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Beyond Species Richness for Biological Conservation

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ABSTRACT

Recent global policy developments have highlighted the need for straightforward, robust, and meaningful biodiversity metrics. However, much of conservation science is dominated by the use of a single metric, species richness, despite several known limitations. Here, we review and synthesize why species richness (i.e., the number of species in a local area) is a poor metric for a variety of topical- and policy-relevant conservation problems. We identify the following three key issues: (1) increasing evidence emphasizes that species richness is often not a robust metric for identifying biodiversity change, (2) species richness ignores species identity and so may often not reflect impacts on species of concern, and (3) species richness does not provide information needed on the persistence of biodiversity or the provision of ecosystem services. We highlight the unappreciated practical outcomes of these limitations with examples from three ongoing conservation debates: whether local biodiversity is declining, how habitat fragmentation affects biodiversity, and the extent to which land sharing or sparing is more beneficial for biodiversity conservation. To address these limitations, we offer a set of guidelines for the use of biodiversity metrics in conservation policy and practice.

1 | Introduction

Biological conservation has a breadth of aims and ambitions, with most goals focused on preventing extinction, promoting ecosystem services, and ensuring the persistence of all existing elements of biodiversity into the future (Ehrlich and Daily 1993; Mace 2014; Rounsevell et al. 2020). This focus has been emphasized by Targets 2 and 3 of the Kunming-Montreal Global Biodiversity Framework (CBD 2022), which aim to conserve and restore biodiversity and ecosystem services, and Target 4, which explicitly aims to reduce human-induced extinctions. This focus is accompanied by, and driving, a rapidly growing range of private and third sector initiatives focused on biodiversity offsetting, net gain, and credits (e.g., Borges-Matos et al. 2023; Wauchope et al. 2024; White et al. 2023). Achieving these international goals and ensuring effective private initiatives depend on biodiversity accounting that tracks changes in biodiversity, determining how conservation and management strategies affect biodiversity, and predicting effects of future global change. Hence, robust metrics to measure the status of biodiversity are needed (Lamb et al. 2009; Santini et al. 2017; van Strien et al. 2012).

The most common metric used in assessing the status of biodiversity across many fields (e.g., sustainability, conservation, ecology) is species richness, or the number of species recorded or estimated to be present in a local area (e.g., a quadrat, forest patch, wetland;

Hillebrand et al. 2018; Purvis and Hector 2000). Gotelli and Colwell (2001) provide a more standardized perspective where they distinguish species density, or the number of species per unit area, from that of species richness, or the number of species for a standardized sample of individuals; here we consider both of these perspectives broadly as species richness metrics. In general, species richness is an intuitively appealing metric for biodiversity conservation because a reduction in the number of species in an area seems obviously to reflect a failure to prevent local extirpations in that area. Collection of data used to estimate local species richness is often straightforward and there are a wide range of well-developed quantitative approaches for deriving metrics of species richness from field observations (Chao et al. 2014; Kery and Royle 2016). Simply put, species richness is a logistically feasible and appealing biodiversity metric because it is easy to measure, intuitive, and is straightforward to communicate to decision makers (Fleishman et al. 2006).

These attractive features of species richness and its widely perceived utility have led to it often being used as the principal, and sometimes the sole, biodiversity metric considered in ecological- and conservation-focused research and decision-making (e.g., Paillet et al. 2010). Based on a collection of 14,720 articles, Hillebrand et al. (2018) found that species richness was more frequently used than any other biodiversity metric and emphasized that "Unfortunately, a single facet of biodiversity, species richness, has become the most dominant measure of biodiversity and its change." In a recent summary of articles that synthesized biodiversity responses to environmental change, 80% of 237 comparisons from 194 articles considered species richness and 18% (43) focused exclusively on this metric (Liu et al. 2023). Species richness dominates debates about different approaches to conservation (e.g., Cardinale et al. 2018; Dornelas et al. 2014; Fahrig 2015; Hanski 2015) and future scenarios of global change (Leclère et al. 2020; Newbold et al. 2015). It is also prominent in emerging issues in conservation such as the use of nature-based solutions, biodiversity positive infrastructure, and biodiversity credits (van Rees et al. 2023; Wauchope et al. 2024).

Species richness metrics also feature prominently in policy targets and guidance documents. For instance, the EU Directive on the promotion of energy use from renewable sources states that energy from biomass should not count toward EU targets for renewable energy if obtained from conversion of species-rich habitats unless production did not affect the biodiversity value of that area (EU 2018). The ubiquitous usage of this indicator in conservation practice is exemplified by its prevalence in policy documents and gray literature: searching for the term "species richness" in the Overton database (Overton 2024) yields 19,174 policy documents or reports between 1985 and 2023, where the number increased considerably between 1995 and 2015 and has been stable annually since that time (Figure 1). This is clearly an underestimate as policy documents frequently use related terms (e.g., number of species) not captured in this search. While some policies and agencies concerned with implementing conservation actions focus on biodiversity metrics that capture population status of individual species and aggregates thereof (Collen et al. 2009), research often focuses on richness (Hillebrand et al. 2018), leading to a disconnect between research results and practitioner needs.

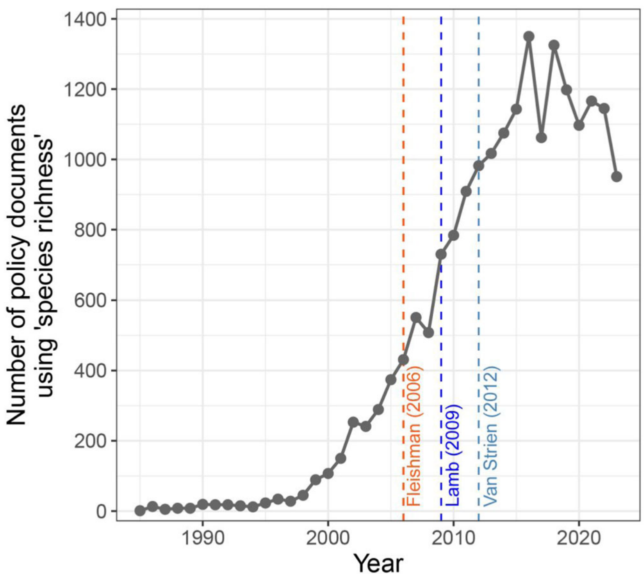

FIGURE 1 | The number of policy documents that mention species richness has increased considerably over time, and increases continued despite research between 2006 and 2012 that highlighted its limitations for conservation. Shown are the number of policy documents between 1985 and 2023 based on the Overton database and reference years for key publications that illustrated the limitations of using species richness in general (Fleishman et al. 2006) and specifically as an indicator metric in conservation (Lamb et al. 2009; van Strien et al. 2012).

