Virtual special issue: Insights from a landscape ecological perspective for tropical biology and conservation

James I. Watling | J. Nicolás Urbina-Cardona

1John Carroll University, University Heights, Ohio, USA
2Facultad de Estudios Ambientales y Rurales, Pontificia Universidad Javeriana, Bogotá, Colombia

Correspondence
James I. Watling, John Carroll University, University Heights, OH 44118, USA.
Email: jwatling@jcu.edu

Associate Editor: Jennifer Powers
Handling Editor: Jennifer Powers

Abstract
We conducted a keyword search to sample a subset of research on landscape ecology published in Biotropica between 2016 and mid-2021. Our search returned 112 studies, which we summarize in terms of focal taxon and habitat. From this pool of studies, we selected 14 papers for the virtual special issue “Insights from a Landscape Ecological Perspective for Tropical Biology and Conservation.” The 14 papers selected exemplify notable trends in recent research in landscape ecology and provide an opportunity to highlight suggestions for high-impact future research: 1) continuing to expand how we think about responses to landscape change by embracing new measures of immunology and gene expression, 2) documenting the conservation value of small habitats as essential reservoirs of biodiversity, 3) clarifying the relative impacts of habitat loss and fragmentation, with particular emphasis on cross-scale studies from a variety of landscapes and taxonomic groups.

KEYWORDS
habitat patch, matrix, rain forest, savanna, spatial ecology, species diversity

1 | INTRODUCTION

Deforestation rates have been trending upwards since the year 2000, with a 12% increase in primary tropical forest loss between 2019 and 2020 (Weisse & Goldman, 2021). Global assessments indicate that grasslands (Bardgett et al., 2021) and wetlands (McInnes et al., 2020) are similarly, if not more degraded than forest. As habitat is lost, primarily as a result of agricultural expansion (Barnosky et al., 2012), remnant habitat tends to occur in an ever-larger number of increasingly small fragments (Taubert et al., 2018). The fate of these fragments for the species and ecological processes they maintain has inspired decades of scientific inquiry. From early tests of island biogeography (Lovejoy et al., 1983; Simberloff & Wilson, 1969), to contemporary debates on the relative importance of habitat loss and fragmentation (Fahrig et al., 2019; Fletcher et al., 2018), the tropics have been an essential laboratory for inspiring landscape ecology theory (e.g., the equilibrium theory of island biogeography and the unified neutral theory of biodiversity and biogeography; Hubbell, 2001; MacArthur & Wilson, 1967) and testing its predictions (Betts et al., 2019; Laurance et al., 2002). In light of the recent loss of two of the leading figures in tropical landscape ecology, Thomas Lovejoy and E. O. Wilson, we take this opportunity to briefly review recent landscape ecology work from Biotropica. We emphasize the community and ecosystem levels of biological organization that have been the focus of much of the landscape ecology theory inspired by and tested in the tropics, and discuss current research trends and future directions. Fourteen studies from our review are highlighted in the accompanying virtual special issue.
2 | METHODS

On July 9, 2021, we conducted a keyword search in the Web of Science database for articles from Biotropica published between January 2016 and July 2021 that included the terms LANDSCAPE and (COMMUNITY or ECOSYSTEM) in the title or abstract. There were 112 articles that included those terms (Table S1). Using the total pool of 112 articles, we classified studies by taxon and habitat, and visualized the classifications using FoamTree (https://carrotsearch.com/foamtree/). A Foam Tree is a hierarchical Voronoi Treemap that efficiently uses space in the figure to create non-rectangular polygons whose size is proportional to the number of observations in each category. To assess the degree to which studies from Biotropica represent the species and habitats of conservation concern, we extracted taxonomic and habitat data for non-marine species from tropical countries from the IUCN Red List using the package rredlist (Chamberlain, 2020) for the R computing platform (R Core Team, 2021) and created similar foam trees for the Red List data. For the Red List comparison group, we included species in all threat categories (including “Least Concern” and “Data Deficient,” a total of 87678 species). We then read the abstracts of the 112 studies, and independently scored them on a scale of 1–5, with the highest score for studies that used a robust experimental design to evaluate effects of at least one landscape metric on a community- or ecosystem-level response variable. While our review synthesizes results from all 112 studies, the 14 studies for the special issue were selected based on three criteria: (1) a score of 4 or 5 in our evaluation; (2) at least one study each from the Neotropics, Africa, and Asia; (3) author diversity (e.g., career stage and institutional affiliation).

