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Opinion

Fragmentation in patchy ecosystems: a call for a functional approach

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Habitat fragmentation is a major threat to biodiversity, but existing literature largely ignores naturally patchy ecosystems in favor of forests, where deforestation creates spatially distinct fragments. Here, we use savannas to highlight the problems with applying forest fragmentation principles to spatially patchy ecosystems. Identifying fragmentation using landscape functionality, specifically connectivity, enables better understanding of ecosystem dynamics. Tools and concepts from connectivity research are well suited to identifying barriers other than vegetation structure contributing to fragmentation. Opportunities exist to improve fragmentation mapping by combining remote-sensing data with field measurements related to connectivity to empirically test whether landscapes are functionally fragmented. Advancements in deep learning and increasingly accessible data open many possibilities for comprehensive maps of fragmentation.

Highlights

Habitat fragmentation is often conceived though a patch–matrix dichotomy, but this is conceptually and practically complicated, especially for patchy ecosystems.

Vegetation structure alone is insufficient to quantify fragmentation because the causes of fragmentation are diverse and some land uses cause fragmentation without altering vegetation.

To improve conservation outcomes, landscape function should be used to define fragmentation in patchy ecosystems.

Fragmented thinking

Human-mediated conversion of **habitat** (see Glossary) has caused a multitude of negative impacts on biodiversity globally [1]. This leads to habitat loss and, often, **habitat fragmentation**, which is frequently associated with loss of biodiversity and ecosystem services as well as trophic collapses [2]. Most definitions of fragmentation focus on the structural component of fragmentation, characterizing it by strong contrasts between contiguous **patches** of habitat and a surrounding **matrix** of nonhabitat [2,3]. Definitions based on contrasts between patch and matrix are popular in the forest ecosystems literature, where it is easy to distinguish ‘natural’ patches from a nonforest matrix by breaks in the canopy. The popularity of this definition has been aided by the wide availability of satellite imagery in which tree canopies are easy to distinguish.

However, fragmentation becomes more difficult to define and identify in ecosystems where there is little to no contiguous vegetation cover, including tree canopy, or where it naturally varies. Of the 25 biomes identified by the IUCN global ecosystem typology, only two are forest biomes [4]. For the remaining 23 biomes (e.g., savannas, tundra, and wetlands), fragmentation is more difficult to identify and quantify with structural metrics because it is often hard to distinguish between patch and matrix. The complexity of identifying fragments in continuous but patchy ecosystems makes it difficult to determine when landscape and land-use changes will result in fragmentation, and, thus, to manage and mitigate future fragmentation and associated degradation of patchy ecosystems.

To overcome these difficulties in distinguishing patches, we suggest quantifying **functional fragmentation** instead of relying on structure. We define functional fragmentation as the separation of habitat by barriers that impede the flow of agents between areas, or more simply, a loss of functional **connectivity**. Barriers may be changes to vegetation structure or human activities that form barriers unrelated to vegetation. We believe that habitat fragmentation should not be quantified based solely on vegetation structure (height, canopy cover, and biomass) without

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evidence that the structure is indicative of barriers. Determining which features and human activities alter dispersal capabilities through landscapes is vital for managing complex socioecological systems, but remains a challenge. We use **savannas** as a case study to show how fragmentation definitions based solely on the patchiness of vegetation structure do not work well for many ecosystems. We then explain how conceptualizing fragmentation using connectivity offers greater flexibility and ecological meaning, and describe potential data sources and analytical techniques that will improve quantification of functional fragmentation.

When patches become problematic

Savannas are the largest land cover in the tropics [5] and provide significant environmental, economic, and cultural value to nearly 1 billion people [6]. Savannas and other grassy biomes are predicted to be heavily altered by climate and land-use change [7]. Methods for identifying fragmentation based on vegetation structure are especially problematic for savannas because: (i) savannas are naturally heterogeneous with areas of high and low woody biomass in the same contiguous landscape (Figure 1); (ii) regular natural disturbances cause frequent changes to the vegetation structure, which make identifying fragmentation more difficult; and (iii) major drivers of fragmentation in savannas can be unrelated to vegetation structure.

