Essay

Applying the dark diversity concept to nature conservation

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Abstract: *Linking diversity to biological processes is central for developing informed and effective conservation decisions. Unfortunately, observable patterns provide only a proportion of the information necessary for fully understanding the mechanisms and processes acting on a particular population or community. We suggest conservation managers use the often overlooked information relative to species absences and pay particular attention to dark diversity (i.e., a set of species that are absent from a site but that could disperse to and establish there, in other words, the absent portion of a habitat-specific species pool). Together with existing ecological metrics, concepts, and conservation tools, dark diversity can be used to complement and further develop conservation prioritization and management decisions through an understanding of biodiversity relativized by its potential (i.e., its species pool). Furthermore, through a detailed understanding of the population, community, and functional dark diversity, the restoration potential of degraded habitats can be more rigorously assessed and so to the likelihood of successful species invasions. We suggest the application of the dark diversity concept is currently an underappreciated source of information that is valuable for conservation applications ranging from macroscale conservation prioritization to more locally scaled restoration ecology and the management of invasive species.*

Keywords: absent species, completeness, conservation ecology, conservation prioritization, invasion ecology, metacommunity, restoration ecology, species co-occurrence

Aplicación del Concepto de Diversidad Oscura a la Conservación de la Naturaleza

Resumen: *Enlazar la diversidad con los procesos biológicos es esencial para el desarrollo de decisiones informadas y efectivas de conservación. Desafortunadamente, los patrones observables brindan sólo una proporción de la información necesaria para entender por completo los mecanismos y los procesos que actúan sobre una población o comunidad en particular. Le sugerimos a los administradores de la conservación que usen la información que es ignorada continuamente en relación a la ausencia de especies y que le presentar particular atención a la diversidad oscura (es decir, un conjunto de especies que está ausente de un sitio pero que podría dispersarse a y establecerse ahí, en otras palabras, la porción ausente de un acervo de especies específicas de hábitat). Junto con las medidas y conceptos ecológicos y las herramientas de conservación, la diversidad oscura puede utilizarse para complementar y desarrollar a fondo la priorización de la conservación y las decisiones administrativas por medio del entendimiento de la biodiversidad relativizada por su potencial (es decir, su acervo de especies). Más allá, a través del entendimiento detallado de la población, la comunidad y la diversidad oscura funcional, el potencial de restauración de los hábitats degradados puede ser valorado*

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a fondo de manera más rigurosa, así como la probabilidad de invasiones exitosas de especies. Sugerimos que la aplicación del concepto de diversidad oscura actualmente es una fuente de información poco valorada que es valiosa para las aplicaciones de la conservación, que van desde la priorización de la conservación a macroescala hasta la ecología de restauración con escalas más locales y el manejo de especies invasoras.

Palabras Clave: co-ocurrencia de especies, ecología de la conservación, ecología de la invasión, ecología de la restauración, especies ausentes, integridad, metacomunidad, priorización de la conservación

Introduction

Conservation biology has strong scientific underpinnings (e.g., Tansley 1949). Early in its formalization as a science, the necessity for ecologically relevant metrics for use in quantifying the diversity of plant and animal communities was recognized. Nevertheless, formulating and empirically testing theory to support observed biodiversity patterns has always presented the greater challenge. Linking patterns to processes is absolutely central to nature conservation because it allows one to identify and resolve problems that adversely impact biodiversity (Watt 1947), one of the ultimate goals of conservation. Still, the large number of mechanisms and processes underpinning observed ecological patterns is of such complexity that attributing patterns to processes has been described as an inseparable "mess" (Lawton 1999). However, what if ecological mechanisms and processes can only be partially linked to observable patterns? From this perspective, perhaps it becomes less alarming that observable patterns reflect only a proportion of the bigger picture. It also raises an interesting question. Can knowledge of absences complement the understanding of ecological processes?

The recently developed concept of dark diversity (which sets absences within the species-pool framework) (Fig. 1) emphasizes the value of understanding absent species in addition to observed species. Strictly, dark diversity encompasses all species that are currently absent from a site but have the potential to disperse and establish there (Pärtel et al. 2011) (i.e., those species belonging to a site's habitat-specific species pool, also referred to as the "filtered" species pool [Cornell & Harrison 2014; Zobel 2016]). We considered the state of the art surrounding absent species in ecology, specifically dark diversity, and how including both absent and observed species has vast potential to improve understanding of how biological diversity is governed and maintained. We illustrate our viewpoint by clarifying how measuring, monitoring, and understanding dark diversity can prove beneficial in the context of 3 facets of conservation biology: biodiversity conservation, habitat restoration, and species invasion management.

