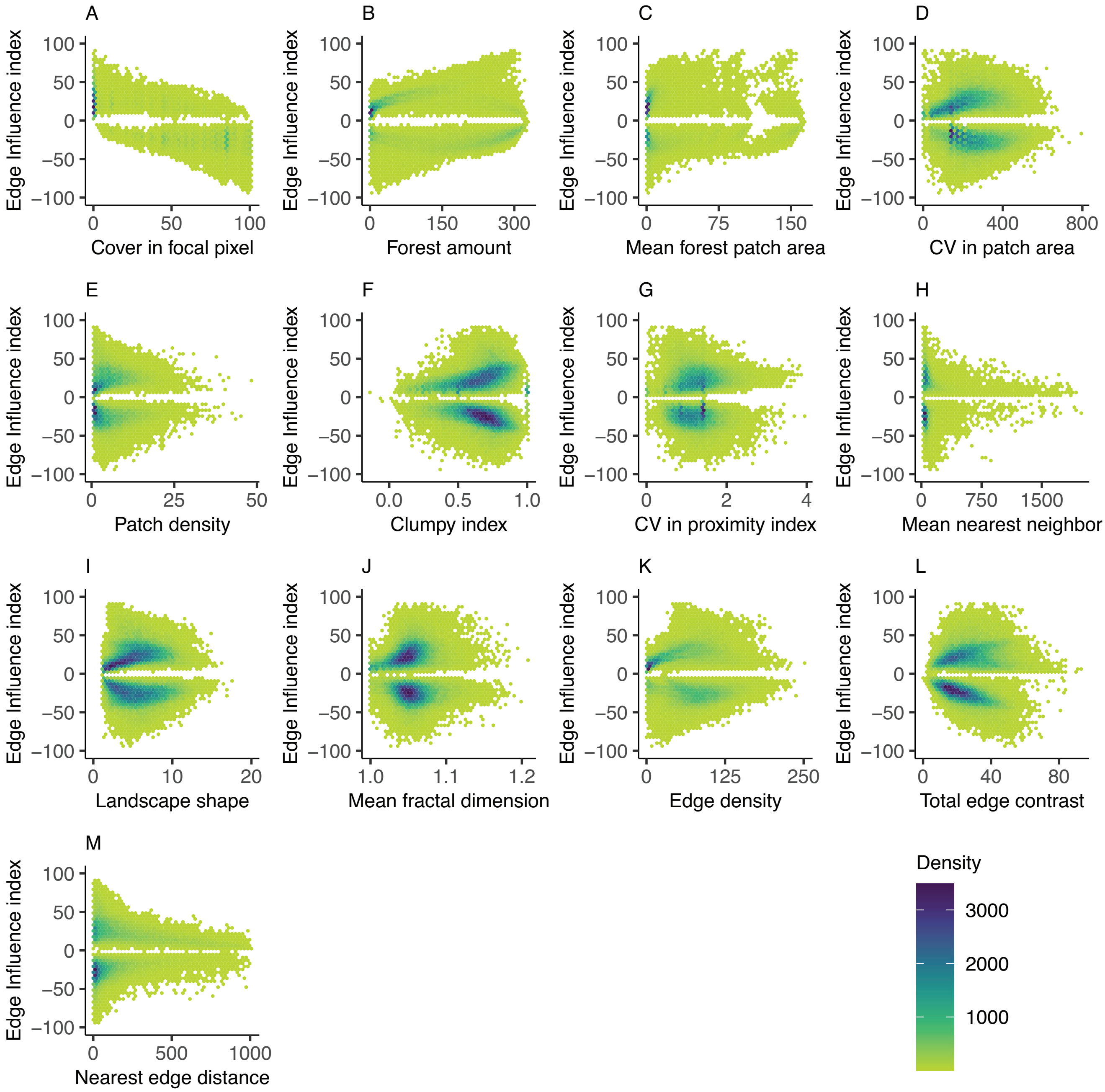

FIGURE 4 | Plots of the relationship between the Edge Influence index and each of the 13 measures representing different aspects of forest amount, fragmentation, and edge, including all data (n = 69,758 landscapes). The color scale indicates point density, from low (light green) to high (dark purple). See Table S1 for metric descriptions.

