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# Dark diversity: shedding light on absent species

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**Ecological theory and nature conservation have traditionally relied solely on observed local diversity. In this review, we recommend including those species that are absent from an ecosystem but which belong to its species pool; that is, all species in the region that can potentially inhabit those particular ecological conditions. We call the set of absent species 'dark diversity'. Relating local and dark diversities enables biodiversity comparisons between regions, ecosystems and taxonomic groups, and the evaluation of the roles of local and regional processes in ecological communities. Dark diversity can also be used to counteract biodiversity loss and to estimate the restoration potential of ecosystems. We illustrate the dark diversity concept by globally mapping plant dark diversity and the local:dark diversity ratio.**

## Local diversity and the species pool

Biological diversity is a central topic of ecological theory and conservation biology. A plethora of approaches exists just to quantify species diversity [1]. Describing patterns of species diversity and understanding the underlying processes presents a major challenge for ecologists [2–4]. Different authors have attributed the variation in the observed number of locally coexisting species either to small-scale biotic interactions [5,6], or to large-scale processes, such as diversification and historic migration [7–9] or dispersal [10,11]. Various aspects and measures of biodiversity have also served as conservation indicators and objectives [12–16]. Species diversity is widely surveyed within local monitoring schemes [17–21] and maximizing biodiversity is often regarded as a major goal of nature conservation to 'compensate' for extinctions [22] and to support ecosystem services [23,24]. The main focus of all these approaches is on, almost without exception, the absolute quantity of observed local diversity.

However, considering only observed local diversity in ecological theory and biodiversity conservation constitutes a major pitfall. The absolute values of biodiversity are unlikely to be suitable for the comparison of biodiversity in relative terms across ecosystems, regions or taxonomic groups. For instance, should one consider 100 vertebrate species recorded in a tropical forest to be species rich or species poor? How many more species can this forest potentially house? Is the local community saturated with species or are open niches available to newcomers? Can diversity increase if more habitat area is restored? To address these theoretical and applied challenges, there is a need to not only make suitable quantifications of local observed diversity, but also, more importantly, to address the absent part of biodiversity that theoretically can inhabit a particular site.

To measure the absent part of biodiversity requires a habitat-specific approach. One cannot estimate the missing part simply by surveying diversity within a larger area, because this would include species from different habitat types, many of which cannot tolerate the ecological conditions in the study site. Instead, attention needs to be focused on the regional species pool: that is, the set of species in a region that can potentially inhabit a site owing to suitable local ecological conditions [25–27]. This seemingly subtle change in approach, shifting from the total number of species in a region to only the portion that can inhabit the study site, enables the ecologically meaningful set of absent species in a particular site to be measured.

## Defining dark diversity

It is possible to specify species that belong to a particular species pool but that are not locally present. We call this unaccounted set of species 'dark diversity'. Exploring 'missing species' is rare in ecology, with infrequent exceptions [28], although the absence of a species might be as scientifically interesting as its presence. The absence of species can also reflect local extinctions, which are of major concern to nature conservationists.

The concept of local and dark diversity is seemingly similar to, but does not recapitulate, concepts of local–regional diversity or alpha–beta–gamma diversity (Box 1). Local observed diversity is frequently called 'alpha diversity' and regional diversity is termed 'gamma diversity'. Beta diversity, or species spatial turnover, is the association between these two [29], either multiplicative (beta = gamma/alpha) or additive (beta = gamma – alpha) [30]. Our approach maintains local observed diversity as alpha diversity, but species pool and dark diversity differ fundamentally from regional (gamma) and beta diversities. Species pools are affiliated with specific habitat conditions, whereas regional diversity encompasses a variety of existing habitats. With gamma or beta diversity, the focus is either on biodiversity owing to habitat diversity (gamma) or on diversity among various habitats (beta). By contrast, dark diversity focuses on the portion of regional diversity potentially able to occur in one particular habitat type. Regional lists of species (i.e. faunas and floras) are sometimes referred

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### Box 1. Theoretical examples of measuring dark diversity

Each of the examples in Figure I has a local observed diversity (alpha diversity). The species pool consists of all species in the region that can potentially inhabit particular ecological conditions. Dark diversity is defined as the portion of species pool absent from the study site. For comparison, we present in Figure I both gamma diversity and additive beta diversity (gamma–alpha). Species are designated by letters.

