

VIEWPOINT

Principles for area-based biodiversity conservation

Federico Riva¹  | Nick Haddad²  | Lenore Fahrig³  | Cristina Banks-Leite⁴ ¹Institute for Environmental Studies, Vrije Universiteit Amsterdam, Amsterdam, the Netherlands²Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan, USA³Geomatic and Landscape Ecology Research Laboratory, Carleton University, Ottawa, Ontario, Canada⁴Department of Life Sciences, Imperial College London, Ascot, UK

Correspondence

Federico Riva, Institute for Environmental Studies, Vrije Universiteit Amsterdam, 1081 HV Amsterdam, the Netherlands.
Email: f.riva@vu.nl

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Abstract

Recent international agreements have strengthened and expanded commitments to protect and restore native habitats for biodiversity protection (“area-based biodiversity conservation”). Nevertheless, biodiversity conservation is hindered because how such commitments should be implemented has been strongly debated, which can lead to suboptimal habitat protection decisions. We argue that, despite the debates, there are three essential principles for area-based biodiversity conservation. These principles are related to habitat geographic coverage, amount, and connectivity. They emerge from evidence that, while large areas of nature are important and must be protected, conservation or restoration of multiple small habitat patches is also critical for global conservation, particularly in regions with high land use. We contend that the many area-based conservation initiatives expected in the coming decades should follow the principles we identify, regardless of ongoing debates. Considering the importance of biodiversity for maintenance of ecosystem services, we suggest that this would bring widespread societal benefits.

KEYWORDS

connectivity, COP 15, Global Biodiversity Framework, habitat fragmentation, habitat loss, land sharing, land sparing, nature reserves, protected areas

Identifying adequate policies to regulate land use is crucial following the 2022 United Nations Biodiversity Conference (COP 15) because habitat loss and degradation contribute most to ongoing biodiversity loss (Fahrig, 2017; Haddad et al., 2015). At the same time, such policies are especially delicate because the complexity of species responses to habitat change has spurred a heated debate regarding the importance and influence of different strategies for habitat protection and restoration (Bateman & Balmford, 2023; Fahrig et al., 2019; Fletcher Jr et al., 2018), that is “area-based biodiversity conservation” (Maxwell et al., 2020). Unanswered questions include how often does habitat fragmentation exacerbate or interact with the effects of habitat loss on biodiversity? And when should land sparing or land sharing be the preferred strategy?

Because different contexts can produce different answers to such questions, deciding which habitat is most valuable based on its location and amount has proven difficult. Managers and policymakers might therefore

believe that scientists cannot agree on how biodiversity should be preserved in the face of widespread and increasing global land use. We contend that ongoing debates should not distract from shared principles based on decades of research in biodiversity conservation. To identify and articulate such principles, we decided to collaborate as conservation scientists with a history of contrasting views (Fahrig et al., 2019; Fletcher Jr et al., 2018). The three resulting principles relate to the geographic and ecological coverage, total surface, and connectivity of native habitat areas (or “patches”) (Figure 1):

1. To protect Earth's biodiversity, we must protect and restore native habitats in all threatened ecoregions (Figure 1[1]). This will safeguard their unique contributions to the Earth's biological heritage (Olson et al., 2001). Broadly distributed cover of native habitats across all ecosystem types is a prerequisite for any effort in global biodiversity conservation.

Federico Riva, Nick Haddad, Lenore Fahrig, Cristina Banks-Leite contributed equally to this study.

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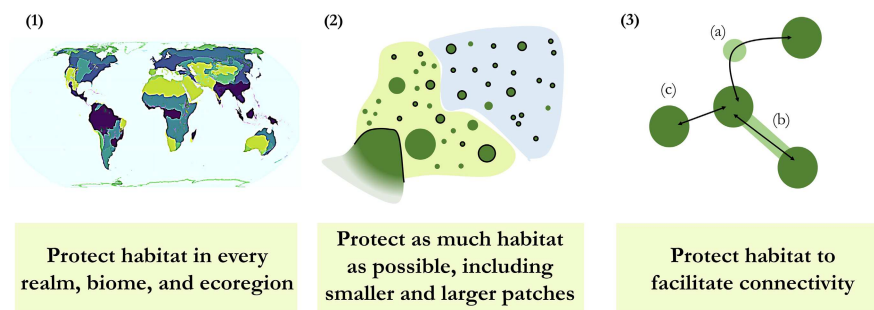