subsets of 26,038 and 43,720 landscapes with focal pixels located within forest and in non-forest, respectively (Figures S6 and S7). We note that the EI index value was typically negative when the focal pixel was forested and positive when the focal pixel was not forested (Figure S8). We also conducted sensitivity analyses to assess whether our conclusions were sensitive to our choice of (a) thresholds for classifying forest/non-forest and (b) landscape size (see Additional Methods S2 in the Supporting Information).

Our results indicate that the EI index is primarily a proxy for habitat cover in the focal pixel and the surrounding landscape. By far, the best individual predictors of the EI index were the percent forest cover in the focal pixel (i.e., C in the EI index formula) and the forest amount in the landscape (Figure 5A). After controlling for the effects of all fragmentation and edge metrics in the analysis, the effect sizes for percent forest cover in the focal pixel and the forest amount in the landscape were 10× and 5× the size of the next-largest effect, respectively. Relationships between the EI index and metrics of forest fragmentation and edge were generally weak. However, they were stronger (and the relationship with forest cover in the focal pixel was weaker) when we considered only the subset of landscapes with forest at the focal pixel (Figure 5A–C). Nevertheless, the effect size for forest amount in the landscape was still more than twice the magnitude

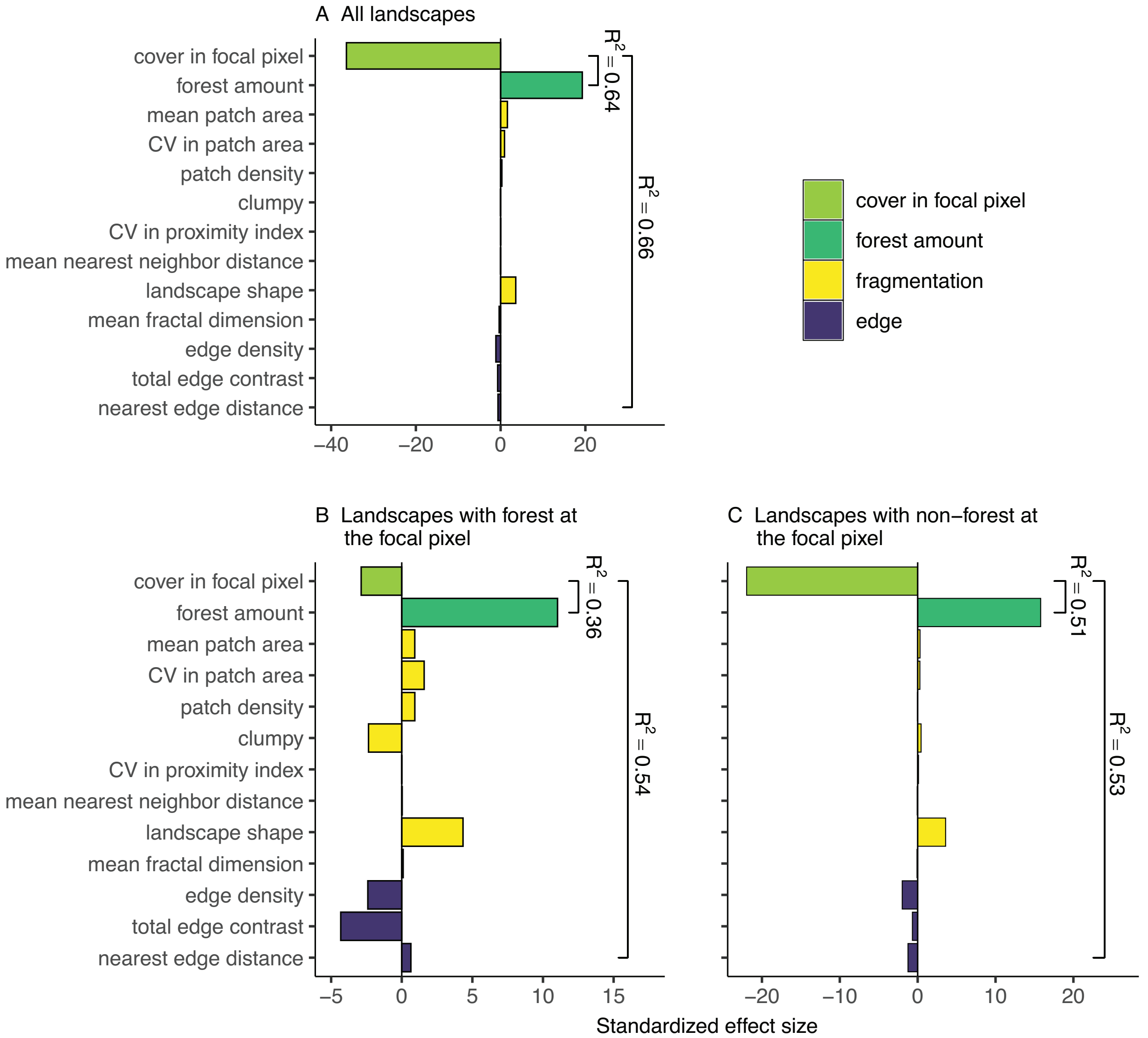

FIGURE 5 | Relationships between the Edge Influence (EI) index and 13 measures representing different aspects of forest amount, fragmentation, and edge. Effect sizes were estimated using nonparametric median regression for models including (A) all data ($n = 69{,}758$ landscapes), (B) the subset of data where the focal pixel was located in