

Characteristic and derived diversity: implementing the species pool concept to quantify conservation condition of habitats

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ABSTRACT

Anthropogenic environmental changes in climate, land use and disturbance regimes, as well as mass propagule transport are having dramatic effects on many ecosystems. Both conservationists and ecologists need ecologically relevant metrics to quantify the condition of plant and animal communities. However, current metrics fail to address the invasion of species native to different community types in the same region, even though these 'native aliens' can serve as valuable indicators of recent changes in habitat condition. We propose a novel approach to reconceptualize community biodiversity based on the composition of historically developed habitat-specific species pools. Total observed community diversity can be divided to characteristic diversity, consisting of species belonging to habitat-specific species pool, and derived diversity, consisting of either native or nonnative species not typical to a given community and whose presence is driven by adverse human impact. Characteristic and derived diversity in communities have different historical backgrounds; thus, the ecological patterns of these components, effects on ecosystem functioning as well as actions necessary for their conservation are likewise different. We propose the Index of Favourable Conservation Status – the log ratio of characteristic to derived diversity – as an easily quantified, ecologically relevant and universal indicator of biodiversity integrity and community condition. The Index of Favourable Conservation Status provides valuable information on habitat conservation needs and recent adverse human impact in relative terms and can be compared between regions and across a wide range of ecosystems. It can also be used to monitor restoration success or characterize biodiversity degradation. We present standardized procedure of determining habitat-specific species pools and bring several examples of how the concept of characteristic and derived diversity can be applied in conservation and research and how expert knowledge on habitat-specific species pool composition can expand our understanding of community biodiversity.

Keywords

Anthropogenic impact, biodiversity index, biodiversity integrity, biological invasions, community composition, native and non-native invaders, species pools.

TOTAL NATIVE BIODIVERSITY AND THE RATIO OF NATIVE TO NON-NATIVE SPECIES CAN FAIL AS MEASURES OF HABITAT CONDITION

Human-related changes in environmental conditions and dramatically enhanced dispersal over great geographic distances have provided the opportunity for species to establish in communities where they were previously absent (Hobbs *et al.*, 2009; Cameron & Bayne, 2012). In this context, the invasion by non-native species has received the most attention due to its unambiguous anthropogenic cause, observable and strong effects on ecosystems (Sax & Gaines, 2003; Vilà *et al.*, 2011) and negative public perception (Simberloff *et al.*, 2013). However, changes in abiotic and biotic

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conditions also make communities susceptible to 'native introductions' by species from other local habitat types (Valéry et al., 2009, 2013). Although the effects of non-native species invasions on ecosystems are considered to be substantially greater (Simberloff et al., 2012), the ecological consequences and causes of the arrival of untypical native species also merit discussion (Davis et al., 2011; Valéry et al., 2013). Invasion of untypical species can also reflect in total species number - another widely used indicator of community conservation value - and in some cases, lead to erroneous conclusions. For example, in dry calcareous semi-natural grasslands in Estonia and Sweden, total plant species richness has shown to increase temporarily following the cessation of traditional habitat management due to the invasion of shade-tolerant forest species and habitat generalist species that benefit from increasing shrub cover (Rejmánek & Rosén, 1988; Pärtel et al., 1999; Kasari et al., 2013). It can take several decades before the eventual extinction of light-demanding grassland species, resulting in temporarily high total species number in communities that actually have urgent conservation need (Helm et al., 2006).

Here, we show that the focus on total observed native diversity or on alien versus native diversity in community ecology can be complemented by an approach that considers recent invasions and historical role of species in ecosystems. Defining the habitat-specific species pools for communities allows us to quantify the historical and recent (humanrelated) components of observed biodiversity. The historically developed habitat-specific species pool is a set of species that occur naturally in the region, are able to disperse to studied habitat and have life history characteristics that enable them to establish, survive and reproduce under environmental conditions that are typical to the particular habitat (Eriksson, 1993; Pärtel et al., 1996, 2011). The development of the species pool of each community represents a long-term process, led by evolutionary and dispersal events (Zobel et al., 2011). Ecological relationships, assembly rules and species' temporal dynamics in habitats are related directly to the composition of community species pool (Lessard et al., 2012). Therefore, it is of utmost importance to consider the habitat-specific species pool when studying the diversity or planning conservation of natural communities (Cam et al., 2000; Pärtel, 2014).

CHARACTERISTIC AND DERIVED DIVERSITY

We suggest a reconceptualization of total observed community biodiversity into two components – characteristic and derived diversity. *Characteristic diversity* consists of those species that belong to a habitat-specific species pool and are currently present in a particular habitat (Fig. 1). We define characteristic diversity as the component of biodiversity that represents to the best of our knowledge the natural and typical part of a particular community, including both rare and common native species. How this 'natural state' is defined depends on a region, ecosystem, existing knowledge and





conservation targets, but characteristic diversity would mostly be typical to given habitat type without recent humaninduced environmental changes. In the context of habitat conservation, researchers and managers may be particularly interested in the composition of species pool during the period of interest (for example in pre-European times or in times prior to the onset of intensive agriculture). Ideally, communities would contain only species that belong to their species pool, making their characteristic diversity equal to the observed total diversity. The term 'characteristic' is also previously used in ecological literature to depict the desired and typical part of biodiversity, for example as put by G. C. Ray: 'The description of characteristic diversity - including indicator and keystone species - must be our immediate focus, and the preservation of that diversity our ultimate challenge' (Ray, 1988, pp. 42). The identification of 'original' species pool of habitats has likewise been suggested to be essential in determining conservation need and tools (Cam et al., 2000).

