Dark diversity: Its potential application for nature conservation.

Rob J Lewis[1,2], Francesco de Bello[3,4], Jonathan A Bennett[1], Pavel Fibich[4], Genevieve E Finerty[3,5], Lars Götzenberger[3], Inga Hiiesalu[1,3], Liis Kasari[1], Jan Lepš[4], Maria Májeková[3,6], Ondřej Mudrák[3], Kersti Riibak[1], Argo Ronk[1], Terezie Rychtecká[4], Alena Vitová[4] and Meelis Pärtel[1].

[1] Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, Tartu 51005, Estonia; Fax +372 737 6380
[2]Department of Bioscience – Ecoinformatics and Biodiversity, Ny Munkegade 116, DK-8000 Aarhus C, Denmark
[3]Institute of Botany, Czech Academy of Sciences, Dukelská 135, 379 82 Třeboň, Czech Republic
[4]Department of Botany, Faculty of Science, University of South Bohemia, CZ-37005, České Budějovice, Czech Republic
[5]Department of Environmental Research, University of Oxford, Oxford, OX1 3PS.
[6]Department of Soil Science, Faculty of Natural Science, Comenius University, SK-842 15, Bratislava, Slovak Republic

Corresponding author: rob.lewis@bios.au.dk

Running title: Dark diversity and nature conservation

Key Words: Absent species, conservation ecology, conservation prioritisation, completeness, invasion ecology, meta-community, species co-occurrence, restoration ecology

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 upon a particular population or community. Here, we suggest conservation managers utilise the often overlooked information imbedded in species absences, paying particular attention to the dark diversity (i.e. a set of species that are absent from a site but can potentially 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 prioritisation 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 further, 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 macro-scale conservation prioritization to more locally-scaled restoration ecology and the management of invasive species.

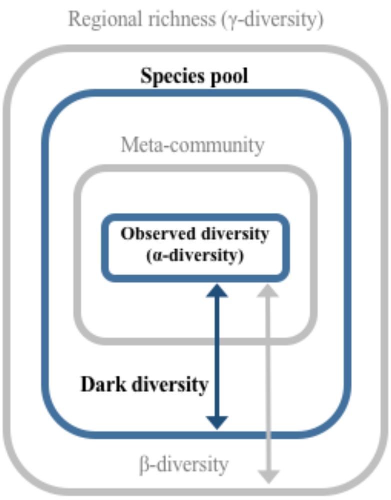
Introduction

Conservation biology has strong scientific underpinnings (e.g. Tansley 1949). Early in its formalisation as a science, the necessity for ecologically relevant metrics able to quantify the biodiversity 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 as it allows us 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 to our understanding of ecological processes?

The recently compiled concept of dark diversity (which sets absences within the species pool framework; Fig. 1), emphasizes the value of understanding absent species in addition to those observed. 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. belonging to a sites habitat-specific species pool (also referred to as the 'filtered' species pool, Cornell & Harrison 2014; Zobel 2016). Here, we discuss 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 our understanding of how biological diversity is governed and maintained. We illustrate this viewpoint by clarifying how measuring, monitoring and understanding dark diversity can prove beneficial in the context of three facets of conservation biology: biodiversity conservation, habitat restoration and species invasion management.

Dark Diversity Concept

At a regional-scale, absent species fall broadly into two 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, belonging to a 'habitat-specific' species pool (*sensu* Erikson 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 can be termed 'dark diversity' (Pärtel et al. 2011) and is complementary to the multi-fold 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).