Classifying landscapes into habitat patches and surrounding matrix is the foundation of much of the fragmentation literature. Typically, methods for defining patch and matrix in fragmentation studies are based on differences in vegetation structure, such as height, aboveground biomass, or tree cover. Differentiating patch and matrix relies on assigning thresholds, above which is habitat and below which is matrix [8]. In savannas, where trees are typically shorter, further apart, and average aboveground biomass is lower, setting ecologically meaningful thresholds is difficult. The ecology of savannas is reliant on vegetation heterogeneity, which is a key driver of species richness, abundance, and composition at multiple spatial scales [9]. Between different savanna types, the spatial scale of this heterogeneity can be variable, with some savannas having heterogeneity on a wide scale with large continuous patches of trees and grasslands, while others have highly variable vegetation types within a single hectare (Figure 1).

Quantification of fragmentation typically focuses on woody vegetation (e.g., [10]). This works well in forests, where ecosystem functionality is closely linked to tree-dominated vegetation structure [11], but the relationship between structure and function in savannas is linked to both woody and herbaceous vegetation [12]. Overlooking grasses and forbs in savannas overlooks their importance as crucial habitat and resource for savanna animals, which often are adapted to utilize the herbaceous patches. Moreover, the literature on woody encroachment highlights the many disadvantages of reduced herbaceous cover [13], not only in savannas, but also in other ecosystems, such as tundra [14].

Spatial heterogeneity of vegetation is not the only aspect that makes fragmentation difficult to conceptualize and study in savannas. Savanna vegetation structure can also change rapidly over time due to natural disturbances and feedbacks. **Disturbance regimes** are crucial for the persistence of many savanna species and overall landscape heterogeneity [9], and a reduction in disturbance can lead to fragmentation via woody encroachment, where the continuity of herbaceous vegetation is lost [13]. The frequent changes to vegetation from disturbance pose a challenge when trying to detect lasting ecosystem structural changes that may represent fragmentation. Many fragmentation studies have relied on satellite remote sensing to quantify change associated with land use and vegetation structure, but more subtle changes due to vegetation growth and human use that can fragment savannas are difficult to detect [15]. While successes have been made in detecting vegetation change in savannas [15–17], it is complex to link these

Glossary

Connectivity: flow of materials, energy, and/or organisms, genes, and so on within a region of interest.
Disturbance regime: pattern of natural processes that impact ecosystems and landscapes.
Functional fragmentation: separation of habitat by barriers that impede the flow of agents between areas, or more simply, a loss of functional connectivity.
Habitat: environment (area and resources) used by an organism to live and reproduce.
Habitat fragmentation: separation of habitat into two or more areas independent of habitat loss.
Matrix: portion of the landscape in which patches of 'habitat' are embedded. The matrix can still serve as 'habitat', but may not represent ideal or untransformed habitat.
Patch: area of contiguous habitat surrounded by land that is classified as nonhabitat.
Landscape-independent factors: when anthropogenic disturbances alter species interactions and cause barriers not directly linked to the physical landscape.
Occurrence data: detections of species or activities at a single position in space and time.
Savannas: ecosystems that include a mixture of trees and grasses and are characterized by a continuous herbaceous or grassy understory and a discontinuous tree canopy. This broad definition can define a wide variety of habitat types as a savanna, including grasslands with trees every few kilometers, or woodlands with hundreds of trees in a single hectare. Variation within savanna habitats is due to drastic differences in precipitation, edaphic features, and disturbance regimes, which can lead to stark contrasts in adjacent vegetation structures that are part of the same contiguous landscape.