However, we often record species in biodiversity surveys that are not historically characteristic of the studied community, but derive due to anthropogenic causes and environmental change from either other habitat types or other geographic regions. These species can serve as valuable indicators of adverse changes in habitat condition. We assign these species to *derived diversity*, as they are novel to the community and do not belong to the habitat-specific species pool. Derived diversity includes not only non-native species from different geographic regions, but also native 'aliens' that are either specialist species from other habitat types (including weeds, opportunistic species) or generalist species that are otherwise widespread, but have not historically been part of this particular habitat. The new term *derived diversity* stems from the concept of derived habitats such as derived grasslands where human impact has profoundly changed the fire and grazing regime of natural grasslands, resulting in altered species composition and augmented occurrence of non-native species (Groves, 2000), or derived forests and scrubs that depict degraded state of previously good-quality forest habitats (Putz & Redford, 2010).

There are variety of processes that can lead to infiltration of habitats by species belonging to derived diversity, including change in physical-chemical conditions of communities (e.g. Duprè et al., 2010), change in historically developed disturbance regimes (Moles et al., 2012), fluctuation in resource availability (Davis et al., 2000), habitat alteration by invasive species (Vilà et al., 2011) and change in the surrounding landscape (Wiser & Buxton, 2008). In addition, derived diversity may increase with the loss of characteristic species and resulting reduced invasion resistance (Zavaleta et al., 2010), excessive flow of alien diaspores (i.e. propagule pressure, Simberloff, 2009), climate change (Williams & Jackson, 2007; Lenoir et al., 2010) and habitat loss and fragmentation (Helm et al., 2006). Facilitation by already established new species and promotion via development of new biotic relationships can increase the habitat susceptibility to additional species (Stevens & Beckage, 2009).

Most of the above-mentioned reasons are triggered by adverse human impact during the Anthropocene (Ellis et al., 2010). Thus, an increasing number of derived species can indicate recent environmental changes and anthropogenic impact. Increasing dominance of derived species can also lead to variety of functional and structural alterations in ecosystems. For example, the human-induced encroachment of indigenous shrubs to semi-arid and arid grasslands around the world has increased net ecosystem productivity and significantly altered the quantity and distribution of soil and plant C and N pools (Eldridge et al., 2011). With increasing derived diversity, novel traits and novel phylogenetic lineages are introduced to the community, possibly inducing a change in functional community structure and diversity (Mouillot et al., 2013). Eventually, novel ecosystems can develop from combinations of species that have never coexisted previously (sensu Hobbs et al., 2009), resulting in long-term effects on the local network of biotic interactions and the intrinsic dynamics of the ecosystems. If there are more generalists among derived diversity than among characteristic diversity, the invasion is likely to result in local and regional biotic homogenization (Clavel et al., 2011). From a conservation perspective, knowledge of the identity and effect of novel species in the ecosystems by quantifying derived diversity allows us to detect habitat alteration and employ conservation actions when necessary.

The idea of identifying native species that could serve as indicators of human influence is not utterly new. In a number of Central and Eastern European countries, the synanthropic component of native floras has been distinguished. For instance, native plant species that benefit from humanrelated disturbances are described as apophytes (Wittig, 2004; Sukopp, 2006). Similarly, specialist versus generalist species can be distinguished according to the width of their ecological niches and are thought to be differently influenced by anthropogenic changes (Krauss *et al.*, 2004; Devictor *et al.*, 2008). Our approach provides a broader and more ecological distinction that is built on historical assembly and development of communities rather than properties of individual species. The concept of derived and characteristic diversity allows us to encompass both native and non-native invaders and is also applicable to animal communities.

QUANTIFYING CHARACTERISTIC AND DERIVED DIVERSITY

Composition of habitat-specific species pools, as well as conservation targets, is unique for each region and habitat. Characteristic diversity can only be described when there is knowledge of the composition of the habitat-specific species pool of a particular habitat in its desired conservation state.

We hereby propose standardized workflow that can be used to estimate the composition of habitat-specific species pools (Fig. 2). In the described approach, the first and the last steps are inevitable, that is, it is always necessary to determine the range of species (step 1) and use local experts to confirm the species list (step 3). Step 2 lists number of approaches encompassing ecological filters that can be selected depending on the availability of background information. They are broadly listed in an order of preferential use, that is, more informative are listed first. Alternatively, in case there is information available to use several approaches on step 2, they can be applied consecutively to elaborate the selection based on previous filter(s). The use of ecological filters should always be pursued while determining species pools. However, in regions and habitats where the amount of existing information is very poor, only steps 1 and 3 can be applied to determine species pool composition until additional data are accumulating.