- **Regional richness (γ-diversity)**: species richness within a landscape or region, likely encompass multiple different habitat types (Whittaker 1960); sometimes cumulative number of species over a set of sites or samples (Loreau 2000).
- **Species pools**: species pools by the following definition are 'habitat-specific' (or 'filtered') i.e. they refer to species which are present in the region and can potentially inhabit a focal site because of suitable ecological conditions (Erikson 1993, Pärtel et al. 1996, Zobel 2016); defined according to species' ecological requirements (**β-niche**, Silvertown 2006). Note that sometimes ('unfiltered') species pool has been used synonymously with γ-diversity.
- **Meta-community**: a set of local communities that are linked by dispersal (Gilpin & Hanski 1991; Wilson 1992); defined according to similar sites.
- **Observed diversity (α-diversity)**: species diversity within a site (Whittaker 1960).
- **Dark diversity**: the set of species that are currently absent from a site but which belong to its habitat specific species pool (Pärtel et al. 2011). Can be used to calculate a **completeness index** which expresses the diverse of a local site relative to its species pool; expressed as *log*(*observed diversity/dark diversity*) (Pärtel et al. 2013).
- **β-diversity**: difference in diversity between sites within a region (Whittaker 1960), or set of samples (Loreau 2000).

Figure 1. Conceptual diagram illustrating the hierarchical structure of following ecological concepts: Species pools, alpha (α), beta (β) and gamma (γ) diversity, the meta-community and dark diversity. Definitions of terminologies used in the main text are provided

Although dark diversity appears seemingly similar to other ecological concepts (for example, β-diversity; Weiher et al. 2011), dark diversity can contribute new and complementary information. To reinforce Pärtel et al. (2011), β-diversity (i.e. species turnover) focuses on diversity among various habitats for the entire flora/fauna within a region (i.e. γ-diversity; Fig. 1). In contrast, dark diversity focuses only on a portion of γ-diversity that can potentially occur within a particular habitat or rather particular environmental conditions. Similar parallels can also be drawn between dark diversity and the meta-community concept (cf. 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), it describes processes that occur across varying spatial scales (i.e. the meta-community scale) linking local population dynamics to landscape patterns. However, a meta-community 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 (Lewis et al. 2016; Smart et al. 2015). Species distribution modelling, which has origins 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 & Thuiller 2005). While commonly viewed with respect to species occurrences, the models provide equally as much information concerning species absences. 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 methodology also integrates flexible species-specific thresholds that act to select, or reject, species into a community's dark diversity depending on the research question. The thresholds themselves are user-defined, and therefore, non-discrete, as species ecological preferences (i.e. species beta-niche *sensu* Silvertown 2006) are non-discrete in nature. Via this approach, dark diversity estimates can be tailored to specific habitats and/or regions.

There are, however, certain limitations to using co-occurrence based dark diversity estimates. Affined but rare species are often underestimated within dark diversity simply due to the limited co-occurrence patterns. In such instances, comprehensive species distribution data, functional traits or ecological requirements of species have been shown as alternatives. For example, Lessard et al. (2016) estimated hummingbird species pools across northwestern South America, Belmaker & Jetz (2013) estimated ecological suitable species pools for both bird and mammal species, and Pärtel et al. (1996) estimated plant species pools across Estonian plant communities. Nevertheless, 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 which 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 utilised 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 localised habitat or an entire biome). At the global-level, prioritisation focuses on identifying areas that fall within a framework of 'irreplaceability' and 'vulnerability' (Brooks et al. 2006). Irreplaceability quantifies species endemism, identifying biodiversity hotspots (Myers et al 2000; Mittermier et al. 2003), while quantifying vulnerability can take multiple forms (Wilson et al. 2005). Interpreting patterns from various prioritisation templates help 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' *sensu* 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 prioritisation 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. how complete a habitat/region is 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 (*sensu* Olsen & Dinerstein 1998), coupled with high irreplaceability and vulnerability (*sensu* Brooks et al. 2006) can be said to especially require conservation priority. Diverse yet complete communities should imply greater functional stability with higher levels of ecosystem services. Communities with a high completeness in northern boreal and temperate regions might even represent areas of last glacial maxima refugia. Here, species can be in disequilibrium with their current environment, absent across much of their potential range due to a combination of dispersal limitation and priority effects during post-glacial recolonization (Svenning & Skov 2004). Relatively complete communities, therefore, have the potential to act as an important source for trailing edge populations, which can even give rise to high ecosystem diversity, thereby providing refuge for many taxa irrespective of changing environmental conditions, as found for long-lived remnant tree populations (Svenning & Sandel 2013).