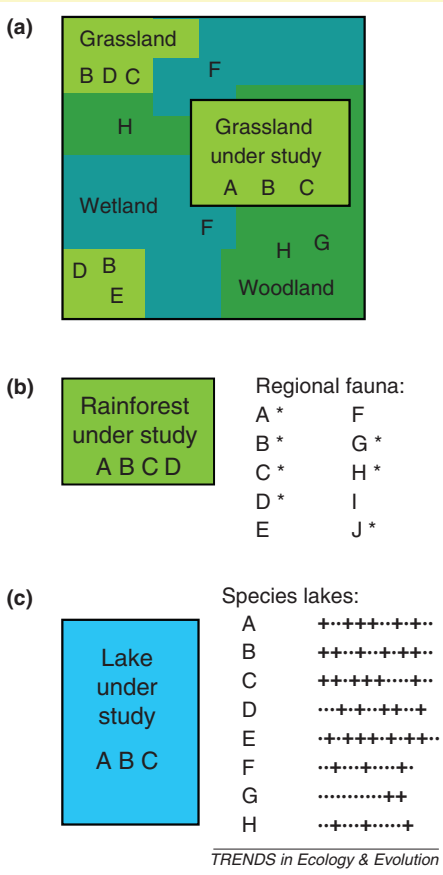


**Figure I**. Defining dark diversity in three theoretical situations. **(a)** Dark diversity of plants for a grassland patch. Local observed diversity in the study grassland includes species A, B and C. The grassland species pool determined by inventories over all grasslands in the region includes species A, B and C, and also D and E. The dark diversity in the study grassland includes species D and E. The region also contains ecosystems other than grasslands. Gamma diversity includes all species from all ecosystems in the region (i.e. A, B, C, D, E, F, G and H), and beta diversity includes species D, E, F, G and H. **(b)** Dark diversity of birds for a tropical rainforest. This region contains a single rainforest stand and the local observed diversity includes species A, B, C and D. The species pool contains species from the regional fauna that can potentially inhabit rainforest (marked by asterisk, i.e. A, B, C, D, G, H and J), as dictated by the nesting and food requirements of regional bird fauna based on monograph data. Many rainforest bird species are not present in the single small rainforest fragment, but persist in the small secondary forest stands of the region. Locally absent rainforest bird species form the dark diversity (G, H and J). Because there is only a single rainforest stand, gamma and beta diversities cannot be calculated. **(c)** Dark diversity of fishes in a lake. Local observed diversity includes species A, B and C. A data set indicating the presence (+) and absence (·) of fish species in all lakes in the region is used to define the species pool. The species pool contains species that probably coexist with the set of species in the lake (i.e. A, B, C, D and E). Thus, the species pool is limited to species with similar ecological requirements. Gamma diversity includes all species in all lakes (i.e. A, B, C, D, E, F, G and H). Dark diversity includes species D and E, whereas beta diversity includes species that do not coexist with the local set of species (i.e. D, E, F, G and H).

to as 'species pools' [31,32], but we find this definition imprecise and suggest that 'species pool' should only be used to refer to species that are ecologically suitable for a particular habitat.