Standardized workflow to determine habitat-specific species pool composition:

1. The first and obligatory step is to identify a range of species that occur naturally in a region from where they can potentially disperse to a given community. This region can be, for example, a small country, a county, a nature reserve or a single relatively uniform biogeographic region (Pärtel *et al.*, 1996, 2011).

2. Application of ecological filters depending on the availability of information and objectives of study. To obtain a representative estimate of characteristic diversity, filters 2b-2d have to be applied to good-quality habitat patches.

a. Use of species-specific information on habitat requirements. Species habitat requirements, preference of certain environmental conditions or an affiliation to particular habitat type are available in number of databases. For



Figure 2 Standardized procedure to identify species pool composition. Step 1 and step 3 are inevitable and have to be always applied. Step 2 provides several approaches that can be selected depending on the availability of background information for particular region and habitat. More informative approaches are listed first, but if suitable information is available, each step can also be sequentially applied to elaborate the selection based on previous stage. In case there is no ecological information available, one can move from step 1 straight to step 3. See the main text for more detailed descriptions.

example, there is existing semi-quantitative information about habitat requirements available for plants in Central Europe (Ellenberg et al., 1991), Italy (Pignatti et al., 2005) or UK (Hill et al., 1999). Lists of typical habitats for European plants can be found in several databases, e.g. BiolFlor (Klotz et al., 2002); Grime (2006), and such information is becoming increasingly available for other species groups (e.g. Speight, 2012). Species habitat requirements have been used in number of studies to determine habitat-specific species pools (Kelt et al., 1995; Pärtel et al., 1996; Duprè, 2000; Diekmann, 2003; Chessman & Royal, 2004; Harrison & Grace, 2007; Sádlo et al., 2007; Zobel et al., 2011; de Bello et al., 2012). In many regions and for many species groups, this approach can still be impracticable due to a lack of data. However, we believe that together with increasing knowledge of natural communities world-wide, information on species habitat requirements is starting to accumulate.

b. Use of community-specific databases to determine species co-occurrence patterns (Ewald, 2002; Münzbergová & Herben, 2004; Pärtel *et al.*, 2011; González-Caro *et al.*, 2012; Lessard *et al.*, 2012). This approach requires a large dataset of species-site descriptions from good-quality habitat patches to identify species belonging to the habitatspecific species pool. Where available, large compilations such as Global Index of Vegetation-Plot Databases (Dengler *et al.*, 2011) can be helpful.

c. Use of fine-scale spatial species distribution data and GIS layers of environmental data to link species occurrence to environmental conditions and habitat distribution. As data with necessary precision are increasingly available in well-studied regions, distribution modelling can serve as a valuable tool to reveal patterns of species assemblages (Elith & Leathwick, 2009; Guisan & Rahbek, 2011; Mokany & Paini, 2011).

d. Use of regional community surveys and classifications. An inventory of species encountered in a specific habitat type, or habitat classifications studies typically present a list of characteristic species for particular community type (Cam *et al.*, 2000; Duprè, 2000; Tofts & Silvertown, 2002; Losvik, 2007; Sádlo *et al.*, 2007; Kirmer *et al.*, 2008). This information can also be obtained from increasingly available data papers (Chavan & Penev, 2011). Some authors have also used 'reference sites' to quantify species composition of good-quality habitat patches and applying the results to assess the change in degraded sites (Hughes *et al.*, 1986; Zampella & Bunnell, 1998).

e. Use of local descriptive data about communities. Historical species lists from the same sites enable to evaluate recent changes in species composition due to adverse human impact (Saar *et al.*, 2012). Materials from case studies or unpublished information that is kept in data repositories or by individual researchers can help to assess the species pool composition.

3. Use of experts to confirm the list of characteristic species should always be final, essential step (Sádlo *et al.*, 2007).

Following the identification of the species pool, all species that are present in the observed community, but do not belong to the characteristic species pool, should be assigned to derived diversity.

The period of infiltration of derived diversity in most regions can coincide with the increase in human population density, related habitat loss and changes in environmental conditions of historically developed habitats. However, numerous ecosystems in Europe and Asia have developed during long-term human influence in the landscape, and moderate anthropogenic impact is a key component necessary for their persistence (Blondel, 2006; Ellis & Ramankutty, 2008). For example, historical land use and related facilitation of invasions from different species pools has resulted in the development of semi-natural grassland habitats in Europe, harbouring remarkable biodiversity (Poschlod et al., 2009; Eriksson, 2013). To determine the derived and characteristic diversity in ecosystems that have evolved handin-hand with humans, it is necessary to match the habitat quality requirements with the onset of rapid changes in traditional land use, that is intensification of agriculture (Duprè et al., 2010).

In summary, the identification of species pools requires a good knowledge of the local biota and its dynamics. We call on experts and ecologists world-wide not only to focus on ecological patterns, but also always to note thoroughly and publish the underlying biodiversity data to increase the general knowledge of biodiversity patterns. We would also encourage researchers to publish a thorough description of their chosen methodology in any publication that deals with habitat specificity or with characteristic versus derived diversity.