Macro-scale variation in biodiversity (and in-turn co-variation 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, decreasing towards the poles. Resultant patterns thus correlate well with macro-scale 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 European-scale. The study revealed stronger patterns between regional completeness and human influence – with higher completeness in regions with low human influence (e.g. Scandes, Pyrenees) and lower in regions with high human influence (e.g. central Europe; Ronk et al. 2015). As 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); process that are pivotal in protecting against regional extinctions.

Processes shaping ecological communities (e.g. dispersal and biotic interactions) vary among regions and habitat types due to differences in species, environmental conditions, climate and land use (Lenoir et al. 2010). This in turn complicates the interpretation of large-scale habitat assessments across regions and habitats. As a relativized metric, the 'completeness index' is advantageous in this respect, as 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). In addition, it can compare communities of different trophic levels such as plants, insects and birds (Pärtel et al. 2011). Its application is not restricted to biological taxa, being easily augmented to measure completeness across genes, functions or phylogeny, or even stratified into informative classes (e.g. differentiating between native and alien species). Knowledge of completeness (taxonomic, genetic and/or functional) with respect to the species pool can therefore prove an invaluable and informative biodiversity metric, 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 its ecological trajectory shifts, impacting abiotic and biotic processes and ultimately ecosystem functions. 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 'best as possible'. Another important, but less obvious consideration, is an understanding of the local species pools from which lost species are to be recouped (see Sundermann et al. 2011). Frequently, restoration requires a reference ecosystem to be defined, typically that of the original, 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 two 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 impacted negatively upon 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 habitats dark diversity. Where species pools are not conserved, i.e. they are depauperate, reference assemblages cannot be expected to be successfully restored, as for assemblages of fish species following river restoration in Germany (Stoll et al. 2012). From this perspective, conservation of a habitat's dark diversity is vital if localized species extinctions are to be reversed and ecosystem functions re-instated.

The use of reference sites to define restoration targets is not always straightforward. First, suitable reference sites may not exist or compositionally similar sites exist, but are subject to contrasting abiotic influences relative to the restoration site. Second, the restoration site may be degraded to the extent that its species pool is simply non-comparable with any reference pool during early phases of restoration. Such situations are not uncommon, especially for highly dynamic and/or rare ecosystems with limited spatial extent. These systems require effective restoration monitoring and adaptive management (Westgate et al. 2013), i.e. systematically re-building the species pool. In this situation, understanding and monitoring even transient species pools (i.e. observed and dark diversities through time) of 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, measuring the restoration sites dark diversity (though not expressed this way) through defining target plant species from the regional species pool.

Ultimately, monitoring is an essential part of any ecological restoration and/or conservation management, 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, resulting in a useful turnover metric in which to measure restoration success (for example, see Koch et al. 2014), as well as gauge wider-context biodiversity conservation targets (for a review, see Carwardine 2009). Knowledge of dark diversity can also help identify potential threats to restoration success. Not all species are wanted (see section on dark diversity and invasion ecology). Identification of potential undesirable species facilitates preventative measure to be implemented into restoration management plans early on. For example, Funk et al. (2008) propose that introduced natives be selected based on their functional similarity to potential invaders, limiting available niche-space (Mitchell et al 2000). Monitoring dark diversity can therefore help to initiate pre-planned adaptive management measures (*sensu* Lindenmayer & Likens 2009) in the event the restoration trajectory goes off course. Similarly, pre-specified structures and/or 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).