FIGURE 1 Three shared principles for area-based biodiversity conservation. (1) To protect Earth's biodiversity, we must protect and restore native habitat in all ecoregions. For illustration purposes, we show Earth's 14 biomes (Olson et al., 2001), each of which encompasses multiple ecoregions. (2) Protecting as much native habitat as possible is our best way to safeguard biodiversity, and requires protecting both smaller and larger patches. For instance, while in some tropical ecoregions forest may exist in large, continuous patches, other ecoregions have been reduced to highly fragmented habitat. Green circles represent habitat patches separated by anthropogenic land use in two adjacent ecoregions (lime and blue background); black outlines represent habitat patches under protection; the fading, green area on the bottom-left corner of the inset represents a large expanse of wilderness. (3) Habitat patches must be functionally connected. Habitat connectivity can increase with stepping stone habitat (a), corridors (b), or by reducing distances between patches (i.e. increasing patch density in the landscape) (c).

2. Protecting as much native habitat as possible is key to safeguard biodiversity (Figure 1[2]). This requires protecting both the remaining large native ecosystems and the many small native patches in working landscapes. Considering the costs of habitat restoration, effort should be focused on preserving remnant native habitats and restoring habitat in regions that have been already extensively transformed by humans.
3. Habitat patches must be functionally connected (Figure 1[3]). Connectivity ensures access to sufficient and complementary resources when remnant habitat patches are too small for a single patch to sustain a species. Connectivity is also fundamental when patches are larger, as migration between them decreases population extinction risk, facilitates re-colonization, and may allow species to shift their ranges in response to climate change.

These principles are not exhaustive. For instance, they do not cover issues of habitat quality (Betts et al., 2022) or overexploitation within protected areas (Plumptre et al., 2014), nor the biology of the species or ecosystems of interest. When detailed information is available about threats to a particular system, the principles might be superseded by other actions. Still, because biodiversity is poorly understood across most of the Earth (Hortal et al., 2015; Hughes et al., 2021), the design of ad hoc actions in most ecosystems and for most species is not possible. Given the dominant role of habitat change in the current biodiversity crisis and unresolved biodiversity knowledge shortfalls, we argue that the application of effective, “coarse-filter” (Schwartz, 1999) general principles will be very beneficial. Therefore, the three simple principles we identify should be at the core of conservation action in response to the recent Global Biodiversity Framework, complementing the broader Targets and Goals identified in the Kunming-Montreal meeting of the Conference of the Parties (COP 15).

PUTTING DISAGREEMENT INTO CONTEXT

Highlighting these three principles is important because ecologists and conservation biologists have long discussed how best to manage native habitat to sustain biodiversity. Earlier discussions revolved around SLOSS (Diamond, 1975; Simberloff & Abele, 1976)—should conservation prioritize “a Single Large Or Several Small” habitat patches? Through time, SLOSS matured into a debate around the effects of habitat fragmentation relative to effects of habitat amount. More recently, the debate has been on whether habitat fragmentation has positive or negative effects on biodiversity (Fahrig et al., 2019; Fletcher Jr et al., 2018). The problem is, while disagreement is healthy in an academic setting, it jeopardizes pragmatic solutions for management and policy-making, even when those solutions exist.

Still, the extensive body of literature addressing these topics has not been sufficient to reach consensus on them. Some scientists have concluded that landscapes containing many small patches of native habitat can sustain rare and/or habitat specialist species (Fahrig et al., 2019; Shafer, 1995), whereas others have suggested that reduced patch sizes inevitably decrease biodiversity even if the total amount of habitat remains unchanged (Bateman & Balmford, 2023; Fletcher Jr et al., 2018). Underlying different perspectives are several factors, including differences among ecosystems (Banks-Leite et al., 2022; Betts et al., 2019) or intraspecific variation (Bellotto-Trigo et al., 2023), or theoretical considerations of spatial scaling and stochasticity (Fahrig, 2024; Riva & Fahrig, 2023a). As a result, authors even differ in what they consider relevant habitat, from “at least 100-1000 ha” (Balmford, 2021) to “smaller than 1 ha” (Riva & Fahrig, 2023b).