Native and non-native species can have ecologically relevant differences in their life history traits (Knapp & Kühn, 2012). Non-native species have arrived mostly via anthropogenic pathways, they can lack natural enemies in the new environment, and they are more likely to turn invasive than native colonizers (Knapp & Kühn, 2012; Simberloff *et al.*, 2012; Simberloff & Vitule, 2014). Thus, in regions and communities where derived diversity consists of native and nonnative species, separate analysis of both can additionally reveal trends in ecosystem invasibility and colonization processes.

APPLYING THE INDEX OF FAVOURABLE CONSERVATION STATUS

For conservation and scientific purposes, we suggest using the Index of Favourable Conservation Status ($FCS_i = log$ (characteristic/derived)), that is, the log ratio of characteristic diversity to derived diversity. This index can describe the ongoing dynamics and habitat condition in relative terms. Metaphorically, this metric captures the fact that the addition of a dozen new species would likely have a considerably greater effect on a species-poor community with ten characteristic species than on a diverse community with hundred of characteristic species. To avoid the limitations of division by zero, both numerator and denominator should be increased by one in case there are no derived species in studied community. As with a large proportion of non-native species in the habitat (Sivicek & Taft, 2011; Catford *et al.*, 2012), a low Index of Favourable Conservation Status can indicate habitat degradation and the necessity for conservation management. Our index can be used as a tool to evaluate the biodiversity recovery following habitat restoration. For example, it can be applied to measure the status of habitat biodiversity and serve as an operational indicator for the Aichi Biodiversity Targets, required by the EU strategic Plan for Biodiversity 2011–2020 (Secretariat of the Convention on Biological Diversity, 2010).

In contrast to simple proportions, the log ratio between characteristic and derived species richness provides not only a measure of relative difference independent of species richness (Szava-Kovats *et al.*, 2012), but places the data in an unbounded line in real space (theoretically from $-\infty$ to $+\infty$), which is a fundamental assumption for all conventional statistics (Bacon-Shone, 2011). As such, the metric displays an effect size like a log odds ratio (Koricheva *et al.*, 2013). When FCS_i is < 0, the characteristic diversity constitutes less than half of the total community diversity. A similar assessment of community status can be performed using species compositional data by calculating characteristic and derived diversity as 'effective species numbers' (Hill, 1973).

We provide an example of the additional insight gained from using the Index of Favourable Conservation Status by examining vascular plant and bryophyte species composition in polluted and intact peat bogs data (Paal et al., 2010; Fig. 3). Peat bogs in Estonia are very well studied, and the species pool composition characteristic of disturbance-free raised bogs has been thoroughly compiled through extensive botanical surveys by habitat experts (Paal & Leibak, 2011). Since the 1950s, many native calciphilous species, including protected orchids from nearby grassland habitats, have invaded the Sphagnum-dominated ombrotrophic (raised) bogs due to alkaline pollution from oil-shale-fuelled power plants (Paal et al., 2010). Although total observed species diversity is even greater in polluted bogs than in pristine bogs (Welch two-tailed t-test, vascular plants: t = 3.14, d.f. = 4.9; P = 0.026; bryophytes: t = 2.26, d.f. 8.62, P = 0.05), the Index of Favourable Conservation Status (FCSi - the log ratio of characteristic:derived diversity) reveals a substantial decline of biodiversity integrity in polluted bogs (vascular plants: t = -2.65, d.f. = 5.09, P = 0.044; bryophytes t = -5.45, d.f. = 8.95, P < 0.001). Consequently, total biodiversity as an index would lead us to conclude that the polluted bogs exhibit good-quality habitat with no pressing need for conservation, especially given that no non-native species are present. Interestingly also, the plant characteristic diversity has even increased also in polluted bogs, which might be related to additional niche construction for bog species in more calcareous habitats (Ewald, 2003). However, as the derived diversity has increased even more, Index of Favourable Conservation Status allows us to distinguish the effects of pollution on biodiversity integrity.

Other similarly straightforward examples in which the Index of Favourable Conservation Status can provide useful



Figure 3 An example of a lower Index of Favourable Conservation Status in degraded raised bogs where current conservation measures have been insufficient. Alkaline fly ash pollution has triggered an invasion of native calciphilous bryophytes and vascular plants that are historically characteristic of nutrient-rich and calcareous subneutral wet meadows or rich fens. Figure is based on Table 3 in Paal *et al.* (2010); see main text for statistics.

information on the change of integrity of community biodiversity include the establishment of shade-tolerant understorey species from nearby forests in unmanaged grasslands in Europe (Duprè *et al.*, 2010) or plant species from saline coastal communities finding a new habitat in salt-polluted grasslands adjacent to motorways (Scott & Davison, 1985).

As the Index of Favourable Conservation Status compares the characteristic and derived diversity in terms of a ratio, it is independent of total species number and can be applied to a range of ecosystems, including both plant and animal communities, in aquatic and terrestrial environments. The Index of Favourable Conservation Status could be applied to measuring climate-induced changes in coral reef assemblages (Yakob & Mumby, 2011), to quantifying the shift in nematode communities due to pollution (Bongers & Ferris, 1999) or assessing the impact of change in pollinator and pollinated plant communities on mutualistic networks (Carvalheiro et al., 2008). For instance, Zampella & Bunnell (1998) have studied aquatic degradation in streams in Pinelands, New Jersey (USA), and found that in streams degraded by eutrophication due to agricultural and urban pollution, species richness of fish had not declined, but they were more colonized by non-Pineland (both native and non-native) species. Application of Index of Favourable Conservation Status in this case can reveal relative decline in restricted native (i.e. characteristic) fish species and emphasize the necessity of conservation.