While ecological monitoring is necessary for tracking restoration progress, progress itself requires an understanding of the ecological processes limiting species to dark diversity. Identifying the mechanisms that explain why some species inhabit suitable sites and others belong to the dark diversity can be achieved through exploring species functional characteristics. For example, many species in temperate semi-natural grasslands are constrained to the dark diversity due to dispersal limitation (Riibak et al. 2015). This is valuable knowledge for implementing effective restoration, indicating some form of facilitated dispersal may be key for enhancing the biodiversity value of temperate semi-natural 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 available habitats. Here co-occurrence patterns are likely to suggest their presence in the dark diversity, nevertheless, restoration through facilitated dispersal should always respect bio-geographical constraints.

Dark diversity and invasion ecology

As mentioned in the previous section, one of the aims of conservation can be to promote certain absences. However, affined but absent from a community does not imply a species should be part of the community automatically. Such a view-point would be dangerous from a conservation perspective by promoting managed invasions. This is because dark diversity estimates consider only a species ecological affinity. Subsequently all species irrespective of whether it is 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 too can help prevent unwanted presences.

A large expense and research effort is channelled 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. Kalusova 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's regional pool, will not only increase the probability of these species becoming successful invaders, but also increase its own invasibility (i.e. the 'donor' habitat; see also Kalusova 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. Whilst valid for understanding island biogeography, in particular niche vacancy and community saturation (see Shea & Chesson 2002), such hypotheses are nowadays dismissed. Species richness alone is a poor predictor for invasion resistance of plant assemblages (Moore et al. 2001). More influential are the ecological mechanisms governing species co-existence i.e. biotic and abiotic interactions, as well as 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, yet this is likely because their species pool and its dark diversity (i.e. potential diversity) are large, confounding 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 prove to be a better measure of community saturation and niche vacancy, and a useful proxy for invasibility. As a result, in the same way completeness provides a useful tool for macro-scale assessment of conservation and restoration priorities, it too can be used to provide effective macro-scale comparisons of biotic resistance among different habitats and regions, helping to develop a clearer understanding of the general relationship between diversity and invasion.

At a local-scale, understanding invasion potential requires knowledge regarding the inter-play 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 match between the invader, community and resident species. Therefore, understanding functional similarity and/or dissimilarity to potential invasives requires knowledge of a community's dark diversity, in particular that of the alien species pool (Smith & Knapp 2001; Perelman et al. 2007). Further efforts should be made towards understanding 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 towards 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 also important is an ability to identify potential threats of new invaders (Groves et al. 2001). Non-native invasions often result in negative ecological and socio-economic impacts (Levine et al. 2003; Mack et al. 2000; 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.

Concluding Remarks

Over much of its history, conservation ecology has developed in situ with community ecology, linking observable patterns 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. Dark diversity facilitates comparisons of biodiversity, irrespective of habitat types and taxa, it 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 our understanding of fundamental ecological processes governing biological diversity. However, to what extent is broadly unknown. Here, we have discussed 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 implemented more widely. After all, scrutinizing additional patterns other than observed diversity only adds to the arsenal from which to guide both the development and implementation of conservation actions.

Acknowledgements

This work resulted from a workshop discussion between colleagues of the Macroecology workgroup, Tartu, Estonia, the Institute of Botany, Třeboň, Czech Republic and the Department of Botany, České Budějovice, Czech Republic, and supported by the institutional research funding (IUT 20-29) of the Estonian Ministry of Education and Research, the Estonian Research Council postdoctoral research grant PUTJD15, the Czech Science Foundation, grant P505/12/1296 and project 14-36079G (Centre of Excellence PLADIAS), and the European Regional Development Fund (Centre of Excellence EcolChange).. We thank Jakub Tešitel, Jitka Klimešová, Petra Janečekova, Petr Šmilauer, Petr Blazek and Štěpán Janeček for helpful discussions. In particular, we thank Rob Marrs, (University of Liverpool, UK) for valuable comments on an earlier version.

Literature Cited

Andreu J, Vila M. 2010. Risk analysis of potential invasive plants in Spain. Journal for Nature Conservation **18:** 34–44.