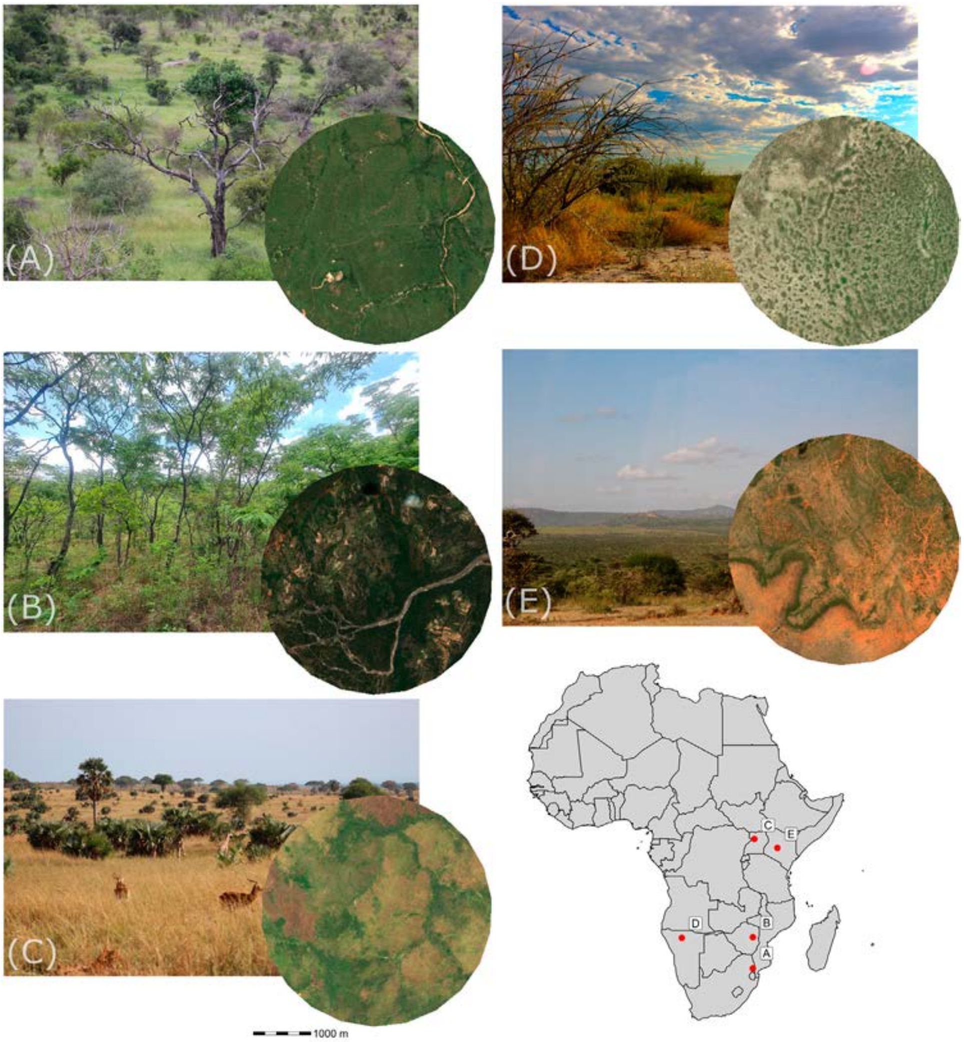

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Figure 1. Examples of savanna ‘patchiness’. Savannas can vary widely in their vegetation structure, with different amounts and configurations of woody and herbaceous biomass. This structural heterogeneity makes it difficult to determine from remote sensing whether patchiness of the landscape is the result of fragmentation. Here, we compare ground photographs of African savannas to images from RGB images from Sentinel-2 to show how variable and ‘patchy’ unfragmented savannas can look. (A) Kruger National Park, South Africa; (B) community woodland in Hwedza District, Zimbabwe; (C) Murchison Falls National Park, Uganda; (D) Etosha National Park, Namibia; and (E) Laikipia plateau, Kenya.

changes to ecological impacts when increasing and decreasing vegetation biomass may have both positive and negative outcomes (e.g., distinguishing vegetation growth recovery vs. encroachment) [16].

Many of the factors that fragment ecosystems are not directly related to vegetation change (Box 1). Changes in land use and management may result in human activities that will deter some taxa. For example, increased human presence and noise pollution may deter some keystone species (e.g., [18]). Fences can fragment landscapes even before they lead to changes in the

Box 1. Drivers of fragmentation in savannas

Changing vegetation structure

Heterogeneity is critical for savannas to remain biodiverse [9,49,50]. Thus, homogenization of savanna vegetation can be a form of degradation. While trees are a keystone structure in savannas the removal of which can be detrimental [51], increases in woody vegetation are a major threat to savanna ecosystems worldwide. Woody encroachment has negative impacts on soil carbon storage [52], grazing potential [53], and biodiversity as grassland species are displaced [13]. Many causal factors contribute to woody encroachment and the alternation of savanna structure, including fire suppression, changing grazing regimes, and land abandonment [13]. Invasive species also contribute to changes in landscape vegetation structure and fire suppression [54]. Invasive grasses are especially problematic and may exacerbate fragmentation caused by other drivers [55].

Agricultural expansion

The conversion of land to agriculture is a major driver of biodiversity loss [2]. As human populations continue to grow, estimates are that 2–10 million km^2 of new land for agriculture is needed [56]. Savanna habitats in Africa and Latin America are the most threatened by land conversion [57]. Anthropogenic disturbances associated with agriculture are known to cause loss of taxonomic and phylogenetic diversity as well as alter biomass stock patterns [58]. However, these relationships can be nonlinear. For example, declines in tree and mammal abundance in African savannas are only evident at extreme levels of land-use change [59].