ECOLOGICAL PATTERNS OF CHARACTERISTIC AND DERIVED DIVERSITY

Quantification of characteristic and derived diversity has also high theoretical significance in aiming to understand ecological relationships and patterns. Establishment success of species belonging to derived diversity can be considered a natural experiment that tests community saturation (Stohlgren *et al.*, 2008) and creates opportunities for rapid evolution of both the invading species and the recipient community (Phillips & Shine, 2006).

Due to their different historical backgrounds, characteristic and derived diversity can exhibit dissimilar relationships with environmental and landscape parameters. In a number of publications, species-area relationships, the effect of habitat loss on diversity or occurrence of extinction debt have been detected only when researchers have defined a habitat-specific species pool (e.g. Steffan-Dewenter, 2003; Krauss et al., 2010; Cousins & Vanhoenacker, 2011; Matthews et al., 2014). Dynamics of species diversity might not be observable immediately following environmental change, as compositional instability can result from extinction debt or colonization credit (Kuussaari et al., 2009; Jackson & Sax, 2010). Such time-lags in species response to environmental change create a challenge in the observations and interpretation of compositional dynamics (Bertrand et al., 2011). In Figure 4, we use data from fragmented and deteriorated calcareous grasslands in Estonia (originally published in Helm et al., 2006; Krauss et al., 2010; Sang et al., 2010) to demonstrate how the detection of the species-area relationship and species time-lag can depend on which biodiversity components are considered. Only native plant and butterfly species occur in these grasslands, and the composition of characteristic diversity was determined by local habitat experts who selected typical species of the total species lists by engaging both their expert assessment and previously available information such as data from numerical habitat classification for calcareous grasslands in Estonia, habitat surveys and monitoring. In these grasslands, the rapid loss of habitat area during previous decades has resulted in extinction debt, and there is no positive relationship between current habitat area and characteristic plant richness (Helm et al., 2006). At the same time, the derived diversity is negatively related to current habitat area, thus inducing a significant relationship with total diversity (Fig. 4, left column). Higher derived diversity in smaller habitat fragments is a result of their greater perimeter-area ratios and otherwise poorer quality. Butterflies, that is, species with shorter life cycles than plants, exhibit no extinction debt, but the relationship with current habitat area is significant only for specialized calcareous



Figure 4 Characteristic and derived diversity can exhibit contrasting ecological relationships due to their dissimilar background in their development. In highly fragmented alvar grasslands in Estonia, total observed diversity, derived diversity and characteristic diversity of plants (left column) and butterflies (right column) are related differently to current habitat area. Regression lines depict statistically significant relationships with corresponding P-values and coefficients of determination (R^2) . Figure is based on data presented in Helm et al. (2006), Sang et al. (2010) and Krauss et al. (2010) with the permission of data owners. See main text for the explanations of observed patterns.

grassland species (Fig. 4, right column). In this case, pooling derived and characteristic diversity and examining total diversity alone would have hidden some of the mechanisms underlying biodiversity patterns. The Index of Favourable Conservation Status is positively related with remaining habitat area in both datasets ($R^2 = 0.20$ for plants and $R^2 = 0.33$ for butterflies), indicating greater biodiversity integrity in currently larger habitats although the occurrence of extinction debt hides this pattern from direct observation of characteristic or total species richness.

In conclusion, environmental changes can render communities susceptible to invasion by both non-native species as well as native species from different habitats. Knowledge of the habitat-specific species pool composition is vital for efficient habitat conservation. Quantifying only observed total (native) diversity as a biodiversity measure can lead to erroneous conclusions about habitat condition and conservation value, as decreases in the characteristic diversity can be masked by increase in derived diversity. The Index of Favourable Conservation Status, that is, log ratio of characteristic:derived diversity, can serve as an efficient biodiversity metric to monitor biodiversity and explore past and future species extinctions. Measured over time, a decrease in the Index of Favourable Conservation Status indicates community alteration. The distinction between characteristic and

derived diversity is necessary to understand fully various ecological processes within and among communities, for planning habitat restoration and evaluating restoration success, for estimating the impact of invading species or for recognizing novel species assemblages.

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REFERENCES

Bacon-Shone, J. (2011) A short history of compositional data analysis. Compositional data analysis: theory and

applications (eds by V. Pawlowsky-Glahn and A. Buccianti), pp. 3–11. John Wiley & Sons, Ltd, Chichester.