Despite the prevalence of using species richness metrics, several serious limitations to the value of species richness for conservation assessments have been identified (Fleishman et al. 2006; Margules and Usher 1981; Robinson et al. 2014). Nonetheless, its use continues to be common (Figure 1), and the extent to which these limitations may hamper conservation in practice remains unclear. We contend that several disagreements in the conservation literature stem, in part, from the use of species richness obscuring fundamental issues relevant to the evaluation of conservation strategies. Here, we argue that species richness often fails to provide reliable answers for biodiversity conservation when the goal is to promote the persistence of biodiversity now and into the future. Co, establishing that a conservation intervention enhances species richness may not mean that it helps achieve long-term conservation goals.

We synthesize evidence on the value of species richness as a conservation metric and offer general guidance for moving beyond the use of species richness as a primary metric for conservation. We have three overarching objectives. First, we identify three key issues that hamper its utility. The first issue is that increasing evidence suggests that species richness is often not a robust metric—it is more prone to bias and sensitive to effort, study design, and scale than several other metrics. The other two issues are more fundamental, in the sense that species richness hides species identity and does not capture information needed for promoting the persistence of biodiversity. Second, we illustrate the practical importance of these issues with examples from recent conservation assessments and ongoing conservation debates. Lastly, we propose guidance about the use of biodiversity metrics for conservation purposes.

2 | Desirable Characteristics of Biodiversity Metrics and the Utility of Species Richness

2.1 | Biodiversity Metrics Need to be Robust

> The number of species in a sample (sample richness) is a very flawed measure of diversity. (Roswell et al. 2021)

Studies of local species richness typically aim to estimate the number of species occurring within a defined area. The ideal data would be a complete census, identifying every species and covering the entire area over a biologically relevant time period. However, this ideal is rarely, if ever, achieved for obvious practical reasons. Rather, studies use sampling strategies (e.g., transects) to estimate richness for a given spatial extent and time period. The resulting estimates of local species richness are therefore usually subject to both sampling error and bias, and are sensitive to effort, study design, and scale. This sensitivity is often greater for species richness than for other metrics (Lamb et al. 2009; van Strien et al. 2012).

Sampling error leads to a lack of precision, which can make a metric insensitive for capturing true variation in biodiversity, whereas bias can lead to incorrect conclusions due to inaccurate or skewed estimates. Sampling error and bias come from five common sources: incomplete detection, limited sampling effort, size of plot and study system relative to the question of interest, location of plots, and time period considered (Williams et al. 2002). The problems of incomplete detection and effort are often linked, where limited sampling effort is likely to increase chances of imperfect detection. Richness is well-known to be sensitive to imperfect detection and sampling effort, and both interpolation and extrapolation approaches have been developed to adjust estimates to address these issues (Chao et al. 2014; Kery and Royle 2016). For instance, rarefaction is a resampling-based interpolation method commonly applied to address the limited sampling effort problem that as more individuals are sampled, more species will be observed (Gotelli and Colwell 2001). Yet, it is often less clear how conservation applications should address sampling problems. For example, there is increasing use of multispecies occupancy modeling as a "gold standard" for reliably accounting for sampling error and imperfect detection when estimating species richness (Roswell et al. 2021). Despite their utility, when applying such models to conservation interventions, the ability of models to capture intervention effects on rare species is poor because models rely on "borrowing information" from common species to inform estimates for rare species. However, rare species often differ from common ones in key ecological attributes, meaning that such approaches may obscure intervention effects on rare species. Consequently, it is often recommended that rare species are not included in richness estimates when assessing interventions (Kery and Royle 2016). While excluding rare species may increase the reliability of biodiversity metrics, it comes at the expense of no longer estimating true richness of the entire community and unfortunately omitting the species of most concern in designing or evaluating conservation efforts.

Species richness is also well-known to be highly sensitive to changes in spatial scale in complex ways (Chase et al. 2019), particularly in terms of changing plot (or grain) size (Palmer and White 1994). Furthermore, the spatial location of plots matters: if plots are located near areas with different environmental conditions, "spatial spillover" can occur (Blitzer et al. 2012). Species often occur in areas adjacent to those they inhabit most of the time and depend upon, which can be particularly problematic if areas with high sampling effort are more likely to be near areas with different environmental conditions (e.g., sampling near roads or edges). Finally, richness estimates are not robust over time. This is because changes in species richness over time are asymmetric: a single individual of a new species increases richness, but all individuals of a species must be lost to cause a decrease in richness (Chase et al. 2019). He and Hubbell (2011) find that this asymmetry helps explain why species-area relationships overestimate extinction rates from habitat loss for birds in the United States by potentially 160%. Such asymmetries pose challenges for interpreting biodiversity changes over time and may be contributing, in part, to the ongoing debate on whether local biodiversity is declining (Box 1).

