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A multidimensional framework for measuring biotic novelty: How novel is a community?

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Abstract

Anthropogenic changes in climate, land use, and disturbance regimes, as well as introductions of non-native species can lead to the transformation of many ecosystems. The resulting novel ecosystems are usually characterized by species assemblages that have not occurred previously in a given area. Quantifying the ecological novelty of communities (i.e., biotic novelty) would enhance the understanding of environmental change. However, quantification remains challenging since current novelty metrics, such as the number and/or proportion of non-native species in a community, fall short of considering both functional and evolutionary aspects of biotic novelty. Here, we propose the Biotic Novelty Index (BNI), an intuitive and flexible multidimensional measure that combines (a) functional differences between native and non-native introduced species with (b) temporal dynamics of species introductions. We show that the BNI is an additive partition of Rao's quadratic entropy, capturing the novel interaction component of the community's functional diversity. Simulations show that the index varies predictably with the relative amount of functional novelty added by recently arrived species, and they illustrate the need to provide an additional standardized version of the index. We present a detailed R code and two applications of the BNI by (a) measuring changes of biotic novelty of dry grassland plant communities along an urbanization gradient in a metropolitan region and (b) determining the biotic novelty of plant species assemblages at a national scale. The results illustrate the applicability of the index across scales and its flexibility in the use of data of different quality. Both case studies revealed strong connections between biotic novelty and increasing urbanization, a measure of abiotic novelty. We conclude that the BNI framework may help building a basis for better understanding the ecological and evolutionary consequences of global change.

Conrad Schittko and Maud Bernard-Verdier contributed equally to this work.

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1 | INTRODUCTION

Ecological novelty has received growing attention in the recent literature (e.g., Heger et al., 2019; Hobbs et al., 2006) focusing on novel organisms (Jeschke, Keesing, & Ostfeld, 2013), novel species interactions (Carthey & Banks, 2014; Pearse & Altermatt, 2013), novel communities (Lurgi, López, & Montoya, 2012), or novel ecosystems (Higgs, 2017; Hobbs, Higgs, & Hall, 2013; Hobbs, Higgs, & Harris, 2009). Ecological novelty can be defined as the degree of dissimilarity of a system, measured in one or more dimensions, relative to a reference baseline (Radeloff et al., 2015). Heger et al. (2019) recently broadened this definition, by proposing to use ecological novelty as an umbrella term for addressing consequences of global change for organisms, communities, ecosystems, and landscapes, which can be approached from multiple perspectives. One major aspect of ecological novelty is the emergence of abiotic and biotic conditions that are beyond the historical range of conditions at a given site or area (Mora et al., 2013), sometimes without present or past analog conditions anywhere else (Williams & Jackson, 2007). A site can be novel in terms of abiotic conditions, resulting, for example, from changes in climate, nitrogen deposition, or pollution by microplastics. Novelty can also result from changes in species composition, structure, or ecological processes generating biotic novelty (Heger et al., 2019). Furthermore, abiotic novelty can cause biotic novelty (Bogan & Lytle, 2011; Chapin & Starfield, 1997; Correa-Metrio et al., 2012; Williams & Jackson, 2007), such as when a reshuffling of species is induced by climate change (Williams & Jackson, 2007). At the same time, biotic novelty can occur without abiotic novelty: a non-native species introduction may create novelty in species composition, whereas abiotic conditions remain essentially unchanged. Hence, rigorously measuring novelty requires explicit definition of the relevant variables (Radeloff et al., 2015).

Why is ecological novelty relevant and why is it important to provide methods for measuring it? From a scientific perspective, highly novel ecosystems offer new systems to study and opportunities to test ecological and evolutionary theories (Radeloff et al., 2015). From a management perspective, their widespread emergence and the ongoing presence of global change challenge a traditional goal of restoring historical ecosystems. Instead, it can be argued that restoration could broaden its reference frame to consider how novel ecosystems might be used to maintain global biodiversity and provide ecosystem functions and services and, in doing so, avoid potentially vain efforts in attempting to fulfill traditional goals (Evers et al., 2018; Perring, Standish, & Hobbs, 2013). In this context, being able to compare the novelty of two sites can, for example, help setting priorities in environmental management or choosing among

different possible management options. Thus, measuring ecological novelty may both clarify communication and guide the development of future environmental policy.

However, the question of how to quantify ecological novelty in a standardized and comparable manner has rarely been considered. A straightforward approach to measuring abiotic novelty is to compare current abiotic variables, for instance climatic variables, in an area with their historic values by applying dissimilarity metrics (Garcia, Cabeza, Rahbek, & Araújo, 2014; Radeloff et al., 2015; Williams, Jackson, & Kutzbach, 2007). This approach has become increasingly common in climate change science, and may be applied to any abiotic factor for which reference data are available.

A common measure of biotic novelty is simply the number and/or proportion of novel species (e.g., non-native species) in a community (Catford, Vesk, Richardson, & Pyšek, 2012; Korell, Schmidt, Bruelheide, Hensen, & Auge, 2016; Parker, Burkepile, & Hayt, 2006; Qian & Ricklefs, 2006; Wilsey, Teaschner, Daneshgar, Isbell, & Polley, 2009). However, assigning species to one of these two categories is a broad generalization, and temporal dynamics of novel species introductions and their interactions with native species are reduced to a binary view. In a given community, species usually differ in their residence time in the focal region, depending on the time of arrival mediated by natural or anthropogenic pathways (Figure 1). This has evolutionary consequences since both native and non-native species may gradually adapt to their new interaction partner(s) over time (Carthey & Banks, 2012; Hulme & Bernard-Verdier, 2018; Strauss, Lau, & Carroll, 2006; Verhoeven, Biere, Harvey, & van der Putten, 2009), which may lead to a decrease in novelty in the community (Saul & Jeschke, 2015). A gradual decrease in novelty is supported by experimental multispecies studies showing that the initial benefits of enemy release in non-native plants disappear with increasing residence time (Hawkes, 2007; Mitchell, Blumenthal, Jarošík, Puckett, & Pyšek, 2010; Schultheis, Berardi, & Lau, 2015) and that native plant communities more strongly reduce the fitness of non-native plant species with longer residence times (Sheppard & Schurr, 2019). Consequently, we argue that a quantification method of biotic novelty should include a component that captures the different time spans of coexistence of the species in a given community.

Another limitation of assessing biotic novelty only by quantifying native versus non-native species is the omission of functional differences between species. A novel species that enters a community may be functionally similar or different to the resident species (Figure 1; Hulme & Bernard-Verdier, 2018). We argue that a species that is functionally dissimilar from the resident species (e.g., in terms of production of secondary compounds in plants, ability

FIGURE 1 Scheme of two aspects of biotic novelty in a hypothetical plant community that are both captured by the Biotic Novelty Index (BNI). Left side: A novel species that enters a community of resident species may be functionally different (scenario a) or similar (scenario b) to the resident species. Right side: In a given community, there is typically not only one non-resident species but also multiple species that may have arrived at different points in time in the focal region
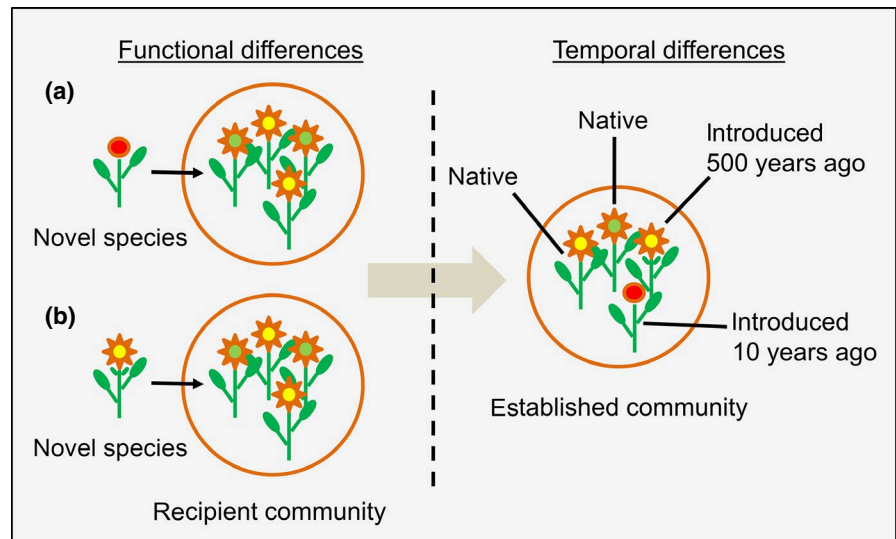
to use atmospheric nitrogen, more efficiently forage for nutrients, etc.) represents greater biotic novelty than one that is similar to the pre-existing community.

Several recent studies proposed new approaches to capture the biotic novelty of ecological communities (Baselga, 2010; Helm, Zobel, Moles, Szava-Kovats, & Pärtel, 2015; Saul, Jeschke, & Heger, 2013; Shimadzu, Dornelas, & Magurran, 2015). These approaches mainly focus on community dynamics and species turnover over time. For example, Shimadzu et al. (2015) converted commonly used measures of β-diversity, such as Jaccard's index of dissimilarity, to a measure of temporal β-diversity that compares the species composition of one community at two points in time (i.e., at an initial state and the current state). A similar approach is given by Harris, Murphy, Nelson, Perring, and Tognetti (2013) who propose to measure novelty in ecosystem composition, structure, or function by comparing current conditions at a site to the historical conditions at this site or to non-novel reference sites as a proxy. These measures provide a powerful way to quantify novelty compared to past "reference states" (Heger et al., 2019), but it is not easily applicable to compare two existing communities for which local temporal dynamics data are missing.

We propose a new multidimensional measure of biotic novelty called Biotic Novelty Index (BNI), which serves to capture the two components of novelty as described by Heger et al. (2019): (a) a change-dependent ("different") component and (b) a time-dependent ("before") component. In this sense, a situation is ecologically novel if the new situation is "different" (e.g., in terms of species composition or functional diversity) from the situation that was present "before" (e.g., compared to historic baseline conditions). Accordingly, our index relies on (a) pairwise dissimilarities between species (e.g., functional or phylogenetic distances) and (b) the residence time of each species in the area considered. The index was designed to make comparisons of novelty between several communities (e.g., along gradients) at the present point in time, without prior knowledge of the local communities' assembly history. The BNI is based on the formula for Rao's quadratic entropy (hereafter Rao's

Q; Botta-Dukát, 2005; Rao, 1982), which is one of the most common indices of functional diversity (Ricotta et al., 2016; Schleuter, Daufresne, Massol, & Argillier, 2010).

Consequently, the BNI shares a number of characteristics with Rao's Q. Both indices are primarily based on pairwise distances between species, which are calculated from relevant attributes of species, such as functional trait values or phylogenetic distances. In the same way that pairwise distances are weighted by relative abundances in Rao's Q, pairwise distances are weighted by a pairwise temporal coexistence coefficient in the BNI. This temporal coefficient is calculated based on the estimated residence time of each species in the reference area and captures how long pairs of species have coexisted in the area. For example, if a given pair of species consists of a native and a recently introduced species, their pairwise trait distance will be weighted more heavily than the distance between a native and another non-native species which arrived earlier in the area. This temporal coefficient allows us to take into account the temporal erosion of novelty in a community, and differentiate between non-natives in such a way that a recently introduced species may be seen as "more novel" compared to the established non-native species.