Dark Diversity Concept

At a regional scale, absent species fall broadly into 2 groups: those that have an ecological affinity to prevailing abiotic conditions at a focal site and those that do not. The former, despite the lack of established populations, are species with a reasonable probability of occurrence that belong to a habitat-specific species pool (Eriksson 1993; Pärtel et al. 1996; Zobel 1997) (Fig. 1) For example, many galliforme bird species have fragmented distributions throughout much of their natural range (World Pheasant Association and IUCN/SSC Re-introduction Specialist Group 2009). Suitable habitats can often be void of species that would otherwise have viable populations in identical habitats elsewhere within the region. It is this specific type of absence that is termed dark diversity (Pärtel et al. 2011), and it is complementary to the multifold species-pool concept (Cornell & Harrison 2014; Zobel 2016). Accordingly, dark diversity is gaining attention as an ecologically meaningful and valuable biodiversity metric (Pärtel 2014; Fraser et al. 2015; Pouteau et al. 2015; Riibak et al. 2015; Ronk et al. 2015; Lessard et al. 2016).

Although dark diversity appears similar to other ecological concepts (e.g., β diversity), dark diversity can contribute new and complementary information. Beta diversity (i.e., species turnover) focuses on diversity among different habitats for the entire flora and fauna within a region (Pärtel et al. 2011) (Fig. 1). In contrast, dark diversity relates only to a portion of γ diversity that can potentially occur within a particular habitat or under particular environmental conditions. Similar parallels can also be drawn between dark-diversity and the metacommunity concept (Leibold et al. 2004). Defined as a set of local communities that are linked by dispersal of multiple, potentially interacting species (Gilpin & Hanski 1991; Wilson 1992), a metacommunity encompasses processes that occur across different spatial scales (i.e., the metacommunity scale) and that link local population dynamics to landscape patterns. However, a metacommunity approach requires an a priori classification from sets of observations. In contrast, the dark-diversity concept is much more holistic and merges information about species availability within the region with information on species' ecological requirements. The dark-diversity concept, therefore, brings together additional ecological information and techniques to describe the local study system while still complementing existing approaches and concepts.

Estimating dark diversity, while not straightforward, is nonetheless achievable (Smart et al. 2015; Lewis et al. 2016). Modeling species distributions, which has origins
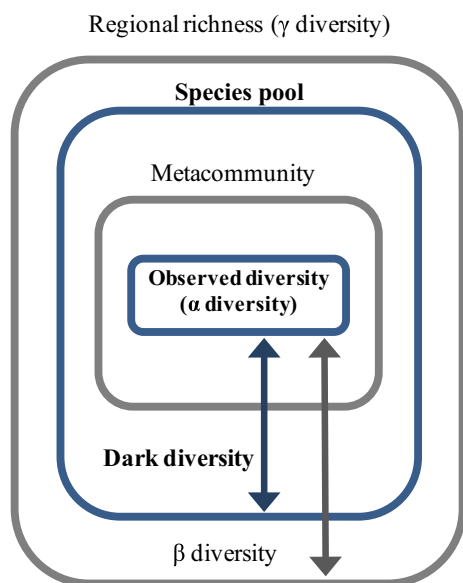
Regional richness (γ diversity)

Figure 1. Conceptual diagram illustrating the hierarchical structure of the following ecological concepts: species pools, alpha (α), beta (β), and gamma (γ) diversity, metacommunity, and dark diversity. Regional richness (γ diversity) is species richness within a landscape or region that likely encompasses multiple habitat types (Whittaker 1960) (sometimes defined as cumulative number of species over a set of sites or samples [Loreau 2000]). Species pools refer to species that are present in the region and can potentially inhabit a focal site because of suitable ecological conditions (Eriksson 1993; Pärtel et al. 1996; Zobel 2016) and are defined according to species' ecological requirements (β niche) (Silvertown et al. 2006). By this definition, species pools are habitat specific (or filtered). Sometimes (unfiltered) species pool has been used synonymously with γ diversity. A metacommunity is a set of local communities linked by dispersal (Gilpin & Hanski 1991; Wilson 1992) and defined according to similar sites. Observed diversity (α diversity) is species diversity within a site (Whittaker 1960). Dark diversity is the set of species that are currently absent from a site but that belong to its habitat-specific species pool (Pärtel et al. 2011). Dark diversity can be used to calculate a completeness index that expresses the diversity of a local site relative to its species pool and is expressed as log(observed diversity/dark diversity) (Pärtel et al. 2013). Beta diversity is the difference in diversity among sites in a region (Whittaker 1960) or set of samples (Loreau 2000).