Many of the above factors are not only relevant to species richness but are more broadly relevant to other biodiversity metrics. However, several investigations have contrasted the sensitivity of species richness to these (and other) issues relative to other biodiversity metrics. Lamb et al. (2009) contrasted 13 different metrics for capturing biodiversity change under several scenarios, finding that species richness had low power in detecting trends and was sensitive to detection error relative to other metrics. van Strien et al. (2012) proposed six desirable properties for biodiversity indicators and found that species richness was poor at satisfying them relative to some other metrics considered. Valdez

BOX 1 | Species richness is not a robust metric for interpreting temporal trends in local biodiversity

There is an enduring and heated debate on whether local biodiversity is declining, much of which has centered on changes in species richness over time (Cardinale et al. 2018; Dornelas et al. 2014; Vellend et al. 2013). For example, Vellend et al. (2013) report no net changes in plant species richness over time based on a global meta-analysis. But changes in species richness over time are asymmetric—a single individual of a new species increases richness, whereas all individuals of a species must be lost to cause a decline in richness—which can lead to a tendency for species richness to be stable or increase even in situations where most species are declining in abundance. Kucynski et al. (2023) illustrate systematic biases in species richness estimates when environments change because richness tends to capture earlier detections of colonizations than extinctions for the same change in population numbers. In contrast, when species abundance is considered, providing more symmetrical information on population change, declining local trends frequently emerge (e.g., Jandt et al. 2022). Recent analyses also suggest that the ability to reliably assess trends in species richness across broad scales may be limited (Santini et al. 2017; Valdez et al. 2023). Taken together, these findings indicate that species richness as a metric of biodiversity change over time is not robust.

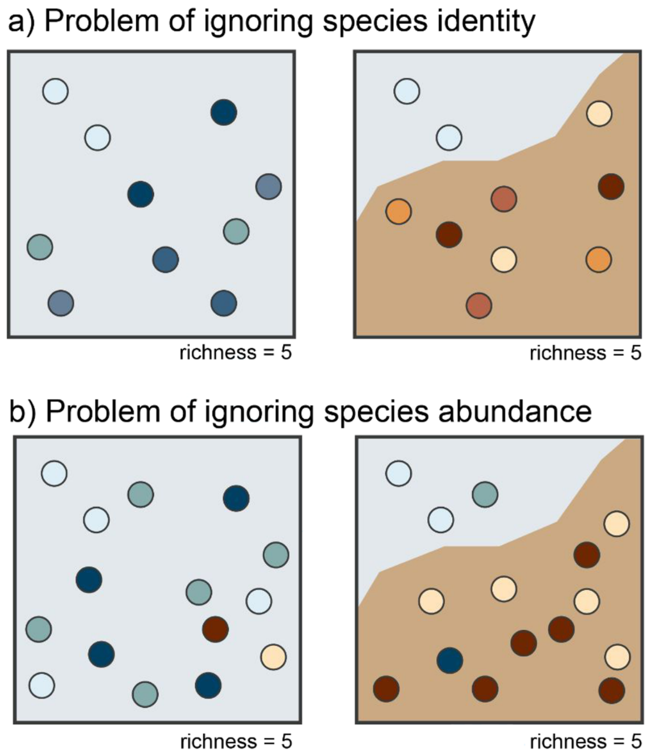

FIGURE 2 | Problems arising when species richness is used to assess management, interventions or environmental change. Shown are hypothetical species records before (left) and after (right) habitat management is implemented (brown shaded). Species are dots, with species identity coded as a color. (a) Four species are gained with habitat management, but richness is unchanged. (b) Each species changes in abundance but richness is again constant.

BOX 2 | Species richness, species identity, and assessing interventions

Species richness is a common metric used in assessing habitat restoration and rewilding interventions. In this context, richness can be misleading when the species included are not associated with intervention goals. We illustrate this problem by reanalyzing data on changes in bird assemblages over time with passive rewilding of an abandoned farmland area over a 33-year period in northeast England, with the goal of restoring woodland habitats (Broughton et al. 2022). Broughton et al. sampled bird communities with the passive rewilding of a farmland. Over time, succession occurred and the abandoned farm transitioned into shrubland. Woodland bird species increased in both number and abundance over time (Figure B1), which highlights the success of the intervention goals. However, total species richness declined over this period. If considered in isolation, total species richness would provide the wrong answer in terms of whether goals were met. The decline in total richness was driven by a loss of farmland species. Using a metric of extrapolated richness (the Chao estimator) produced similar conclusions, as does Shannon diversity based on Hill's numbers. Overall Simpson diversity based on Hill's numbers slightly increased, as this metric places greater weight on common species than rare ones.

et al. (2023) assessed the extent to which local species richness could detect global biodiversity trends, testing how several factors (e.g., sample size, sample interval, scale, measurement error) may influence trend assessment; they concluded that species richness was simply not a robust and sensitive metric for accurately detecting global biodiversity trends. One key reason why species richness is not robust for detecting biodiversity trends is that it ignores species identity.

2.2 | Biodiversity Metrics Need to Address Species Identity

> Focusing on total species richness, without considering the number of conservation-relevant species, may lead to misleading conclusions for conservation purposes. (Lelli et al. 2019)

Species richness has a well-known limitation of ignoring species identity in that it is a count or estimate of the total number of a selected set of species present at a site or in a region (Figure 2; Fleishman et al. 2006). Ignoring species identity has resulted in much disagreement in the literature, such as whether edge effects are positive or negative for biodiversity (Pfeifer et al. 2017). The principal problems in this regard concern the set or sets of species chosen for study and comparisons. When a study ignores differences in the conservation significance of the species (e.g., IUCN status) included in it, this can greatly obscure or diminish the value of the results for conservation. Fundamental issues for conservation may be masked, such as biotic homogenization occurring through the replacement of specialists with generalists (Newbold et al. 2018), whether differences in richness are driven by non-native or invasive species (Vila and Ibanez 2011), and the extent to which the most conservation-relevant species (e.g., restricted range, endemic, threatened) are affected (Lelli et al. 2019; Simberloff 1998). Thus, species are often included in richness metrics even though they are not relevant to the intended purpose of a conservation intervention, masking or even reversing the apparent conservation effect of an intervention (Box 2).