The BNI is not restricted to specific taxa, scales, or geographic areas. It can be applied to communities and species assemblages for which two kinds of data are available or measurable: trait data that characterize species functionally, and information whether a species is novel to an area or not (and ideally with additional information on its residence time). Here, we describe how to calculate the BNI from various data sources, and how it associates with traditional measures of biotic novelty, abiotic novelty, species richness, and functional diversity. By presenting simulations and two case studies, we show that this new method to quantify biotic novelty is intuitive and versatile, as it is easily adaptable to datasets of different scale, scope, and resolution. We demonstrate in this paper that the BNI framework is a helpful tool whenever the assessment of novel species assemblages or communities is needed, which may not only be useful in invasion ecology but also in global change ecology, restoration ecology, or urban ecology.

2 | METHODS

2.1 | The new index of biotic novelty

There are seven steps to calculate the BNI: (1) obtaining a trait matrix, (2) converting the trait matrix into a distance matrix, (3) obtaining species' first records, (4) converting the first records into a temporal coexistence matrix, (5) weighting the distance matrix by the temporal coexistence matrix, (6) multiplying the distance matrix by the species' relative abundance (optional), and (7) calculating the sum of all pairwise comparisons from the distance matrix (Figure 2). The resulting BNI is expressed as:

$$\text{BNI} = \sum_{i=1}^{s-1}\sum_{j=i+1}^{s-1} d_{ij} \times c_{ij} \times p_i p_j, \tag{1}$$

where d_{ij} is the distance between species i and j, c_{ij} is the temporal coexistence coefficient of species i and j in the local area, and $p_i p_j$ are the relative abundances of species i and j. Note that the equation of the BNI corresponds to the calculation of Rao's Q (Botta-Dukát, 2005; Rao, 1982), but with the temporal coexistence coefficient c_{ij} added to the product term. Steps 1, 2, 6, and 7 are standard multivariate methods to obtain Rao's Q; steps 3, 4, and 5 are the implementation of the temporal coexistence component. Both components are explained in detail in the following sections.

2.2 | The functional diversity component

The general rule to calculate functional diversity indices is that traits must be linked to the function(s) of interest. For instance, specific leaf area, maximum growth rate, and leaf nitrogen concentration are important components of plant functional diversity when primary production is the process of interest (Garnier et al., 2004; Wright et al., 2004). Similarly, the choice of traits for the BNI can be related to the novelty aspects of interest. For example, if the aim is to assess
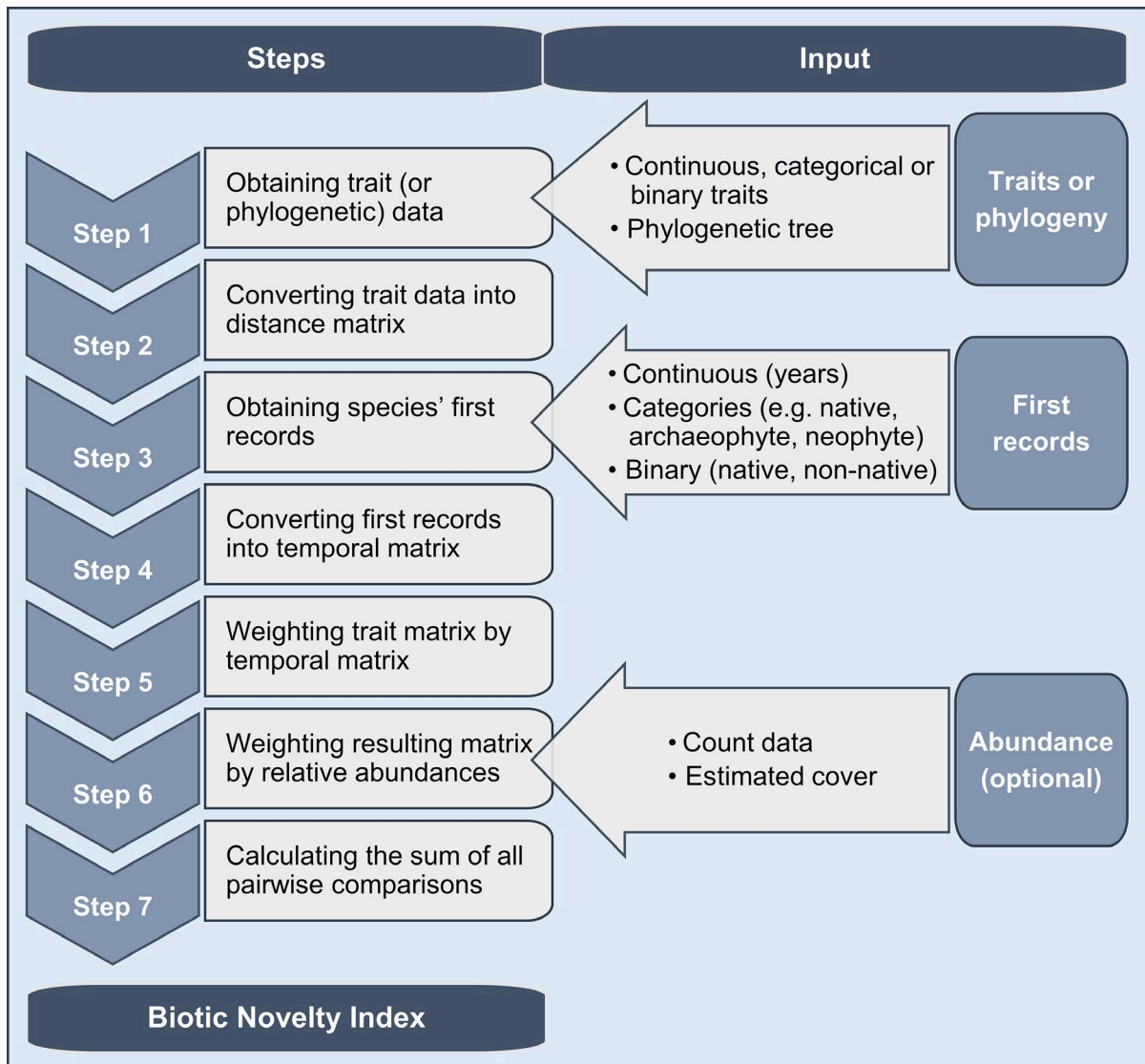

FIGURE 2 Standardized procedure for calculating the biotic novelty of a community with the Biotic Novelty Index

the biotic novelty of an invertebrate herbivore community, feeding preference, feeding type (e.g., chewing or sucking), and the number of generations per year are traits where novelty could play a relevant role for the consumed plant. If some traits are more important for evaluating biotic novelty than others, they should be given greater weights in the trait matrix. Careful decisions about which traits to include and how to weigh them depends on the purpose to which the index will be applied and should rely on expert knowledge of the system (Laliberté & Legendre, 2010). Traits can be continuous (e.g., leaf nitrogen concentration), binary variables (e.g., legume or non-legume), or categorical (e.g., flower color).

Distance measures calculate the difference between pairs of species based on their characteristics (e.g., functional traits). There are many distance measures to choose from, which have different mathematical properties and should be chosen carefully (Pavoine, Ollier, & Pontier, 2005). Two are most commonly used for trait datasets: the Euclidean distance and the Gower distance (Laliberté & Legendre, 2010). The Euclidean distance is calculated on complete and continuous trait datasets, and emphasizes absolute differences (Poos, Walker, & Jackson, 2009), whereas the Gower distance has the advantage that it allows incomplete datasets and mixed (categorical, ordinal, and continuous) data types (Gower, 1971; Laliberté & Legendre, 2010). Distances may be scaled between 0 and 1 (=maximum pairwise distance), as is sometimes recommended for Rao's Q in cases when the goal is to compare Rao's Q to other indices of functional diversity, or to partition diversity in into alpha, beta, and gamma diversity (De Bello, Lavergne, Meynard, Lepš, & Thuiller, 2010). When distances are scaled, then the BNI will be bounded between [0, 1]. To illustrate the absolute amount of functional novelty contributed by species, we chose to keep the distances unscaled throughout this article.

2.3 | The temporal coexistence component

In the BNI, pairwise trait distances are weighted by a pairwise temporal coexistence coefficient. The first step in calculating this coefficient is to define whether each species belongs to the historical native species pool or not. Second, we use information such as first records (or time of establishment) of the non-native species in the local region. This information can be obtained either from publications (e.g., Seebens et al., 2017 collected first records of alien species worldwide: http://dataportal-senckenberg.de/database/metacat/bikf.10029/bikf), regional databases (e.g., the BiolFlor database for plants in Germany, Klotz, Kühn, & Durka, 2002), or expert knowledge. For native species, time of establishment needs to be estimated as well (e.g., for many plant species in Central Europe a reference to the end of the last glacial period will be reasonable). From this information, the residence time for each species is calculated. The residence time tells us how many years before today each species was introduced or has been established. For example, a species that was introduced in 1720 has a residence time of 300 years in the year 2020 (the current year). Next, residence times are scaled between 0 and 1, with 0

corresponding to species that arrived in the current year, and 1 for the oldest residents (i.e., native species), as follows:

$$r_i' = \frac{r_i}{r_{max}}, \tag{2}$$

where r_i' is the standardized residence time of species i, r_i is the residence time of species i (in years), and r_{max} the maximum residence time of all species (i.e., residence time of native species). Once residence times have been scaled for all species, the temporal coexistence coefficient can be calculated for each pair of species as follows:

$$c_{ij} = 1 - \min\left(r_i', r_j'\right), \tag{3}$$

where c_{ij} is the temporal coexistence coefficient of species i and j, r_i' is the normalized residence time of species i, and r_j' is the normalized residence time of species j.

Note that the minimum of both normalized residence times is used in Equation (3) because the latest arrival in the species pair determines how long both species have coexisted in the focal area. For example, if the two species have residence times of, respectively, 300 and 100 years, their temporal coexistence in the focal area is 100 years. We then take the complement of the minimum normalized residence time in Equation (3), such that the coefficient is maximized when species have had the lowest local coexistence time (i.e., maximum novelty). Eventually, the temporal coexistence coefficient is calculated for each possible species pair and a new temporal matrix can be constructed with the same dimension as the trait distance matrix described before. The values of the temporal matrix range between 0 and 1 (due to the normalization step given in Equation 2) and functions as weighting factor for the trait distance matrix. In this way, trait differences between species with low coexistence time are weighted heavily, whereas trait differences between species coexisting for millennia (such as a pair of native species) will be given no weight in the BNI.