the forest ($n = 26{,}038$ landscapes), and (C) the subset of data where the focal pixel was in non-forest ($n = 43{,}720$ landscapes). Pseudo-R^2 values were estimated for the full model (13 metrics) and for a model of the EI index as a function of forest cover in the focal pixel + forest amount in the landscape.

of any other metric (Figure 5B). Our conclusions were similar for analyses using the alternative forest/non-forest maps (Figures S9–S12) and landscape sizes (Figures S13–S15).

Given the strong relationships between the EI index and forest cover in the focal pixel and forest amount in the landscape (Figure 5) and the expectation that this index will simultaneously represent many measures of fragmentation and edge but not individual metrics, we asked a follow-up question. Do fragmentation and edge measures collectively explain substantial variation in the EI index above what is explained by forest cover in the focal pixel and forest amount in the landscape? To answer this question, we compared the pseudo-R^2 value for the model specified above to a model of the EI index as a function of only the forest cover in the focal pixel + forest amount in the landscape. Pseudo-R^2 values were estimated using the formula in Koenker and Machado (1999). For analyses of all landscapes and the subset of landscapes with non-forest at the focal pixel, adding all 11 measures of fragmentation and edge only increased the pseudo-R^2 by 0.02 (Figure 5A,C). For landscapes with forest at the focal pixel, the suite of fragmentation and edge metrics explained an additional 0.18 of variation in the EI index; this was half the variation explained by forest cover in the focal pixel and forest amount in the landscape (Figure 5B). This finding was consistent whether we modeled linear or nonlinear relationships between the EI index and other metrics (see Figures S16–S19).