The existence of different schools of thought might cast doubt on the generality of the principles we propose,

yet this is a misconception. The principles we outline (Figure 1) instead help to put disagreements into perspective. For instance, there is no debate about the need to conserve habitat: the effects of increasing native habitat on biodiversity are overwhelmingly positive. It is true that large areas of nature are important and must be protected from threats (Bateman & Balmford, 2023; Haddad et al., 2015), as much as it is true that ensuring the conservation or restoration of multiple small habitat patches is critical for global conservation, particularly in human-dominated landscapes (Arroyo-Rodriguez et al., 2020; Riva & Fahrig, 2022). These are neither incompatible nor competing strategies; they are complementary approaches to protect biodiversity across all regions. Disagreement can be unintentionally translated into a false dichotomy between the protections of large or small patches, a mistake that must be avoided at all costs for the sake of biodiversity conservation because both are important.

The risks of ignoring these principles are clear. Habitat existing as small patches is often deemed less valuable than large swaths of habitat in less modified regions, which is inadvertently leading to widespread cumulative loss of habitat from millions of small patches across the globe (Riva et al., 2022). For instance, smaller (<1000 ha) forest patches are more likely to suffer a given amount of habitat loss than larger (>10,000 ha) patches (Riva et al., 2022). While the recent agreement of the parties involved in COP 15 is agnostic on patch area, policies that protect only patches larger than a minimum size are widespread (Riva & Fahrig, 2023b). Such policies hinder conservation because they fail to protect biodiversity in highly modified regions where protection is clearly needed. Similarly, focusing habitat protection solely in biodiversity-rich regions and/or large habitat patches risks neglecting extensive areas of the planet with unique flora and fauna persisting in many small habitat patches surrounded by anthropogenic land uses (Haddad et al., 2015). Finally, failing to maintain small habitat patches reduces landscape connectivity among larger patches due to the loss of “stepping stones” (Terborgh, 1974), where small patches distributed through a landscape can facilitate movement between larger patches.

At the same time, very large tracts of native habitat are now limited to fewer regions (Haddad et al., 2015), and their conversion to human land uses is placing several species—many of which have not yet been identified by science (Hortal et al., 2015)—at risk. For instance, continued deforestation in the Amazon has been predicted to trigger an ecosystem state-shift. This biome persists thanks to feedback between vegetation and climate (Albert et al., 2023). Losing 20% of the Amazonian forest could trigger a shift from forest into savanna, a death-knell for the forest-dependent species of the Amazon (Albert et al., 2023). Similarly, while the few remaining extensive grasslands worldwide sequester large amounts of carbon and host unique species, they

remain poorly protected and continue to shrink (Scholtz & Twidwell, 2022).

PROTECTING BIODIVERSITY WITH PEOPLE AND FOR PEOPLE

While the principles we propose are essential to sustain biodiversity, conservation is destined to fail unless the rights and needs of people also enter the equation. This implies that the three principles, even if best for biodiversity, cannot always be applied. Trade-offs with other priorities in landscape management must also be considered. For instance, the provision of food, water, shelter, and energy to humans often implies the sacrifice of large areas of native habitat. How can we sustain biodiversity, while at the same time supporting the needs of an increasing global human population?

Careful planning that does not affect the total area reserved to nature can optimize conservation investments. For example, natural habitats can be maintained within agricultural landscapes to sustain several crucial services (e.g. pollination, pest control, and nutrient retention). In the Midwestern United States, removing from crop production sub-field areas that are consistently under-yielding makes conservation possible across millions of hectares (Basso & Antle, 2020). Avoiding growing food in such locations can reduce the total surface of land needed to feed humanity. As a further example, restoration of small (≤ 0.16 ha) forests in oil palm plantations can enhance biodiversity and multiple ecosystem services without compromising yield (Zemp et al., 2023). Thus, it is possible to reduce under-productive areas and increase land for nature, while also maintaining the services that people rely on.