2.4 | The BNI as a framework

The BNI is in essence the sum of two components: the mean functional distance between novel species in the community, and the mean functional distance between native and novel species. Furthermore, we can show that the BNI is an additive partition of Rao's Q (see Supplementary Material 1 for details). According to this partitioning, we can express the BNI relative to Rao's Q, and define a standardized version of the BNI as:

$$BNIs = \frac{BNI}{Rao\,Q}. \tag{4}$$

This standardized version is a proportion of Rao's Q, which can be described as the proportion of functional diversity contributed by novel species pairs (for an application, see the simulations below and in Supplementary Material 2). A detailed R code

to calculate the BNI and the BNIs is provided in Supplementary Material 3.

We purposely refer to the BNI as a framework because it is built upon the idea to combine two relevant aspects into one measure, which can be easily adapted to the needs of the user (e.g., by adding or replacing relevant components) depending on the goal of the study. For example, the BNI as described above captures the functional novelty of communities because it uses functional traits to calculate differences between species. However, if the user aims to assess phylogenetic aspects of novelty, or to compare phylogenetic aspects with functional aspects, then the functional diversity component of the BNI may be replaced with a measurement of phylogenetic distances between species (see case study 2 for an application). While phylogeny has sometimes been used as a substitute for functional or ecological niche differences between species (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009; Helmus, Bland, Williams, & Ives, 2007; Webb, Ackerly, McPeek, & Donoghue, 2002), it has become clear that phylogenetic distances are, at best, an imperfect proxy (Emerson & Gillespie, 2008; Mason & Pavoine, 2013). Calculating the BNI using phylogenetic distances may be useful in cases when trait data are difficult to obtain or the evolutionary history and relatedness of species are the focus of interest (Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015). As for Rao's Q, some care should be taken when comparing functional to phylogenetic novelty using the BNI index (cf. Pavoine & Ricotta, 2014). As has been demonstrated for Rao's Q, the properties of the indices may only be comparable when calculated from distance matrices with similar mathematical properties, such as ultrametric matrices (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009) and comparisons should account for the expected redundancy driven by the similar abundance weighting of the indices (Pavoine, Gasc, Bonsall, & Mason, 2013).

While the temporal component of the BNI was designed to use species residence times as the most accurate way to weigh the novelty of species cooccurrences, there will often be situations where dates of first records are imprecise, incomplete, or even entirely missing. For these cases, we suggest the use of temporal categories to characterize each species in the community. The generation of these categories, for example, could be based on corresponding decades or centuries. Another approach would be to adopt already existing temporal categorizations such as the three-level classification scheme of European plant species by Schroeder (1968): non-native species are classified according to their time of human introduction, either before Europe's discovery of the New World in 1492 (archaeophytes or more generally archaeobiota) or after 1492 (neophytes, neobiota). Species that colonized a given area after the end of the last glacial period without human assistance are classified as native (see case study 1 for an application). "Neonative" species could be added as another category for species establishing due to climate change in the Anthropocene, that is, since the middle of the 20th century (Essl et al., 2019). If even these data are not available, the user may opt for the most basic categorization method which classifies species as either native or non-native (i.e., a binary categorization). In this case, the corresponding temporal coexistence coefficient would be either 0 for pairs of native species or 1 for pairs involving at least one non-native species. Sensitivity of the BNI to the estimation of residence times is presented in Supplementary Material 2.

The BNI as described above is a multispecies approach since it captures the functional novelty of communities and species assemblages. However, by modifying the BNI equation, it would also be possible to focus on the biotic novelty of particular novel target species in relationship to the interacting resident species. A similar approach was proposed by Saul and Jeschke (2015), which consider the implications of different degrees of eco-evolutionary experience of interacting resident and novel species.

2.5 | Simulations

We carried out a series of simulations to explore the range of values taken by the index, and its sensitivity to different scenarios of functional differences and species arrival times. Each simulation consisted of generating an artificial regional pool of species based on a given scenario of arrival times and a given scenario of functional novelty, that is, how functionally different are the non-native species from the coexisting natives in the region (cf. Table 1). Within each simulated region, we used a simple weighted lottery model to simulate the assembly of local communities along a gradient of increasing proportion of non-native species. Our goal was to assess the behavior of the BNI and the BNIs within each scenario, and to compare it to our expectations.

For each simulation, we first created a regional pool of 250 species, comprising 70% natives and 30% non-natives. To simulate species residence times realistically, we followed the three-level classification of European plant species described before (see also case study 1), and separated non-natives into long established non-natives (i.e., archaeobiota, 15% of all species in the pool) and recently arrived non-natives (i.e., neobiota, 15% of all species). We defined species residence time based on these three categories: 8,518 years for natives, 2,786 years for archaeobiota, and a uniformly generated year of arrival between 1492 and 2018 for the neobiota. The mean dates of arrival for natives and archaeobiota originate from the respective class limits of native plants and archaeophytes in the Berlin-Brandenburg area, that is, around 10,000 BC (end of the last glacial period) for natives and around 3,000 BC for the introduction of the first archaeophytes (Haas, Giesecke, & Karg, 2003; cf. Supplementary Material 2 for alternative estimates of residence times).

Next, we randomly generated functional trait values for each species in the pool. Three continuous traits were sampled from normal distributions, whose mean and variance were determined according to one of four non-native trait scenarios. Since the BNI is designed to capture functional novelty, we explored scenarios where neobiota species are bringing different functional trait values to the historical pool of natives and archaeobiota (hereafter referred to as the "resident" species). We present four trait scenarios from low to high novelty (Table 1): (1) low novelty, in which traits for all species are sampled from the same distribution; (2) medium–low novelty, in which traits of neobiota have on average higher values

TABLE 1 Scenarios of functional novelty explored in the simulations. Scenarios 1–4 were designed to represent increasing levels of biotic novelty, with neobiota contributing an increasing amount of functional diversity to the resident communities

Scenario	Description	Expected level of biotic novelty
1	No functional difference between residents and neobiota	Low
2	Neobiota have on average higher trait values than residents	Medium–low
3	Neobiota are more functionally diverse than residents	Medium–high
4	Neobiota are both more functionally diverse and have on average a higher trait value than residents	High

than the residents (i.e., different mean); (3) medium–high novelty, in which traits of neobiota are more diverse (i.e., higher variance parameter) than the residents; and (4) high novelty, in which traits of neobiota have both a higher mean and a higher variance than the traits of residents (cf. Supplementary Material 2 for details and additional scenarios).

We then assembled 100 local communities of 25 species each by drawing species from the simulated regional species pool. Species were not drawn entirely at random from the pool, but following an increasing proportion of neobiota across communities, from 0% (communities made up entirely of natives and archaeobiota) to 100% (communities made up only of neobiota). To avoid complicating the simulations further, we did not consider local trait selection during community assembly based on environmental filters or competition; however, such scenarios have been treated extensively elsewhere (Gallien, Carboni, & Münkemüller, 2014; Lemoine, Burkepile, & Parker, 2016).

Simulations were repeated 200 times, with incremental changes in the functional parameters for each scenarios every 10 simulations (cf. Supplementary Material 2). We calculated Rao's Q, the BNI and the BNIs for each simulated community. All simulations and calculations were done in R version 3.6.0 (R Core Team, 2019), and all R scripts are included in Supplementary Material 3.

2.5.1 | Case study 1: Biotic novelty of plant communities along an urbanization gradient

To illustrate the strengths and weaknesses of the newly proposed measure, we analyzed changes in biotic novelty along an urbanization gradient in dry grassland communities in Berlin, Germany. These urban dry grasslands have been selected as a model ecosystem within the CityScapeLab Berlin, an experimental platform with a network of 56 permanent plots, established for the evaluation of biodiversity in urban environments (von der Lippe, Buchholz, Hiller, Seitz, & Kowarik, 2020). From April 18 to May 19 and June 21 to July 28, 2017, two vegetation surveys were carried out in a 4 × 4 m plot within each of the 56 grasslands, recording the abundance (percent cover) of 234 vascular plant species. Trait data for the calculation of the BNI and Rao's Q were extracted from the TRY database (Kattge et al., 2011) and the BiolFlor database (Klotz et al., 2002). We used data for 12 plant functional traits (plant height, specific

leaf area, life form, flower color, flower class, clonal growth organs, length of dispersal unit, seed mass, leaf area, leaf nitrogen content, nitrogen fixation, and mycorrhizal infection). Information on the first record of neophytes is based on the atlas of the Berlin flora (Seitz et al., 2012). All other species were classified as native or as archaeophytes (introduced by human agency before 1492) according to the BiolFlor database (Klotz et al., 2002). Note that exact first record information (dates) were only available for neophytes, but not for archaeophytes, nor native species, which is a typical situation of data availability for plant species in Europe. Hence, we used for these two categories a mid-range value for each species in the respective category and the exact first records for neophytes only. The mid-range value for natives and archaeophytes was calculated from the respective class limits in the focal area, that is, around 10,000 BC (end of the last glacial period) for natives and around 3,000 BC for the introduction of the first archaeophytes in the Berlin-Brandenburg region (Haas et al., 2003). This resulted in an estimated residence time of 8,518 years for natives and 2,786 years for archaeophytes.

To analyze the relationship between the biotic novelty of plant communities and the level of urbanization (as a driver of ecological novelty), we applied a commonly used indicator of urbanization: the percentage of sealed surfaces (i.e., impervious soils) in the surrounding landscape (Lu & Weng, 2006; Schwarz, 2010). We calculated the mean percentage of sealed surfaces in a 500 m buffer area around each of the 56 plots using publicly available urban habitat maps from the Berlin Senate Department for Urban Development and Housing and QGIS 2.18.0 (QGIS Development Team, 2016). Relationships of the BNI and the BNIs with the percentage of sealed surfaces, Rao's Q, and species richness were analyzed with linear models. All calculations were carried out using R version 3.4.3 (R Core Team, 2017).

2.5.2 | Case study 2: Biotic novelty of co-occurring vascular plants in Germany

The second case study demonstrates the application of the BNI in conjunction with big datasets. Here, we aimed to calculate the BNI for co-occurring vascular plants in Germany and to evaluate how their biotic novelty is spatially related to the extent of urban areas. It is a feature of this case study that it extensively used freely accessible

data from online databases. From the Global Biodiversity Information Facility (GBIF: The Global Biodiversity Information Facility, 2019), we downloaded the occurrence dataset "Flora von Deutschland (Phanerogamen)" which includes 9,577,887 records of 5,721 vascular plant species in Germany (Bundesamt für Naturschutz/Netzwerk Phytodiversität Deutschland, 2018). These occurrence records are aggregated in 11 × 11 km grid cells of the grid of topographic maps (TK 25, scale 1:25,000), which are officially used for the design of species distribution maps in Germany. We used phylogenetic pairwise distances to calculate the BNI. In this case, the BNI thus captures phylogenetic novelty rather than the functional novelty we calculated in our simulations and in case study 1. To do so, we pruned the extensive phylogeny "Daphne" (Durka & Michalski, 2012) for our species set. Daphne is a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. Information whether a plant species is native or non-native in Germany plus information on first records for neophytes were obtained from the BiolFlor (Klotz et al., 2002) database. We calculated the BNI for each of the 3,003 grid cells and created a map using QGIS version 3.2.1 (QGIS Development Team, 2018). A second layer, which indicates the extent of urban areas based on MODIS satellite data (Schneider, Friedl, & Potere, 2009) was added to the map. All calculations were carried out using R version 3.4.3 (R Core Team, 2017) and the R package "picante" (Kembel et al., 2010) for phylogenetic tree pruning.

