Functionalizing ecological integrity: using functional ecology to monitor animal communities

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Ecological integrity—the degree to which an ecosystem supports ecological structure, composition, diversity, function, and connectivity typical of natural conditions—has been a guiding principle in ecosystem monitoring around the world. However, in terrestrial ecosystems, integrity-based monitoring often excludes animal communities, even though they are critical drivers of integrity. Methodological advances in monitoring and data science have made it easier to document animal communities. We highlight examples of these advances and how they remove barriers to adopting animal-specific integrity metrics. We then illustrate how describing animal communities in terms of functional ecology, which has also undergone substantial development over the past several decades, can provide a generalizable approach to incorporating animal communities into integrity-based monitoring across taxa and ecosystems. Incorporating animal communities into ecological integrity monitoring is a vital step toward understanding how human-driven change, restoration, and conservation shape terrestrial ecosystems worldwide.

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Ecological integrity is an important guiding concept for ecosystem assessment and monitoring globally. Despite having a range of definitions (Parrish *et al*. 2003), ecological integrity is considered here as the ability of an ecosystem to support a natural range of structure (eg canopy cover), composition/diversity (eg species richness), function (eg nutrient cycling), and connectivity (eg corridors). In both conservation and management contexts, ecological integrity provides a cohesive framework for assessing whether ecosystems exist within a natural or expected range of biotic and abiotic conditions. The concept has been and continues to be applied across environments worldwide, occasionally described either as one cohesive "integrity score" for an ecosystem (Faber-Langendoen *et al*. 2006; Woodley 2010) or as a set of desirable or target conditions (eg a combination of metrics depending on management or conservation goals, such as forest stand structure, size, and species composition; Carter *et al*. 2019; Nordman *et al*. 2021). At its core, the concept of ecological integrity aims to describe how an ecosystem looks and functions relative to a desired condition or range of conditions.

In a nutshell:

- Ecological integrity, or the degree to which an ecosystem's structure, composition, diversity, function, and connectivity falls within a natural range, is an important guiding principle for ecosystem monitoring
- Ecological integrity monitoring for terrestrial ecosystems has historically excluded animal communities
- Advances in monitoring technology, data availability, statistical methods, and computation have removed historical barriers to monitoring animal communities
- Using functional traits linked to ecology, including diet, habitat, behavior, and body size, provides a biologically meaningful way to generalize across animal communities and ecosystems

Because ecological integrity has a broad, multifaceted definition, the monitoring of ecological integrity has taken on different appearances across environments as well as across conservation and management agencies. For example, in land management, integrity-based monitoring emphasizes the structure and composition of vegetation (eg trees; Nordman *et al*. 2021). Conversely, in aquatic ecosystems, integrity-based monitoring emphasizes indicator species of pollution and land use (eg the composition and diversity of macroinvertebrate and fish communities; Karr 1981; Carter *et al*. 2019). Within the scope of their respective definitions of ecological integrity, conservation and management agencies have been successful in re-establishing aspects of ecological integrity through

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management actions (eg tree thinning [Cannon *et al.* 2018], stream restoration [Birnie-Gauvin *et al.* 2020]). However, how agencies apply the concept of ecological integrity stems from traditional or current agency-specific mandates for monitoring to historical establishment of standardized protocols (eg Karr 1981). As a result of these differences, creating generalizable metrics across ecosystems, taxa, and agencies has been challenging.

