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Opinion

Resurrecting habitat fragmentation as a process over time

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Habitat loss and fragmentation occur over time. Despite this truism, understanding the effects of habitat fragmentation has, in recent years, predominantly focused on interpreting snapshots of current landscape configuration, effectively focusing on spatial patterns rather than the process of change over time. This recent emphasis on current patterns is haunted by implicit assumptions regarding changes over time, thereby obstructing ecological understanding and the ability to provide clear and actionable guidance for conservation. We identify many issues that emerge from focusing solely on current landscape patterns and discuss the implications of shifting from the current paradigm to a time-focused, process-based paradigm for interpreting the effects of fragmentation, including its relevance for conservation policy and practice.

Highlights

Habitat fragmentation has long been argued to impact biodiversity, but recent research has challenged the extent and ways in which fragmentation effects may occur.

Space-for-time substitutions that compare snapshots of biodiversity across landscapes dominate current research. Consequently, understanding the effects of fragmentation as a process of the 'breaking apart' of habitat over time has been limited.

As biodiversity is often far from equilibrium with its environment, viewing fragmentation as a temporal process to understand biodiversity impacts is needed.

Recent advances in causal methods and growing longitudinal data streams provide new opportunities to refocus evaluations of the effects of the temporal processes of loss and fragmentation.

By refocusing on habitat fragmentation over time, guidance for conservation will become less contentious and more effective.

The evolution of the fragmentation concept

Habitat loss and fragmentation are considered key threats to biodiversity across the planet [1]. While the effects of habitat loss are clear, the role of habitat fragmentation has led to confusion and ongoing debate [2–5]. A large part of this confusion stems from how the fragmentation concept has evolved over time [6,7]. Some of the earliest uses of the term 'fragmentation' envisioned that it increased if the remaining habitat became more 'broken up' over time as habitat was destroyed. For instance, Curtis [8] showed in Green County, Wisconsin, USA, that between 1831 and 1950, as forest was cleared, the number of forest patches increased, average patch size declined, and more edge resulted. Thus, in this early work, fragmentation occurred to various degrees as habitat was lost over time [8,9].

How scientists envisioned habitat fragmentation changed substantially in the late 1990s and early 2000s. Pioneering work by Fahrig argued that fragmentation should be interpreted independent of habitat loss (Figure 1) [10,11]. This perspective coincided with a shift in the literature regarding how studies were conceived and implemented, in which the focus is now on using **space-for-time substitutions** (see Glossary) that compare snapshots of patterns across different landscapes, aiming to account for habitat amount when interpreting fragmentation. For instance, of the 25 most cited articles on habitat fragmentation over the past 5 years (2021–2025), all interpreted biodiversity response data as a single snapshot in time (see the Supplemental Information online). Yet substituting space-for-time means that rather than emphasizing habitat loss, the focus is on current habitat amount. Rather than emphasizing that fragmentation is a process of 'breaking apart' (a verb that implies change over time), the focus is on **landscape configuration** patterns or the patchiness of current landscapes. This new framing also led, in part, to a heated debate on the effects of habitat fragmentation [4,5,12–14]. As the pattern-based perspective has taken hold, we contend that the conception of habitat fragmentation as a dynamic process of 'breaking apart' through time has been lost.