in conceptual models based on expert opinion, is now a major field of ecological research (Franklin 2010). With computational improvements, new techniques for dynamic mechanistic species distribution models (Dullinger et al. 2012) can alleviate some of the limitations of static niche models (for an overview, see Guisan and Thuiller [2005]). Although commonly viewed with respect to species occurrences, the models provide equally as much information concerning species absences. Nevertheless, more holistic approaches to predicting species absences also exist. Lewis et al. (2016) demonstrate that dark diversity can be estimated with a reasonable degree of accuracy through species co-occurrence patterns. Here, species that commonly co-occur with each other are used to infer probabilities that a given absence belongs to dark diversity. For example, where species A, C, E, and F commonly co-occur across space and where a community comprising species A, C, and E is observed, species F will have a high probability of belonging to the dark diversity of that community. The co-occurrence methodology also integrates flexible species-specific thresholds that act to select or reject species in a community's dark diversity depending on the research question. The thresholds themselves are user defined and therefore nondiscrete, just as species ecological preferences (i.e., species beta niche [Silvertown et al. 2006]) are nondiscrete in nature. Via this approach, dark diversity estimates can be tailored to specific habitats and regions.

There are, however, certain limitations to using co-occurrence-based dark diversity estimates. Affined but rare species are often underestimated within dark diversity due to the limited co-occurrence patterns. In such instances, comprehensive species distribution data, functional traits, or ecological requirements of species are alternatives. For example, Lessard et al. (2016) estimated species pools for hummingbird species across northwestern South America; Belmaker and Jetz (2013) estimated ecologically suitable species pools for both bird and mammal species; and Pärtel et al. (1996) estimated plant species pools across Estonian plant communities. Irrespective of the method, accurate estimates of dark diversity depend heavily on data quality. Insufficient sampling can result in those species that could potentially colonize and persist in the focal assemblage being excluded from the species pool. It can also present difficulties in disentangling low incidence and hidden species from those that are truly absent. Still, where good quality data exists, accurate species-pool estimations are achievable.

Dark Diversity and Biodiversity Conservation

Conserving biodiversity is a serious global challenge. Scale and extent of the challenge notwithstanding, social, political, and economic restraints further the requirement that conservation activities be prioritized so that resources are used effectively and efficiently (Carwardine et al. 2009; Wilson et al. 2009). Implementing conservation priorities first requires a thorough understanding of conservation objectives at a range of scales (e.g., conservation of species, communities,

habitats, ecosystem functions), constraints (e.g. land-use disturbance, exploitation, climate change), and the ecology of the system (e.g., single localized habitat or an entire biome). At the global level, prioritization focuses on identifying areas that fall within a framework of irreplaceability and vulnerability (Brooks et al. 2006). Irreplaceability quantifies species endemism and is used to identify biodiversity hotspots (Myers et al 2000; Mittermier et al. 2003), whereas quantifying vulnerability can take multiple forms (Wilson et al. 2005). Interpreting patterns from different prioritization templates helps facilitate an informed process of identifying target areas most at risk of biodiversity loss. For example, a large overlap between the global spatial extent of biodiversity hotspots and "crisis ecoregions" (Hoekstra et al. 2005) can provide an initial broad-scale identification of particularly vulnerable regions which, if degraded or lost, would contribute significantly to global biodiversity loss.