Roads

In forests, roads disrupt canopies, causing changes to microclimate and other key aspects of ecology [60]. While roads in savannas do not have the same impacts, they are linked to changes in vegetation structure. Woody canopy has been found to be higher on the edges of roads [61]. Road mortality also has major impacts on animals of all groups and limits foraging, dispersal, migration, and range expansion for many species [62]. Alternatively, roads in savannas provide new opportunities for some species (e.g., [63,64]).

Fences

Fences can inhibit the dispersal of animals and cause mortality [65]. Exclosure experiments reveal how inhibiting herbivore movements can impact vegetation [66]. Fences are hard to detect and have largely gone unnoticed by remote sensing [65]. Unlike roads and railways, there are no global fence data sets to understand how they are changing ecosystems. Furthermore, since many fences exist in more remote areas, areas with high densities of fences can still be labeled as having low human impacts [65].

Other human activities

Humans are superpredators who create a widespread landscape of fear, which influences wildlife behavior across the globe [67]. Fragmentation can be caused by anthropogenic disturbances independent of alteration of the physical landscape [68]. These include changes to pollination and seed dispersal or avoidance due to increased predation or competition, which can alter wider ecosystem processes.

vegetation from altered grazing or seed dispersal patterns. In the Greater Maasai Mara Ecosystem in Kenya, increased fencing is rapidly fragmenting the landscape by inhibiting animal movements [19,20] (Figure 2). Yet, fence changes are largely omitted from global products for human modification and are not included in maps of land cover and biomass, which are frequently used in fragmentation assessment. Given the limitation of satellite remote sensing to detect some types of fragmentation, savannas globally could be more at risk than currently thought [21].

We are not the first to call for a more nuanced view of fragmentation that moves away from strict patch–matrix binary conceptualization and incorporates more complex ecological factors. Fischer and Lindenmayer [22] proposed a continuum model for fragmentation, which advocated for inclusion of other ecological variables, such as climate and food availability. Similarly, Didham *et al.* [23] called for incorporating the interdependence of species and landscapes in fragmentation models. Both regarded the use of continuous metrics as an improvement to binary models of patch and matrix. Yet, 74% of the literature still conforms to the binary conceptual model [24]. Continuous maps provide more information compared with binary ones [25], but the use of the binary model is only decreasing at a slow rate [24] and it is still common to see studies that use