3 | RESULTS

3.1 | Simulations

Our simulations showed that the BNI varies broadly with the proportion of non-native species and with the size of trait differences between species (Figure 3). As expected, in each scenario of increasing functional novelty (scenarios 2–4), the larger the trait difference among neobiota and residents, the higher the BNI and the BNIs (color-coded curves are stacked vertically in Figure 3c–h), with no upper bound value except the maximum trait difference existing in the regional pool.

The amount of biotic novelty quantified in each of the scenarios mostly followed our expectations (Table 1). The highest BNI values were obtained in scenario 4 (max = 4.07), when neobiota were both different on average, and more diverse, than the residents. BNI values were somewhat lower in scenarios 3 (max = 3.36) and 2 (max = 2.82), but, as expected, the lowest values were found in scenario 1 (max = 1.18). Simulations reveal that a high variance of neobiota traits contributes more to increasing the BNI than a simple difference in mean trait values from the residents. In other words, the more diverse the pool of neobiota, the higher the functional novelty of the communities.

The shape of the BNI response curve along the invasion gradient was determined by the type of functional novelty (difference in mean vs. variance) brought by neobiota. Overall, as long as neobiota made up less than half of the community, the BNI increased

monotonously as more neobiota were added. Beyond this point, however, the BNI did not always increase with the proportion of neobiota, depending on the diversity of neobiota relative to residents.

In scenario 1, where neobiota were similar to natives, the BNI increased monotonously with the proportion of neobiota (Figure 3a). In this scenario, the mean pairwise trait differences (i.e., total functional diversity or Rao's Q, cf. Supplementary Material 2) remained constant, while the contribution of neobiota increased with their relative abundance in the community. The BNI curve tended to saturate at high neobiota proportions as new neobiota species were less likely to add new trait differences. In scenarios 2 and 4, where neobiota were on average functionally different from the residents, the simulated BNI often showed a humped-shaped curve, with a maximum at intermediate proportions of neobiota (Figure 3c,g). This pattern is due to the fact that the BNI is based on mean pairwise differences between species, which reaches its maximum when one half of the community (i.e., the neobiota here) is different from the other (i.e., the resident species). A similar pattern is observed for Rao's Q (cf. Supplementary Material 2). Beyond this mid-point, the variance of neobiota (SD_{neo}) determined the behavior of the BNI. As illustrated in scenarios 3 and 4 (Figure 3e,g), as long as the trait values of the neobiota were more variable than those of the resident species ($SD_{neo} > SD_{residents}$), the BNI increased monotonously with the proportion of neobiota and the amount of variance in neobiota traits. When neobiota had a lower trait variance (i.e., they were more similar among themselves) than the residents ($SD_{neo} < SD_{residents}$), then the BNI tended to decrease with the proportion of neobiota in the community (cf. Supplementary Material 2).

By contrast, the standardized value of the BNI (BNIs) showed no such changes in behavior across scenarios: the BNIs always increased monotonously with the proportion of neobiota and the amount of functional diversity added by neobiota. The rate of increase was always higher than 1, with steeper curves generated by neobiota traits being different on average from residents (scenarios 2 and 4), or with higher variance than residents (scenarios 3 and 4).

3.2 | Case study 1: Biotic novelty of plant communities along an urbanization gradient

The observed BNI values for the 56 Berlin grassland plots ranged from 0.002 to 0.092 and had a mean at 0.020 ± 0.016 SD. The plot with the lowest BNI value contained 13 species of which 12 were native and 1 was non-native, specifically an archaeophyte species. The plot with the highest BNI value contained 32 species of which 19, 6, and 7 were native, archaeophytes and neophytes, respectively. Statistical analyses of the BNI across the 56 plots indicated that the BNI was positively related to the urbanization indicator sealed surface area (Figure 4). Fifteen percent of the variation in the BNI was explained by the percentage of sealed surfaces
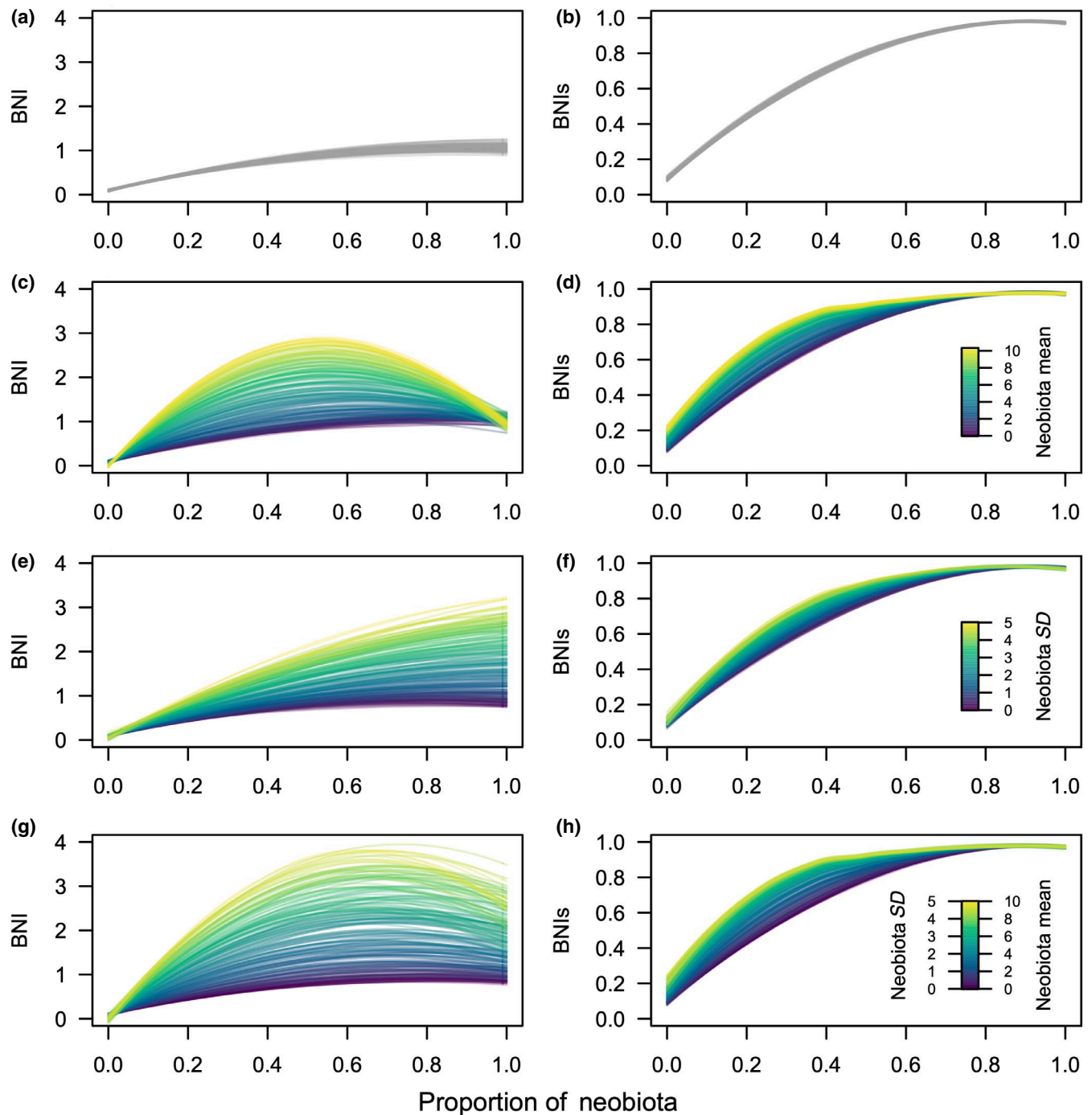
FIGURE 3 Variation of the Biotic Novelty Index (BNI) and its standardized value (BNIs) in four simulation scenarios. Communities were simulated with an increasing proportion of neobiota (x-axis). Scenarios explore different parameters (mean and *SD*) of the normal distribution from which neobiota species traits were sampled. In the first scenario (a, b), traits of residents and neobiota follow the same normal distribution (trait mean = 0, *SD* = 1). In scenario 2 (c, d), the traits of neobiota are increasingly different from the residents. Colors (or grayscales in the printed version) represent variation in neobiota trait mean from 0 to 10; *SD* = 1. In the third scenario (e, f), residents and neobiota have the same trait mean (mean = 0), but neobiota are more diverse than the residents (neobiota trait *SD* increases from 0 to 5). In the fourth scenario (g, h), neobiota are both different and more diverse than the residents (both the mean and *SD* of neobiota increase simultaneously from 0 to 10 and 0 to 5, respectively). Lines represent LOESS regressions fitted on the 100 communities corresponding to one simulated regional species pool

