

1 **A multidimensional framework for measuring biotic novelty:**

2 **How novel is a community?**

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22 Running head: A new framework for measuring biotic novelty

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26 **Abstract**

27 Anthropogenic changes in climate, land use and disturbance regimes, as well as in-
28 troductions of non-native species can lead to the transformation of many ecosystems.
29 The resulting novel ecosystems are usually characterized by species assemblages
30 that have not occurred previously in a given area. Quantifying the ecological novelty
31 of communities (i.e. biotic novelty) would enhance the understanding of environmen-
32 tal change. However, quantification remains challenging since current novelty met-
33 rics, such as the number and/or proportion of non-native species in a community, fall
34 short of considering both functional and evolutionary aspects of biotic novelty. Here,
35 we propose the Biotic Novelty Index (BNI), an intuitive and flexible multidimensional
36 measure that combines (1) functional differences between native and non-native in-
37 troduced species with (2) temporal dynamics of species introductions. We show that
38 the BNI is an additive partition of Rao's quadratic entropy, capturing the novel inter-
39 action component of the community's functional diversity. Simulations show that the
40 index varies predictably with the relative amount of functional novelty added by re-
41 cently arrived species, and they illustrate the need to provide an additional standard-
42 ized version of the index. We present a detailed R-code and two applications of the
43 BNI by (1) measuring changes of biotic novelty of dry grassland plant communities
44 along an urbanization gradient in a metropolitan region and (2) determining the biotic
45 novelty of plant species assemblages at a national scale. Results illustrate the ap-
46 plicability of the index across scales and its flexibility in the use of data of different
47 quality. Both case studies revealed strong connections between biotic novelty and
48 increasing urbanization, a measure of abiotic novelty. We conclude that the BNI
49 framework may help in building a basis for a better understanding of the ecological
50 and evolutionary consequences of global change.

51 Introduction

63 Ecological novelty has received growing attention in the recent literature (e.g. Hobbs
64 *et al.* 2006; Heger *et al.* 2019) focusing on novel organisms (Jeschke *et al.* 2013),
65 novel species interactions (Pearse & Altermatt 2013; Bezemer *et al.* 2014; Carthey &
66 Banks 2014), novel communities (Lurgi *et al.* 2012) or novel ecosystems (Hobbs *et*
67 *al.* 2009, 2013; Higgs 2017). One major aspect of ecological novelty is the emer-
68 gence of abiotic and biotic conditions that are beyond the historical range of condi-
69 tions at a given site or area (Mora *et al.* 2013), sometimes without present or past
70 analog conditions anywhere else (Williams & Jackson 2007). A site can be novel in
71 terms of abiotic conditions, resulting for example from changes in climate, nitrogen
72 deposition or pollution by microplastics. Novelty can also result from changes in spe-
73 cies composition, structure or ecological processes, generating biotic novelty (Heger
74 *et al.* 2019). Furthermore, abiotic novelty can cause biotic novelty (Chapin & Starfield
75 1997; Williams & Jackson 2007; Bogan & Lytle 2011; Correa-Metrio *et al.* 2012),
76 such as a when a reshuffling of species is induced by climate change (Williams &
77 Jackson 2007) – and vice versa when introduced species, for example, strongly af-
78 fect the nutrient cycling (Vilà *et al.* 2011; Jäger *et al.* 2013). At the same time, biotic
79 novelty can occur without abiotic novelty: a non-native species introduction may cre-
80 ate novelty in species composition, whereas abiotic conditions remain essentially un-
81 changed. Hence, rigorously measuring novelty requires explicit definition of the rele-
82 vant variables (Radeloff *et al.* 2015).

83 However, the question of how to quantify ecological novelty in a standardized and
84 comparable manner has rarely been considered. A straightforward approach to
85 measuring abiotic novelty is to compare current abiotic variables, for instance climatic
86 variables, in an area with their historic values by applying dissimilarity metrics

87 (Williams *et al.* 2007; Garcia *et al.* 2014; Radeloff *et al.* 2015). This approach has
88 become increasingly common in climate change science, and may be applied to any
89 abiotic factor for which reference data are available.

90 A common measure of biotic novelty is simply the number and/or proportion of novel
91 species (e.g. non-native species) in a community (Parker *et al.* 2006; Qian & Ricklefs
92 2006; Wilsey *et al.* 2009; Catford *et al.* 2012; Korell *et al.* 2016). However, assigning
93 species to one of these two categories is a broad generalization and temporal dy-
94 namics of novel species introductions and their interactions with native species are
95 reduced to a binary view. In a given community, species usually differ in their resi-
96 dence time in the focal region, depending on the time of arrival mediated by natural
97 or anthropogenic pathways (Fig. 1). This has evolutionary consequences since both
98 native and non-native species may gradually adapt to their new interaction partner(s)
99 over time (Strauss *et al.* 2006; Verhoeven *et al.* 2009; Carthey & Banks 2012; Hulme
100 & Bernard-Verdier 2018), which may lead to a decrease of novelty in the community
101 (Saul & Jeschke 2015). Consequently, we argue that a quantification method of biotic
102 novelty should include a component that captures the different time spans of coexist-
103 ence of the species in a given community.