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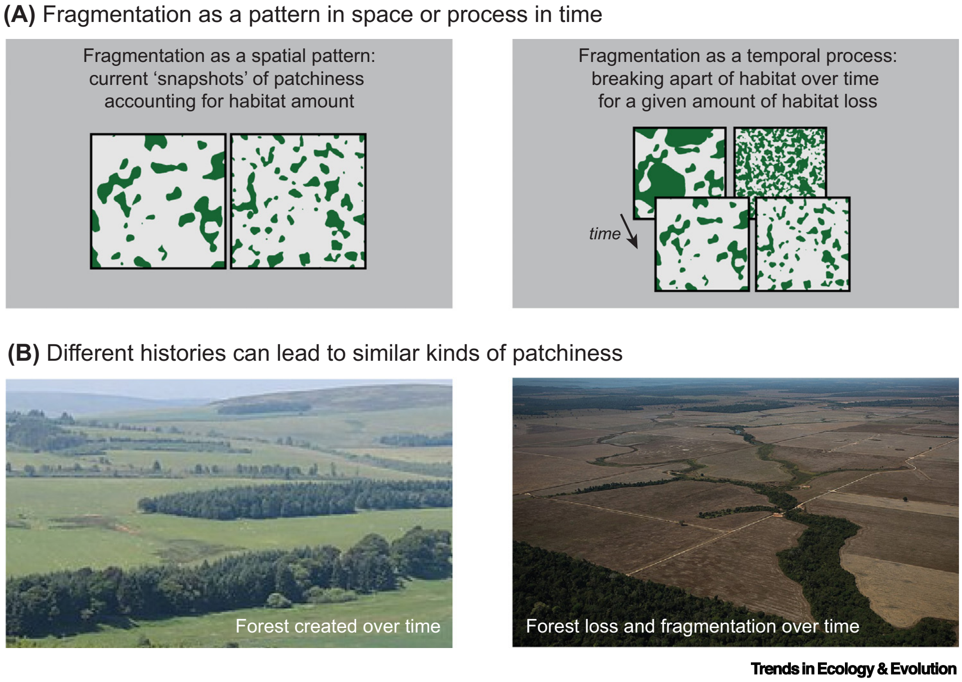

Figure 1. Habitat fragmentation in space and time. (A) In recent years, the dominant perspective on habitat fragmentation focuses on current spatial pattern, where fragmentation *per se* describes the configuration of habitat, for a given habitat amount. In contrast, earlier perspectives focused on habitat fragmentation as a temporal process of the breaking apart of habitat that occurs with habitat loss over time. (B) Current landscapes can have different histories, such as afforestation and restoration of woodland in the UK (lower left) generating current patchiness of woodlands in contrast to recent loss and fragmentation of tropical forests in the Amazon (lower right). Thus, current spatial patterns may be driven by fundamentally different processes and histories. Landscape photos from Wikimedia Commons.

To advance understanding of habitat fragmentation and its relevance to conservation, we offer a time-focused, process-based perspective for interpreting habitat fragmentation and discuss why this perspective is needed to reliably interpret the 'breaking apart' of habitat and its consequences. Doing so can unite opposing perspectives under a common theme of landscape change. We conclude by highlighting the implications of resurrecting a temporal perspective for understanding the effects of fragmentation on biodiversity.

Pattern in space, process in time

In recent years, it has often been argued that habitat fragmentation can only be understood as the pattern resulting from the breaking apart of habitat and which is 'independent' of habitat amount, what has been termed **habitat fragmentation *per se*** [2,4]. In this context, 'independent' is often used in a statistical sense, whereby habitat amount may serve as a covariate in the analysis of fragmentation effects to isolate the effects of the 'breaking apart' of habitat. This pattern-based definition is useful because it can potentially separate the effects of **landscape composition** (habitat amount) and configuration (e.g., number of patches and proportion of edge). Yet this separation has been criticized operationally, as statistical models may not adequately address the often collinear nature of loss and fragmentation [15,16], and conceptually, as fragmentation in general requires habitat loss to occur over time (and thus, how could it be 'independent' of loss?) [17]. Earlier descriptions of habitat fragmentation emphasized that it is a process by which habitat gets 'broken' into fragments over time [8,18,19]. However, this process-based definition has also been criticized because it can confound the effects of habitat loss with habitat fragmentation [10].