## Measuring dark diversity

Local diversity can be recorded by careful inventory. To define dark diversity, species pools also need to be defined. To determine species pools, the concepts of geographical and ecological filters must be applied: species must be present in the region and must be able to inhabit ecological conditions in the study site. Geographical filters are applied by considering all taxa from a specific region only (e.g. a country, county or island). This information can be obtained from regional faunas and floras. Distinguishing a subset of species with particular ecological requirements from the regional fauna or flora is a more demanding task (Box 1). Extensive inventories of a single habitat type within a region can provide a good approximation of species pool composition. However, inventories typically include

### Box 2. Examples of the potential application of the concept of dark diversity

The concept of dark diversity enables biodiversity estimates to be meaningfully compared across regions, ecosystems and taxonomic groups. We illustrate this in Figure I using theoretical examples with simulated data. We present both local and dark diversity and their corresponding ratio.

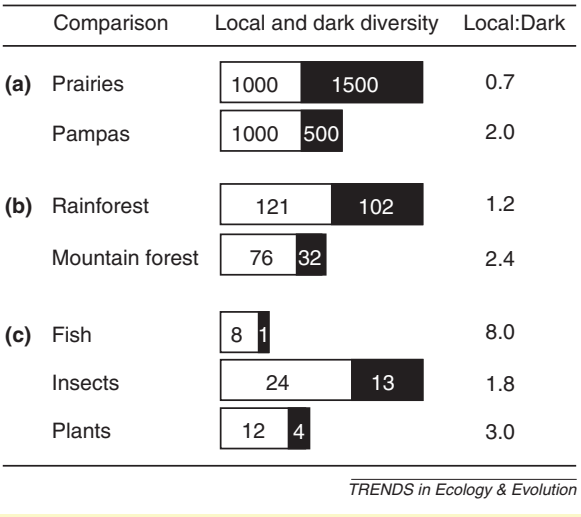


**Figure I**. Theoretical examples for comparing biodiversity across regions, ecosystems and taxonomic groups with the help of dark diversity. **(a)** We compare plant diversity in analogous grassland ecosystems, notably North American prairies and South American pampas. Although observed local diversity is the same in both (1000 vascular plant species in a 10 000 $km^2$ area), dark diversity (estimated for each region by habitat-specific inventories: ca 1500 species in the North America compared with ca 500 in South America) is notably different. Therefore, local diversity is relatively higher in the pampas. **(b)** A tropical region contains a single, virgin lowland rainforest fragment and areas of mountain forests. We want to know how local bird diversity in 10 $km^2$ in the rainforest (121 species) compares with that in a similar area in mountain forest (76 species). Knowing the ecology of local bird fauna, we estimate dark diversity for both the lowland and mountain forests in this region. Because, in our example, many lowland rainforest species persist in secondary habitats, the dark diversity of the rainforest is higher (102 species) than that of mountain forests (32 species). Therefore, the rainforest patch is relatively less diverse than the mountain forest. High dark diversity of lowland rainforest birds shows that biodiversity in this rainforest can be maintained or even increased if some adjacent areas can be restored. **(c)** Eight species of fishes, 24 species of insects and 12 plant species are found in a small temperate lake. Dark diversity can suggest which taxonomic groups are relatively more diverse. We examined a large set of lakes with species presence–absence data from the same region and compiled a list of species that probably coexist with the present set of species. We found that one fish, 13 insect and four plant species are likely to be absent, but potentially able to inhabit the lake. These absent species form dark diversities and demonstrate that this lake is especially rich in fish species.