One of the key gaps in applying ecological integrity to monitoring is the exclusion of animal communities from terrestrial monitoring (Carter *et al.* 2019). After conducting a qualitative literature review of five journals—*Biological Conservation*, *Conservation Biology*, *Ecological Applications*, *Ecological Indicators*, and *Forest Ecology and Management*—that published papers on ecological integrity between 1990 and 2023, we found that while 50% (89 out of 178) of the papers included metrics for animal communities, only 12% (21 out of 178) were conducted in terrestrial environments (Figure 1; Appendix S1: Figure S1 and Panel S1). Animal communities provide information about ecological integrity that is frequently lacking from common indices based on abiotic factors and vegetation characteristics. For instance, because animal communities comprise multiple trophic levels, their inclusion in assessments of ecological integrity can help in deciphering top-down influences on ecosystem states (Karr 1981). When considered in terrestrial systems, animals are often evaluated with a habitat-proxy approach (Palmer *et al.* 1997) or through focal species monitoring (Runge *et al.* 2019). Although the habitat-proxy approach captures abiotic and vegetation structure metrics of ecological integrity well, both approaches are generally poor predictors of animal community response to change, for a variety of reasons (Schwartz *et al.* 2015). Animal taxa and communities respond to a variety of landscape features in species- and age-specific ways (Lee-Yaw *et al.* 2022). Animal communities also influence, and are influenced by, the ecosystems they occupy (Russo *et al.* 2023). Thus, the structure and composition of the animal community shapes ecological integrity directly. As such, excluding animal communities from terrestrial ecological integrity monitoring results in an incomplete picture of the status of ecosystems. Compounded with this oversight is the growing awareness that ecosystem restoration efforts often have unintended or unexpected consequences that ripple across food webs and shape ecological integrity; in the absence of metrics for the status of animal communities, this could lead to degraded, rather than restored, ecosystems (Miller-ter Kuile *et al.* 2021; Pearson *et al.* 2022).

We propose that now is a pivotal moment for adopting animal community metrics of ecological integrity into terrestrial monitoring efforts, for two reasons. First, current and growing technological advances in monitoring and data analysis have alleviated many real or perceived barriers to monitoring animal communities. Second, because ecological integrity is essentially a metric describing how functional an ecosystem is, we can adopt metrics for animal communities using functional ecology and functional traits (eg feeding, habitat, behavioral, and morphological traits that have a measurable effect on ecosystem functions) as a guiding principle because functional traits are generalizable and comparable across taxa and environments. As with monitoring, functional ecology has experienced major advances in the past two decades, in terms of both theory (McGill *et al.* 2006) and technology (eg Frimpong and Angermeier 2009; Tobias *et al.* 2022). We highlight methodological and technological advances that hold the most promise for this endeavor, as well as the literature demonstrating how a functional ecology approach allows for building general protocols, baselines, and understanding of