These criticisms can be reconciled by explicitly interpreting habitat fragmentation as the breaking apart of habitat with respect to a given amount of habitat loss over time. While habitat loss often generates fragmentation, by comparing different landscapes over time that vary in the degree of fragmentation for a given amount of loss, we may be able to better understand the role of the 'breaking apart' of habitat on biodiversity (Box 1). This interpretation blends both pattern- and process-based perspectives [18,19]. It not only acknowledges both the process of change over time but also explicitly aims to understand this configurational effect over time from that of pure compositional effects. It further helps to highlight why time is important for interpreting habitat fragmentation and its effects on biodiversity.

Why a temporal lens is essential

Acknowledging landscape history is needed to reliably interpret the 'breaking apart' of habitat

Focusing only on current landscape patterns to interpret fragmentation assumes similar landscape histories, disregards past changes, and implicitly treats biodiversity as being in equilibrium with the current landscape. Yet the current pattern of habitat can have arisen from a wide range of land trajectories, such that in the absence of information about prior landscapes, it can be challenging to interpret the breaking apart of habitats. Current landscape patterns can be composites of variation in both habitat loss and habitat gain, and changes that both fragment and defragment (or reconnect) habitats. To more reliably interpret fragmentation impacts, we suggest that knowledge of at least two key factors is needed: (i) an understanding of some historical baseline of habitat patterns and (ii) information on the pattern of change in habitat over time (e.g., direction, rate, and timing). Together, these factors can broadly capture the essential components of fragmentation over time, acknowledging that landscapes with the same current pattern may have very different histories (Figure 2).

Nearly all studies on habitat fragmentation that compare across current landscapes implicitly assume that the historical baseline is a largely contiguous landscape such that the landscapes all had the same starting point and are strictly comparable. Yet historical landscapes can have three fundamentally different baselines in relation to the focal habitat: (i) intact and contiguous habitat, (ii) naturally patchy habitat, or (iii) no focal habitat at all (Figure 2A). Classic examples of historical baselines of contiguous habitat come from tropical forests in the Amazon [28]. However, many landscapes have naturally patchy habitats [29], such as savannas, riparian forests, wetlands, and grasslands. Historical baselines can also include scenarios where there was little or no focal habitat, but succession, afforestation, and restoration have led to current landscapes of patchy habitat, giving the impression that fragmentation has occurred [30]. In general, interpreting historical baselines should also be explicit about the assumed time period since the baseline (e.g., 100 years), which is necessary context for interpreting rates of change [31].

The pattern of change in habitat over time is a second key factor for interpreting the history of fragmentation. There are two fundamental issues: directions and rates. In relation to baseline conditions, habitat area may be static (effectively no substantial change), habitat loss can occur, or habitat gain can occur, and both losses and gains can happen alongside changes in configuration. Rates of change over time can be roughly continuous or can be discrete, punctuated events (Figure 2B). The consequences of these changes compound over time, such that even if two landscapes have similar baseline and current states, the rates and timing of change may have varied. For interpreting the consequences of change, both instantaneous and cumulative rates over time may be informative [32]. For example, Ewers *et al.* [28] proposed a **terrageny** framework that focuses on cumulative historical fragmentation over time to better explain current biodiversity patterns.

Glossary

Alternative stable states: when an ecosystem can exist in multiple states that are nontransitory and therefore considered stable over time.

Colonization credit: the number of species committed to eventual colonization following a disturbance event or land clearing.

Ecological memory: the influence of past events on an ecosystem's current and future responses.

Extinction debt: the number of species committed to extinction but not yet extinct, following a disturbance event and/or land clearing.

Extinction filter: the loss of species over time, which can arise from habitat fragmentation.

Habitat fragmentation *per se*: the breaking apart of habitat, independent of the habitat amount.

Inverse priority effect: the effect of the order and timing of species losses on biodiversity.

Landscape configuration: the arrangement of elements, cover types, or habitats.

Landscape composition: the amount and number of elements, cover types, or habitats.

Landscape legacies: long-lasting effects of both natural processes and human activity on a landscape over time.