Brooks TM, Mittermeier RA, da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL. 2006. Global biodiversity conservation priorities. Science **313:** 58–61.

Belmaker J, Jetz W. 2013. Spatial scaling of functional structure in bird and mammal assemblages. The American Naturalist **181:** 464-478.

Carwardine J, Klein CJ, Wilson KA, Pressey RL, Possingham HP. 2009. Hitting the target and missing the point: target-based conservation planning in context. Conservation Letters **2:** 3–10.

Cornell HV, Harrison SP. 2014. What are species pools and when are they important? Annual Review of Ecology, Evolution and Systematics **45:** 45–67

de Bello F, Price JN, Münkemüller T, Liira J, Zobel M, Thuiller W, Gerhold P, Götzenberger L, Lavergne S, Leps J, Zobel K, Pärtel M. 2012. Functional species pool framework to test for biotic effects on community assembly. Ecology, **93**: 2263–2273.

Dullinger S, Gattringer A, Thuiller W, Moser D, Zimmermann NE, Guisan A, Willner W, Plutzar C, Leitner M, Mang T, Caccianiga M, Dirnböck T, Ertl S, Fischer A, Lenoir J, Svenning J-C, Psomas A, Schmatz DR, Silc U, Vittoz P, Hülber K. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature, **2:** 619-622.

Eriksson O. 1993. The species-pool hypothesis and plant community diversity. Oikos **68:** 371–374.

Franklin J. 2010. Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge.

Fraser LH, Pärtel M, Pither J, Jentsch A, Sternberg M, Zobel M. 2015. Response to Comment on “Worldwide evidence of a unimodal relationship between productivity and plant species richness”. Science **350:** 1177.

Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B. 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecology **88:** 3–17.

Funk JL, Cleland EE, Suding KN, Zavaleta ES. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution **23:** 695–703.

Gilpin ME, Hanski IA. 1991. Metapopulation dynamics: Empirical and theoretical investigations. Academic Press, London.

Groves RH, Panetta FD, Virtue JG. 2001. Weed risk assessment. CSIRO Publishing, Collingwood, Australia.

Guisan A, Thuiller W. 2005. Predicting species distributions: Offering more than simple habitat models. Ecology Letters **8:** 993–1009.

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters **8:** 23–29.

Kalusová V, Chytrý M, Kartesz JT, Nishino M, Pyšek P. 2013. Where do they come from and where do they go? European natural habitats as donors of invasive alien plants globally. Diversity and Distributions **19:** 199–214.

Kalusová V, Chytrý M, Peet RK, Wentworth TR. 2014. Alien species pool influences the level of habitat invasion in intercontinental exchange of alien plants. Global Ecology and Biogeography **23:** 1366–1375.

Koch K, Wagner C, Shalén G. 2014. Farmland versus forest: comparing changes in Odonata species composition in western and eastern Sweden. Insect Conservation and Diversity **7:** 22–31.

Lawton JH. 1999. Are there general laws in ecology? Oikos **84:** 177–192.

Lessard J-P, Weinstein BG, Borregaard MK, Marske KA, Martin DR, McGuire JA, Parra JL, Rahbek C, Graham CH, Harrison AES, Bronstein, EJL. 2016. Process-based species pools reveal the hidden signature of biotic interactions amid the influence of temperature filtering. The American Naturalist **187:** in press.

Lewis RJ, Szava-Kovats R, Pärtel M. 2016. Estimating dark diversity and species pools: an empirical evaluation of two methods. Methods in Ecology and Evolution **7:** 104–113.

Lenoir J, Gégout J-C, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Svenning J-C. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography **33:** 295–303.

Levine JM, Vila M, D'Antonio C, Dukes JS, Grigulis K, Lavorel S. 2003. Mechanisms underlying the impact of exotic plant invasions. Philosophical Transactions of the Royal Society B **270:** 775–781.