Because area-based conservation actions are intertwined with socio-political dynamics and ethics (Richardson et al., 2023), they require integrating biodiversity policy with other human goals, for example the United Nations sustainable development goals of “Zero hunger” and “Clean water and sanitation.” In some regions, this can result in situations where actions to sustain biodiversity are not always desirable for people. For instance, human–wildlife conflicts are more likely in human-occupied regions containing significant wilderness areas. This complicates global conservation, especially in the global South where regulations on land use have large impacts on the ability of many people to gain a living.

Conservation action must therefore be implemented equitably, not only for ethical reasons, but also because a loss of social legitimacy often causes nature reserves to be disregarded. Consideration of aspects beyond—but dependent on—biodiversity must therefore be central in the dialogue with stakeholders and decision-makers around how to implement area-based conservation efforts, including sources of uncertainty. Most local- and landscape-scale conservation decisions are taken based on relatively limited information (Hortal et al., 2015;

Hughes et al., 2021) and thus require careful consideration and involvement of local experts and other people. Nevertheless, there is no uncertainty about the need to apply the three principles we outlined, only uncertainty about how to do so in a given context. While the dialogue requires weighing different conservation, ethical, social, and economic priorities, we stress that the principles we identify here must be central to the process of weighing these different priorities. This is because failing to halt biodiversity loss entails a risk of societal collapse as most ecosystem services supporting human societies would disappear (Tilman et al., 2014).

CODA

National and international policies have embraced the principle of conserving 30% of land and water by 2030. To protect biodiversity, this so-called “30×30” must be achieved in each ecoregion, through conservation of the few remaining large habitat areas, combined with protection and restoration of many small habitat patches in regions most affected by human activities. In fact, in highly human-modified regions, reaching area targets will be possible only through a combination of protection of small patches and habitat restoration. In such regions, conservation and restoration of many small areas is essential to get to 30×30, and such areas may represent the greatest net gains for area-based biodiversity conservation going forward.

More broadly, realizing ambitious area-based plans will be possible only if we promptly coordinate and recognize common ground among researchers working on biodiversity conservation (Eckert et al., 2023). Ongoing disagreements such as the fragmentation debate are secondary to the general principles we outline in this letter, and we are confident that they will be resolved as data accumulate and science progresses. In the meantime, to address a global biodiversity emergency, implementation of shared principles will bolster our chances of preserving the Earth's biodiversity heritage.

AUTHOR CONTRIBUTIONS

FR and CB-L wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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No data collected, or analysis performed.

ORCID

Federico Riva  <https://orcid.org/0000-0002-1724-4293>
 Nick Haddad  <https://orcid.org/0000-0002-1591-9322>
 Lenore Fahrig  <https://orcid.org/0000-0002-3841-0342>
 Cristina Banks-Leite  <https://orcid.org/0000-0002-0091-2857>