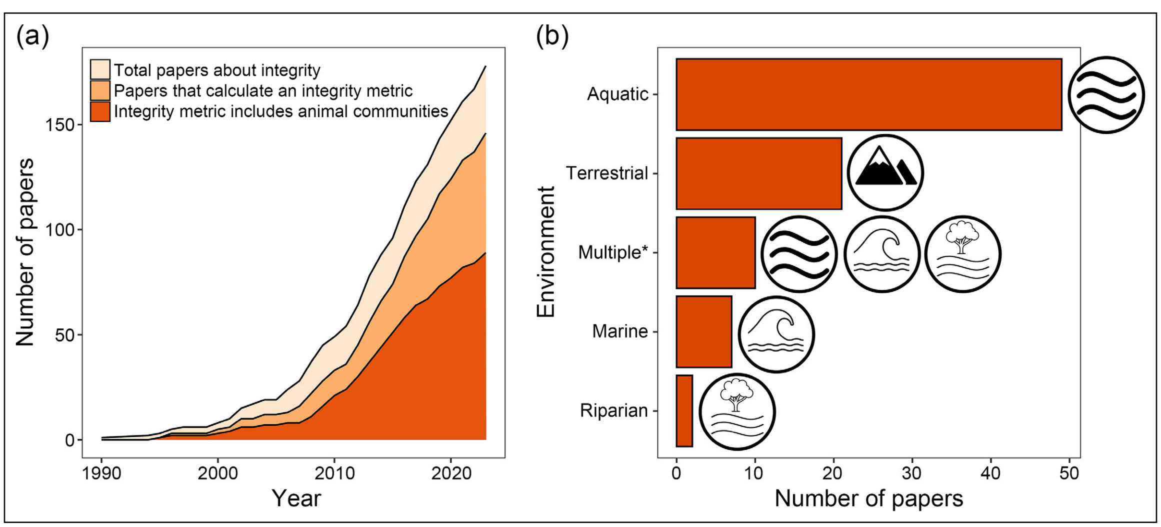

Figure 1. Number of papers on ecological integrity published in the journals *Biological Conservation*, *Conservation Biology*, *Ecological Applications*, *Ecological Indicators*, and *Forest Ecology and Management*. In (a), colors represent the cumulative number of papers that (1) are about ecological integrity (light), (2) are about ecological integrity and calculate one or more metrics (medium), and (3) include animal communities in these metrics (dark). (b) Breakdown by environment for papers that included animal communities in integrity metrics. "Multiple*" environments were the interface between an aquatic and riparian or marine and estuarine environment. Icons are from Microsoft PowerPoint (CC-0 license).

ecological integrity of animal communities across systems, taxa, and monitoring schema.

Growth in monitoring, data, and computational capacity

Historically, animal communities have been difficult to integrate into ecological integrity monitoring because animal communities are difficult to monitor. For example, animals can be mobile, can be cryptic, and/or are rare on the landscape relative to stationary ecosystem components. However, new methods of data collection and analytics are making these barriers a relic of the past. New technologies, such as acoustic recording units (ARUs), Motus Wildlife Tracking Systems (Motus), camera traps, environmental DNA (eDNA), and drones, are facilitating data collection on animal communities at much broader spatial and temporal scales (Rees *et al*. 2014; Steenweg *et al*. 2017; Wood *et al*. 2019). Both new and conventional data collection methods (eg field observations) are contributing to a growing number of long-term monitoring programs, including the Breeding Bird Survey (Ziolkowski *et al*. 2023), the North American Bat Monitoring Program (NABat; Gotthold *et al*. 2024), and the Long Term Ecological Research (LTER) network, and databases, such as AVONET (Tobias *et al*. 2022) and FishTraits (Frimpong and Angermeier 2009), for diverse taxa across many ecosystems.

Technological innovations and a growing amount of data, combined with advanced modeling and computational ability, further erode barriers to monitoring animal communities, and thus to incorporating animal communities into ecological integrity metrics. Modeling approaches such as multispecies occupancy models (Iknayan *et al*. 2014) and data integration (combining multiple sources of data, including that collected by community scientists, such as eBird; Sullivan *et al*. 2009; Miller *et al*. 2019) can accommodate large datasets and help account for deficiencies in historical data collection (eg imperfect detection, biased sampling design, lack of temporal or spatial coverage). Advancements in methods have been paired with increased computational power for efficient analyses of community data (Yackulic *et al*. 2020). Thus, given these analytical and technological advances, now is an ideal time to integrate animals into ecological integrity monitoring.

The goal of monitoring multiple species does not have to replace current single-species monitoring priorities (such as for threatened and endangered species). For instance, many emerging sampling technologies (eg ARUs, camera traps, eDNA) are designed as multispecies sampling approaches that passively or non-invasively sample large areas. Thus, they have the potential to help with the detection of cryptic areas of occupancy for rare species. In addition, while many current single- and multispecies monitoring efforts focus on charismatic fauna (eg birds, large mammals), a growing number of these sampling technologies provide opportunities to include historically excluded but ecologically important taxa (eg invertebrates) (Grodsky *et al*. 2015). Where concerns exist about the additional time or cost of multispecies sampling, community-level monitoring could be simplified over time as part of optimal sampling approaches. Specifically, monitoring can begin with pilot studies that inform the number of sites and survey replicates needed to detect representative species in a community while optimizing project costs (ie Sanderlin *et al*. 2014). Alternatively, long-term datasets with high resolution for one or a few species (eg threatened and endangered species) could be augmented with more general sampling of animal communities to elucidate mechanisms driving changes in single-species trends (eg predation dynamics). As we discuss below, these decisions could also be based on information about species' functional roles that most shape ecosystem integrity.