Relaxation time: the duration of the extinction debt or colonization credit, or how long it takes for full debts or credits to be realized.

Space-for-time substitution: using spatial variation as a proxy for temporal variation.

Stochasticity: variation that occurs with uncertainty.

Temporal lag: a delay in a process or pattern.

Terrageny: a record of how a landscape became fragmented through time, analogous to a phylogeny.

Transient dynamics: short-term changes in a system that do not remain over long periods of time.

Box 1. How to evaluate habitat fragmentation as a temporal process?

To operationalize fragmentation as a temporal process, three key elements are needed: (i) a time period being considered; (ii) a configurational metric quantifying ‘breaking apart’ (e.g., number of patches); and (iii) a compositional metric describing habitat amount. With these elements, the change in configuration relative to the change in habitat amount over time can identify the temporal process of fragmentation. Other metrics could also be considered [20], but the key is that this temporal process operates on a defined time scale and reflects configurational change over time.

We outline four approaches that form a continuum of study designs that vary in the data needed and their reliability to isolate loss and fragmentation effects (Figure I). The first two approaches only require information on organismal responses in present-day landscapes, whereas the others use data on responses across multiple time periods.

- (i) **Use information from historical land use as covariates to statistically or qualitatively account for past land use** [21]. Such approaches have been used to interpret potential extinction debts from past fragmentation [22].
- (ii) **Apply matching to select landscapes with similar historical baselines.** Statistical matching can improve attribution of interventions [23]. Matching landscapes that contain similar prior habitat composition and configuration to test effects of current patterns can improve causal inference for fragmentation effects. Current landscape patterns could also be matched to test for different effects of historical change in habitat.
- (iii) **Test effects from time series of biodiversity and land change.** Either standardized long-term monitoring or long-term studies of land change and biodiversity could be harnessed. In this case, covariates of temporal change of land use can be considered when interpreting fragmentation effects [24].
- (iv) **Implement difference-in-difference designs to contrast landscapes that vary in their land-use change over similar periods of time**. This design is similar to before–after control–impact (BACI) studies, where ‘impact’ reflects the relative degree of fragmentation (more/less) for a given amount of loss (Figure I). BACI designs are known to provide highly reliable evidence when replicated [25].

Experimental designs could also be improved to better interpret fragmentation as a temporal process. Most experiments to date either have designed landscapes that vary in habitat amount and configuration patterns [26] or have manipulated habitat loss and fragmentation once and simply monitored organismal responses after the perturbation [27]. A new generation of experiments that test the timing and pace of change will provide deeper insights into fragmentation as a temporal process.