3 | RESULTS AND DISCUSSION

The vast majority of studies in our review (>90%) focus on biological communities rather than ecosystem properties, with most (66%) focusing on taxonomic diversity. The proportion of papers published in Biotropica on different taxonomic groups was generally representative of the number of species from those groups on the Red List, with roughly a third of studies on plants, and two-thirds on animals, particularly birds, arthropods, and mammals (Figure 1). Most studies in Biotropica took place in forested landscapes, which was also the most commonly used habitat for species on the Red List (Figure 2).

However, grasslands represented about 20% of habitat use observations for species on the Red List, but only 6% from Biotropica studies, implying that native grasslands may be somewhat understudied compared with their use by tropical species. The over-representation of agricultural areas in Biotropica studies (Figure 2) makes sense given that about 40% of Earth’s terrestrial land area is used for agriculture (Barnosky et al., 2012), and many landscape ecology studies take place in agricultural landscapes. The small proportions of studies in karst and urban landscapes were roughly proportional to their use by species on the Red List.

3.1 | The present and future of tropical landscape ecology

One of the points we found most noteworthy in our keyword review was the relatively large number of studies taking a functional approach to measuring biodiversity responses to landscape configuration. Although measures of abundance and species richness remain the most common response variables in the studies we surveyed (66%), a substantial fraction of studies measured at least one response variable describing functional diversity (9%). Scientists have long stressed the need for studies of functional diversity (e.g., Cadotte et al., 2011), and it appears that researchers submitting work to Biotropica are responding to that call. For example, in their study of phyllostomid bats, Ramirez-Mejia et al. (2020) found that functional diversity increased in landscapes with greater forest cover in a 1.25 km buffer around sampling points. Another study used two measures to show that for birds in the Atlantic Forest, phylogenetic diversity was unaffected by vegetation cover even when species richness was (Adorno et al., 2021). Even as we encourage researchers to continue exploring functional diversity, we see great benefit to further expanding how we think about biodiversity responses to landscape configuration. The field of macroimmunology (Becker et al., 2020) offers rich opportunities to enhance our understanding of how remnant populations and communities respond to human influence at landscape scales. In a similar vein, we imagine the "omics" revolution applied spatially to understand, for example, how gene expression for particular traits varies along gradients of succession, habitat amount, or forest quality. Embracing these new response variables can only enhance our understanding of biodiversity persistence in the Anthropocene.

**FIGURE 1**  Treemap comparing taxonomic representation in 112 landscape studies from Biotropica (a) and 87678 species on the International Union for the Conservation of Nature’s Red List of Threatened Species (b). In each panel, polygon size is proportional to the number of observations in each category.
The field of landscape ecology is predicated on the fact that many properties measured at a point are influenced by processes occurring in a landscape surrounding that point (Driscoll et al., 2013). Of course, the distance over which that influence is felt (the scale of effect, Jackson & Fahrig, 2012) varies with many factors, including the response variable, species identity, and conditions in the landscape itself. Such context dependency makes a priori determination of a single spatial scale for landscape analysis difficult and potentially misleading, especially when working with biotic communities comprised of many species with their own, unique scale of effect. Therefore, researchers often determine the scale of effect empirically, by evaluating responses in multiple landscapes defined by concentric circles of increasing area centered on a sampling point. Biodiversity responses to predictors measured in each nested landscape can be evaluated using the appropriate statistical model, and ranked using Akaike’s Information Criterion (or similar) to select the landscape size at which the relationship between predictor and response is greatest. The use of concentric landscape buffers is exemplified by Ghosh and Basu (2020), who found that the scale of effect in a study of Indian herpetofauna depended on taxon, response variable, and landscape predictor. Other highlighted studies took a similar approach (e.g. Almeida-Gomes et al., 2016; Coutinho et al., 2020). We encourage researchers doing such work to include results from different landscape sizes as supplemental material, with the idea that future researchers can test for predictable patterns in the scale of effect by taxon and geography that could ultimately lead to a mechanistic framework for a priori determination of the scale of effect for landscape-scale studies.