Functional ecology as a general framework for monitoring animal ecological integrity

The functional ecology of an animal community describes the traits that underpin the maintenance of ecological processes, making functional ecology a clear and simple approach to monitoring the ecological integrity for animal communities. Functional traits, such as those traits related to diet, morphology, and habitat use that shape an animal's environment, can be generalized across systems, taxa, and data collection practices (Carter *et al*. 2019). Animal communities provide important ecosystem services and functions such as nutrient cycling (Schneider *et al*. 2016) and seed and pollen dispersal (González-Robles *et al*. 2021; Fricke *et al*. 2022). Composition of species within functional groups in an animal community determines how these processes shape ecosystems (eg Donoso *et al*. 2020). These functions and the animal traits that govern them can be generalized across ecosystems, thereby providing a means of describing animal communities and ecological integrity across systems and taxa, as well as a way to predict the mechanisms that may shape ecosystems and ecological integrity (McGill *et al*. 2006).

Ideally, monitoring targets all four components of ecological integrity—structure, composition/diversity, function, and connectivity—through a combination of metrics. We can extend these and other aspects of ecological integrity to animal community monitoring using functional ecology and functional traits. These traits include trophic (eg trophic composition and diet breadth), habitat (eg feeding and nesting sites and geographic range), morphological (eg body size), and behavioral traits (eg migratory behavior, dispersal distances, and range size; Appendix S1: Figure S1b; Gonçalves-Souza *et al*. 2023). These traits describe animals in communities across taxa and environments and could be used to build a general set of ecological integrity metrics (eg Karr 1981). Furthermore, information about many of these traits is already available in large databases (eg AVONET, FishTraits) and could be relatively easy to combine with monitoring data from current and emerging