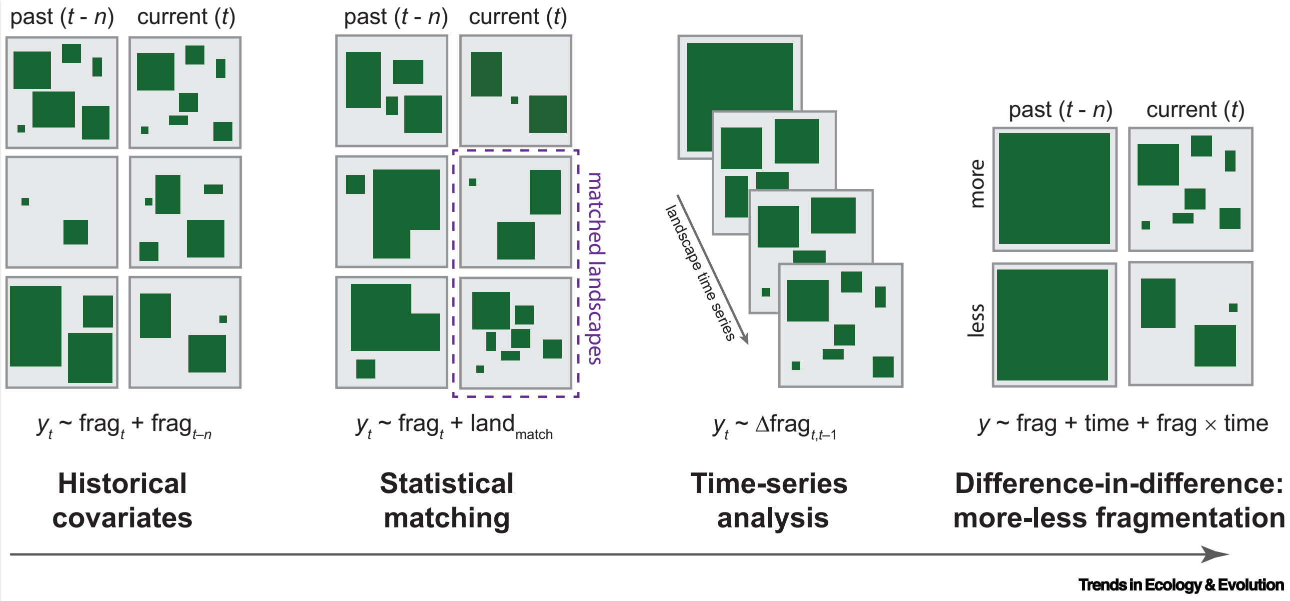

Figure I. Four approaches to use a temporal paradigm for evaluating habitat fragmentation in nonexperimental studies. The use of historical covariates uses historic land-use patterns (e.g., habitat amount, number of patches *n* years prior to current time *t*) as covariates when testing for current fragmentation effects. Statistical matching identifies landscapes with similar histories but different current conditions for sampling organismal responses in current landscapes. In the diagram, only matched landscapes are considered in the study. Time-series analysis explicitly quantifies change (e.g., Δ number of patches for a given change in habitat amount) to predict organism responses. Difference-in-difference approaches, akin to before–after control–impact designs, test for changes in organismal responses for different degrees of fragmentation over time. In this way, the effect size can be described as follows: $\left(y_{\text{more,after}} - y_{\text{more,before}}\right) - \left(y_{\text{less,after}} - y_{\text{less,before}}\right)$.

Biodiversity dynamics over time can muddle spatial comparisons used to infer fragmentation effects

Snapshot studies that use spatial comparisons alone can make reliable inferences about fragmentation challenging due to temporal processes that drive biodiversity patterns [33,34].