The problem of ignoring species identity is not only that inappropriate species may be included for interpreting conservation problems, but also that the conservation problem itself can be ill-defined for the species being considered. For example, when conservation problems focus on managing, restoring, or conserving "habitat," assessments that use species richness often assume a false equivalence of species habitat across the entire community (e.g., a forest is "habitat" for all species counted), despite the fact that "habitat" is perceived and used differently by each individual species (Hall et al. 1997). This leads to the description of habitat being intrinsically incorrect when considered across multiple species, which may invalidate conclusions when the focus is on the pattern, structure, or quality of habitat. Such issues have arisen both when applying species-area relationships in conservation (e.g., Matthews et al. 2014) and when interpreting the effects of habitat loss and fragmentation on biodiversity (Box 3; Betts et al. 2014), which has contributed to contentious debate

BOX 3 | Ill-defined conservation problems and species richness: "habitat" fragmentation

There is ongoing debate on the effects of habitat fragmentation, or the breaking apart of habitat for a given amount of habitat loss (Fahrig 2017), on biodiversity, and species richness has featured prominently in disagreements (Valente et al. 2023). Because species often have dissimilar habitat requirements (Hanski 2015), the aggregation of occurrences across species can lead to inappropriate conclusions when interpreting "habitat" fragmentation. In this way, land-cover categories used to assess fragmentation (e.g., "forest") may not reflect patterns of habitat for individual species, or places where a species can survive and reproduce (Hall et al. 1997). A landscape may, for example, have highly fragmented habitat for a specialist species, but habitat for generalist species may be less fragmented (and more abundant; Figure B2). Thus, the aggregation of species into a species richness metric assumes a false equivalence for habitat of individual species and patterns of land-cover fragmentation may not be relevant to actual habitat fragmentation for species, such that both habitat loss and fragmentation (e.g., number of patches) are ill-defined. When habitat fragmentation is quantified based on species' habitat requirements, positive effects of landcover fragmentation often become negative when based on habitat instead (e.g., Halstead et al. 2019). Results like these help explain why ecological theory, which is grounded in habitat-based principles, can sometimes lead to different conclusions about fragmentation than empirical studies focused on land cover.

on whether fragmentation may be beneficial for biodiversity (Valente et al. 2023).

Some approaches that attempt to circumvent these issues include subsetting the community based on species traits and using complementarity-based approaches. Subsetting species based on traits can help to focus on groups of species intended to be the principal motivation of conservation interventions (Box 2). Such approaches can be helpful but can be ad hoc and are typically based more on what trait data are available rather than on prior definition of conservation-relevant traits (van Strien et al. 2012). Functional diversity metrics based on species traits do not solve these issues and have been shown to poorly capture species trends (Santini et al. 2017). Community composition and beta diversity analyses honor species identity in their calculations. However, these approaches often summarize this information in ways that either make it challenging to relate back to species identities (e.g., nonmetric multidimensional scaling techniques) or make it nuanced for interpretation, such as high beta diversity potentially being both a desirable and undesirable conservation outcome, depending on the situation (Socolar et al. 2016). A focus on species complementarity in spatial conservation planning can help address some issues, where species identity is considered in terms of representation relative to occurrence in other areas (Kukkala and Moilanen 2013). Yet these approaches, while potentially helpful, may still be sensitive to similar problems from ignoring species identities. By keeping track of species identity, it will also become more feasible to track the potential for species persistence.

2.3 | Biodiversity Metrics Need to Address Species Persistence

> Species richness provides no information on density or demography and thus provides no insights to likelihoods of species persistence. (Fleishman et al. 2006)

At its core, species richness says very little about the status of species at a given site or region. Only information on the incidence of species at a location is used. However, incidence alone does not mean that a species' presence is meaningful from a conservation perspective: A single individual, a sink population, an ecological trap, a rapidly declining population, or even transient individuals will be recorded in the same manner as a large, self-sustaining, or increasing population but has very different connotations for conservation (Figure 2). Other measures that reflect abundance, reproductive performance, survival, dispersal, habitat quality, and role in ecosystem functioning provide richer insights for the achievement of conservation goals (Bock and Jones 2004). For example, species richness can be high in the wildlife-friendly agricultural landscapes of Costa Rica, yet species are often less likely to breed in these areas than in nearby protected areas (Ke et al. 2024). Detailed demographic information can be too resource-demanding to be feasible to track for many species in most systems, but information on species abundance is often available or can be estimated from standard biodiversity surveys. In practice, this information is often discarded as not providing robust information on abundance, although in many situations it may still provide useful information to better interpret biodiversity change. As changes in abundance are more closely linked to extinction risk than species incidence, abundance-based metrics have been promoted to better assess goals in biodiversity conservation (Callaghan et al. 2024; Geldmann et al. 2023) and are used in some important conservation assessments, such as the Living Planet Index (Collen et al. 2009).

When abundance is considered, three related summaries include: (1) proportional abundance among species, (2) total abundance summed across species, and (3) (relative) abundance for individual species. Proportional abundance describes the relative dominance of species within a community and is used in metrics such as Simpson's diversity or Shannon's evenness (and related Hill's numbers; Roswell et al. 2021). Incorporating proportional abundance is helpful for understanding problems of species evenness and related properties, but resulting metrics ignore species identity and can be insensitive and misleading for detecting biodiversity change relevant to conservation (Santini et al. 2017; Williams et al. 2017). Total abundance (or biomass) summed across species is commonly reported (see, e.g., Vereecken et al. 2021) but suffers from issues of ignoring species identity as described above. We argue that reporting the absolute abundance of individual species, or each species' abundance relative to some reference value or state such as that in undisturbed habitat (McNellie et al. 2020), is often more helpful for conservation problems (see also Callaghan et al. 2024). Abundance can fluctuate more than occurrence, and may thus better track key changes in the environment, although care should be taken to not overinterpret "noisy" abundance variation. Differences among species in their contributions to ecosystem services and functioning are often driven by abundance (Dee et al. 2023; Gaston and Fuller 2008) and population trends and persistence are driven by changes in abundance (Collen et al. 2011). For instance, incorporating species abundance through density-yield curves in the land-sharing/land-sparing framework illustrates how richness alone can be a misleading metric for this conservation problem (Box 4). Information on abundance is essential for diagnosing decline and recovery of species and may better capture the resilience of biodiversity to ongoing environmental threats (Capdevila et al. 2022). Finally, assessments of the efficacy of biodiversity metrics often conclude that abundance-based metrics are more reliable than incidence-based metrics, as they are more sensitive to different types of pressures and behave more predictably (Lamb et al. 2009; van Strien et al. 2012).