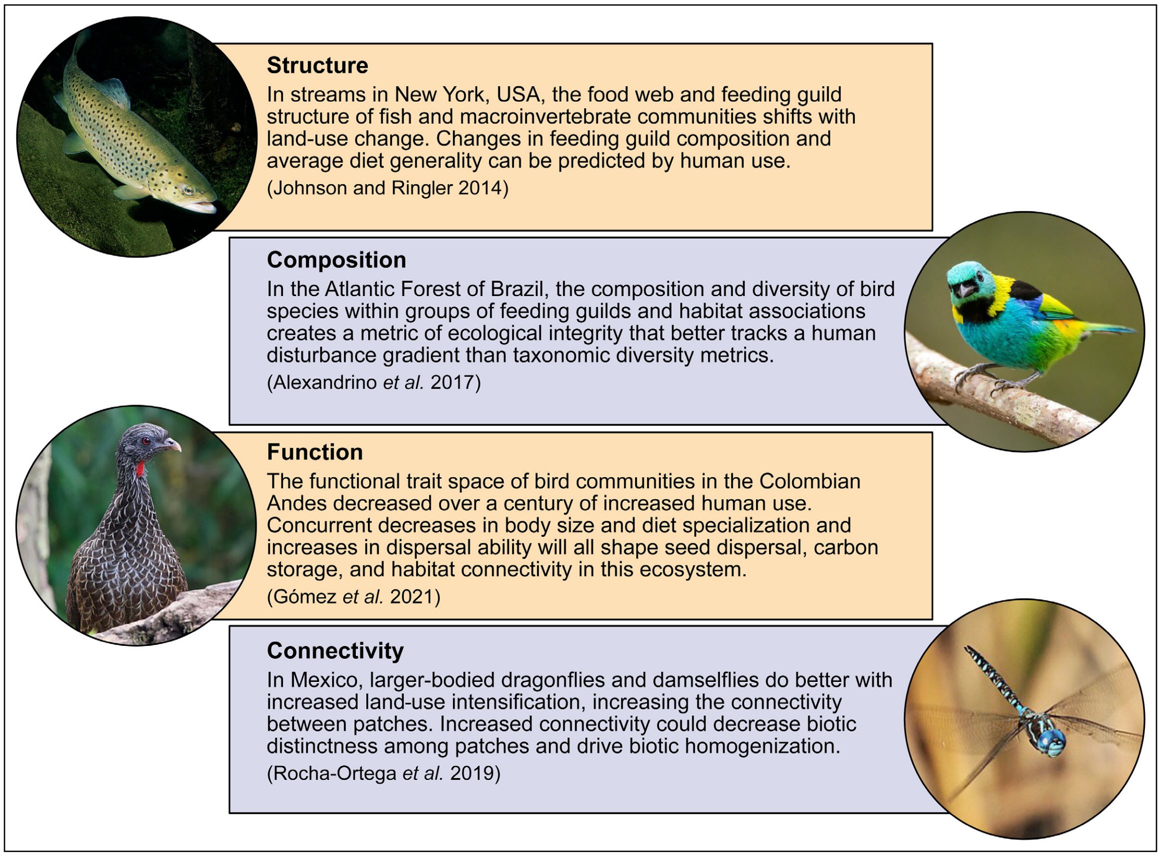

Figure 2. Examples of using the functional ecology of animal communities to track the ecological integrity of ecosystems across the globe. We highlight examples from four common integrity components: structure, composition, function, and connectivity. For these and other studies monitoring integrity with functional traits, field-measured traits and trait databases (eg AVONET, FishTraits) were used in conjunction with other standard monitoring protocols. Images are from Wikimedia Commons (CC-0 license).

monitoring approaches (see above). In the following sections, we highlight studies that demonstrate the benefit of using functional ecology for monitoring animal communities for ecological integrity (Figure 2).

Structure

The *structure* of animal communities includes the networks of biological interactions that shape all communities. Thus, monitoring animal community structure could include monitoring these networks or their component parts (eg primary producers, predators, or keystone species). Johnson and Ringler (2014) demonstrated that stream macroinvertebrate and fish assemblages in New York State respond to human-driven environmental change; specifically, this study highlighted that the functional traits related to network *structure* (trophic composition, feeding guild, and diet breadth) are all influenced by human-driven environmental change, with key implications for ecosystem function. For example, the macroinvertebrate community is less even (more dominated by the three most common taxa) with increased urbanization, a shift that coincides with a dominance of a particular feeding guild (greater numbers of "collector–gatherers" that focus on gathering particles that have precipitated out of the water column versus filtering those particles out of suspension). Furthermore, streams with lower dissolved oxygen concentrations (a result of intensified human use) are dominated by fish with a more generalized diet. Notably, fish and macroinvertebrates respond differently to human-driven change, highlighting the importance of monitoring multiple groups of taxa as indicators of ecological integrity.

Composition and diversity

Measures of the *composition* of animal communities describe which groups or species are present in a community, often with information about their absolute and relative abundances. *Diversity* measures include measures of composition as well as descriptions of the total number of species or groups in a community (eg richness). Alexandrino *et al.* (2017) developed a metric of ecological integrity based on the functional *composition* and *diversity* of the bird communities in the Brazilian Atlantic Forest. The authors computed and compared multiple abundance and richness-based metrics of species composition, separating species into a set of functional trait groups, including traits related to habitat associations (eg forest-dwelling), foraging habits (eg ground versus canopy), endemism, and threat level. From a set of candidate metrics, they selected seven that categorized functional community composition well along a human disturbance gradient, including richness and abundance of species in specific habitat associations and foraging guilds. They then combined these into one ecological integrity index that better detected a gradient of human disturbance than taxonomic diversity metrics, such as total species richness or Shannon diversity.

Function

Animal community *function* metrics describe how the animals in an ecosystem shape how that ecosystem functions, from processes such as nutrient cycling to carbon storage. Gómez *et al.* (2021) demonstrated that functional trait space (a measure of the breadth of many different traits represented in a community) decreased for a bird assemblage in the Andes of Colombia over a century of increased human use. Most of this change in functional diversity was caused by changes in traits related to body size, dispersal ability, and habitat breadth. Over time, specifically for birds in the community, average body size and diet specialization decreased while dispersal ability increased. These changes have implications for ecosystem *functions* such as seed dispersal, carbon storage, and habitat connectivity (Donoso *et al.* 2020; González-Robles *et al.* 2021; Fricke *et al.* 2022).