Finally, we asked whether relationships between the EI index and measures of forest amount, fragmentation, and edge depended on the amount of forest in the landscape. Previous studies have found that the relationships between habitat amount and fragmentation metrics can be different for landscapes with low, intermediate, and high habitat amounts (e.g., Wang et al. 2014, Riva et al. 2024). To assess this, we reran our main analyses for subsets

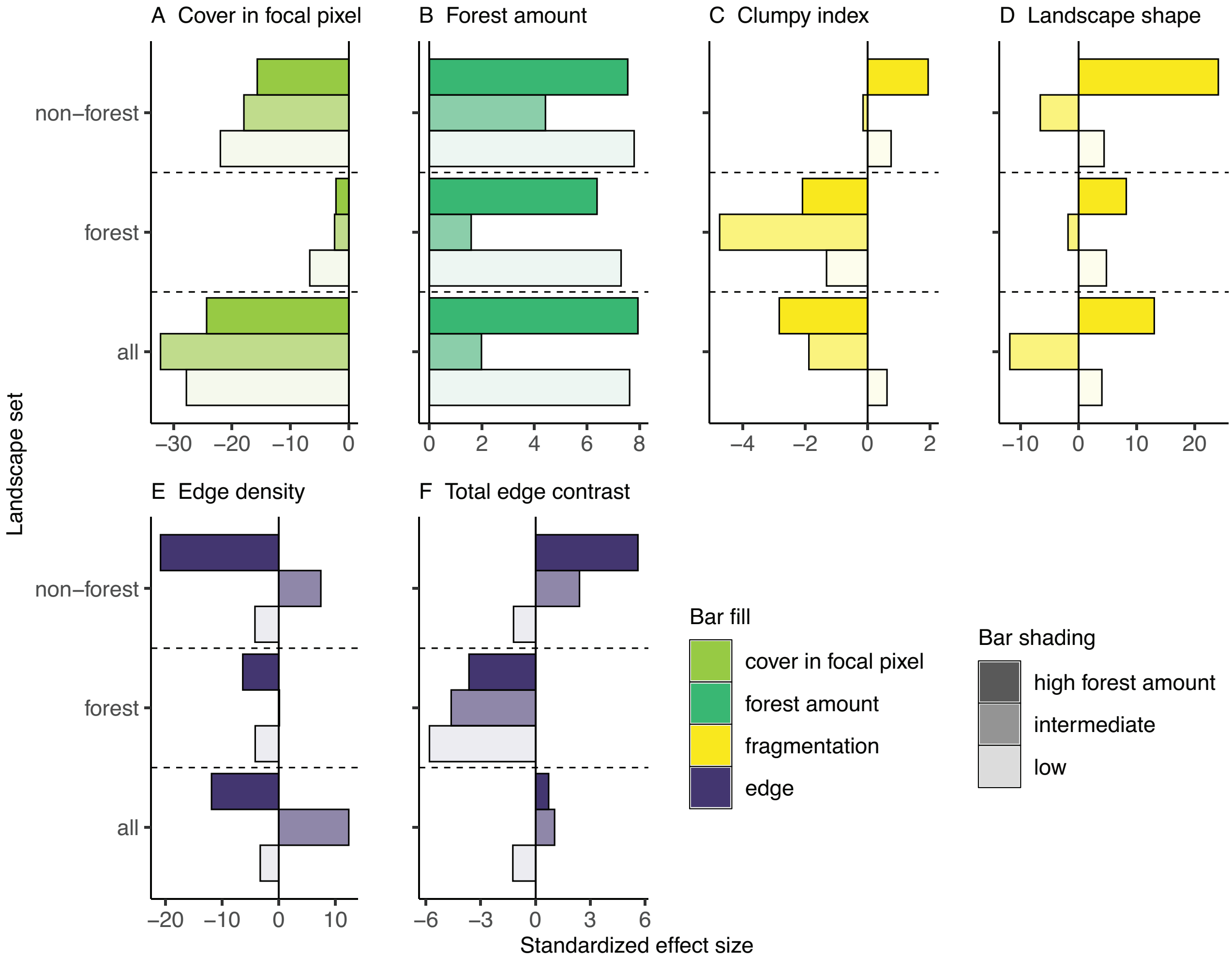

FIGURE 6 | The influence of forest amount in the landscape on the magnitude and direction of relationships between the Edge Influence index and (A) forest cover in the focal pixel, (B) forest amount, and (C–F) the subset of fragmentation and edge metrics with the largest effect sizes (see Figure S23 for remaining metrics). Effect sizes were estimated using nonparametric median regression for models including (A) all data, (B) the subset of landscapes where the focal pixel was located in the forest, and (C) the subset of landscapes where the focal pixel was in non-forest. Each of these three data sets was further subdivided into landscapes with low (<35% of the landscape in the forest), intermediate (35% to <65%), or high (≥65%) forest amounts prior to analyses.

of landscapes with low (<35% of the landscape in the forest), intermediate (35% to <65%), and high (≥65%) forest amounts.

As expected, the relationship with forest amount was weaker in these analyses than in those reported above because its range of values was narrower. However, we still found that the EI index usually maintained stronger relationships with forest cover in the focal pixel and forest amount in the landscape than with individual metrics of fragmentation/edge. Notably, forest cover in the focal pixel and forest amount in the landscape always had larger effects than measures of fragmentation and edge across landscapes with < 35% of the landscape in the forest (Figure S20). Above that threshold, we found larger effects for some individual fragmentation and edge metrics relative to forest amount (Figures S21–S22). Most importantly, while the direction of the relationship between the EI index and forest cover in the focal pixel and forest amount in the landscape were consistent in all conditions—that is, across forest amounts and landscapes with focal pixels in forest and non-forest (Figure 6A,B)—the relationships between the EI index and metrics of fragmentation and edge were not. This was apparent even when we focused on the subset of fragmentation and edge metrics that had the strongest relationships with the EI index (i.e., the largest standardized effect sizes, Figure 6C–F; see also Figure S23). Furthermore, for some combinations of forest amount and focal pixel (forest or non-forest) condition, the index showed different directions of relationship with different fragmentation metrics (Figure 6C,D) and with different edge metrics (Figure 6E,F).