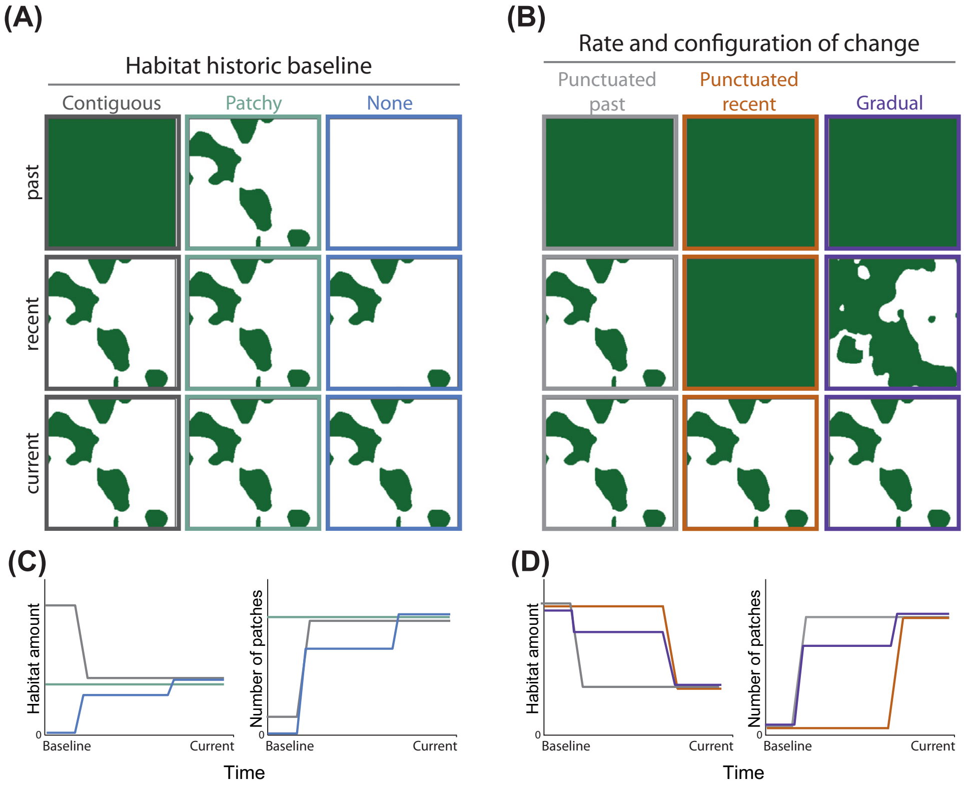

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Figure 2. Examples of how trajectories of habitat loss, gain, and fragmentation over time based on historic habitat conditions and the rate of change over time can all lead to the same current landscape structure. (A) Historic habitat baselines can vary from entirely contiguous habitat in the landscape, which is often implicitly assumed, to no habitat in the landscape (where habitat is created over time through succession, restoration, etc.). (B) Even with consistent historic conditions (shown here, historically contiguous habitat), the rate and configuration of habitat change can vary, including the timing and shape of change (e.g., punctuated or gradual) in habitat loss and fragmentation. (C) Changes in both habitat amount and number of patches over time based on variation in landscapes shown in (A). Note that the breaking apart of habitat cannot occur when there is no historic habitat, such that habitat is created and may be patchy based on the number of patches created but it has not been 'broken apart'. (D) Changes in both habitat amount and number of patches over time based on variation in the rate and shape of change in landscapes shown in (B). For both (C) and (D), line colors link to landscapes in (A) and (B) based on their boundary color.

Among the most important temporal factors that can alter conclusions about habitat fragmentation are stochasticity, transient dynamics, and long-term alternative stable states (Figure 3). These factors can operate directly from habitat loss and fragmentation or can arise irrespective of it.

Stochasticity causes short-term changes in biodiversity that are atypical of long-term averages. When contrasting landscapes with snapshots, stochastic factors may operate distinctly across landscapes and contribute to differences in responses used to assess fragmentation effects [35,36]. As such, stochastic factors may muddle conclusions about fragmentation effects (Figure 3A).

Transient dynamics and associated **temporal lags** can lead to inappropriate conclusions on fragmentation when landscapes differ in the timing and rates of landscape change [24] (Figure 3B), as comparisons implicitly assume that landscape biodiversity is at (quasi-) equilibrium [37]. For example, well-dispersing species can move to remaining habitat during habitat loss, leading to short-term crowding effects in remaining patches. In such cases, conclusions about