Connectivity

Animal community metrics of *connectivity* describe the degree of connectedness between different patches of a habitat, either for species or for communities (eg food webs). Understanding measures of connectivity for animal communities can help explain patterns of genetic diversity in populations of moving animals and the other organisms they can help transport (eg seeds) and can shape how food webs are structured across habitat patches. Rocha-Ortega *et al.* (2019) found that the average body size of dragonfly and damselfly communities tracked past and current land use in Mexico, with large-bodied species, which can fly over greater distances to more disparate patches, exhibiting greater resilience to land-use intensification than their small-bodied counterparts. Communities with superior dispersal abilities overall alter the *connectivity* of patches across the landscape. In some cases (eg seed dispersal, and pollination), increased connectivity can benefit ecological integrity. In the case of dragonfly and damselfly communities, however, increased connectivity may negatively influence ecological integrity by

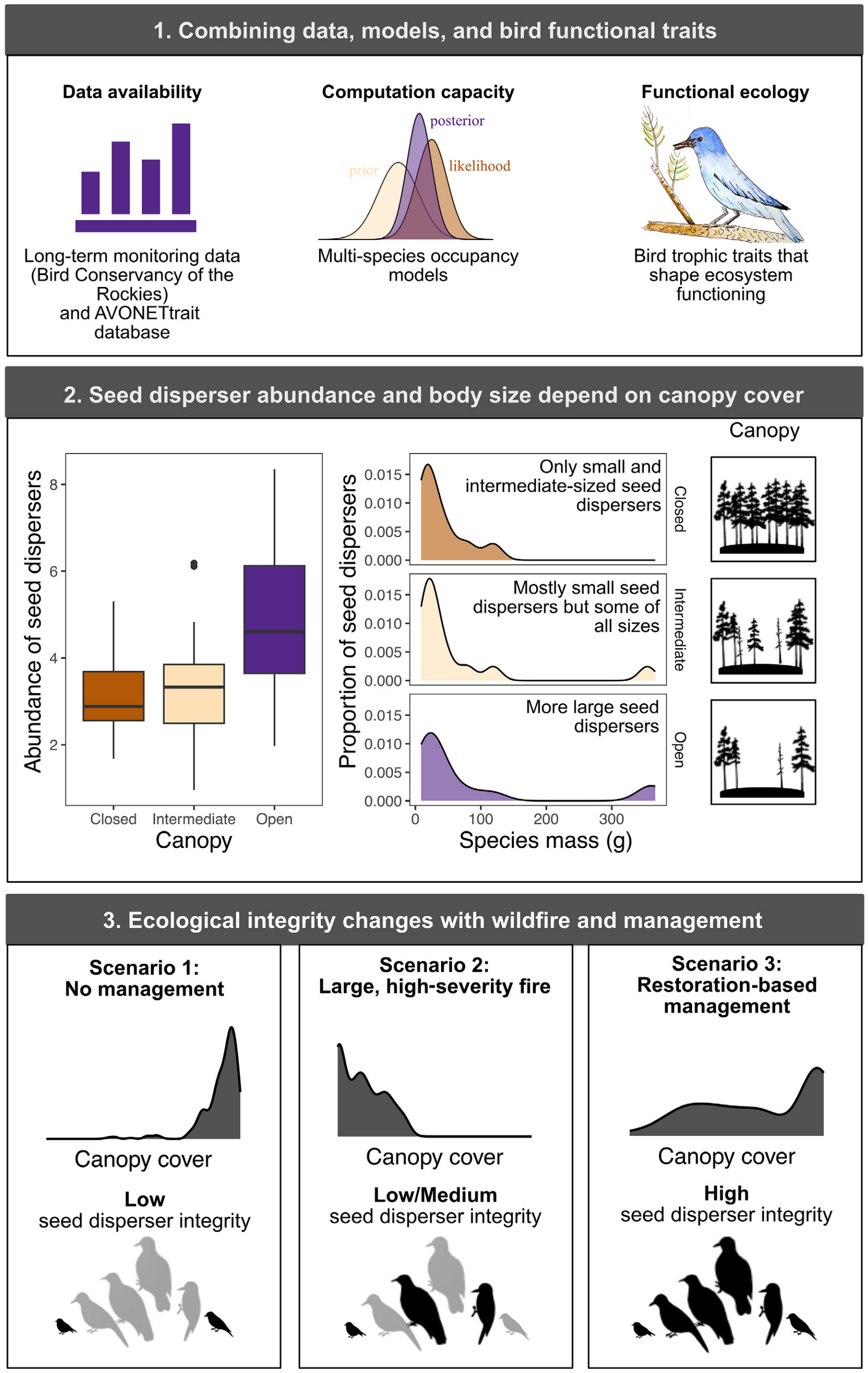

Figure 3. A worked example of monitoring animal communities for ecological integrity using bird community data from Colorado. (1) The combination of expanding data sources and statistical approaches leads to (2) an improved understanding of the functional composition of seed-dispersing birds across a range of habitat conditions, which in turn can lead to (3) predictions of the integrity of seed-dispersing bird communities given a range of land management decisions. Figure was created by Ana Miller-ter Kuile and Jamie S Sanderlin. Bar graph icon is from streamlinehq.com (CC-0 license). Vector images of birds and trees were created by Jamie S Sanderlin. In (2), horizontal lines within boxes depict median values, boxes represent the interquartile range (25th–75th percentiles), whiskers (vertical lines) represent 1.5×interquartile range, and solid circles depict outliers.

increasing the potential for biotic homogenization and loss of patches with distinct biodiversity (Juen and De Marco 2011).

An example for forest restoration and bird community integrity

Using a combination of long-term monitoring of bird communities in Colorado and multispecies occupancy models, Latif *et al.* (2022) reported that many bird species respond to canopy cover conditions in these forests. We combined these results with trait data from the AVONET trait database (Tobias *et al.