BOX 4 | The importance of species abundance versus richness in the land sharing/land sparing framework

The land sharing/land sparing framework was developed to assess how region-wide populations of a set of species are affected by the agricultural yield of the farmed part of the region (Green et al. 2005). Land sharing involves farming much or all of the landscape at relatively low yields so that farmed land supports more biodiversity, while sparing involves producing the same total amount of food at higher yields thereby making more space for natural land elsewhere in the landscape (Phalan et al. 2011). Based on survey data for Ghanaian birds, species richness declined with increasing agricultural yield ($r = -0.837$; $p < 0.001$; Figure B3a), so if richness is taken as a meaningful metric of conservation outcome, land sharing would be identified beneficial for the region's bird fauna. However, farming using only low-yielding methods would (assuming 2007 region-wide food production) result in almost half of species having region-wide population sizes 50% or more below the baseline population size expected with no farming, whereas adopting high-yielding methods and sparing the land not required for production would reduce this proportion to zero (Figure B3b; note that sparing outperforms sharing even more if region-wide food production increases). This result arises because a high proportion of species in the region (48%) have negative-trending convex functions relating local population density to local farm yield (Figure B3c). These species can be considered "land-sparing loser" species (i.e., species that decline with yield but have higher abundance in a sparing than sharing context; Phalan et al. 2011) and include most of the regionally endemic and threatened species. A much smaller proportion (24%) are land-sharing or intermediate losers (i.e., species that decline with yield but reach relatively higher abundance in a sharing context), which typically have hump-shaped or concave density-yield curves. Winner species (28%), or those that increase with yield, were absent or scarce in the absence of farming and are of minimal conservation concern in this region. Abundance-based analyses designed to assess impacts on the persistence of biodiversity thus identify that the most beneficial land-use strategy for birds in this region would be to maintain large areas of native vegetation, even though that requires high-yielding farming with reduced species richness on farmland (for similar conclusions for birds, beetles, and trees in Mexico; see Williams et al. 2017).

3 | Guidance for Better Application of Metrics

> A good index should also be clearly related to particular management objectives or biodiversity outcomes. (McCarthy et al. 2014)

Given these limitations of species richness and their practical consequences (Boxes 1–4), how can metrics move beyond species richness in a helpful way for biodiversity conservation? Metrics for biodiversity assessments and their application to conservation policy and practice should have several desirable properties (Buckland et al. 2005; Lamb et al. 2009; McCarthy et al. 2014; Santini et al. 2017; van Strien et al. 2012). While continued assessments of metrics and their utility are needed, we offer a set of guidelines that involve 10 steps for the general use of metrics to inform biological conservation, including policy guidance on biodiversity reporting (e.g., protocols for evaluating biodiversity offsets or credits; Borges-Matos et al. 2023; Wauchope et al. 2024) and monitoring aimed at understanding conservation interventions (e.g., rewilding; Torres et al. 2018). These guidelines reflect how metrics should be considered in the context of conservation goals; the design of monitoring and research to address those goals; and the analysis, reporting, and interpretation of metrics (Figure 3).

When designing studies

1. Design metrics to address objectives: Be clear what the conservation objectives are and how information like species richness may or may not be relevant to them. For instance, if the goal of an intervention is to increase the persistence of biodiversity, to what extent does species richness inform understanding of that goal? Would other metrics (see, e.g., Lamb et al. 2009; Santini et al. 2017; van Strien et al. 2012) be more informative for reliably addressing the goal? We argue here that for most objectives, species richness is unlikely to be the most appropriate metric and several other metrics may be more useful (Burgess et al. 2024). We emphasize that the solution is not to fall back onto single-species monitoring and conservation strategies but rather to keep track of species identity in such a way that decisions can be made in the context of species attributes, vulnerability, conservation concern, etc. For instance, both the LIFE (Eyres et al. 2025) and STAR metrics (Mair et al. 2021) provide insights into species-specific potential extinction risks that can be summarized across terrestrial vertebrates and used to assess land-use change and restoration interventions.
2. Identify individual species: Collect data that allow for reliable analysis and reporting of individual species, particularly those of conservation concern. If needed, such data can be pooled later for metrics like species richness but provide flexibility for reporting more valuable information on individual species.
3. Measure abundance: Sample in a way that provides robust information on species abundance, or at least abundance

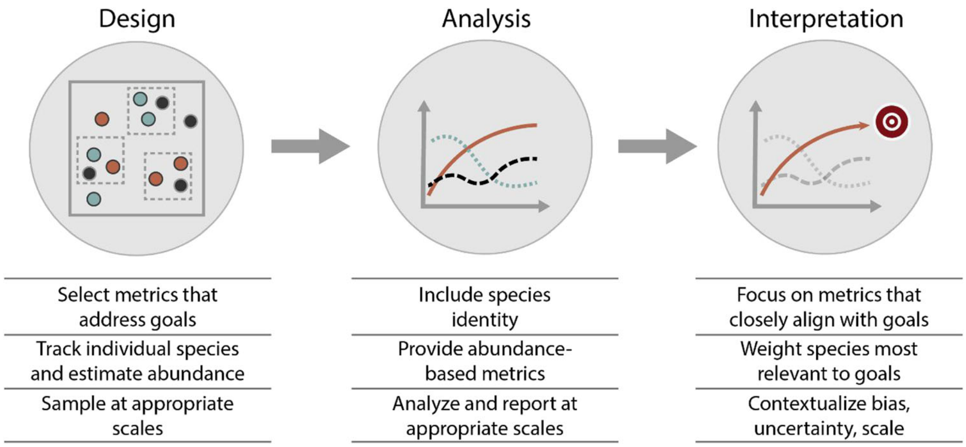

FIGURE 3 | Guidance for moving beyond species richness in conservation assessments, focusing on the design, analysis, and interpretation of studies. Each component aims to reduce the three fundamental limitations of species richness for biological conservation.