- de Bello, F., Price, J.N., Münkemüller, T., Liira, J., Zobel, M., Thuiller, W., Gerhold, P., Götzenberger, L., Lavergne, S. & Lepš, J. (2012) Functional species pool framework to test for biotic effects on community assembly. *Ecology*, **93**, 2263–2273.
- Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.C. & Gégout, J.C. (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, **479**, 517–520.
- Blondel, J. (2006) The 'design' of Mediterranean landscapes: a millennial story of humans and ecological systems during the historic period. *Human Ecology*, **34**, 713–729.
- Bongers, T. & Ferris, H. (1999) Nematode community structure as a bioindicator in environmental monitoring. *Trends in Ecology & Evolution*, **14**, 224–228.
- Cam, E., Nichols, J.D., Sauer, J.R., Hines, J.E. & Flather, C.H. (2000) Relative species richness and community completeness: bird and urbanization in the Mid-Atlantic states. *Ecological Applications*, **10**, 1196–1210.
- Cameron, E.K. & Bayne, E.M. (2012) Invasion by a nonnative ecosystem engineer alters distribution of a native predator. *Diversity and Distributions*, **18**, 1190–1198.
- Carvalheiro, L.G., Barbosa, E.R.M. & Memmott, J. (2008) Pollinator networks, alien species and the conservation of rare plants: *Trinia glauca* as a case study. *Journal of Applied Ecology*, **45**, 1419–1427.
- Catford, J.A., Vesk, P.A., Richardson, D.M. & Pyšek, P. (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. *Global Change Biology*, **18**, 44–62.
- Chavan, V. & Penev, L. (2011) The data paper: a mechanism to incentivize data publishing in biodiversity science. *BMC Bioinformatics*, **12**, S2.
- Chessman, B.C. & Royal, M.J. (2004) Bioassessment without reference sites: use of environmental filters to predict natural assemblages of river macroinvertebrates. *Journal of the North American Benthological Society*, **23**, 599–615.
- Clavel, J., Julliard, R. & Devictor, V. (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*, **9**, 222–228.
- Cousins, S.A.O. & Vanhoenacker, D. (2011) Detection of extinction debt depends on scale and specialisation. *Biological Conservation*, **144**, 782–787.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.
- Davis, M., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Del Tredici, P., Suding, K.N., Ehrenfeld, J.G., Grime, J.P., Mascaro, J. & Briggs, J.C. (2011) Don't judge species on their origins. *Nature*, **474**, 153–154.

- Dengler, J., Jansen, F., Glöckler, F., Peet, R.K., De Cáceres, M., Chytrý, M., Ewald, J., Oldeland, J., Lopez-Gonzalez, G. & Finckh, M. (2011) The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *Journal of Vegetation Science*, 22, 582–597.
- Devictor, V., Julliard, R. & Jiguet, F. (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, **117**, 507–514.
- Diekmann, M. (2003) Species indicator values as an important tool in applied plant ecology – a review. *Basic and Applied Ecology*, **4**, 493–506.
- Duprè, C. (2000) How to determine a regional species pool: a study in two Swedish regions. *Oikos*, **89**, 128–136.
- Duprè, C., Stevens, C.J., Ranke, T., Bleeker, A., Peppler Lisbach, C., Gowing, D.J.G., Dise, N.B., Dorland, E., Bobbink, R. & Diekmann, M. (2010) Changes in species richness and composition in European acidic grasslands over the past 70 years: the contribution of cumulative atmospheric nitrogen deposition. *Global Change Biology*, 16, 344–357.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. & Whitford, W.G. (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters*, **14**, 709–722.
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W.& Paulijen, D. (1991) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, 18, 1–248.
- Ellis, E.C. & Ramankutty, N. (2008) Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, **6**, 439–447.
- Ellis, E.C., Klein Goldewijk, K., Siebert, S., Lightman, D. & Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, **19**, 589–606.
- Eriksson, O. (1993) The species-pool hypothesis and plant community diversity. *Oikos*, **68**, 371–374.
- Eriksson, O. (2013) Species pools in cultural landscapes niche construction, ecological opportunity and niche shifts. *Ecography*, **36**, 403–413.
- Ewald, J. (2002) A probabilistic approach to estimating species pools from large compositional matrices. *Journal of Vegetation Science*, **13**, 191–198.
- Ewald, J. (2003) The calcareous riddle: why are there so many calciphilous species in the Central European flora? *Folia Geobotanica*, **38**, 357–366.
- González-Caro, S., Parra, J.L., Graham, C.H., McGuire, J.A. & Cadena, C.D. (2012) Sensitivity of metrics of phylogenetic structure to scale, source of data and species pool of hummingbird assemblages along elevational gradients. *PLoS ONE*, **7**, e35472.
- Grime, J.P. (2006) *Plant strategies, vegetation processes, and ecosystem properties.* John Wiley & Sons, Chichester.