104 Another limitation of assessing biotic novelty only by quantifying native vs. non-native
105 species is the omission of functional differences between species. A novel species
106 that enters a community may be functionally similar or different compared with the
107 resident species (Fig. 1; Hulme & Bernard-Verdier 2018). We argue that a species
108 that is functionally dissimilar from the resident species represents greater biotic
109 novelty than one that is similar to the pre-existing community.

110 Several recent studies proposed new approaches to capture the biotic novelty of
111 ecological communities (Baselga 2010; Saul *et al.* 2013; Helm *et al.* 2015; Shimadzu

112 *et al.* 2015). These approaches mainly focus on community dynamics and species
113 turnover over time. For example, Shimadzu *et al.* (2015) converted commonly used
114 measures of β -diversity, such as Jaccard's index of dissimilarity, to a measure of
115 temporal β -diversity that compares the species composition of one community at two
116 points in time (i.e. at an initial state and the current state). This provides a powerful
117 way to quantify novelty compared to past "reference states" (Heger *et al.* 2019), but it
118 is not easily applicable to compare two existing communities for which local temporal
119 dynamics data are missing.

120 We propose a new multidimensional measure of biotic novelty called Biotic Novelty
121 Index (BNI), which serves to capture the two components of novelty as described by
122 Heger *et al.* (2019): (1) a change-dependent ("different") component and (2) a time-
123 dependent ("before") component. In this sense, a situation is ecologically novel if the
124 new situation is "different", e.g. in terms of species composition, from the situation
125 that was present "before", e.g. compared to historic baseline conditions. Accordingly,
126 our index relies on: (1) pairwise dissimilarities between species (e.g. functional or
127 phylogenetic distances), and (2) the residence time of each species in the area
128 considered. The index was designed to make comparisons of novelty between
129 several communities (e.g. along gradients) at the present point in time, without prior
130 knowledge of the local communities assembly history. The BNI is based on the
131 formula for Rao's quadratic entropy (hereafter Rao's Q; Rao 1982; Botta-Dukát
132 2005), which is one of the most common indices of functional diversity (Schleuter *et*
133 *al.* 2010; Ricotta *et al.* 2016).

134 Consequently, the BNI shares a number of characteristics with Rao's Q. Both indices
135 are primarily based on pairwise distances between species, which are calculated
136 from relevant attributes of species, such as functional trait values or phylogenetic

137 distances. In the same way that pairwise distances are weighted by relative
138 abundances in Rao's Q, pairwise distances are weighted by a pairwise temporal
139 coexistence coefficient in the BNI. This temporal coefficient is calculated based on
140 the estimated residence time of each species in the reference area and captures how
141 long pairs of species have coexisted in the area. For example, if a given pair of
142 species consists of a native and a recently introduced species, their pairwise trait
143 distance will be weighted more heavily than the distance between a native and
144 another non-native which arrived earlier in the area. This temporal coefficient allows
145 us to take into account the temporal erosion of novelty in a community, and
146 differentiate between non-natives in such a way that a recently introduced species
147 may be seen as "more novel" compared to the established non-native species.

148 We describe how to calculate the BNI from various data sources, and how it
149 associates with traditional measures of biotic novelty, abiotic novelty, species
150 richness and functional diversity. By presenting simulations and two case studies, we
151 show that this new method to quantify biotic novelty is intuitive and versatile, as it is
152 easily adaptable to datasets of different scale, scope and resolution. We demonstrate
153 in this paper that the BNI framework is a helpful tool whenever the assessment of
154 novel species assemblages or communities is needed, which may not only be useful
155 in invasion ecology, but also in global change ecology, restoration ecology or urban
156 ecology.

157 **Methods**

158 **The new index of biotic novelty**

159 There are seven steps to calculate the BNI: (1) obtaining a trait matrix, (2) converting
160 the trait matrix into a distance matrix, (3) obtaining species' first records, (4) convert-
161 ing the first records into a temporal coexistence matrix, (5) weighting the distance

162 matrix by the temporal coexistence matrix, (6) multiplying the distance matrix by the
163 species' relative abundance (optional), and (7) calculating the sum of all pairwise
164 comparisons from the distance matrix (Fig. 2). The resulting BNI is expressed as:

$$166 \quad BNI = \sum_{i=1}^{s-1} \sum_{j=i+1}^{s-1} d_{ij} \times c_{ij} \times p_i p_j$$

165 (Equation 1)