The concept of dark diversity can complement and improve the robustness of existing approaches in conservation prioritization and management decisions. For example, extant irreplaceability and vulnerability indices do not provide information on a region's current biodiversity relative to its potential biodiversity. Pärtel et al. (2013) recently formulated a "completeness index" (i.e., the completeness of a habitat or region relative to its respective species pool; completeness = log(observed diversity/dark diversity)). High completeness (i.e., high observed diversity and low dark diversity) within an ecoregion (Olson & Dinerstein 1998) coupled with high irreplaceability and vulnerability (Brooks et al. 2006) indicate an area should have a high conservation priority. Diverse yet complete communities should imply high levels of functional stability and ecosystem services. Communities with a high completeness in northern boreal and temperate regions may even represent the last areas of glacial maxima refugia. Here, species can be in disequilibrium with their current environment and absent across much of their potential range due to dispersal limitation and priority effects during postglacial recolonization (Svenning & Skov 2004). Relatively complete communities, therefore, have the potential to act as an important source for trailing-edge populations. These populations can even give rise to high ecosystem diversity and thereby provide refuge for many taxa irrespective of changing environmental conditions, as is found for long-lived remnant tree populations (Svenning & Sandel 2013).

Macroscale variation in biodiversity (and in-turn covariation in dark diversity) often reflects variation in species pool sizes (Zobel 1997; Pärtel et al. 2011), a pattern well understood to gradate across latitudinal gradients and to decrease toward the poles. Resultant patterns thus correlate well with macroscale ecological descriptors (e.g., climate). Patterns of completeness, in contrast, are different. For example, Ronk et al. (2015) found no latitudinal relationship for completeness of vascular plants at a Euro-pean scale. The study revealed stronger patterns between regional completeness and human influence, pointing to high completeness in regions with low human influence (e.g., Scandes, Pyrenees) and low completeness in regions with high human influence (e.g., central Europe) (Ronk et al. 2015). Because completeness detects relative diversity hotspots across regions, its patterns can be used to identify the effects of landscape-scale disturbances and metapopulation dynamics on biodiversity (Mosblech et al. 2011), processes that are pivotal in protecting against regional extinctions.

Processes shaping ecological communities (e.g., dispersal and biotic interactions) vary among regions and habitat types because of differences in species, environmental conditions, climate, and land use (Lenoir et al. 2010). These differences complicate the interpretation of large-scale habitat assessments across regions and habitat types. As a relativized metric, the completeness index is advantageous in this respect because it can be used to make informative biodiversity comparisons among dissimilar communities within or across regions, an attribute shared by few biodiversity indices (but see The Living Planet Index [Loh et al. 2005]). It could also be used to compare communities of different trophic levels such as plants, insects, and birds (Pärtel et al. 2011). Furthermore, its application is not restricted to biological taxa; it can be easily augmented to measure completeness across genes, functions, or phylogeny or even to stratify informative classes (e.g., differentiating between native and alien species). Knowledge of completeness (taxonomic, genetic, or functional) with respect to the species pool can therefore prove an invaluable and informative biodiversity metric that is beneficial for addressing conservation decisions (e.g., when and where to initiate conservation actions) and helpful for sustaining representative samples of regional biodiversity and ecosystem functions (Margules & Pressey 2000).

Dark Diversity and Ecological Restoration

Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2004) to the extent that left undisturbed the ecosystem's ecological trajectory shifts through which abiotic and biotic processes and ultimately ecosystem functions are affected. Before restoration, sites must be scrutinized carefully in terms of their restoration potential to maximize restoration success from limited resources (Wilson et al. 2011). One obvious consideration is to ensure causes of degradation have been eradicated as much as possible. Another important, but less obvious consideration, is an understanding of the local species pools from which lost species are to be recouped (Sundermann et al. 2011). Frequently, restoration requires a reference ecosystem to be defined, typically the pre-disturbance state. Comparing a

habitat-specific species pool of the reference habitat with the degraded habitat can provide additional and valuable information concerning the likelihood of achieving successful restoration. For example, if large dissimilarities exist between the 2 species pools (i.e., the species pool of the restoration community and species pool of the reference community), restoration success is unlikely to be effective in the short term, that is, without further intervention (e.g., species translocation, biomass removal). Conversely, where species are conserved as part of a degraded habitat's dark diversity (i.e., the species exists in the wider region and has a probability to disperse and establish), the chances of successful restorations should be greater. For example, habitat fragmentation and disturbance have negatively affected primate diversity for particular lowland tropical rainforests of northeast India. Despite this, the regional, habitat-specific species pool remains conserved (Sharma et al. 2013); for a given habitat fragment, the absent species remain part of that habitat's dark diversity. Where species pools are not conserved (i.e., where they are depauperate), reference assemblages cannot be expected to be successfully restored, as occurred with assemblages of fishes following river restoration in Germany (Stoll et al. 2012). From this perspective, conservation of a habitat's dark diversity is vital if extirpations are to be reversed and ecosystem functions reinstated.