One of the key theoretical developments in the field of landscape ecology in the last decade is the habitat amount hypothesis (Fahrig, 2013). The habitat amount hypothesis predicts that, when measured at the appropriate scale of effect, total habitat area in a landscape is as good or a better predictor of biodiversity responses than properties of the habitat patches where samples are collected. Perhaps because tropical ecosystems are generally (although not universally) home to many disturbance-averse species (Bettis et al., 2019) with relatively specialized habitat requirements (Pfeifer et al., 2017), the tropics have been a rich source of studies evaluating empirical support for the habitat amount hypothesis. Six of the studies in the special virtual issue referenced the habitat amount hypothesis, while others evaluated the importance of total habitat cover in a landscape (e.g. Borges et al., 2016; Quiroga et al., 2021). In one noteworthy study, Rabelo et al. (2019) showed that species composition of mammals on islands in the central Amazon basin was more related to habitat amount (forest cover) within 3 km of sampling points than the size of the individual islands in which surveys were conducted. Although Lion et al. (2016) did not directly measure habitat amount in their study of reptiles in the Atlantic Forest, they found a strong negative effect of patch area on species richness, which they attribute to the possibility of release from predation on small habitat patches. Both studies are part of a larger recent trend highlighting the importance of small habitat areas for conservation (Wintle et al., 2019). In a world where most of the world’s forest occur within 1 km of an edge (Haddad et al., 2015), and small patches are disproportionately likely to be lost (Hansen et al., 2020), protecting small patches helps maintain remaining habitat in a landscape. Further investigation on how best to enhance the conservation value of small habitats is essential to safeguard species in increasingly human-dominated landscapes.

Half of the selected studies framed their research questions in terms of habitat fragmentation (Borges et al., 2016; Hadley et al., 2018; Iop et al., 2020; Lion et al., 2016; Olivier & Aarde, 2017; Regolin et al., 2020; Silva & Rossa-Feres, 2017). The magnitude and direction of fragmentation effects on biodiversity have been the subject of recent, renewed debate (Fahrig et al., 2019; Fletcher et al., 2018). In part, disagreements about habitat fragmentation are related to whether the term is used to define a landscape-level spatial pattern in which habitat occurs in multiple, isolated patches, or a more general shorthand for a variety of disturbances that influence species distributions within or among habitat patches in human-modified landscapes. Furthermore, because fragmentation and habitat amount are often correlated, it is important to separate their effects as much as possible, either experimentally or statistically (Smith et al., 2009). Indeed, the term "fragmentation per se" is used to refer to an effect of fragmentation independent of (or accounting for) the amount of habitat in a landscape. In the interest of clarifying the magnitude and direction of fragmentation effects, we encourage researchers to (1) reserve use of the term habitat fragmentation to refer to the landscape spatial pattern, and identify other types of disturbances that may occur in fragmented landscapes (e.g., hunting, roadkill, proximity to population centers) explicitly, and (2) infer an effect of fragmentation only when the units of observation in an analysis are landscapes, and after accounting for the influence of habitat amount in each landscape. An important area of future research.
for which the tropics provide rich opportunity is whether negative effects observed at the patch scale (e.g., negative species-area relationships, or declining abundance in proximity to habitat edge, Schneider-Manoury et al., 2016) are associated with negative fragmentation effects at the landscape scale, or whether compensatory mechanisms such as competitive release or refuge from disturbance can maintain populations and species in landscapes even as they decline or are lost from some individual patches (Fahrig et al., 2019). Indeed, even for research themes as well-studied as edge or matrix effects (Driscoll et al., 2013; Ries et al., 2004), new insights await from the judicious application of a landscape perspective. We look forward to many years more of insightful and impactful landscape ecology research in Biotropica.