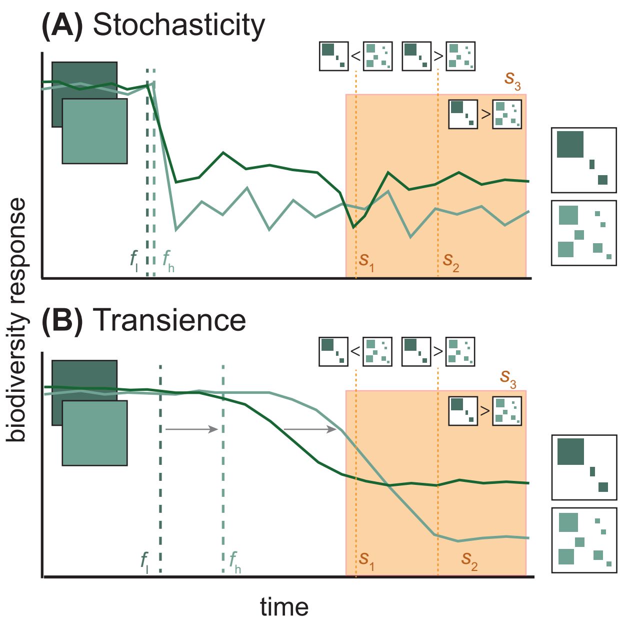

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Figure 3. Biodiversity dynamics can alter the interpretations of fragmentation effects when landscapes are sampled as snapshots in time. Shown are time series of biotic responses in two landscapes (dark/light green), which vary in fragmentation over time (dashed lines denote timing of relatively low, f_l, or high, f_h, fragmentation). Sampling for biodiversity is shown at different snapshot times (s_1 and s_2; orange dashed lines) and over a longer time interval (s_3, orange window), leading to different conclusions about the effects of fragmentation due to stochastic variation in responses and transient dynamics (shown at the top of sampling line/window). (A) Stochasticity leads to temporal variation in responses, such that current short-term snapshots may be unreliable. (B) Transience in dynamics from temporal lags arises from different timing of low or high fragmentation, leading to variation in delays of biotic responses (delay shown as a gray arrow), which can impact conclusions when comparing current landscapes.

fragmentation effects depend on when sampling occurs [38]. The concepts of **extinction debts** and **colonization credits** also reflect transience, where the extent of these effects is driven by both the timing of habitat loss and fragmentation and the **relaxation time** of species [22,39]. On longer timescales, **extinction filters** can shape current biodiversity in relation to historic fragmentation. Such filters might explain why tropical species may be more sensitive to fragmentation than temperate species [40]. The order of species loss through variation in debts and filters over time with fragmentation has the potential to have cascading effects on communities, which has been termed **inverse priority effects** [41].

More complex issues can arise when landscapes continually change, and ecosystems respond in tandem with them. The concept of **alternative stable states** suggests that landscapes with similar properties may nonetheless have different community compositions and ecosystem functions, depending on initial conditions [42]. As such, two landscapes may exist in different stable states because of historical differences alone [43].

In all these cases, past temporal dynamics create **ecological memory** that complicates the relationship between current landscape patterns and biodiversity [31,44]. For example, there is compelling evidence for temporal lags in long-term fragmentation experiments [45,46], which suggests that more information is needed than current landscape patterns alone to infer the loss and fragmentation effects on biodiversity. Emerging theory and statistical models provide a means to glean understanding from these **landscape legacies** [47,48] and to predict whether populations and communities can nonetheless remain stable and resilient in the face of persistent, ongoing change [49].

Implications for fragmentation research and practice

Shifting from the current paradigm to a time-focused, process-based paradigm for fragmentation has multiple implications. Here, we consider implications for interpreting the existing evidence of habitat loss and fragmentation, study design and analysis, and conservation policy and practice.

There has been substantial debate on the evidence for the impacts of habitat fragmentation, both in terms of separating the effects of habitat loss from those of fragmentation and diagnosing whether fragmentation may have negative or positive consequences for biodiversity, which has delivered mixed messages to the conservation community [3]. For instance, isolation and patch-size effects have been argued to be simply habitat amount effects because of their covarying patterns when comparing current snapshots of different landscapes [10]. Yet, a time-focused paradigm allows for interpreting isolation and patch-size effects separately from the effects of habitat loss by tracking changes over time, whereby habitat loss at the landscape scale can occur with or without changes in the isolation or size of focal patches in a landscape (e.g., protected areas). This approach is useful because, mechanistically, patch size and isolation can have effects that are unique from the direct effects of habitat loss across entire landscapes [50].