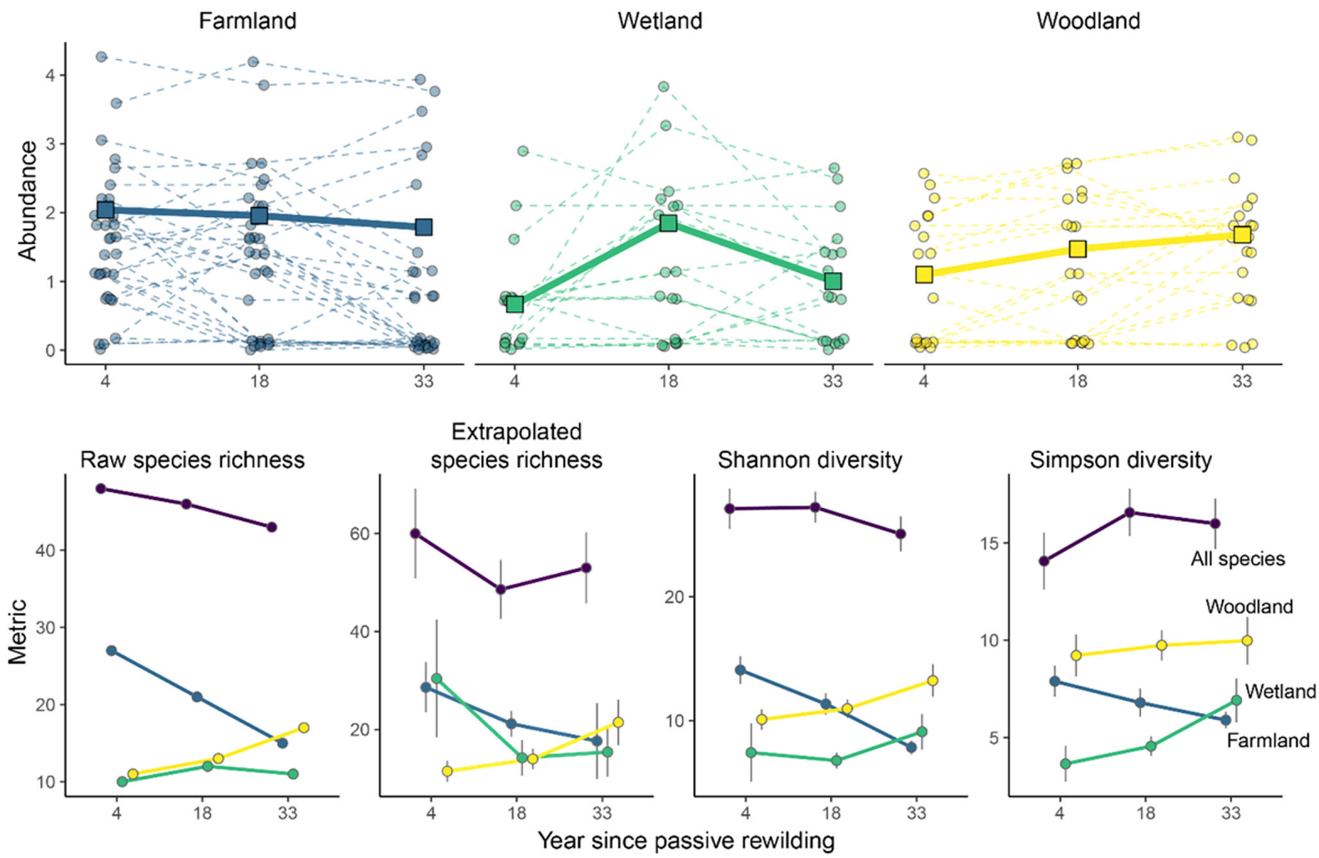

FIGURE B1 | Contrasting changes in individual species abundance, species richness, and diversity with passive rewilding based on the entire assemblage and by habitat association. Data from Broughton et al. (2022), reanalyzed for this paper. For species abundance, values were log-transformed and jittered for visualization, with individual species shown as dashed lines and the average across species shown as solid lines.

relative to that in other locations. Survey methods that allow for incomplete detection are desirable. There are several emerging prospects for rapid estimation of (relative) abundance, such as the use of passive acoustic recordings (Gibb et al. 2019; Van Parijs et al. 2009). In addition, spatial and temporal variation in occurrence can be used to quantify relative abundance (Farr et al. 2022; Yin and He 2014). While abundance estimation can be more challenging than occurrence in many situations, we contend that imperfect abundance information may often still be preferred to an alternative of not considering such information at all.

4. Sample at appropriate scales: Sample at appropriate scales for addressing objectives (both in terms of grain and extent). Species richness is well-known to be sensitive to scale (Chase et al. 2019), and while other metrics are often less