Lindenmayer DB, Likens GE. 2009. Adaptive monitoring: a new paradigm in long-term studies. Trends in Ecology and Evolution **24:** 482–86.

Lindenmayer DB, Likens GE. 2010. Effective ecological monitoring. Melbourne, Australia, and London, UK: CSIRO Publishing and Earthscan.

Loh J, Green RE, Ricketts T, Lamoreux J, Jenkins M, Kapos V, Randers J. 2005. The Living Planet Index: using species population time series to track trends in biodiversity. Philosophical Transactions of the Royal Society B **360:** 289–295.

Loreau M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos **91:** 3–17.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications **10:** 689–710.

Margules CR, Pressey RL. 2000. Systematic conservation planning. Nature **405:** 243–253.

Mitchell RJ, Auld MHD, Le Duc MG, Marrs RH. 2000. Ecosystem stability and resilience: a review of their relevance for the conservation management of lowland heaths. Perspectives in Plant Ecology, Evolution and Systematics **3:** 142–160.

Mittermeier RA, Mittermeier CG, Brooks TM, Pilgrim JD, Konstant WR, da Fonseca GAB, Kormos C. 2003. Wilderness and biodiversity conservation**.** Proceedings of the National

Academy of Science **100:** 10309–10313.

Moore JL, Mouquet N, Lawton J H, Loreau M. 2001. Coexistence, saturation and invasion resistance in simulated plant assemblages. Oikos **94:** 303–314.

Mosblech NAS, Bush MB, van Woesik R. 2011. On metapopulations and microrefugia: palaeoecological insights. Journal of Biogeography **38:** 419–429.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature **403:** 853–858.

Olson DM, Dinerstein E. 1998. The global 200: A representation approach to conserving the earth's most biologically valuable ecoregions. Conservation Biology **12:** 502–515.

Pärtel M. 2014. Community ecology of absent species: hidden and dark diversity (R Kalamees, Ed.). Journal of Vegetation Science **25:** 1154–1159.

Pärtel M, Szava-Kovats R, Zobel M. 2013. Community completeness: Linking local and dark diversity within the species pool concept. Folia Geobotanica **48:** 307–317.

Pärtel M, Szava-Kovats R, Zobel M. 2011. Dark diversity: shedding light on absent species. Trends In Ecology And Evolution **26:** 124–128.

Pärtel M, Zobel M, Zobel K, van der Maarel E. 1996. The species pool and its relation to species richness: Evidence from Estonian plant communities. Oikos **75:** 111–117.

Perelman SB, Chaneton EJ, Batista WJ, Burkart SE, León RJC. 2007. Habitat stress, species pool size and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands. Journal of Ecology **95:** 662–673.

Pimentel D, Zuniga R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics, **52:** 273–288.

Pouteau R, Bayle E, Blanchard E, Birnbaum P, Cassan J-J, Hequet V, Ibanez T, Vandrot H. 2015. Accounting for the indirect area effect in stacked species distribution models to map species richness in a montane biodiversity hotspot. Diversity and Distributions **21:** 1329–1338.

Rejmánek M, Richardson DM, Pyšek P. 2005. Plant invasions and invasibility of plant communities In: van der Maarel, E. ed. Vegetation Ecology, p. 332–355 Blackwell, Oxford.

Riibak K, Reitalu T, Tamme R, Helm A, Gerhold P, Znamenskiy S, Bengtsson K, Rosén E, Prentice HC, Pärtel M. 2015. Dark diversity in dry calcareous grasslands is determined by dispersal ability and stress-tolerance. Ecography **38:** 713–721.

Ronk A, Szava-Kovats R, Pärtel M. 2015. Applying the dark diversity concept to plants at the European scale. Ecography **38:** 1015–1025.

SER (2004). The SER Primer on Ecological Restoration, Version 2. Society for Ecological Restoration Science and Policy Working Group. Silvertown, J., M. Dodd, D. Gowing, C. Lawson, and K. McConway. 2006. Phylogeny and the hierarchical organization of plant diversity. Ecology, **87**, S39–S49.