REFERENCES

- Albert, J.S., Carnaval, A.C., Flantua, S.G.A., Lohmann, L.G., Ribas, C.C., Riff, D. et al. (2023) Human impacts outpace natural processes in the Amazon. *Science*, 379, eabo5003.
- Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M. et al. (2020) Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecology Letters*, 23, 1404–1420.
- Balmford, A. (2021) Concentrating vs. spreading our footprint: how to meet humanity's needs at least cost to nature. *Journal of Zoology* (1987), 315, 79–109.
- Banks-Leite, C., Betts, M.G., Ewers, R.M., Orme, C.D.L. & Pigot, A.L. (2022) The macroecology of landscape ecology. *Trends in Ecology & Evolution*, 37(6), 480–487.
- Basso, B. & Antle, J. (2020) Digital agriculture to design sustainable agricultural systems. *Nature Sustainability*, 3, 254–256.
- Bateman, I. & Balmford, A. (2023) Current conservation policies risk accelerating biodiversity loss. *Nature*, 618, 671–674.
- Bellotto-Trigo, F.C., Uezu, A., Hatfield, J.H., Morante-Filho, J.C., dos Anjos, L., Develey, P.F. et al. (2023) Intraspecific variation in sensitivity to habitat fragmentation is influenced by forest cover and distance to the range edge. *Biological Conservation*, 284, 110167.
- Betts, M.G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D.B. et al. (2019) Extinction filters mediate the global effects of habitat fragmentation on animals. *Science*, 366, 1236–1239.
- Betts, M.G., Yang, Z., Hadley, A.S., Smith, A.C., Rousseau, J.S., Northrup, J.M. et al. (2022) Forest degradation drives widespread avian habitat and population declines. *Nature Ecology & Evolution*, 6, 709–719.
- Diamond, J.M. (1975) The Island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, 7, 129–146.
- Eckert, I., Brown, A., Caron, D., Riva, F. & Pollock, L.J. (2023) 30×30 biodiversity gains rely on national coordination. *Nature Communications*, 14, 7113.
- Fahrig, L. (2017) Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, 48, 1–23.
- Fahrig, L. (2024) Patch-scale edge effects do not indicate landscape-scale fragmentation effects. *Conservation Letters*, 17(1), e12992.
- Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J. et al. (2019) Is habitat fragmentation bad for biodiversity? *Biological Conservation*, 230, 179–186.
- Fletcher, R.J., Jr., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J. et al. (2018) Is habitat fragmentation good for biodiversity? *Biological Conservation*, 226, 9–15.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D. et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1, e1500052.
- Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015) Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 46, 523–549.
- Hughes, A.C., Orr, M.C., Ma, K., Costello, M.J., Waller, J., Provoost, P. et al. (2021) Sampling biases shape our view of the natural world. *Ecography*, 44(9), 1259–1269.

- Maxwell, S.L., Cazalis, V., Dudley, N., Hoffmann, N., Rodrigues, A.S.L., Stolton, S. et al. (2020) Area-based conservation in the twenty-first century. *Nature*, 586, 217–227.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C. et al. (2001) Terrestrial ecoregions of the world: a new map of life on earth. *Bioscience*, 51, 933.
- Plumptre, A.J., Fuller, R.A., Rwetsiba, A., Wanyama, F., Kujirakwinja, D., Driciru, M. et al. (2014) Efficiently targeting resources to deter illegal activities in protected areas. *Journal of Applied Ecology*, 51, 714–725.
- Richardson, K., Steffen, W., Lucht, W., Bendtsen, J., Cornell, S.E., Donges, J.F. et al. (2023) Earth beyond six of nine planetary boundaries. *Science Advances*, 9, eadh2458.
- Riva, F. & Fahrig, L. (2022) The disproportionately high value of small patches for biodiversity conservation. *Conservation Letters*, 15(3), e12881.
- Riva, F. & Fahrig, L. (2023a) Landscape-scale habitat fragmentation is positively related to biodiversity, despite patch-scale ecosystem decay. *Ecology Letters*, 26, 268–277.
- Riva, F. & Fahrig, L. (2023b) Obstruction of biodiversity conservation by minimum patch size criteria. *Conservation Biology*, 37(5), e14092.
- Riva, F., Martin, C.J., Millard, K. & Fahrig, L. (2022) Loss of the world's smallest forests. *Global Change Biology*, 28, 7164–7166.
- Scholtz, R. & Twidwell, D. (2022) The last continuous grasslands on Earth: identification and conservation importance. *Conservation Science and Practice*, 4(3), e26.
- Schwartz, M.W. (1999) Choosing the appropriate scale of reserves for conservation. *Annual Review of Ecology and Systematics*, 30, 83–108.
- Shafer, C.L. (1995) Values and shortcomings of small reserves. *Bioscience*, 45, 80–88.
- Simberloff, D.S. & Abele, L.G. (1976) Island biogeography theory and conservation practice. *Science*, 191, 285–286.
- Terborgh, J. (1974) Preservation of natural diversity: the problem of extinction prone species. *Bioscience*, 24, 715–722.
- Tilman, D., Isbell, F. & Cowles, J.M. (2014) Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45, 471–493.
- Zemp, D.C., Guerrero-Ramirez, N., Brambach, F., Darras, K., Grass, I., Potapov, A. et al. (2023) Tree islands enhance biodiversity and functioning in oil palm landscapes. *Nature*, 618, 316–321.

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