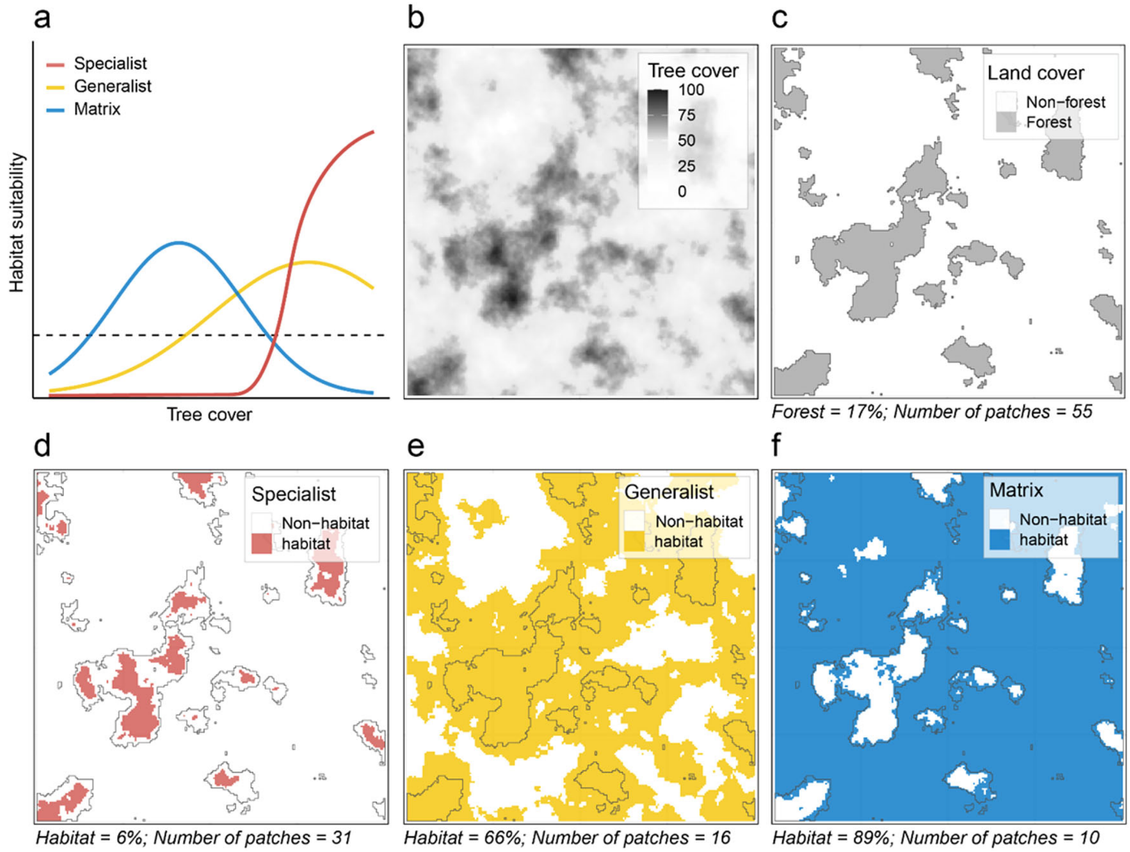

FIGURE B2 | The problem of pooling species when interpreting habitat fragmentation. Consider three species across a gradient of tree cover, with one that specializes on forest habitats ("specialist"), a second that uses forest but is a "generalist" and can have high fitness in areas of relatively low tree cover, and a third that specializes on non-forest (or "matrix"). (a) Habitat suitability relationships as a function of tree cover, with the horizontal dashed line showing a minimal suitability value for persistence. (b) A landscape that varies in tree cover, which is (c) categorized as forest and non-forest. The habitats for these species are different, where (d) the specialist largely tracks forest land cover, (e) the habitat generalist spills over into many non-forested areas, leading to less fragmented habitat, and (f) the habitat for the matrix species is largely the opposite to that of the specialist and is abundant and relatively contiguous. For each species, the proportion of habitat remaining in the landscape and the number of patches differs. For (d–f) forest polygons are overlaid for comparison to species habitat.

so (van Strien et al. 2012), it remains imperative that scales considered are relevant to objectives. Often fine-grained sampling can be helpful because samples can be combined to consider larger grains. Extents should generally be large to capture the potential for spillover and leakage that may alter conclusions.

When analyzing and reporting metrics

1. Include species identity in metric reporting: Never report only total species richness or use total species richness exclusively for conservation guidance. Breaking down richness into its components that honor species identity can be helpful but be mindful of the limitations when information is based on incidence alone (See Section 2.3).
2. Report abundance-based metrics: Provide and use information on species abundance when it is available. Often data on abundance are collected in field campaigns that estimate species richness but are discarded because abundance information may be less accurate than that of occurrence. Examples of abundance-based metrics include estimators of abundance from repeated sampling such as *N*-mixture models or dynamic *N*-occupancy models (Rossman et al. 2016), and indices such as the geometric mean abundance index (Buckland et al. 2011) and Nielson's abundance index (Nielsen et al. 2007). Avoid simple lumping of counts into "total abundance" across species to avoid obscuring species-specific differences.
3. Report at appropriate scales: Assess outcomes at relevant scales for the conservation objective, which is often at large (landscape) scales, but report information in a way that allows conclusions to be made across scales (Fletcher et al. 2023). In addition, acknowledge potential for spatial spillover, leakage, etc., which may alter conclusions in conservation assessments.

When interpreting metrics

1. Focus on metrics that align with objectives: Focus on the metrics that are most closely aligned with conservation goals (Burgess et al. 2024). In doing so, this will typically de-emphasize reliance on species richness in favor of met-