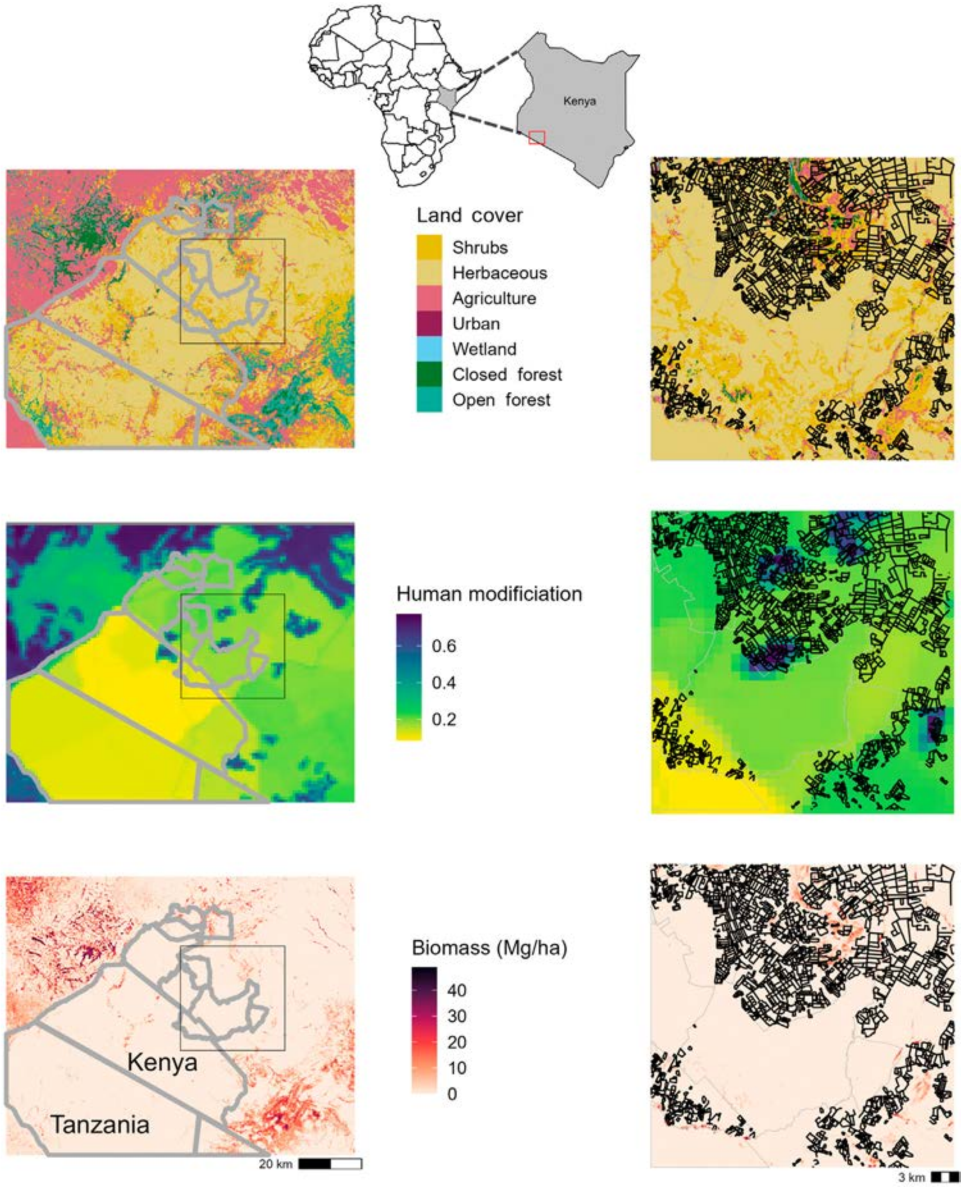

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Figure 2. Limitations to existing products for fragmentation. The Greater Maasai Mara landscape in Kenya is highly fragmented by fencing [20], but existing global products for land cover (A) [76], human modification (B) [77], and aboveground woody biomass (C) [78] are insufficient for mapping functional fragmentation because the majority of fenced areas are in areas labeled as natural vegetation and low human modification. Images on the right are zoomed in images of the area indicated by the black box in the images on the left. Gray polygons represent protected areas and black lines are fences recorded from the LandDX project [20].

binary metrics to separate out habitat and nonhabitat based on vegetation cover (i.e., [19]). For fragmentation to be a meaningful metric that is useful for conservation in nonforest ecosystems, we need to move away from binary classifications based on vegetation structure to classifications based on ecosystem functioning, explicitly model key ecosystem dynamics, and incorporate additional drivers of fragmentation.

Moving beyond structure to functional fragmentation

While patch-based metrics can be problematic, their use continues because it is comparatively easy to quantify fragmentation this way. Adding nuance to address the issues mentioned earlier means adding conceptual and computational complexity. Instead of reinventing the wheel, we suggest that tools already exist for quantifying functional fragmentation within the field of landscape connectivity. Connectivity occurs over a variety of spatial and temporal scales and can be as varied as the flow of nutrients, spread of fire, or dispersal of individuals or seeds [26], giving it the necessary flexibility to be used in patchy and otherwise complex ecosystems. Connectivity methods mostly use continuous metrics, have a greater emphasis on drivers, and are particularly good at combining data types into comparable landscape representations [27].

The main limitation of the connectivity approach to date is that studies tend to focus on a single species or process that is not indicative of all aspects of the ecosystem [28], and is more tractable for some taxa than others (e.g., easier for vertebrates than for invertebrates). To address this, there is an active community of researchers developing multispecies connectivity methods, which show promise for bringing further understanding of wider landscape dynamics by aggregating maps from species with different dispersal capabilities [27,28]. Another issue is that innovation tends to be related to processing species data (response data, also known as the labels in machine learning), rather than to the environmental data layers used as predictors (or features) in these models. For example, a map of global functional connectivity for mammals relied only on normalized difference vegetation index (NDVI) and human footprint index (HFI) for the predictor data [29]. These covariates have limited and very context- and species-dependent impacts on connectivity, and are, at best, crude descriptors of ecosystem function. Further landscape information is available via high-resolution optical, radar, and hyperspectral sensors, for example on human use, vegetation structure and vegetation health, respectively, but these are largely not used by vertebrate animal ecologists, who dominate the connectivity field [30].