* 2022) to link bird responses to canopy cover to the key functional role of seed dispersal (Figure 3). Abundance and body size distributions of seed-dispersing birds depend on canopy class ("open", "intermediate", and "closed" canopies). We highlight the consequences for the ecological integrity of seed-dispersing bird communities in three scenarios: (1) "no management" (forests with high tree density due to fire suppression); (2) "a large, high-severity wildfire"; and (3) "restoration-based management" aimed at creating a heterogenous habitat. Due to their limited ranges of canopy conditions, the "no management" and "large, high-severity wildfire" scenarios (scenarios 1 and 2) have lower integrity of seed-dispersing bird communities (both diversity and structure), whereas the "restoration-based management" scenario (scenario 3) has higher integrity of seed-dispersing bird communities due to a distribution of canopy cover that supports bird community preferences across canopy conditions.

The future of ecological integrity monitoring includes animal communities

In conservation and restoration, there is a growing awareness that even actions intended to improve the resiliency and integrity of an ecosystem can have ripple effects that lead to positive, negative, and neutral outcomes for a variety of interconnected ecosystem components (Miller-ter Kuile *et al.* 2021; Pearson *et al.* 2022). Here, we highlighted two reasons why today is a key moment for reconsidering how ecological integrity is quantified, especially for terrestrial ecosystems. First, recent methodological and computational advances permit better monitoring of how management, restoration, and conservation efforts shape ecosystems. Second, characterizing communities in terms of their functional traits is a unifying way in which the ecological integrity of animal communities can be documented. In an applied context, trait-based approaches can employ current and new monitoring approaches (eg field surveys, ARUs) combined with information from trait databases (eg AVONET, FishTraits) and a growing number of computational options for combining historical and modern sampling (eg data integration models). Expanding integrity-based monitoring to include animal community metrics will improve understanding of how communities are structured and how conservation and management actions shape ecosystems, without disregarding crucial players in ecosystems.

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Data Availability Statement

Data and code (Miller-ter Kuile and Jones 2024) for the literature review, a worked example, and generation of figures can be found on Zenodo at https://doi.org/10.5281/zenodo.14520173.

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Supporting Information

Additional material can be found online at http://onlinelibrary.wiley.com/doi/10.1002/fee.2852/suppinfo