**DATA AVAILABILITY STATEMENT**

The data that support the findings of this study are openly available in the Dryad at https://doi.org/10.5061/dryad.hqbxkhj4

**ORCID**

James I. Watling https://orcid.org/0000-0003-4445-4808

**REFERENCES**

Adorno, B. F. C. B., Barros, F. M., Ribeiro, M. C., da Silva, V. X., & Hasui, E. (2021). Landscape heterogeneity shapes bird phylogenetic responses at forest-matrix interfaces in Atlantic Forest, Brazil. *Biotropica*, 53, 409–421. https://doi.org/10.1111/btp.12881

Almeida-Gomes, M., Rocha, C. F. D., & Vieira, M. V. (2016). Local and landscape factors driving the structure of tropical anuran communities: Do ephemeral ponds have a nested pattern? *Biotropica*, 48, 365–372. https://doi.org/10.1111/btp.12285

Bardgett, R. D., Bullock, J. M., Lavelle, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan, G., Fry, E. L., Johnson, D., Lavallee, J. M., Le Provost, G., Luo, S., Png, K., Sankaran, M., Hou, X., Zhou, H., Ma, L., Ren, W., ... Shi, H. (2021). Combatting global grassland degradation. *Nature Reviews Earth & Environment*, 2, 720–735. https://doi.org/10.1038/s43017-021-00207-2

Baranosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., Getz, W. M., Harte, J., Hastings, A., Marquet, P. A., Martínez, N. D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J. W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., ... Smith, A. B. (2012). Approaching a state shift in Earth's biosphere. *Nature*, 486, 52–58. https://doi.org/10.1038/nature11018

Becker, D. J., Albery, G. F., Kessler, M. K., Lunn, T. J., Falvo, C. A., Czirják, G. A., Martin, L. B., & Plowright, R. K. (2020). Macroimmunology: the drivers and consequences of spatial patterns in wildlife immune defense. *Journal of Animal Ecology*, 89, 972–995.

Bets, M. G., Wolf, C., Pfeiffer, M., Banks-Leite, C., Arroyo-Rodriguez, V., Ribeiro, D. B., Barlow, J., Eigenbrod, F., Faria, D., Fletcher, R. J. Jr, Hadley, A. S., Hawes, J. E., Holt, R. D., Klingberg, B., Kormann, U., Lens, L., Levi, T., Medina-Rangel, G. F., Mezger, D., ... Ewers, R. M. (2019). Extinction filters mediate the global effects of fragmentation on animals. *Science*, 366, 1236–1239.

Borges, S. H., Cornelius, C., Moreira, M., Ribas, C. C., Conh-Haft, M., Capuruchu, J. M., Vargas, C., & Almeida, R. (2016). Bird communities in Amazonian white-sand vegetation patches: Effects of landscape configuration and biogeographic context. *Biotropica*, 48, 121–131.

Cadotte, M. W., Carssadden, K., & Mirochnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Chamberlain, S. (2020). rredlist: ‘IUCN’ Red List Client. Retrieved from: https://CRAN.R-project.org/package=rredlist

 Coutinho, J. G. E., Angel-Coca, C., Boscolo, D., & Viana, B. F. (2020). Heterogeneous agroecosystems support high diversity and abundance of trap-nesting bees and wasps among tropical crops. *Biotropica*, 52, 991–1004. https://doi.org/10.1111/btp.12809

da Silva, F. R., & Rossa-Feres, D. D. (2017). Fragmentation gradients differentially affect the species range distributions of four taxonomic groups in semi-deciduous Atlantic forest. *Biotropica*, 49, 283–292. https://doi.org/10.1111/btp.12362

Driscoll, D. A., Banks, S. C., Barton, P. S., Lindenmayer, D. B., & Smith, A. L. (2013). Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology & Evolution*, 28, 605–613. https://doi.org/10.1016/j.tree.2013.06.010

Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, 40, 1649–1663. https://doi.org/10.1111/jbi.12130

Fahrig, L., Arroyo-Rodriguez, V., Bennett, J. R., Boucher-Lalonde, V., Cazetta, E., Currie, D. J., Eigenbrod, F., Ford, A. T., Harrison, S. P., Jaeger, J. A. G., Koper, N., Martin, A. E., Martin, J.-L., Metzger, J. P., Morrison, P., Rhodes, J. R., Saunders, D. A., Simberloff, D., Smith, A. C., ... Watling, J. I. (2019). Is habitat fragmentation bad for biodiversity? *Biological Conservation*, 230, 179–186. https://doi.org/10.1016/j.biocon.2018.07.022