- Groves, R.H. (2000) Temperate grasslands of the Southern hemisphere. *Grasses: systematics and evolution* (eds by S.W.L. Jacobs and J. Everett), pp. 356–360. CSIRO Publishing, Collingwood, Vic., Australia.
- Guisan, A. & Rahbek, C. (2011) SESAM–a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography*, **38**, 1433–1444.
- Harrison, S. & Grace, J.B. (2007) Biogeographic affinity helps explain productivity-richness relationships at regional and local scales. *The American Naturalist*, **170**, S5–S15.
- Helm, A., Hanski, I. & Pärtel, M. (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters*, **9**, 72–77.
- Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**, 427–432.
- Hill, M.O., Mountford, J., Roy, D. & Bunce, R. (1999) *Ellenberg's indicator values for British plants*. ECOFACT Vol. 2. Technical Annex: Institute of Terrestrial Ecology, Huntingdon, UK.
- Hobbs, R.J., Higgs, E. & Harris, J.A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution*, **24**, 599–605.
- Hughes, R.M., Larsen, D.P. & Omernik, J.M. (1986) Regional reference sites: a method for assessing stream potentials. *Environmental Management*, **10**, 629–635.
- Jackson, S.T. & Sax, D.F. (2010) Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology and Evolution*, **25**, 153–160.
- Kasari, L., Gazol, A., Kalwij, J.M. & Helm, A. (2013) Low shrub cover in alvar grasslands increases small-scale diversity by promoting the occurrence of generalist species. *Tuexenia*, **33**, 293–308.
- Kelt, D.A., Taper, M.L. & Meserve, P.L. (1995) Assessing the impact of competition on community assembly: a case study using small mammals. *Ecology*, **76**, 1283–1296.
- Kirmer, A., Tischew, S., Ozinga, W.A., von Lampe, M., Baasch, A. & van Groenendael, J.M. (2008) Importance of regional species pools and functional traits in colonization processes: predicting re-colonization after large-scale destruction of ecosystems. *Journal of Applied Ecology*, 45, 1523–1530.
- Klotz, S., Kühn, I. & Durka, W. (2002) *BIOLFLOR-Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland*. Bundesamt für Naturschutz, Bonn.
- Knapp, S. & Kühn, I. (2012) Origin matters: widely distributed native and non-native species benefit from different functional traits. *Ecology Letters*, 15, 696–703.
- Koricheva, J., Gurevitch, J. & Mengersen, K. (2013) *Handbook of meta-analysis in ecology and evolution*. Princeton University Press, Princeton.
- Krauss, J., Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2004) Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. *Biodiversity and Conservation*, **13**, 1427–1439.

- Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, 13, 597–605.
- Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution*, 24, 564–571.
- Lenoir, J., Gégout, J.C., Dupouey, J.L., Bert, D. & Svenning, J.C. (2010) Forest plant community changes during 1989-2007 in response to climate warming in the Jura Mountains (France and Switzerland). *Journal of Vegetation Science*, **21**, 949–964.
- Lessard, J.-P., Belmaker, J., Myers, J.A., Chase, J.M. & Rahbek, C. (2012) Inferring local ecological processes amid species pool influences. *Trends in Ecology and Evolution*, 27, 600–607.
- Losvik, M.H. (2007) Regional species pools of hay meadows: a case study. *Applied Vegetation Science*, **10**, 239–248.
- Matthews, T.J., Cottee-Jones, H.E. & Whittaker, R.J. (2014) Habitat fragmentation and the species–area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists. *Diversity and Distributions*, **20**, 1136–1146.
- Mokany, K. & Paini, D.R. (2011) Dark diversity: adding the grey. *Trends in Ecology & Evolution*, **26**, 264–265.
- Moles, A.T., Flores-Moreno, H., Bonser, S.P. *et al.* (2012) Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology*, **100**, 116–127.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, **28**, 167–177.
- Münzbergová, Z. & Herben, T. (2004) Identification of suitable unoccupied habitats in metapopulation studies using co-occurrence of species. *Oikos*, **105**, 408–414.
- Paal, J. & Leibak, E. (2011) *Estonian mires: inventory of habitats.* Regio, Tartu.
- Paal, J., Vellak, K., Liira, J. & Karofeld, E. (2010) Bog recovery in Northeastern Estonia after the reduction of atmospheric pollutant input. *Restoration Ecology*, **18**(Suppl S2), 387–400.
- Pärtel, M. (2014) Community ecology of absent species: hidden and dark diversity. *Journal of Vegetation Science*, **25**, 1154–1159.
- 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.
- Pärtel, M., Mändla, R. & Zobel, M. (1999) Landscape history of a calcareous (alvar) grassland in Hanila, western Estonia,

during the last three hundred years. *Landscape Ecology*, 14, 187–196.