around the plots (*p* = .003, Figure 4a). However, there were no significant relationships detectable between the sealed surface area and traditional measures of biotic novelty, that is, the number of non-native species (R^2 = .01, *p* = .443, Figure 4b) or their proportion (R^2 = .04, *p* = .130, data not shown). Furthermore, when considering total functional diversity (expressed as Rao's *Q*), we
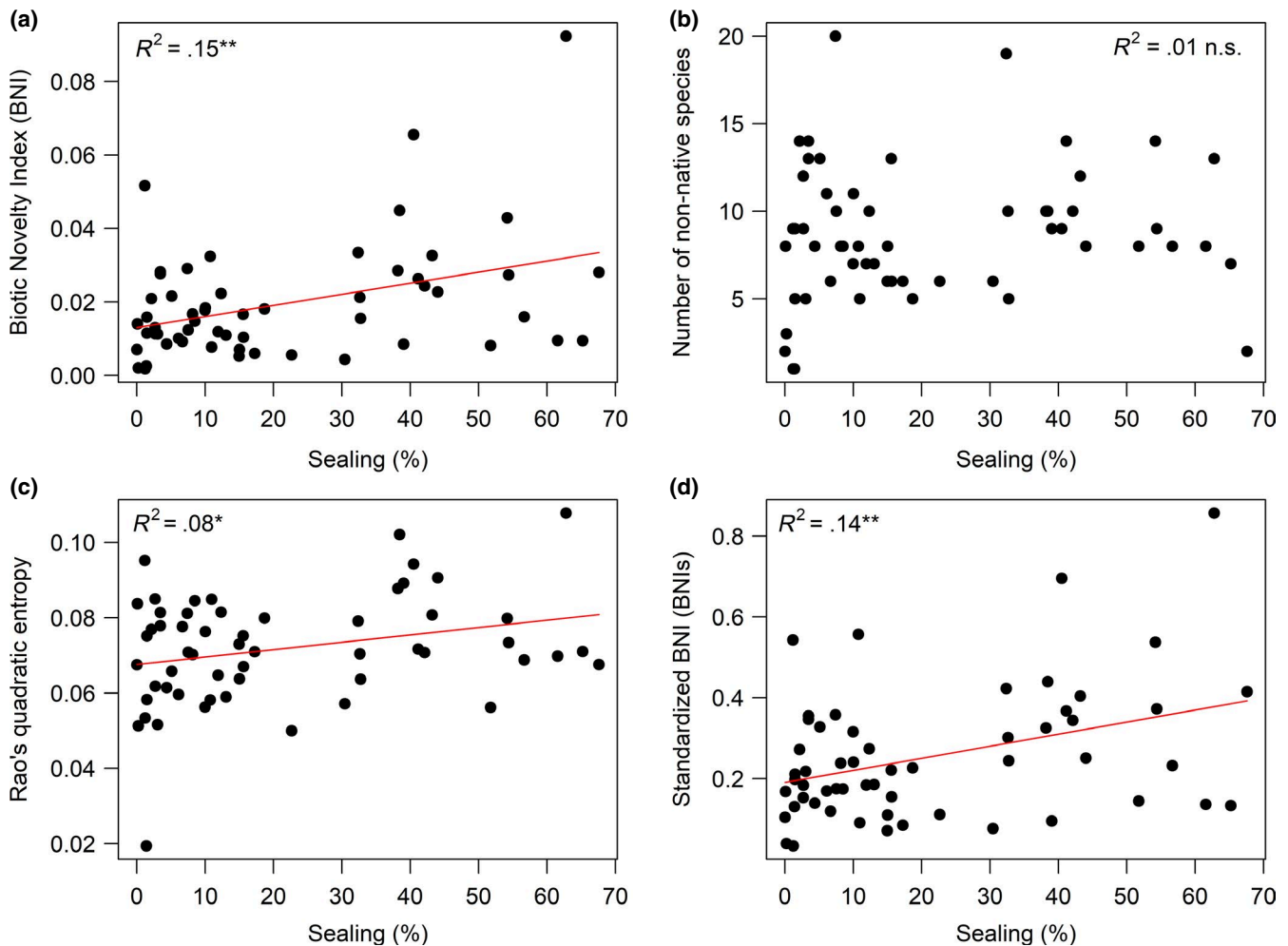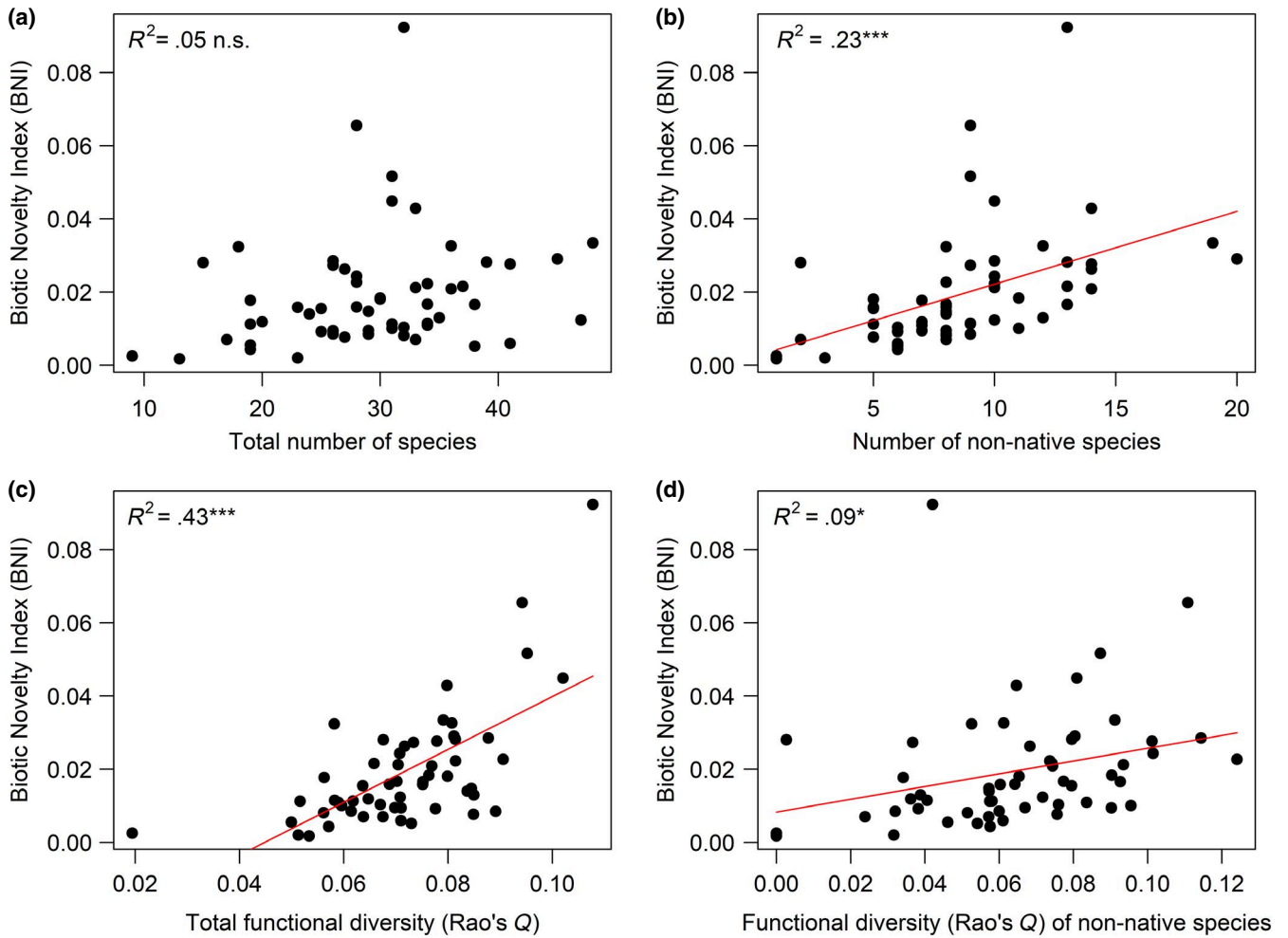
FIGURE 4 Case study 1: relationships between the percentage of sealed surface area in a 500 m buffer zone around the 56 urban grassland plots and (a) the Biotic Novelty Index (BNI), (b) the number of non-native species, (c) Rao's *Q* as a measure of functional diversity and (d) the standardized BNI. Asterisks indicate statistical significance using linear models ("**" = $p < .01$, "*" = $p < .05$, "n.s." = $p \geq .05$)

also identified a positive relationship with the sealed surface area ($R^2 = .08$, $p = .040$, Figure 4c), but less strong than the one for the BNI. Finally, we investigated how the BNI varies independently of the variation in Rao's *Q* by calculating the standardized version of the BNI. The standardized BNI (BNIs) showed a similar relationship with the sealed surface area ($R^2 = .14$, $p = .004$, Figure 4d) than the non-standardized BNI.

We were also interested in how the BNI associates with community parameters such as species richness and functional diversity. The BNI was not related to the total number of species in the plots ($R^2 = .05$, $p = .103$, Figure 5a), but showed a moderately positive relationship with the number of non-native species ($R^2 = .23$, $p < .001$, Figure 5b). On the other hand, the BNI was strongly positively related with the functional diversity (expressed as Rao's *Q*) of all species ($R^2 = .43$, $p < .001$, Figure 5c), but weakly positively related to the functional diversity of the group of non-native species ($R^2 = .09$, $p = .028$, Figure 5d). The standardized version of the BNI (BNIs) showed almost identical relationships to all four community parameters (Figure S4.1 in Supplementary Material 4).

3.3 | Case study 2: Biotic novelty of co-occurring vascular plant species in Germany

The nationwide assessment of biotic phylogenetic novelty identified large areas with high novelty in Germany, indicated by the distribution map and the slightly right-skewed histogram of the BNI (Figure 6). The BNI values ranged from 0 (at Zugspitze, the highest mountain in Germany) to 64.18 (in Leipzig, the most populous city in the German federal state of Saxony). Areas of very high novelty were clearly concentrated in and around urban areas: in addition to Leipzig, other areas of high novelty were the cities Cologne (62.72), Bamberg (62.39), and Mülheim an der Ruhr (62.15). The capital and largest city of Germany, Berlin, had the ninth highest BNI (61.06). That the city surroundings also showed a higher extent in biotic novelty may be indicative for a spatial spillover effect from cities to adjacent areas. Areas of low novelty were visible predominantly in southern and partly in central Germany, presumably due to the ranges of the Alps and the central uplands, respectively, in these regions. The standardized

FIGURE 5 Case study 1: relationships between the Biotic Novelty Index and (a) the total number of species, (b) the number of non-native species, (c) Rao's Q as a measure of functional diversity, and (d) the functional diversity of non-native species in the 56 urban grassland plots. Asterisks indicate statistical significance using linear models ("***" = $p < .001$, "*" = $p < .05$, "n.s." = $p \geq .05$)

FIGURE 6 Case study 2: biotic novelty of co-occurring vascular plants in Germany aggregated in 11 × 11 km grid cells calculated with the Biotic Novelty Index (BNI). Areas outlined in black indicate the extent of urban areas based on MODIS satellite data (Schneider et al., 2009)
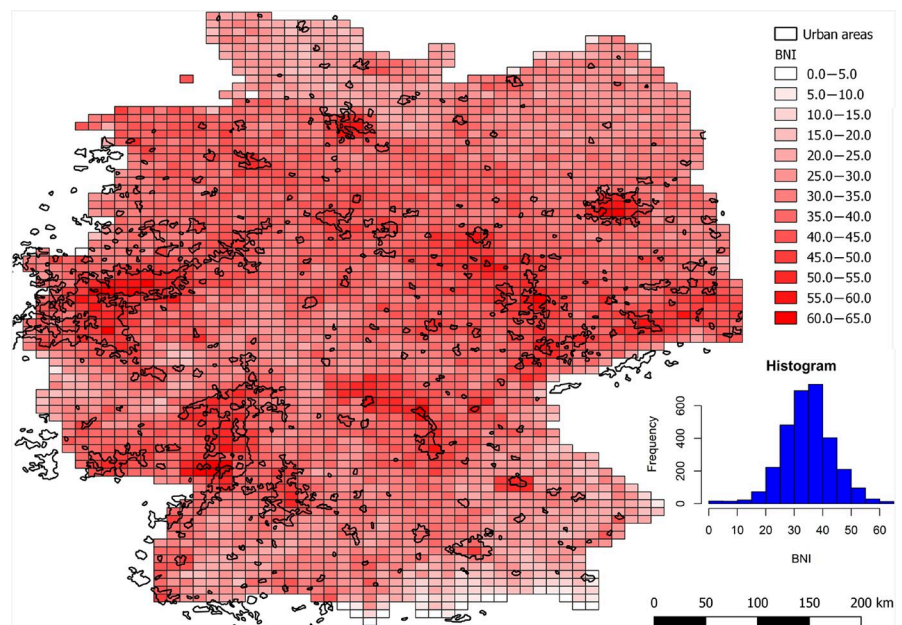
version of the BNI (BNIs) showed an almost identical distribution map (Figure S4.2 in Supplementary Material 4).