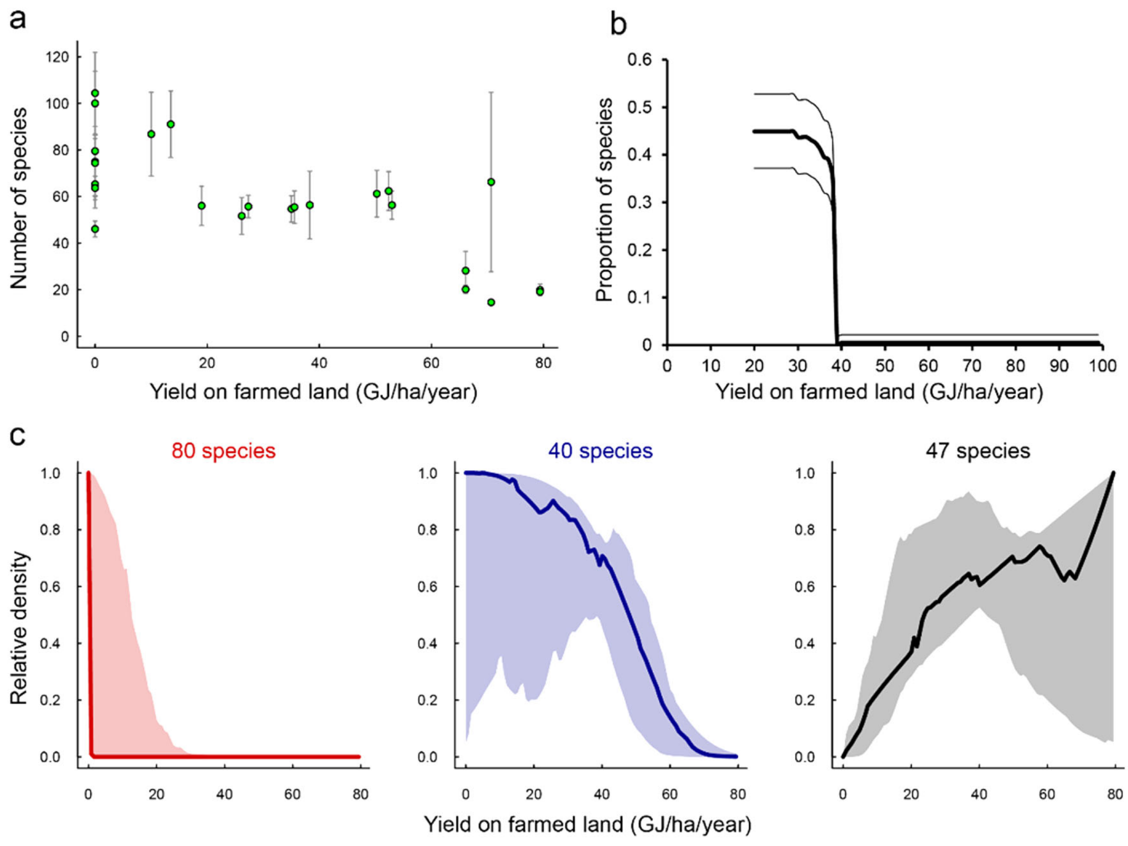

FIGURE B3 | (a) Estimated species richness (Chao2, mean ± SD) of birds on 25 1-km square plots in southwestern Ghana in relation to local annual food energy yield (GJ/ha/year) from the whole of each plot in the same plots. (b) Proportion of bird species with modeled region-wide population size less than half of the baseline population level expected if the whole region was forest in relation to modeled average farm yield in the farmed part of the region, assuming region-wide food production is at 2007 levels. The thin lines show Clopper–Pearson exact 95% confidence intervals for the proportion. (c) Median density-yield curve for bird species divided into three broad categories: land sparing losers (left), which are species that always have a higher population when agriculture is concentrated on as small an area as possible and other land is retained as native vegetation; land sharing and intermediate losers (center), which do best with more extensive farming at yields below the maximum; and winners (right), which are either absent from areas of native vegetation, or which have larger populations under any farming scenario than they would in the absence of agriculture. For further details see Phalan et al. (2011).

rics that more closely reflect the likelihood of population persistence or ecosystem services.

2. Emphasize species appropriate to objectives: Conservation interventions often focus on altering potential habitats via creation, restoration, or rewilding. Focusing on appropriate species, such as habitat specialists and endemics (Lelli et al. 2019), is particularly relevant when assessing "habitat" in land-use change, restoration, and management (see Box 3).
3. Contextualize potential bias and uncertainty: To the extent that the above suggestions are not possible, provide assessment for potential errors or provide information as to why limitations are not relevant given the conservation objective(s).

The application of these recommendations will often require a structured approach to conservation assessments and investment in better (or more intensive) monitoring. But doing so will improve understanding of the effectiveness of conservation policy and provide more reliable guidance for future decision-making. For example, to assess ecosystem condition in both tropical and temperate forests, the UN System of Environmental Economic Accounting—Ecosystem Accounting (SEEA) proposed both tree and bird species richness as indicators for monitoring and reporting on status and trends (UN 2021). Given that the objective is to assess ecosystem condition, our guidelines emphasize that indicators more closely aligned to ecosystem function (and potential services), such as the abundances of key species that are important to limiting functions (e.g., pollination) would provide better information to address this goal. In many situations, addressing objectives (like ecosystem condition) may require multiple indicators, more intensive monitoring, and a greater funding investment than is presently the norm. In this and other situations, we emphasize reliable indicators may require a more precise or detailed description of goals, such as rather than having a goal of "ecosystem condition," a more detailed set of goals (e.g., pollination services) may be required. Such indicators should be sampled and interpreted at the ecosystem scale. Policy for biodiversity offsetting is rapidly evolving and based on an analysis of policies from 108 countries, with the exception of habitat-based metrics (e.g., habitat area, condition), species richness is the most common biodiversity metric being applied (Marshall et al. 2024). Given the known limitations of habitat-based and species richness metrics (Hanford et al. 2017; Marshall et al. 2022), our recommendations provide a general template for devising more appropriate offset metrics.

4 | Looking Forward

There is an increasing need and urgency for metrics to support public and private sectors in reducing their impacts on biodiversity (Burgess et al. 2024). In the private sector, increasing regulation around biodiversity net gain, or no-net-loss, as well as increasing awareness of reputational risks, and the potential emergence of biodiversity credit markets are together driving the development of a range of reporting systems for calculating and monitoring biodiversity impacts (Marshall et al. 2024; White et al. 2023). The success of both public and private sector initiatives is dependent on robust, reliable, and relevant biodiversity metrics.

While species richness is a straightforward summary statistic and will no doubt continue to be reported, it is rarely an appropriate primary metric for conservation assessments. Mounting evidence also suggests that it can obscure fundamental issues regarding the persistence of biodiversity and the provision of ecosystem services, and that it has in turn led to misleading conclusions about what actions to take to achieve conservation goals. We urge the conservation community not to use species richness as anything other than the barest of starting points for understanding biodiversity data, and to base conservation policy and decisions on richer, more informative metrics (Burgess et al. 2024). Our guidance provides a template for realigning assessments to achieve conservation goals.

Author Contributions

R.J.F., R.E.G., B.T.P., P.W.A., and A.B. conceived the study. R.J.F. wrote the first draft of the manuscript. All authors contributed substantial effort in ideas and revisions of the manuscript.

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Data Availability Statement

The authors have nothing to report.

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