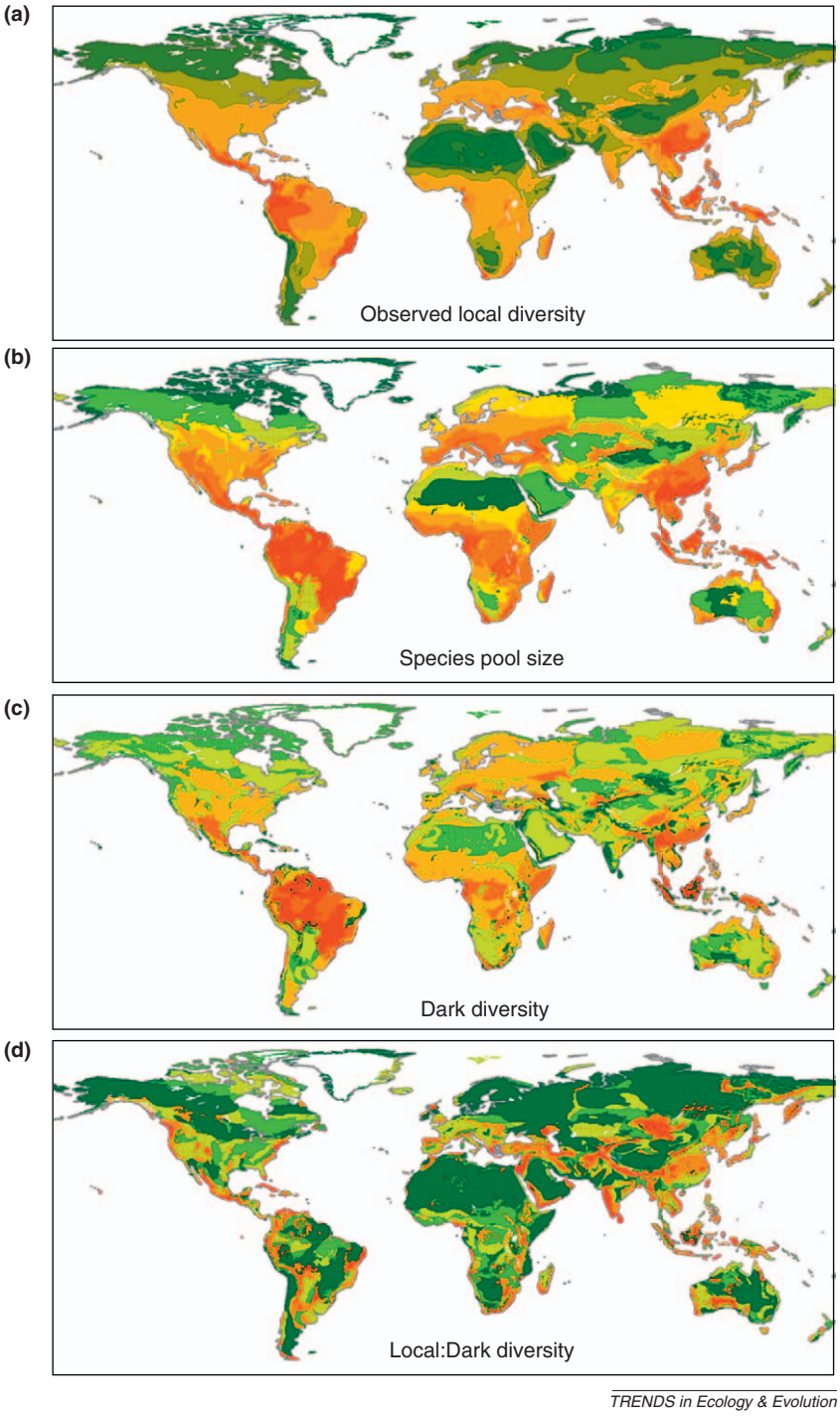


**Figure 1**. The biodiversity of vascular plant species on a global scale. **(a)** Local observed diversity on a 100 km × 100 km scale; **(b)** species pool size (i.e. the number of species inhabiting different ecoregions); **(c)** absolute value of dark diversity (i.e. the portion of the species pool not observed locally); and **(d)** the local:dark diversity ratio, demonstrating the relative quantity of local diversity. Green and red shading indicate low and high values, respectively. Redrawn, with permission, from [43,44] **(a)** and [46] **(b)**.

all species within a particular area without accounting for habitat specificity, which is not suitable for distinguishing dark diversity. Additionally, it is possible to use species-specific ecological information, particularly information on species habitat requirements. For example, habitat affinities of rodents are available in monographs [31,33] and ecological requirements of plants across main environmental gradients are obtainable from databases [34]. When such information is absent, the geographical distribution patterns of species (i.e. their biogeographical affinity) [35] or species co-occurrence patterns [36,37] might serve as a proxy of species ecological requirements. Such data are becoming increasingly more available in various depositories, such as vegetation sample plot archives, data papers and ecological archives. A policy of archiving ecological data sets as a requirement for publication is emerging [38].