The use of reference sites to define restoration targets is not always straightforward. First, suitable reference sites may not exist, or compositionally similar sites may exist, but they may be subject to different abiotic influences relative to the restoration site. Second, the restoration site may be degraded to the extent that its species pool is simply not comparable with any reference pool during early phases of restoration. Such situations are not uncommon, especially for highly dynamic and rare ecosystems with limited spatial extent. These systems require effective restoration monitoring and adaptive management (Westgate et al. 2013) (i.e., systematic rebuilding of the species pool). In this situation, understanding and monitoring even transient species pools (i.e., observed and dark diversities through time) at restoration sites can provide benchmarks in which to gauge and address management decisions. Wolters et al. (2005) demonstrated such an approach to be effective for salt-marsh communities. They measured the restoration sites dark diversity (though not expressed this way) by defining target plant species from the regional species pool.

Ultimately, monitoring is an essential part of any ecological restoration or conservation program, yet monitoring designs are often poor (Lindenmayer & Likens 2010). Suding (2011) stressed the necessity for a comprehensive evaluation tool if restoration decisions are to be improved. Tracking the exchange of species in and out of dark and observed diversity provides a step in this direction and results in a useful turnover metric in which to

measure restoration success (e.g., Koch et al. 2014) and a gauge to wider-context biodiversity conservation targets (reviewed in Carwardine et al. [2009]). Knowledge of dark diversity can also help identify potential threats to restoration success. Not all species are wanted (see "Dark Diversity and Invasion Ecology"). Identification of potentially undesirable species facilitates integration of preventative measures in restoration management plans early on. For example, Funk et al. (2008) propose that introduced native species be selected based on their functional similarity to potential invaders so as to limit available niche space (Mitchell et al 2000). Monitoring dark diversity can therefore help initiate preplanned adaptive management measures (Lindenmayer & Likens 2009) in the event the restoration trajectory goes off course. Similarly, pre-specified structures of and temporal patterns in the observed and dark diversities can act as trigger points that initiate general shifts in the course of restoration management (i.e., active adaptive management [Williams 2011]).

Although ecological monitoring is necessary to track restoration progress, progress itself requires an understanding of the ecological processes that limit species to dark diversity. Identifying the mechanisms that explain why some species inhabit sites and others belong to the dark diversity can be achieved through the exploration of species functional characteristics. For example, many species in temperate seminatural grasslands are part of dark diversity due to dispersal limitation (Riibak et al. 2015). This is valuable knowledge for implementing effective restoration because it indicates some form of facilitated dispersal may be the key, for example, to enhancing the biodiversity value of temperate seminatural grasslands. It is, however, also important to single out those species among the dark diversity that are naturally absent. In Europe, many species from the Alps do not occur north of the Danube, despite the presence of habitat. Here co-occurrence patterns are likely to suggest their presence in dark diversity; nevertheless, restoration through facilitated dispersal should always respect biogeographical constraints.

Dark Diversity and Invasion Ecology

As mentioned previously, one of the aims of conservation can be to promote certain absences. However, the absence of affined species from a community should not automatically imply that species should be part of the community. Such a view would be dangerous from a conservation perspective because it could potentially promote managed invasions. This is because dark diversity estimates consider only a species' ecological affinity. Subsequently, all species, irrespective of whether they are native, non-native, locally introduced, or invasive, can be included as part of dark diversity. Therefore, in the same way dark diversity provides information that

can help prevent undesirable absences, it can also help prevent unwanted presences.

A large amount of funds and research effort is channeled into understanding ecological mechanisms and management processes to ensure certain species remain absent from observed diversity (i.e., part of dark diversity). Understanding the process of invasion is critical to both ecological theory and conservation efforts; identifying the likelihood of potential invaders and habitat invasibility is of particular concern. Habitat-specific species pools that reflect species ecological preferences (i.e., abiotic and biotic selection [Vellend 2010]) have proven useful in this respect. Kalusová et al. (2014) demonstrated how analogous, yet geographically disparate, habitats influence each other's invasibility via direct and reciprocal species pool effects. In other words, a habitat that contributes large numbers of species to another habitat's regional pool will not only increase the probability of these species becoming successful invaders but will increase its own invasibility (i.e., the donor habitat) (see also Kalusová et al. 2013).