4 | A Path Forward

Taken together, our findings indicate that the EI index is mainly a proxy for local- and landscape-scale habitat amount, not for the spatial configuration of habitat (fragmentation or edge). Thus, researchers interested in using this index to represent the complexities of fragmentation and edge would need to control for correlations with habitat amount via study design or statistical approaches (Smith et al. 2009). Otherwise, the effects of the EI index on ecological responses will largely reflect the influences of habitat amount. Furthermore, our analyses indicate that the EI index's relationships with measures of fragmentation and edge are complicated—these relationships can change in both strength and direction depending on the amount of habitat in the landscape, whether the landscape is centered on habitat or non-habitat, and the particular measure of fragmentation or edge. Thus, it is challenging to interpret or make inferences about the effects of habitat fragmentation and edges on ecological responses from studies using the EI index.

We stress that the challenges of selecting fragmentation metrics appropriate for each research question are not unique to this index. There is a wealth of fragmentation metrics that range from simpler (e.g., the number of habitat patches in a landscape) to more complex ones (e.g., L–Z complexity; Shuangcheng et al. 2009), but as a rule of thumb, we suggest that "simplest is best." Results from simple fragmentation metrics are both easier to interpret and more easily translated into clear and effective conservation policy and practice. In particular, policies/practices aimed at altering fragmentation should rely on evidence from studies using direct indicators of fragmentation. This means studies should use metrics that explicitly represent the subdivision or breaking apart of habitat (e.g., patch density) while controlling for habitat amount via study design or statistical analyses. This allows for inferences that can be directly translated into conservation action. For example, it is easier to imagine how a forest restoration project could be designed to increase/decrease patch density for a given addition of forest cover than how one would plan a project to increase/decrease a metric that has different—and sometimes contradictory—associations with various aspects of the landscape structure. Such plans will be crucial for addressing the ongoing crisis of biodiversity loss in human-modified landscapes.