4 | DISCUSSION

This study introduced the BNI and demonstrated its applicability as a framework to measure the ecological novelty of communities and species assemblages. We regard ecological novelty as a continuous gradient ranging from historic or analog to novel (Heger et al., 2019) rather than a binary classification. Accordingly, we have designed the BNI to be able to gradually measure ecological novelty. More specifically, the BNI focuses on the biotic rather than abiotic component of ecological novelty (i.e., biotic novelty). It measures the extent of trait differences among novel and non-novel species and, simultaneously, takes temporal dynamics into account. Arithmetically, the BNI represents the expected functional novelty between two randomly picked individuals in the community.

4.1 | The BNI captures novelty in both functional diversity and introduction history

We designed the BNI to combine two aspects of ecological novelty: historical novelty, captured by the sequence of arrivals of new species in a given region, and functional novelty contributed by the new species (Heger et al., 2019). Together with the optional weighting of relative abundances (which is inherited from Rao's Q), these components capture three crucial dimensions of biotic novelty. However, it should be noted that not all possible aspects of ecological novelty are covered by the BNI. Besides abiotic novelty, which is beyond the scope of this article, biogeographic origins and trophic interactions of non-native species (Saul et al., 2013) are not captured by the BNI in its current form. However, we refer to the BNI as a framework because it can be adapted to the needs of the user, for example, by adding or replacing relevant components such as the biogeographic origins of non-natives. The BNI was conceived for a community defined by a single taxonomic group or guild (i.e., whose members can all be equally characterized by a given set of traits). Cross-taxon assessments (e.g., novel predator–prey interactions) would require the integration of multiple trait sets which could be imagined by further modifying the BNI equation.

Due to its similarities with Rao's Q, the BNI is a continuous measure which quantifies novelty as a gradient. However, in the concept of novel ecosystems as presented by Hobbs et al. (2013), specific pre-defined thresholds separate novel ecosystems from hybrid and historic ones, which is a categorical approach to novelty. The threshold concept of novelty inevitably faces the challenge to compare the focal system to a reference system or a reference state which is not required for the BNI. However, we think both views are not necessarily contradictory (see Heger et al., 2019 for a detailed discussion) and that the BNI may even have the potential to identify thresholds or step changes in a system. A helpful

statistical tool might be piecewise regression, a technique used to identify ecological thresholds in a regression context (Toms & Lesperance, 2003).

4.2 | Properties and limitations of the BNI

By design, the BNI shares a number of properties with Rao's Q: it is not correlated to species richness and increases monotonously with mean species trait differences (Botta-Dukát, 2005; Petchey & Gaston, 2006). Accordingly, we have shown in our simulations that the BNI captures functional novelty in a predictable manner: for a given proportion of non-native species, increasing trait differences between native and non-native species increases the functional novelty of the community. The BNI has no upper bound and is expressed in units of trait (or phylogenetic) distance between species. However, as for Rao's Q, it may be modified to be bounded between 0 and 1 by simply scaling the pairwise trait distances to set the maximum distance equal to 1 (Botta-Dukát, 2005), which enables comparisons across regions and traits. As for other diversity indices (e.g., Chase, Kraft, Smith, Vellend, & Inouye, 2011), null modeling may be necessary to compare expected values across systems, as well as to test specific hypotheses of community assembly or biological invasions.

The BNI also shares a perhaps counterintuitive property of Rao's Q: adding new species to the community does not necessarily increase functional novelty, and may sometimes decrease it (Botta-Dukát, 2005). If the new species introduced is very similar to some existing species in the community, then both Rao's Q and the BNI will decrease, as the average dissimilarity between species will decrease. This property implies that the behavior of the BNI is not always linear in response to the proportion of non-native species in the communities. In our simulations, the BNI was often maximized at intermediate proportions of non-native species, when the most functionally different pairs of species (in our case, the pairs of resident species vs. neobiota) were also the most frequent. This behavior might be counterintuitive depending on the goal of the study and the user's viewpoint on biotic novelty. Some solutions have been proposed to overcome this limitation in Rao's Q, based on transforming the distance matrix to make it ultrametric (Pavoine et al., 2009) or using Hill numbers (Chiu & Chao, 2014). Future studies may investigate similar methods for the BNI, but these remain beyond the scope of this study. Instead, we propose a simple standardization (BNIs), which partly overcomes some of these issues.

The BNIs offer an additional description of biotic functional novelty of the community by quantifying the proportion of functional diversity (measured as Rao's Q) that is contributed by novel species interactions in the community. The advantage of this standardization is that, by construction, it is monotonous with regard to increasing proportions of non-native species, and the size of trait differences. This standardized version may therefore provide a more objective measure to compare the level of biotic novelty between communities with different levels of

functional diversity, or assembled from a different species pool. Nevertheless, the untransformed value of the BNI remains a valuable measurement when the goal is to quantify the absolute amounts of functional diversity contributed by novel species in a community. For instance, this may be particularly relevant when investigating impacts of novel species traits on ecosystem functioning (Cleland, 2011; Drenovsky et al., 2012). Depending on a study's goal, either of the two versions of the index may be more relevant, but using both will give a fuller picture of variation in novelty across communities.

4.3 | Case studies

Both case studies revealed strong connections of biotic novelty with abiotic novelty. The first study showed that the BNI of 56 dry grassland plant communities in Berlin was positively related to the observed urbanization indicator (i.e., percentage of sealed surfaces). This is not surprising, as previous studies demonstrated that the construction and expansion of towns and cities promote the loss of native species and their replacement by non-native species (Chocholoušková & Pyšek, 2003; DeCandido, Muir, & Gargiullo, 2004; Knapp, Kühn, Stolle, & Klotz, 2010; Tait, Daniels, & Hill, 2005). However, in the present study system (dry grasslands), this relationship between increasing urbanization and non-native plant species richness was not supported since we found no relationship between the sealed surface area and non-native species richness (nor their proportion on total species richness). This finding underlines that the BNI captures different aspects of biotic novelty than the simple number and/or proportion of non-native species.

Our analyses also showed a strong relationship of the BNI with Rao's Q. This was expected, given that the BNI is actually an additive partition of Rao's Q (see Supplementary Material 1 for details). Several recent studies also examined whether invasions of non-native species change the structure of native communities by increasing or decreasing functional diversity (Castro-Díez, Pauchard, Traveset, & Vilà, 2016; de la Riva, Godoy, Castro-Díez, Gutiérrez-Cánovas, & Vilà, 2019 ; Loiola et al., 2018). These measures that compare invaded and uninvaded communities functionally and calculate the magnitude of change share a similar basis with the BNI. However, the BNI includes all possible species pairings weighted by the temporal coexistence coefficient rather than a comparison of categories (which Castro-Díez et al., 2016; de la Riva et al., 2019; and Loiola et al., 2018 do). These conceptual differences in how biotic novelty is assessed were reflected in the result that the BNI was only weakly positively related to the functional diversity of the group of non-native species (Figure 5d).

Furthermore, by applying the standardization of the BNI (the BNI in proportion to Rao's Q), we showed in the first case study that the BNI was not driven by the inherent variation in functional diversity along the urbanization gradient (since BNI and BNIs varied to a very similar extent along the gradient). As shown in our methods section,

this standardization of the BNI can be easily applied by the user for a validation of the BNI results.

The second case study demonstrated the applicability of the BNI to nationwide datasets. The grid-cell map showed that areas of very high novelty of vascular plant species were predominantly concentrated in and around urban areas in Germany, which is partially in line with former nationwide assessments of vascular plants in Germany (Kühn, Brandl, & Klotz, 2004) and the UK (Botham et al., 2009). These studies described that neophytes were very strongly associated with urban land cover, but do not appear to be spreading out of urban habitats into the wider countryside. Our finding that the BNI is also higher around urban areas might be due to spread of novel species along transportation pathways, such as roads (von der Lippe & Kowarik, 2008) and rivers (Maskell, Bullock, Smart, Thompson, & Hulme, 2006), which connect cities and are located in corresponding grid cells in the map.

We observed on the grid-cell map that areas of low novelty were visible predominantly in southern Germany and partly in central Germany, which coincidences with mountain ranges in Germany. Previous studies also showed that non-native species richness typically declines along elevational gradients (Alexander et al., 2011; Averett et al., 2016; Seipel et al., 2012). This pattern has been explained by two factors: (a) special adaptations are required to invade extreme environments (Alexander et al., 2011; Alpert, Bone, & Holzapfel, 2000; Pauchard et al., 2009), making mountains inherently resistant to invasions and (b) anthropogenic disturbance decreases with increasing elevation, leading to fewer species introductions (i.e., lower propagule pressure) and also higher resistance to invasions (Arévalo et al., 2005; Averett et al., 2016).

We are aware that analyzing a dataset with the extent of our second case study is not free of concerns. For example, the large grid-cell size (11 × 11 km) and the spatial autocorrelation of grid cells (Kühn et al., 2004) may be problematic sources of error. Sampling bias (i.e., there are more botanical institutes and experts in urbanized areas than in less urbanized areas) and other potential explanatory variables (e.g., geological types of grid cells) may play important roles for such an analysis as well. However, since it is the scope of this paper to demonstrate possible applications of the BNI rather than disentangling various factors that structure biotic novelty, we refrained to perform complex statistical analysis and chose to present a map without underlying models. Therefore, it is up to future studies to focus on this demanding task.

In our two case studies, we investigated the relationship between biotic novelty and urbanization (as an indicator of abiotic novelty). However, it is unknown how novelty is related to other global ecological trends. For example, the loss of native species and the increase in exotic species as a landscape becomes more urban has led to the concept of biotic homogenization (McKinney, 2006; McKinney & Lockwood, 1999; Olden, 2006). Due to their conceptual parallels, we suspect that biotic novelty and biotic homogenization are related and will co-occur (especially in cities), but this needs further study.

5 | CONCLUSIONS

Human-induced changes are generating novel communities composed of new combinations of species which may result in increased biotic novelty. Previous methods for quantifying biotic novelty, such as counting the number of non-native species, appear limited in that they do not consider whether these new species are functionally novel, or how long these species have been residents, possibly over- or under-estimating the amount of novelty contributed by these new species. Our framework of measuring biotic novelty may have an advantage over a number of measures by combining these relevant aspects of biotic novelty into a single formula, accompanied by an additional standardization method. It allows for a nuanced comparison of communities, as it considers the trait differences between species. It is also versatile, since it allows species differences, hence novelty, to be measured in different ways according to the focus of the study. It is a helpful tool whenever the assessment of novel species assemblages is needed, which is not only the case in invasion ecology but also in global change ecology, restoration ecology, or urban ecology. We encourage further use and development of the BNI framework for different purposes in the future.