Previously, community invasibility has been linked to species diversity (i.e., species-rich sites have fewer available niches and therefore greater resistance to invasions). Although valid for understanding island biogeography, in particular, niche vacancy and community saturation (Shea & Chesson 2002), such hypotheses are nowadays dismissed. Species richness alone is a poor predictor of invasion resistance of plant assemblages (Moore et al. 2001). More influential are the ecological mechanisms governing species coexistence (i.e., biotic and abiotic interactions and regional process and patch dynamics), which ultimately maintain regional species pools.

Species richness as a predictor of invasibility is a much more informative metric when relativized to habitat-specific species pools. It is well known that habitat-type influences invasibility (Andreu & Vila 2010), yet assessing risk from an understanding of both observed and dark diversity remains unexplored. For example, habitats subject to disturbance or adjacent to transport pathways are more at risk of invasion, but this is likely because their species pool and its dark diversity (i.e., potential diversity) are large, which confounds the relationship between diversity and biotic resistance (Moore et al. 2001; Shea & Chesson 2002; Fridley et al. 2007). In theory, the relationship between diversity and biotic resistance should be much more consistent across sites if local diversities are standardized (Shea & Chesson 2002). Once more, relativizing observed diversities with species pools augments such a measure. Used in this way, completeness ratios may provide a suitable measure of community saturation and niche vacancy and be a useful proxy for invasibility. Thus, in the same way a completeness index provides a useful tool for macroscale assessment of conservation and restoration priorities. It too can be used to provide effective macroscale comparisons of biotic resis-

tance among different habitat types and regions, which helps clarify understanding of the general relationship between diversity and invasion.

At a local scale, understanding invasion potential requires knowledge regarding the interplay between an invading species and the invasible community. Invasion patterns depend on the functional traits of communities and invaders (Perelman et al. 2007; Funk et al. 2008) and are arguably best viewed in terms of functional matches among the invader, community, and resident species. Therefore, understanding functional similarity and dissimilarity to potential invasive species requires knowledge of a community's dark diversity, in particular that of the non-native species pool (Smith & Knapp 2001; Perelman et al. 2007). Further efforts should be made to understand the functional structure of dark as well as observed species. This is achievable and has been demonstrated to help disentangle trait dissimilarity (i.e., convergence vs divergence patterns) resulting from fine-scale biotic processes (e.g., phenotypic exclusion, pollination [de Bello et al. 2012]). Enhancing our understanding of community assembly in this way should prove useful in facilitating restoration and conservation plans aimed at the eradication and conservation of non-native and native species, respectively.

Under global-change scenarios, not only is it important to understand the threat of potential invasive species present in dark diversity, but it is also important to be able to identify potential threats of new invaders (Groves et al. 2001). Non-native invasions often have negative ecological and socioeconomic impacts (Mack et al. 2000; Levine et al. 2003; Pimentel et al. 2005). Moreover, for plants, once established, they are exceptionally difficult to eradicate or control (Rejmánek et al. 2005). In view of this, dark diversity has the potential to aid the development of early-warning models capable of detecting non-native invasives with reasonable probabilities of successful establishment.

Summary

Over much of its history, conservation ecology has developed in situ with community ecology, through which observable patterns have been linked to ecological processes. However, in much the same way patterns of observable species provide valuable information so too can patterns of absent species, specifically dark diversity. Knowledge of dark diversity facilitates comparisons of biodiversity, irrespective of habitat type and taxa; is beneficial for restoration and target-based monitoring; and can prove valuable for forecasting potential impacts of invasions and developing subsequent mitigation measures. Therefore, there are many reasons to expect an understanding of dark diversity to contribute to an understanding of fundamental ecological processes governing

biological diversity. However, to what extent is broadly unknown. We considered this expectation (i.e., potential benefits resulting from understanding dark diversity patterns) in light of core challenges in conservation ecology. Given dark diversity can, with relative ease, be reasonably well estimated from extant data (e.g., Lewis et al. 2016), we suggest it be used more widely. After all, scrutinizing additional patterns other than observed diversity only adds to the arsenal of information that can be used to guide both the development and implementation of conservation actions.

Acknowledgments

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