Acknowledgments

This work was funded by a grant from the Natural Sciences and Engineering Research Council of Canada to LF. AEM is supported by funding through Environment and Climate Change Canada. The authors thank members of the Geomatics and Landscape Ecology Research Laboratory at Carleton University for discussions that helped motivate this work, Dr. James Watling for his assistance with the BioFrag software, and the peer reviewers for their constructive feedback.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

See Hansen et al. (2013a) and Resolve (2017) for access to publicly available data sets. Other data and analysis scripts are here: https://doi.org/10.6084/m9.figshare.25810126.

References

Arroyo-Rodríguez, V., L. Fahrig, M. Tabarelli, et al. 2020. "Designing Optimal Human-Modified Landscapes for Forest Biodiversity Conservation." *Ecology Letters* 23: 1404–1420.

Betts, M. G., C. Wolf, M. Pfeifer, et al. 2019. "Extinction Filters Mediate the Global Effects of Habitat Fragmentation on Animals." *Science* 366: 1236–1239.

Dinerstein, E., D. Olson, A. Joshi, et al. 2017. "An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm." *Bioscience* 67: 534–545.

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

Fahrig, L. 2017. "Ecological Responses to Habitat Fragmentation Per Se." *Annual Review of Ecology, Evolution, and Systematics* 48: 1–23.

Fletcher, R. J. Jr., R. K. Didham, C. Banks-Leite, et al. 2018. "Is Habitat Fragmentation Good for Biodiversity?" *Biological Conservation* 226: 9–15.

Galán-Acedo, C., V. Arroyo-Rodríguez, S. J. Cudney-Valenzuela, and L. Fahrig. 2019. "A Global Assessment of Primate Responses to Landscape Structure." *Biological Reviews* 94: 1605–1618.

Haila, Y. 2002. "A Conceptual Genealogy of Fragmentation Research: From Island Biogeography to Landscape Ecology." *Ecological Applications* 12: 321–334.

Haila, Y., and I. K. Hanski. 1984. "Methodology for Studying the Effect of Habitat Fragmentation on Land Birds." *Annales Zoologica Fennici* 21: 393–397.

Hansen, M. C., P. V. Potapov, R. Moore, et al. 2013a. "Global 2010 Tree Cover (30 m)." Global Land Analysis & Discovery. https://glad.umd.edu/dataset/global-2010-tree-cover-30-m.

Hansen, M. C., P. V. Potapov, R. Moore, et al. 2013b. "High-resolution Global Maps of 21st-century Forest Cover Change." *Science* 342: 850–853.

Harper, K. A., S. E. Macdonald, P. J. Burton, et al. 2005. "Edge Influence on Forest Structure and Composition in Fragmented Landscapes." *Conservation Biology* 19: 768–782.

Hesselbarth, M. H. K., M. Sciaini, K. A. With, K. Wiegand, and J. Nowosad. 2019. "landscapemetrics: An Open-Source *R* Tool to Calculate Landscape Metrics." *Ecography* 42: 1648–1657.

Koenker, R., and J. A. F. Machado. 1999. "Goodness of Fit and Related Inference Processes for Quantile Regression." *Journal of the American Statistical Association* 94: 1296–1310.

Kremen, C., and A. M. Merenlender. 2018. "Landscapes That Work for Biodiversity and People." *Science* 362: eaau6020.

Lefebvre, V., M. Pfeifer, and R. Ewers. 2016. BioFrag|Edge Response-The BioFrag Software. https://github.com/VeroL/BioFrag.

Lindenmayer, D., R. J. Hobbs, R. Montague-Drake, et al. 2008. "A Checklist for Ecological Management of Landscapes for Conservation." *Ecology Letters* 11: 78–91.

Martin, A. E., J. R. Bennett, and L. Fahrig. 2021. "Habitat Fragmentation." In *The Routledge Handbook of Landscape Ecology*, edited by R. A. Francis, J. D. A. Millington, G. L. W. Perry, and E. S. Minor, 118–139. Routledge.