The exact procedure to define species pools depends on data availability, and on whether the need is to estimate

only the size of a particular biodiversity component or its composition. Often the estimated size of dark diversity is sufficient.

## Application of dark diversity

The concept of dark diversity enables one to compare readily the status of biodiversity in different ecosystems by circumventing the confounding effects of the different absolute diversity values inherent to these systems. Even if the diversity of different ecosystems differs by several magnitudes, the local:dark diversity ratio indicates how many potential species are present compared with the missing portion. This ratio is dimensionless and makes it possible to compare different ecosystems, regions or taxonomic groups. Relative richness (i.e. the proportion of local diversity with respect to regional diversity) has already demonstrated its usefulness, for example in comparing fish diversity in temperate and tropical regions [39], or bird communities across the urbanization gradient [40]. This kind of approach deserves wider application, in both theoretical ecology and biodiversity conservation (Box 2).

In addition to diversity comparisons, dark diversity has the potential to reconcile the role of regional and local processes underlying community assembly. The usual approach to addressing this issue is to study whether local richness is independent of biotic interactions occurring in the local habitat and increases proportionately with regional richness, or whether it is independent of regional richness (i.e. the system is species saturated) [31,34,41]. Although the relationship between local and regional richness has been addressed in numerous studies, this approach is suspect if regional richness includes species from ecosystems that differ from the habitat in which local diversity is measured. Moreover, by comparing biodiversity components directly (i.e. local diversity vs dark diversity), one is freed from the non-independence of small- and large-scale diversity.

The concept of dark diversity is also readily applicable to the exploration of temporal changes in biodiversity. Transitions of species from local to dark diversity sound a warning that local extinctions are occurring. However, the extinction process remains potentially reversible if species are still present in the region (i.e. present as dark diversity). By contrast, high dark diversity might reveal a potential for ecosystem restoration: the aim of community restoration is to increase local diversity at the expense of dark diversity [42].

We illustrate the concept of dark diversity by using a global map of vascular plant diversity (Figure 1). Local diversity at the scale of 100 km $\times$ 100 km was derived from a global map based on more than 3300 observed species richness measurements from different regions of the world [43–45]. Despite the unusually large scale, this compilation still reflects the observed local diversity at the global scale. Species pool sizes were defined as the number of plant species in each ecoregion [46]; that is, relatively homogeneous areas having distinct types of natural communities [47]. Because each ecoregion contains one main broadly defined community type, we expect that the total number of species within ecoregions is a suitable proxy for the potential species for each locality within this ecoregion. Dark diversity was calculated by subtracting local diversity from the species pool size. Dark diversity for plants sees high values in both tropical and temperate regions (especially in Europe). Therefore, in several parts of the world, fewer species are observed locally than are present in the species pool of the ecoregion. A striking pattern emerges for the plant local:dark diversity ratio: temperate areas are often more diverse in relative terms compared with well-known biodiversity hotspots in the tropics (Figure 1). We also observe only limited regions exhibiting a relatively high local:dark diversity ratio. We suggest that these areas deserve serious attention from a nature conservation perspective.

## Conclusions

Dark diversity is a useful concept for understanding processes underlying diversity patterns. Each ecosystem 'owns' an unseen evolutionary background, its dark diversity, which provides insight into processes underlying observed local diversity. Even if estimated rather than measured, dark diversity is needed to understand the behaviour of ecological communities. Dark diversity is vital when comparing biodiversity across regions, ecosystems and taxonomic groups, and estimating the relative loss of local diversity. Similarly, dark diversity provides an opportunity to estimate the restoration potential of degraded ecosystems.

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