- Pärtel, M., Szava-Kovats, R. & Zobel, M. (2011) Dark diversity: shedding light on absent species. *Trends in Ecology and Evolution*, **26**, 124–128.
- Phillips, B.L. & Shine, R. (2006) An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1545–1550.
- Pignatti, S., Menegoni, P. & Pietrosanti, S. (2005) Bioindicazione attraverso le piante vascolari. Valori di indicazione secondo Ellenberg (Zeigerwerte) per le specie della Flora d'Italia. *Braun-Blanquetia*, **39**, 1–97.
- Poschlod, P., Baumann, A. & Karlik, P. (2009) Origin and development of grasslands in Central Europe. *Grasslands in Europe of high nature value* (eds by P. Veen, R. Jefferson, J. De Smidt and J. Van Der Straaten), pp. 15–25. KNNV Publishing, Zeist, The Netherlands.
- Putz, F.E. & Redford, K.H. (2010) The importance of defining 'forest': tropical forest degradation, deforestation, longterm phase shifts, and further transitions. *Biotropica*, **42**, 10–20.
- Ray, G.C. (1988) Ecological diversity in coastal zones and oceans, pp. 36–50. Biodiversity. National Academy Press, Washington, DC.
- Rejmánek, M. & Rosén, E. (1988) The effects of colonizing shrubs (*Juniperus communis* and *Potentilla fruticosa*) on species richness in the grasslands of Stora Alvaret, Oeland (Sweden). *Acta Phytogeographica Suecica*, **76**, 67–72.
- Saar, L., Takkis, K., Pärtel, M. & Helm, A. (2012) Which plant traits predict species loss in calcareous grasslands with extinction debt? *Diversity and Distributions*, **18**, 808–817.
- Sádlo, J., Chytrý, M. & Pyšek, P. (2007) Regional species pools of vascular plants in habitats of the Czech Republic. *Preslia*, **79**, 303–321.
- Sang, A., Teder, T., Helm, A. & Pärtel, M. (2010) Indirect evidence for an extinction debt of grassland butterflies half century after habitat loss. *Biological Conservation*, **143**, 1405–1413.
- Sax, D.F. & Gaines, S.D. (2003) Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution*, **18**, 561–566.
- Scott, N.E. & Davison, A.W. (1985) The distribution and ecology of coastal species on roadsides. *Plant Ecology*, **62**, 433–440.
- Secretariat of the Convention on Biological Diversity (2010) Convention on biological diversity. Strategic plan for biodiversity 2011–2020, including Aichi biodiversity targets. Available at: http://www.cbd.int/sp/ (accessed 26 August 2014), Montreal.
- Simberloff, D. (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology Evolution and Systematics*, **40**, 81–102.
- Simberloff, D. & Vitule, J.R.S. (2014) A call for an end to calls for the end of invasion biology. *Oikos*, **123**, 408–413.

- Simberloff, D., Souza, L., Nuñez, M.A., Barrios-Garcia, M.N. & Bunn, W. (2012) The natives are restless, but not often and mostly when disturbed. *Ecology*, **93**, 598–607.
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E. & Vilà, M. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution*, 28, 58–66.
- Sivicek, V.A. & Taft, J.B. (2011) Functional Group Density as an index for assessing habitat quality in tallgrass prairie. *Ecological Indicators*, **11**, 1251–1258.
- Speight, M. (2012) Species accounts of European Syrphidae (Diptera), 2012. Syrph the Net publications, Dublin.
- Steffan-Dewenter, I. (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology*, **17**, 1036–1044.
- Stevens, J.T. & Beckage, B. (2009) Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). *New Phytologist*, **184**, 365–375.
- Stohlgren, T.J., Barnett, D.T., Jarnevich, C.S., Flather, C. & Kartesz, J. (2008) The myth of plant species saturation. *Ecology Letters*, **11**, 313–322.
- Sukopp, H. (2006) Apophytes in the flora of Central Europe. *Polish Botanical Studies*, **22**, 473–485.
- Szava-Kovats, R.C., Zobel, M. & Pärtel, M. (2012) The localregional species richness relationship: new perspectives on the null-hypothesis. *Oikos*, **121**, 321–326.
- Tofts, R. & Silvertown, J. (2002) Community assembly from the local species pool: an experimental study using congeneric species pairs. *Journal of Ecology*, **90**, 385–393.
- Valéry, L., Fritz, H., Lefeuvre, J.C. & Simberloff, D. (2009) Invasive species can also be native. *Trends in Ecology and Evolution*, 24, 585.
- Valéry, L., Fritz, H. & Lefeuvre, J.-C. (2013) Another call for the end of invasion biology. *Oikos*, **122**, 1143–1146.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a metaanalysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14, 702–708.
- Williams, J.W. & Jackson, S.T. (2007) Novel climates, noanalog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.
- Wiser, S.K. & Buxton, R.P. (2008) Context matters: matrix vegetation influences native and exotic species composition on habitat islands. *Ecology*, **89**, 380–391.
- Wittig, R. (2004) The origin and development of the urban flora of Central Europe. *Urban Ecosystems*, **7**, 323–329.
- Yakob, L. & Mumby, P.J. (2011) Climate change induces demographic resistance to disease in novel coral assemblages. *Proceedings of the National Academy of Sciences* USA, **108**, 1967–1969.
- Zampella, R.A. & Bunnell, J.F. (1998) Use of reference-site fish assemblages to assess aquatic degradation in Pinelands streams. *Ecological Applications*, **8**, 645–658.

- Zavaleta, E.S., Pasari, J.R., Hulvey, K.B. & Tilman, G.D. (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings* of the National Academy of Sciences USA, **107**, 1443–1446.
- Zobel, M., Otto, R., Laanisto, L., Naranjo-Cigala, A., Pärtel, M. & Fernández-Palacios, J.M. (2011) The formation of species pools: historical habitat abundance affects current local diversity. *Global Ecology and Biogeography*, **20**, 251–259.

BIOSKETCH

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