McGarigal, K., and W. C. McComb. 1995. "Relationships Between Landscape Structure and Breeding Birds in the Oregon Coast Range." *Ecological Monographs* 65: 235–260.

Melo, F. P. L., V. Arroyo-Rodríguez, L. Fahrig, M. Martínez-Ramos, and M. Tabarelli. 2013. "On the Hope for Biodiversity-Friendly Tropical Landscapes." *Trends in Ecology & Evolution* 28: 462–468.

Miller-Rushing, A. J., R. B. Primack, V. Devictor, et al. 2019. "How Does Habitat Fragmentation Affect Biodiversity? A Controversial Question at the Core of Conservation Biology." *Biological Conservation* 232: 271–273.

Morrissey, M. B., and G. D. Ruxton. 2018. "Multiple Regression Is Not Multiple Regressions: the Meaning of Multiple Regression and the Non-Problem of Collinearity." *Philosophy, Theory, and Practice in Biology* 10: 003.

Pfeifer, M., V. Lefebvre, C. A. Peres, et al. 2017. "Creation of Forest Edges Has a Global Impact on Forest Vertebrates." *Nature* 551: 187–191.

Püttker, T., R. Crouzeilles, M. Almeida-Gomes, et al. 2020. "Indirect Effects of Habitat Loss via Habitat Fragmentation: A Cross-Taxa Analysis of Forest-Dependent Species." *Biological Conservation* 241: 108368.

Resolve. 2017. Ecoregions 2017. https://ecoregions.appspot.com/.

Riva, F., N. Koper, and L. Fahrig. 2024. "Overcoming Confusion and Stigma in Habitat Fragmentation Research." *Biological Reviews* 99: 1411–1424.

Rivas, C. A., J. Guerrero-Casado, and R. M. Navarro-Cerrillo. 2022. "A New Combined Index to Assess the Fragmentation Status of a Forest Patch Based on Its Size, Shape Complexity, and Isolation." *Diversity* 14: 896.

Semper-Pascual, A., C. Burton, M. Baumann, et al. 2021. "How Do Habitat Amount and Habitat Fragmentation Drive Time-Delayed Responses of Biodiversity to Land-Use Change?" *Proceeding of the Royal Society B: Biological Sciences* 288: 20202466.

Shuangcheng, L., C. Qing, P. Jian, and W. Yanglin. 2009. "Indicating Landscape Fragmentation Using L–Z Complexity." *Ecological Indicators* 9: 780–790.

Smith, A. C., N. Koper, C. M. Francis, and L. Fahrig. 2009. "Confronting Collinearity: Comparing Methods for Disentangling the Effects of Habitat Loss and Fragmentation." *Landscape Ecology* 24: 1271–1285.

Trzcinski, M. K., L. Fahrig, and G. Merriam. 1999. "Independent Effects of Forest Cover and Fragmentation on the Distribution of Forest Breeding Birds." *Ecological Applications* 9: 586–593.

Valente, J. J., D. G. Gannon, J. Hightower, et al. 2023. "Toward Conciliation in the Habitat Fragmentation and Biodiversity Debate." *Landscape Ecology* 38: 2717–2730.

Wang, X., F. G. Blanchet, and N. Koper. 2014. "Measuring Habitat Fragmentation: An Evaluation of Landscape Pattern Metrics." *Methods in Ecology and Evolution* 5: 634–646.

Weeks, T. L., M. G. Betts, M. Pfeifer, et al. 2023. "Climate-Driven Variation in Dispersal Ability Predicts Responses to Forest Fragmentation in Birds." *Nature Ecology & Evolution* 7: 1079–1091.

Wilson, M. C., X. Y. Chen, R. T. Corlett, et al. 2016. "Habitat Fragmentation and Biodiversity Conservation: Key Findings and Future Challenges." *Landscape Ecology* 31: 219–227.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.