Sharma N, Madhusudan MD, Sinha A. 2013. Local and andscape correlates of primate distribution and persistence in the remnant lowland rainforests of the upper Brahmaputra alley, northeastern India. Conservation Biology **28:** 95–106.

Shea K, Chesson P. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution **17:** 170–176.

Smart SM, Jarvis S, Walker KJ, Henrys PA, Pescott OL, Marrs RH. 2015. Common plants as indicators of habitat suitability for rare plants; quantifying the strength of the association between threatened plants and their neighbours. New Journal of Botany **5:** 72–88.

Smith MD and Knapp AK. 2001. Size of the local species pool determines invasibility of a C4-dominated grassland. Oikos **92**, 55-61.

Stoll, S., Sundermann, A., Lorenz, A.W., Kail, J. and Hasse, P. 2012. Small and impoverished regional species pools constrain colonisation of restored river reaches by fishes. Freshwater Biology, **58**, 664-674.

Stoll S, Sundermann A, Lorenz AW, Kail J, Hasse P. 2012. Small and impoverished regional species pools constrain colonisation of restored river reaches by fishes. Freshwater Biology **58:** 664–674.

Sundermann A, Antons C, Cron N, Lorenz AW, Hering D, Haase P. 2011. Hydromorphological restoration of running waters: effects on benthic invertebrate assemblages. Freshwater Biology **56:** 1689–1702.

Suding KN. 2011. Toward an era of restoration in ecology: Successes, failures, and opportunities ahead. Annual Review of Ecology, Evolution, and Systematics **42:** 465–487.

Svenning J-C, Skov F. 2004. Limited filling of the potential range in European tree species. Ecology Letters **7:** 565–573.

Svenning J-C, Sandel B. 2013. Disequilibrium vegetation dynamics under future climate change. American Journal of Botany **100:** 1266–1286.

Tansley AG. 1949. The British Isles and their vegetation. Cambridge University Press, Cambridge, UK.

Vellend M. 2010. Conceptual synthesis in community ecology. The Quarterly Review of Biology **85:** 183–206.

Watt AS. 1947. Pattern and process in the plant community. Ecology **35:** 1–22.

Westgate M J, Likens GE, Lindenmayer, DB. 2013. Adaptive management of biological systems: a review. Biological Conservation **158:** 128–139.

Whittaker RM. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs **30:** 279–338.

Williams BK. 2011. Passive and active adaptive management: approaches and an example. Journal of Environmental Management **92:** 1371–1378.

Wilson DS. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology **73:** 1984–2000.

Wilson KA, Pressey RL, Newton AN, Burgman MA, Possingham HP, Weston CJ. 2005.

Measuring and incorporating vulnerability into conservation planning. Environmental Management **35:** 527–543.

Wilson KA, Carwardine J, Possingham HP. 2009. Setting conservation priorities. Annals of the New York Academy of Sciences, The Year in Ecology and Conservation Biology **1162:** 237–264.

Wilson KA, Lulow M, Burger J, Fang Y, Andersen C, Andersen C, Olson O'Connell M, McBride MF. 2011. Optimal restoration: accounting for space, time, and uncertainty. Journal of Applied Ecology, **28:** 715–25.

Wolters M, Garbutt A, Bakker JP. 2005. Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. Biological Conservation **123:** 249–68.

World Pheasant Association and IUCN/SSC Re-introduction Specialist Group (eds.) 2009. Guidelines for the Re-introduction of Galliformes for Conservation Purposes. Gland, Switzerland: IUCN and Newcastle-upon-Tyne, UK: World Pheasant Association. 86 pp.

Zobel, M. 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? Trends in Ecology and Evolution **12:** 266–269.

Zobel, M. 2016. The species pool concept as a framework for studying patterns of plant diversity. Journal of Vegetation Science **27:** 8–18.