We suggest that integrating connectivity concepts with satellite remote-sensing data provides a way forward for better estimating the functional fragmentation. For patchy ecosystems, special attention needs to be paid to assumptions that are biased toward woody vegetation, and further steps taken to incorporate critical landscape processes beyond vegetation structure. For example, detailed maps of vegetation classification and degradation exist for the Great Maasai Mara Ecosystem, which show that the region is becoming increasingly structurally fragmented as woodland and grassland areas decrease and bare ground cover expands [19]. These vegetation changes are assumed to have negative ecological impacts for wildlife, but the influence of these structural changes on functional connectivity is not well understood. Existing sources of data can be used to confirm when vegetation structure is sufficient to explain fragmentation and where other drivers of fragmentation need to be examined. For example, data on wildebeest (*Connochaetes taurinus*) movements [31] can help determine where fencing inhibits connectivity, and invasive plant occurrences [32] can help separate functional differences in native and non-native species, which are not always distinguishable from vegetation structure alone. Linking changes in ecological flows or rapid changes in composition to what we can easily observe with satellites provides a more nuanced perspective of fragmentation that is rooted in function, not structure.

Functional fragmentation in practice

Functional fragmentation mapping can be improved by looking beyond vegetation structure by incorporating other landscape features and using field data sets to validate that all landscape features impact functional connectivity. In recent years, remote sensing has vastly improved our ability to map landscape features, including buildings [33], roads [34], and field boundaries [35]. These feature-detection algorithms and the data sets they produce should be incorporated in fragmentation maps along with information on vegetation and land cover. Combining object-based classification with landscape connectivity modeling has been shown to be a powerful tool [36], but further work needs to be done to create data sets for other key features (e.g., fences) and parametrize them for specific landscapes (e.g., relative impact of wire vs. electric fences). Additionally, these methods can be used to improve vegetation mapping by identifying invasive species [37] and keystone trees [38]. Furthermore, high-resolution satellite imagery is increasingly available for identifying these small landscape features. Which landscape features need to be identified and the extent to which they contribute to fragmentation are highly landscape dependent; thus, remote-sensing scientists should work closely with ecologists to determine what is crucial for function in each landscape.

A wealth of potential 'label' or response data exists from field ecology, which provide many opportunities for validating functional fragmentation models and associated maps (Box 2). **Occurrence data** can contribute to the assessment of functional fragmentation by confirming habitat locations. Such data are especially powerful when used in occupancy models to determine the probability of dispersal [39]. Animal-borne tags produce thousands of points per individual and

Box 2. Data sets that remote sensing could exploit for evidence of function

Genetic data: whole-genome sequencing and environmental DNA

Pro: DNA samples from individuals can help create maps of genetic variation to assess whether there is gene flow between sites and populations for a given species (e.g., [69]). Environmental (e)DNA is an especially important tool for monitoring species that are difficult to detect or track using other methods.

Con: lower spatial resolution makes it more difficult to identify 'edges' of fragments.

Innovations: eDNA holds potential to be used as a population genetics tool [70].

Databases: Genbank, GBIF, and eBioAtlas.

Animal-borne tags: biotelemetry (GPS collars) and biologging (accelerometers and temperature sensors)

Pros: animal-borne tags produce thousands of points per individual, and often millions of points in a single study at high spatiotemporal frequency. Interpreting animal behaviors from these data can be useful for identifying hard-to-see landscape features in satellite images such as fences, or areas where landscape independent factors contribute to fragmentation.

Cons: their use is mostly limited to large taxa and usually only a few species at any given site. There are also ethical considerations for deploying new tags [71].

Innovations: new technologies allow for recording data at higher temporal frequencies and to track a wider variety of taxa [72]. For example, the open source 'TickTag' weighs ~1 g and can record up to 10 000 fixes on a single battery, making it suitable for very small vertebrates [73].

Databases: Movebank and Euromammals.

Occurrence data: point-count surveys, pit fall traps, vegetation plots, camera traps, and acoustic monitors to assess the presence of species or events at a given location

Pro: occurrence data can be used for a wide variety of taxa and spatial scales. They are especially powerful when used in occupancy models to determine the probability of dispersal [39]. Data for a wide variety of taxa (plants as well as animals) already exist from regular monitoring at many locations.