DATA AVAILABILITY STATEMENT

Supplementary Material 3 contains an R script with a function to calculate the BNI (file *SM 3.1_BNI function.R*). A set of functions to simulate communities and explore the behavior of the BNI, and two functions for plotting results can be found in the file *SM 3.2_ FUNCTION BNI simulation functions.R*. An R script to re-run the nine different simulation scenarios from the article can be found in the file *SM 3.3_Simulation testing.R*. All R code plus a dataset that replicates case study 1 can also be found under https://github.com/maudbv/BioticNoveltyIndex. The occurrence dataset titled "Flora von Deutschland (Phanerogamen)" that supports case study 2 is available from https://www.gbif.org/.

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REFERENCES

Alexander, J. M., Kueffer, C., Daehler, C. C., Edwards, P. J., Pauchard, A., Seipel, T., … Walsh, N. (2011). Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(2), 656–661. https://doi.org/10.1073/pnas.1013136108

Alpert, P., Bone, E., & Holzapfel, C. (2000). Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics*, *3*(1), 52–66. https://doi.org/10.1078/1433-8319-00004

Arévalo, J. R., Delgado, J. D., Otto, R., Naranjo, A., Salas, M., & Fernández-Palacios, J. M. (2005). Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). *Perspectives in Plant Ecology, Evolution and Systematics*, *7*(3), 185–202. https://doi.org/10.1016/J.PPEES.2005.09.003

Averett, J. P., McCune, B., Parks, C. G., Naylor, B. J., DelCurto, T., & Mata-González, R. (2016). Non-native plant invasion along elevation and canopy closure gradients in a middle rocky mountain ecosystem. *PLoS ONE*, *11*(1), e0147826. https://doi.org/10.1371/journal.pone.0147826

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Bogan, M. T., & Lytle, D. A. (2011). Severe drought drives novel community trajectories in desert stream pools. *Freshwater Biology*, *56*(10), 2070–2081. https://doi.org/10.1111/j.1365-2427.2011.02638.x

Botham, M. S., Rothery, P., Hulme, P. E., Hill, M. O., Preston, C. D., & Roy, D. B. (2009). Do urban areas act as foci for the spread of alien plant species? An assessment of temporal trends in the UK. *Diversity and Distributions*, *15*(2), 338–345. https://doi.org/10.1111/J.1472-4642.2008.00539.X

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, *16*(5), 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Bundesamt für Naturschutz/Netzwerk Phytodiversität Deutschland. (2018). Flora von Deutschland (Phanerogamen). Occurrence dataset accessed via GBIF.org on 2018-07-23. https://doi.org/10.15468/dl.7qdzml

Cadotte, M. W., Cavender-Bares, J., Tilman, D., & Oakley, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, *4*(5), e5695. https://doi.org/10.1371/journal.pone.0005695

Carthey, A. J. R., & Banks, P. B. (2012). When does an alien become a native species? A vulnerable native mammal recognizes and responds to its long-term alien predator. *PLoS ONE*, *7*(2), e31804. https://doi.org/10.1371/journal.pone.0031804

Carthey, A. J. R., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. *Biological Reviews*, *89*(4), 932–949. https://doi.org/10.1111/brv.12087

Castro-Díez, P., Pauchard, A., Traveset, A., & Vilà, M. (2016). Linking the impacts of plant invasion on community functional structure and ecosystem properties. *Journal of Vegetation Science*, *27*(6), 1233–1242. https://doi.org/10.1111/jvs.12429

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*(1), 44–62. https://doi.org/10.1111/j.1365-2486.2011.02549.x

Chapin, F. S., & Starfield, A. M. (1997). Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change*, *35*(4), 449–461. https://doi.org/10.1023/A:1005337705025

Chase, J. M., Kraft, N. J. B., Smith, K. G., Vellend, M., & Inouye, B. D. (2011). Using null models to disentangle variation in community dissimilarity from variation in α-diversity. *Ecosphere*, *2*(2), 1–11. https://doi.org/10.1890/ES10-00117.1

Chiu, C. H., & Chao, A. (2014). Distance-based functional diversity measures and their decomposition: A framework based on hill numbers. *PLoS ONE*, *9*(7), e100014. https://doi.org/10.1371/journal.pone.0100014

Chocholoušková, Z., & Pyšek, P. (2003). Changes in composition and structure of urban flora over 120 years: A case study of the city of Plzeň. *Flora - Morphology, Distribution, Functional Ecology of Plants*, *198*(5), 366–376. https://doi.org/10.1078/0367-2530-00109

Cleland, E. E. (2011). Trait divergence and the ecosystem impacts of invading species. *New Phytologist*, *189*(3), 649–652. https://doi.org/10.1111/j.1469-8137.2010.03607.x

Correa-Metrio, A., Bush, M. B., Cabrera, K. R., Sully, S., Brenner, M., Hodell, D. A., … Guilderson, T. (2012). Rapid climate change and no-analog vegetation in lowland Central America during the last 86,000 years. *Quaternary Science Reviews*, *38*, 63–75. https://doi.org/10.1016/j.quascirev.2012.01.025

De Bello, F., Lavergne, S., Meynard, C. N., Lepš, J., & Thuiller, W. (2010). The partitioning of diversity: Showing Theseus a way out of the labyrinth. *Journal of Vegetation Science*, *21*(5), 992–1000. https://doi.org/10.1111/j.1654-1103.2010.01195.x

de la Riva, E. G., Godoy, O., Castro-Díez, P., Gutiérrez-Cánovas, C., & Vilà, M. (2019). Functional and phylogenetic consequences of plant invasion for coastal native communities. *Journal of Vegetation Science*, *30*(3), 510–520. https://doi.org/10.1111/jvs.12748

DeCandido, R., Muir, A. A., & Gargiullo, M. B. (2004). A first approximation of the historical and extant vascular flora of New York City: Implications for native plant species conservation. *Journal of the Torrey Botanical Society*, *131*(3), 243–251. https://doi.org/10.2307/4126954

Drenovsky, R. E., Grewell, B. J., D'Antonio, C. M., Funk, J. L., James, J. J., Molinari, N., … Richards, C. L. (2012). A functional trait perspective on plant invasion. *Annals of Botany*, *110*(1), 141–153. https://doi.org/10.1093/aob/mcs100

Durka, W., & Michalski, S. G. (2012). Daphne: A dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology*, *93*(10), 2297–2297. https://doi.org/10.1890/12-0743.1

Emerson, B. C., & Gillespie, R. G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution*, *23*(11), 619–630. https://doi.org/10.1016/j.tree.2008.07.005

Essl, F., Dullinger, S., Genovesi, P., Hulme, P. E., Jeschke, J. M., Katsanevakis, S., … Bacher, S. (2019). A conceptual framework for range-expanding species that track human-induced environmental change. *BioScience*, *69*(11), 908–919. https://doi.org/10.1093/biosci/biz101

Evers, C. R., Wardropper, C. B., Branoff, B., Granek, E. F., Hirsch, S. L., Link, T. E., … Wilson, C. (2018). The ecosystem services and biodiversity of novel ecosystems: A literature review. *Global Ecology and Conservation*, *13*, e00362. https://doi.org/10.1016/j.gecco.2017.e00362

Gallien, L., Carboni, M., & Münkemüller, T. (2014). Identifying the signal of environmental filtering and competition in invasion patterns – A contest of approaches from community ecology. *Methods in Ecology and Evolution*, *5*(10), 1002–1011. https://doi.org/10.1111/2041-210X.12257

Garcia, R. A., Cabeza, M., Rahbek, C., & Araújo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, *344*(6183), 1247579. https://doi.org/10.1126/science.1247579

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., … Toussaint, J.-P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, *85*(9), 2630–2637. https://doi.org/10.1890/03-0799

GBIF: The Global Biodiversity Information Facility. (2019). What is GBIF? Retrieved from https://www.gbif.org/what-is-gbif

Gerhold, P., Cahill, J. F., Winter, M., Bartish, I. V., & Prinzing, A. (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, *29*(5), 600–614. https://doi.org/10.1111/1365-2435.12425

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, *27*(4), 857–871. https://doi.org/10.2307/2528823

Haas, J. N., Giesecke, T., & Karg, S. (2003). Die mitteleuropäische Subsistenzwirtschaft des 3. bis 2. Jahrtausends v.Chr. aus paläoökologischer Sicht. *Journal of Neolithic Archaeology*, *5*, 1–8. https://doi.org/10.12766/jna.2003.2

Harris, J. A., Murphy, S. D., Nelson, C. R., Perring, M. P., & Tognetti, P. M. (2013). Characterizing novel ecosystems: Challenges for measurement. In R. J. Hobbs, E. S. Higgs, & C. M. Hall (Eds.), *Novel ecosystems: Intervening in the new ecological world order* (pp. 192–204). Chichester, UK: John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118354186.ch24

Hawkes, C. V. (2007). Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. *The American Naturalist*, *170*(6), 832–843. https://doi.org/10.1086/522842

Heger, T., Bernard-Verdier, M., Gessler, A., Greenwood, A. D., Grossart, H.-P., Hilker, M., … Jeschke, J. M. (2019). Towards an integrative, eco-evolutionary understanding of ecological novelty: Studying and communicating interlinked effects of global change. *BioScience*, *69*(11), 888–899. https://doi.org/10.1093/biosci/biz095

Helm, A., Zobel, M., Moles, A. T., Szava-Kovats, R., & Pärtel, M. (2015). Characteristic and derived diversity: Implementing the species pool concept to quantify conservation condition of habitats. *Diversity and Distributions*, *21*(6), 711–721. https://doi.org/10.1111/ddi.12285

Helmus, M. R., Bland, T. J., Williams, C. K., & Ives, A. R. (2007). Phylogenetic measures of biodiversity. *The American Naturalist*, *169*(3), E68–83. https://doi.org/10.1086/511334

Higgs, E. (2017). Novel and designed ecosystems. *Restoration Ecology*, *25*(1), 8–13. https://doi.org/10.1111/rec.12410

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., … Zobel, M. (2006). Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, *15*(1), 1–7. https://doi.org/10.1111/j.1466-822X.2006.00212.x

Hobbs, R. J., Higgs, E. S., & Hall, C. M. (2013). Defining novel ecosystems. In R. J. Hobbs, E. S. Higgs, & C. M. Hall (Eds.), *Novel ecosystems: Intervening in the new ecological world order* (pp. 58–60). Chichester, UK: John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118354186.ch6

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology & Evolution*, *24*(11), 599–605. https://doi.org/10.1016/j.tree.2009.05.012

Hulme, P. E., & Bernard-Verdier, M. (2018). Comparing traits of native and alien plants: Can we do better? *Functional Ecology*, *32*(1), 117–125. https://doi.org/10.1111/1365-2435.12982

Jeschke, J. M., Keesing, F., & Ostfeld, R. S. (2013). Novel organisms: Comparing invasive species, GMOs, and emerging pathogens. *Ambio*, *42*(5), 541–548. https://doi.org/10.1007/s13280-013-0387-5

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., … Wirth, C. (2011). TRY – A global database of plant traits. *Global Change Biology*, *17*(9), 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., ... Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26(11), 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Klotz, S., Kühn, I., & Durka, W. (2002). *BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde* (Vol. 38). Hiltrup, Münster, Bonn-Bad Godesberg, Germany: BfN-Schriftenvertrieb im Landwirtschaftsverl.