Fletcher, R. J. Jr, Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., Holt, R. D., Gonzalez, A., Pardini, R., Damschen, E. I., Melo, F. P. L., Ries, L., Prevedello, J. A., Tscharntke, T., Laurance, W. F., Lovejoy, T., & Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity? *Biological Conservation*, 226, 9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Ghosh, D., & Basu, P. (2020). Factors influencing herpetofauna abundance and diversity in a tropical agricultural landscape mosaic. *Biotropica*, 52, 927–937. https://doi.org/10.1111/btp.12799

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townsend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1, e1500052. https://doi.org/10.1126/sciadv.1500052

Hadley, A. S., Frey, S. J. K., Robinson, W. D., & Betts, M. G. (2018). Forest fragmentation and loss reduce richness, availability, and specialization in tropical hummingbird communities. *Biotropica*, 50, 84–83. https://doi.org/10.1111/btp.12487

Hansen, M. C., Wang, L., Song, X. P., Tyukavina, A., Turubanova, S., Potapov, P. V., & Stehman, S. V. (2020). The fate of tropical forest fragments. *Science Advances*, 6, eaax8574. https://doi.org/10.1126/sciadv.aax8574

Hubbell, S. P. (2001). The unified neutral theory of biodiversity and biogeography. Princeton University Press.

Iop, S., dos Santos, T. G., Cechin, S. Z., Velez-Martín, E., Pillar, V. D., & Prado, P. I. (2020). The interplay between local and landscape scales on the density of pond-dwelling anurans in subtropical grasslands. *Biotropica*, 52, 913–926. https://doi.org/10.1111/btp.12794

Jackson, H. B., & Fahrig, L. (2012). What size is a biologically relevant landscape? *Landscape Ecology*, 27, 929–941. https://doi.org/10.1007/s10109-012-9757-9

Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., Gascon, C., Bierregaard, R. O., Laurance, S. G., Ricketts, T. H., & Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments. *Biotropica*, 34, 265–275. https://doi.org/10.1111/btp.12277
Regolin, A. L., Ribeiro, M. C., Martello, F., Melo, G. L., Sponchiado, J., Campanha, L. F. D., Sugai, L. S. M., Silva, T. S. F., & Caceres, N. C. (2020). Spatial heterogeneity and habitat configuration overcome habitat composition influences on alpha and beta mammal diversity. *Biotropica*, 52, 970–982. https://doi.org/10.1111/btp.12800

Ries, L., Fletcher, R. J. Jr, Battin, J., & Sisk, T. D. (2004). Ecological responses to habitat edges: mechanisms, models, and variability explained.

Annual Review of Ecology, Evolution, and Systematics, 35, 491–522. https://doi.org/10.1146/annurev.ecolsys.35.112202.130148

Schneider-Manoury, L., Lefebvre, V., Ewers, R. M., Medina-Rangel, G. F., Peres, C. A., Somarriba, E., Urbina-Cardona, N., & Pfeifer, M. (2016). Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forests. *Biological Conservation*, 200, 207–215.

Simberloff, D. S., & Wilson, E. O. (1969). Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, 50, 278–296. https://doi.org/10.2307/1934856

Smith, A. C., Koper, N., Francis, C. M., & Fahrig, L. (2009). Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. *Landscape Ecology*, 24, 1271–1285. https://doi.org/10.1007/s10101-009-9383-3

Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M. S., Rödig, E., Wiegand, T., & Huth, A. (2018). Global patterns of tropical forest fragmentation. *Nature*, 554, 519–522. https://doi.org/10.1038/nature25508

Weisse, M., & Goldman, E. (2021). *Primary rainforest destruction increased 12% from 2019 to 2020*. World Resources Institute. Retrieved from: https://research.wri.org/gfr/forest-pulse

Wintle, B. A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Molianen, A., Gordon, A., Lentini, P. E., Cadenhead, N. C. R., & Bekassy, S. A. (2019). Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the National Academy of Sciences USA*, 116, 909–914. https://doi.org/10.1073/pnas.1813051115

**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of the article at the publisher’s website.

**How to cite this article:** Watling, J. I., & Urbina-Cardona, J. N. (2022). Virtual special issue: Insights from a landscape ecological perspective for tropical biology and conservation. *Biotropica*, 54, 546–550. https://doi.org/10.1111/btp.13092