Con: such data have relatively low spatial resolution on the landscape and depending on the survey method. They tend to occur at low temporal resolution.

Innovations: advances in computer vision for identifying animals from camera traps and acoustic monitors have increased the utility of these data sources [74,75].

Database: GBIF, eMammal, Forestplots, Arbimon, and SEOSAW.

provide detailed spatiotemporal information regarding landscape connectivity [40]. In addition, technological advances have increased the possibility of assessing genetic connectivity for entire ecological communities [41]. Previously, these types of data were limited to large and charismatic species, but further technological innovations are opening possibilities for monitoring a wider variety of taxa (e.g., automated bioacoustics models to detect and classify insects [42]).

Satellite remote sensing already uses field data to contextualize and improve maps. For example, data from vegetation plots are used as calibration and validation for satellite-derived biomass maps [43]. However, since vegetation structure is not the only component of fragmentation (Box 1), we recommend looking at other aspects of the landscape to improve fragmentation maps. Data on animals provide many opportunities for adding functional context to fragmentation maps, since animals often strongly influence vegetation structure and ecosystem function (e.g., [44,45]). The importance of animals in maintaining ecosystems processes is well known [46,47], as are the ecosystem-wide changes that occur when animals are absent [48]. Additionally, data regarding animal dispersal may be a good way to test how specific landscape features influence landscape connectivity (e.g., impact of different types of road) or when **landscape-independent fragmentation** is occurring (e.g., avoidance of humans).

Field data sets are underutilized as labels by remote-sensing scientists. Furthermore, combining multiple types of data for the same landscape offers opportunities to assess functional fragmentation across multiple spatiotemporal scales, and multispecies connectivity methods provide avenues for merging data sets [28]. Global analyses of functional connectivity using large quantities of field data are becoming more frequent, thus highlighting people's willingness to share data and collaborate (i.e., [29]). Remote-sensing scientists should be capitalizing on the numerous data available to improve understanding of fragmentation in savannas and other patchy systems.

While availability of the field data provides opportunities to improve models and maps of functional fragmentation and connectivity, they come with their own challenges. First, each additional type of data is prone to different types of error and limitation, which requires expert knowledge to appropriately deduce ecological meaning. Second, ecological data are spatially biased to certain data-rich sites, often protected areas that may not be representative of the wider landscape, and are often taxonomically biased. These issues can be reduced through collaboration between data collectors, remote-sensing specialists, and data scientists. Ecologists should work with remote-sensing specialists to make their data easily useable with satellite images and be clear about the uncertainties and limitations in their data sets. Remote-sensing specialists and data scientists who work with large data sets can help ecologists utilize available computational tools and deep learning methods to detect landscape features that contribute to functional fragmentation. Interdisciplinary collaborations using deep learning are already happening across ecology [30], but further opportunities exist to use collaborations to improve research into fragmentation, especially in difficult-to-delineate ecosystems.

Concluding remarks

Understanding how to mitigate threats to patchy ecosystems from fragmentation will aid greatly in their conservation and the maintenance of the ecosystem services they provide. Yet, progress is hindered by models of fragmentation that are based solely on woody vegetation structure and binary metrics, which do not work well for many ecosystems. We instead suggest that opportunities for better understanding fragmentation and its impacts arise from using connectivity methods to parametrize and combine ecological data. Further integration of data from field-based ecology studies (genetic, movement, and occurrence) and satellite-derived data sets for key landscape features provide a way forward for understanding patchy ecosystems. While many questions

Outstanding questions

How much of the world's ecosystems are functionally fragmented, and what are the consequences?

How do ecosystem processes (e.g., fire spread or seed dispersal) influence functional fragmentation and at which spatiotemporal scales?

How does functional fragmentation compare with delineations based only on land cover or vegetation structure?

Which feature and label data are necessary to make a comprehensive map of functional fragmentation?

How can we most easily gather data describing ecosystem function to meaningfully assess fragmentation?

How can we incorporate smaller taxa (e.g., invertebrates or reptiles) for which fragmentation may occur on smaller spatial scales than is easily represented by landscape data?

remain as to what extent these techniques can be mobilized (see Outstanding questions), the continued advancement of methods, along with increasingly accessible data, creates opportunities for more comprehensive maps and nuanced interpretations of fragmentation.

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Declaration of interests

The authors declare no competing interests.

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