Knapp, S., Kühn, I., Stolle, J., & Klotz, S. (2010). Changes in the functional composition of a Central European urban flora over three centuries. *Perspectives in Plant Ecology, Evolution and Systematics*, 12(3), 235–244. https://doi.org/10.1016/j.ppees.2009.11.001

Korell, L., Schmidt, R., Bruelheide, H., Hensen, I., & Auge, H. (2016). Mechanisms driving diversity–productivity relationships differ between exotic and native communities and are affected by gastropod herbivory. *Oecologia*, 180(4), 1025–1036. https://doi.org/10.1007/s00442-015-3395-2

Kühn, I., Brandl, R., & Klotz, S. (2004). The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, 6(5), 749–764.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305. https://doi.org/10.1890/08-2244.1

Lemoine, N. P., Burkepile, D. E., & Parker, J. D. (2016). Quantifying differences between native and introduced species. *Trends in Ecology & Evolution*, 31(5), 372–381. https://doi.org/10.1016/j.tree.2016.02.008

Loiola, P. P., de Bello, F., Chytrý, M., Götzenberger, L., Carmona, C. P., Pyšek, P., & Lososová, Z. (2018). Invaders among locals: Alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. *Journal of Ecology*, 106(6), 2230–2241. https://doi.org/10.1111/1365-2745.12986

Lu, D., & Weng, Q. (2006). Use of impervious surface in urban land-use classification. *Remote Sensing of Environment*, 102(1–2), 146–160. https://doi.org/10.1016/j.rse.2006.02.010

Lurgi, M., López, B. C., & Montoya, J. M. (2012). Novel communities from climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605), 2913–2922. https://doi.org/10.1098/rstb.2012.0238

Maskell, L. C., Bullock, J. M., Smart, S. M., Thompson, K., & Hulme, P. E. (2006). The distribution and habitat associations of non-native plant species in urban riparian habitats. *Journal of Vegetation Science*, 17(4), 499–508. https://doi.org/10.1111/j.1654-1103.2006.tb02471.x

Mason, N. W. H., & Pavoine, S. (2013). Does trait conservatism guarantee that indicators of phylogenetic community structure will reveal niche-based assembly processes along stress gradients? *Journal of Vegetation Science*, 24(5), 820–833. https://doi.org/10.1111/jvs.12033

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127(3), 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Mitchell, C. E., Blumenthal, D., Jarošík, V., Puckett, E. E., & Pyšek, P. (2010). Controls on pathogen species richness in plants' introduced and native ranges: Roles of residence time, range size and host traits. *Ecology Letters*, 13(12), 1525–1535. https://doi.org/10.1111/j.1461-0248.2010.01543.x

Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., ... Giambelluca, T. W. (2013). The projected timing of climate departure from recent variability. *Nature*, 502(7470), 183–187. https://doi.org/10.1038/nature12540

Olden, J. D. (2006). Biotic homogenization: A new research agenda for conservation biogeography. *Journal of Biogeography*, 33(12), 2027–2039. https://doi.org/10.1111/j.1365-2699.2006.01572.x

Parker, J. D., Burkepile, D. E., & Hayt, M. E. (2006). Opposing effects of native and exotic herbivores on plant invasions. *Science*, 311(5766), 1459–1461. https://doi.org/10.1126/science.1121407

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C. C., Alexander, J., Edwards, P. J., ... Seipel, T. (2009). Ain't no mountain high enough: Plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, 7(9), 479–486. https://doi.org/10.1890/080072

Pavoine, S., Gasc, A., Bonsall, M. B., & Mason, N. W. H. (2013). Correlations between phylogenetic and functional diversity: Mathematical artefacts or true ecological and evolutionary processes? *Journal of Vegetation Science*, 24(5), 781–793. https://doi.org/10.1111/jvs.12051

Pavoine, S., Ollier, S., & Pontier, D. (2005). Measuring diversity from dissimilarities with Rao's quadratic entropy: Are any dissimilarities suitable? *Theoretical Population Biology*, 67(4), 231–239. https://doi.org/10.1016/j.tpb.2005.01.004

Pavoine, S., & Ricotta, C. (2014). Functional and phylogenetic similarity among communities. *Methods in Ecology and Evolution*, 5(7), 666–675. https://doi.org/10.1111/2041-210X.12193

Pavoine, S., Vallet, J., Dufour, A. B., Gachet, S., & Daniel, H. (2009). On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. *Oikos*, 118(3), 391–402. https://doi.org/10.1111/j.1600-0706.2008.16668.x

Pearse, I. S., & Altermatt, F. (2013). Predicting novel trophic interactions in a non-native world. *Ecology Letters*, 16(8), 1088–1094. https://doi.org/10.1111/ele.12143

Perring, M. P., Standish, R. J., & Hobbs, R. J. (2013). Incorporating novelty and novel ecosystems into restoration planning and practice in the 21st century. *Ecological Processes*, 2(1), 1–8. https://doi.org/10.1186/2192-1709-2-18

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, 9(6), 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Poos, M. S., Walker, S. C., & Jackson, D. A. (2009). Functional-diversity indices can be driven by methodological choices and species richness. *Ecology*, 90(2), 341–347. https://doi.org/10.1890/08-1638.1

QGIS Development Team. (2016). QGIS geographic information system. Open Source Geospatial Foundation Project. Retrieved from http://qgis.osgeo.org

QGIS Development Team. (2018). QGIS geographic information system. Open Source Geospatial Foundation Project. Retrieved from http://qgis.osgeo.org

Qian, H., & Ricklefs, R. E. (2006). The role of exotic species in homogenizing the North American flora. *Ecology Letters*, 9(12), 1293–1298. https://doi.org/10.1111/j.1461-0248.2006.00982.x

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

Radeloff, V. C., Williams, J. W., Bateman, B. L., Burke, K. D., Carter, S. K., Childress, E. S., ... Usinowicz, J. (2015). The rise of novelty in ecosystems. *Ecological Applications*, 25(8), 2051–2068. https://doi.org/10.1890/14-1781.1

Rao, C. R. (1982). Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology*, 21(1), 24–43. https://doi.org/10.1016/0040-5809(82)90004-1

Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B. E. L., & Pavoine, S. (2016). Measuring the functional redundancy of biological communities: A quantitative guide. *Methods in Ecology and Evolution*, 7(11), 1386–1395. https://doi.org/10.1111/2041-210X.12604

Saul, W.-C., & Jeschke, J. M. (2015). Eco-evolutionary experience in novel species interactions. *Ecology Letters*, *18*(3), 236–245. https://doi.org/10.1111/ele.12408

Saul, W.-C., Jeschke, J. M., & Heger, T. (2013). The role of eco-evolutionary experience in invasion success. *NeoBiota*, *17*, 57–74. https://doi.org/10.3897/neobiota.17.5208

Schleuter, D., Daufresne, M., Massol, F., & Argillier, C. (2010). A user's guide to functional diversity indices. *Ecological Monographs*, *80*(3), 469–484. https://doi.org/10.1890/08-2225.1

Schneider, A., Friedl, M. A., & Potere, D. (2009). A new map of global urban extent from MODIS satellite data. *Environmental Research Letters*, *4*(4), 044003. https://doi.org/10.1088/1748-9326/4/4/044003

Schroeder, F. G. (1968). Zur Klassifizierung der Anthropochoren. *Vegetatio Acta Geobotanica*, *16*(5–6), 225–238. https://doi.org/10.1007/BF00257018

Schultheis, E. H., Berardi, A. E., & Lau, J. A. (2015). No release for the wicked: Enemy release is dynamic and not associated with invasiveness. *Ecology*, *96*(9), 2446–2457. https://doi.org/10.1890/14-2158.1

Schwarz, N. (2010). Urban form revisited – Selecting indicators for characterising European cities. *Landscape and Urban Planning*, *96*(1), 29–47. https://doi.org/10.1016/j.landurbplan.2010.01.007

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

Seipel, T., Kueffer, C., Rew, L. J., Daehler, C. C., Pauchard, A., Naylor, B. J., … Walsh, N. (2012). Processes at multiple scales affect richness and similarity of non-native plant species in mountains around the world. *Global Ecology and Biogeography*, *21*(2), 236–246. https://doi.org/10.1111/j.1466-8238.2011.00664.x

Seitz, B., Ristow, M., Prasse, R., Machatzi, B., Klemm, G., Böcker, R., & Sukopp, H. (2012). Der Berliner Florenatlas. *Verhandlungen Des Botanischen Vereins Berlin Brandenburg*, *7*, 1–533.

Sheppard, C. S., & Schurr, F. M. (2019). Biotic resistance or introduction bias? Immigrant plant performance decreases with residence times over millennia. *Global Ecology and Biogeography*, *28*(2), 222–237. https://doi.org/10.1111/geb.12844

Shimadzu, H., Dornelas, M., & Magurran, A. E. (2015). Measuring temporal turnover in ecological communities. *Methods in Ecology and Evolution*, *6*(12), 1384–1394. https://doi.org/10.1111/2041-210X.12438

Strauss, S. Y., Lau, J. A., & Carroll, S. P. (2006). Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? *Ecology Letters*, *9*(3), 357–374. https://doi.org/10.1111/j.1461-0248.2005.00874.x

Tait, C. J., Daniels, C. B., & Hill, R. S. (2005). Changes in species assemblages within the Adelaide metropolitan area, Australia, 1836–2002. *Ecological Applications*, *15*(1), 346–359. https://doi.org/10.1890/04-0920

Toms, J. D., & Lesperance, M. L. (2003). Piecewise regression: A tool for identifying ecological thresholds. *Ecology*, *84*(8), 2034–2041. https://doi.org/10.1890/02-0472

Verhoeven, K. J. F., Biere, A., Harvey, J. A., & van der Putten, W. H. (2009). Plant invaders and their novel natural enemies: Who is naïve? *Ecology Letters*, *12*(2), 107–117. https://doi.org/10.1111/j.1461-0248.2008.01248.x

von der Lippe, M., Buchholz, S., Hiller, A., Seitz, B., & Kowarik, I. (2020). CityScapeLab Berlin: A research platform for untangling urbanization effects on biodiversity. *Sustainability*, *12*(6), 2565. https://doi.org/10.3390/su12062565

von der Lippe, M., & Kowarik, I. (2008). Do cities export biodiversity? Traffic as dispersal vector across urban-rural gradients. *Diversity and Distributions*, *14*(1), 18–25. https://doi.org/10.1111/j.1472-4642.2007.00401.x

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, *33*(1), 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, *5*(9), 475–482. https://doi.org/10.1890/070037

Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(14), 5738–5742. https://doi.org/10.1073/pnas.0606292104

Wilsey, B. J., Teaschner, T. B., Daneshgar, P. P., Isbell, F. I., & Polley, H. W. (2009). Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. *Ecology Letters*, *12*(5), 432–442. https://doi.org/10.1111/j.1461-0248.2009.01298.x

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

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