We expect that a time-focused paradigm will also improve understanding of the conservation value of highly fragmented landscapes composed of many small patches [51]. For example, a time-focused paradigm highlights that one value of small patches resides in the current context of remaining habitat structure, rather than suggesting that the fragmentation of habitat over time is beneficial [52]. Similarly, over short time scales, a global analysis of forest change identified that small forest patches were more likely to be lost than the same area in large forest patches [53]. A time-focused paradigm emphasizes that these small forest patches were likely created from previous loss and fragmentation, which ultimately leads to greater current vulnerability of existing small forest fragments (i.e., carryover effects [32]). Consequently, there can be hidden signatures of past fragmentation, or ‘ghosts of fragmentation past’, on current prioritization and value of habitats.

Study designs for interpreting habitat fragmentation need to be recalibrated to address these temporal issues. While it is valuable to have time series of both landscape change and organismal responses to such changes when interpreting fragmentation effects across landscapes [21,27], in many situations, this will not be possible. Nevertheless, it will often be possible to use causal inference methods to account for landscape history when evaluating current landscapes [31,54]. For example, matching methods, either statistical or qualitative [23], could be used to select landscapes with similar histories of landscape change based on remote-sensing data, historical documents, or traditional (including indigenous) knowledge [55] (Box 1). Such matching can address the often-implicit assumptions that landscapes have a shared history of contiguity or that history is unimportant. Despite this potential, current evidence for fragmentation effects has not yet leveraged these powerful causal methods. Even in the absence of statistical methods to address landscape history, we believe the mere process of questioning, acknowledging, and exploring landscape history will enrich our understanding of fragmentation moving forward.

A time-focused paradigm can also provide more reliable information for both policy and practice. Policy often de-emphasizes the conservation of small patches of habitat and instead focuses on large ones [52]. While scientists have disagreed on whether or not this emphasis is warranted, explicitly acknowledging temporal dynamics may help recalibrate where and when policy should focus across landscapes. Knowing landscape history can also guide management [56]. For example, in recently fragmented landscapes, conservation efforts may be best focused on improving within-fragment habitat quality and expanding or buffering patches to increase population viability and prevent further local extinctions. In historically fragmented landscapes, where debts have likely already been paid, actions may be best directed at rebuilding and connecting remnant fragments to support long-term, landscape-scale persistence, in addition to maintaining existing habitat. Patchiness generated by restoration may be driven by different processes than if such patchiness occurred from fragmentation [57], such that interpreting ‘fragmentation’ from restoration activities may be misleading.

Concluding remarks

Interpreting habitat fragmentation as the process of breaking apart habitat for a given amount of habitat loss over time will address long-standing issues in the science and application of land-change concepts for biodiversity. It reconciles the tension between pattern- and process-focused perspectives while also providing new opportunities for better understanding fragmentation effects. In doing so, we anticipate that guidance for conservation will be less contentious and more effective.

The future of ecological and conservation science depends on more precisely understanding how land-use change and conservation actions affect biodiversity now and into the future (see Outstanding questions). Doing so will require new experiments, causal inference methods for broad-scale data, and an understanding of transient versus long-term effects of environmental change. Whether fragmentation is bad or good is not the key question [5,58]; instead, we should focus on the process and pattern of land change and its implications [59]. The benefits will be substantial, as it will not only advance our understanding of habitat fragmentation but will also be key in delivering a unified framework for interpreting the complexity of land change on biodiversity.

Outstanding questions

Does the trajectory of loss and fragmentation over time lead to different cumulative effects on biodiversity?

What metrics are needed to fully capture and understand fragmentation over time with habitat loss (and gain)?

Are time lags similar when habitat amount changes versus when habitat fragmentation changes?

How predictable is the influence of landscape history on life-histories, species traits, and taxonomic groups?

What are the most reliable methods for diagnosing the attribution of fragmentation on biodiversity over time?

How much of the role of landscape history is caused by direct demographic responses of species versus disruptions in species interactions?

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Declaration of interests

The authors declare no competing interests.

Supplemental information

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