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

174 **The functional diversity component**

175 The general rule to calculate functional diversity indices is that traits must be linked to
176 the function(s) of interest. For instance, specific leaf area, maximum growth rate and
177 leaf nitrogen concentration are important components of plant functional diversity
178 when primary production is the process of interest (Garnier *et al.* 2004; Wright *et al.*
179 2004). Similarly, the choice of traits for the BNI can be related to the novelty aspects
180 of interest. For example, if the aim is to assess the biotic novelty of an invertebrate
181 herbivore community, feeding preference, feeding type (e.g. chewing or sucking) and
182 the number of generations per year are traits where novelty could play a relevant role
183 for the consumed plant. If some traits are more important for evaluating biotic novelty
184 than others, they should be given greater weights in the trait matrix. Careful decisions

185 about which traits to include and how to weigh them depends on the purpose to
186 which the index will be applied and should rely on expert knowledge of the system
187 (Laliberté & Legendre 2010). Traits can be continuous (e.g. leaf nitrogen concentra-
188 tion), binary variables (e.g. legume or non-legume) or categorical (e.g. flower color).
189 Distance measures calculate the difference between pairs of species based on their
190 characteristics (e.g. functional traits). There are many distance measures to choose
191 from, but two are most commonly used on trait datasets: the Euclidean distance and
192 the Gower distance (Laliberté & Legendre 2010). The Euclidean distance is calculat-
193 ed on complete and continuous trait datasets, and emphasizes absolute differences
194 (Poos *et al.* 2009), while the Gower distance has the advantage that it allows incom-
195 plete data sets and mixed (categorical, ordinal, continuous) data types (Gower 1971;
196 Laliberté & Legendre 2010).

197 **The temporal coexistence component**

198 In the BNI, pairwise trait distances are weighted by a pairwise temporal coexistence
199 coefficient. The first step in calculating this coefficient is to define whether each spe-
200 cies belongs to the historical native species pool or not. Second, we use information
201 such as first records (or time of establishment) of the non-native species in the local
202 region. This information can be obtained either from publications (e.g. Seebens *et al.*
203 2017 collected first records of alien species worldwide: [http://dataportal-](http://dataportal-senckenberg.de/database/metacat/bikf.10029/bikf)
204 [senckenberg.de/database/metacat/bikf.10029/bikf](http://dataportal-senckenberg.de/database/metacat/bikf.10029/bikf)), regional databases (e.g. the Bi-
205 oFlor database for plants in Germany, Klotz *et al.* 2002), or expert knowledge. For
206 native species, time of establishment needs to be estimated as well (e.g. for many
207 plant species in Central Europe a reference to the end of the last glacial period will
208 be reasonable). From this information, the residence time for each species is calcu-
209 lated. The residence time tells us how many years before today each species was

210 introduced or had been established. For example, a species that was introduced in
211 1719 has a residence time of 300 years in the year 2019 (the current year). Next,
212 resident times are normalized between the oldest residents (i.e. native species) and
213 the newest arrivals, bringing them into the range [0,1] by the following calculation:

$$215 \quad r_i' = \frac{r_i - r_{min}}{r_{max} - r_{min}}$$

214 (Equation 2)

216 where r_i' is the normalized residence time of species i , r_i is the residence time of spe-
217 cies i (in years), r_{min} is the minimum residence time of all species (i.e. the newest ar-
218 rival) and r_{max} the maximum residence time of all species (i.e. residence time of na-
219 tive species). Once the normalized residence time is calculated for each species, for
220 each pair of species the temporal coexistence coefficient can be calculated as fol-
221 lows:

$$223 \quad c_{ij} = 1 - \min(r_i', r_j')$$

222 (Equation 3)

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

226 Note that the minimum of both normalized residence times is used in equation 3 be-
227 cause the latest arrival in the species pair determines how long both species have
228 coexisted in the focal area. For example, if the two species have residence times of
229 300 and 100 years, respectively, their temporal coexistence in the focal area is 100
230 years. We then take the complement of the minimum normalized residence time in
231 equation 3, such that the coefficient is maximized when species have had the lowest
232 local coexistence time (i.e. maximum novelty). Eventually, the temporal coexistence

233 coefficient is calculated for each possible species pair and a new temporal matrix can
234 be constructed with the same dimension as the trait distance matrix described before.
235 The values of the temporal matrix range between 0 and 1 (due to the normalization
236 step given in equation 2) and functions as weighting factor for the trait distance ma-
237 trix. In this way, trait differences between species with low coexistence time are
238 weighted heavily, whereas trait differences between species coexisting for millennia
239 (such as a pair of native species) will be given no weight in the BNI.

240 **The BNI as a framework**

241 The BNI is in essence the sum of two components: the mean functional distance be-
242 tween novel species in the community, and the mean functional distance between
243 native and novel species. Furthermore, we can show that the BNI is an additive parti-
244 tion of Rao's Q (see supplementary material S1 for details). According to this parti-
245 tioning, we can express the BNI relative to Rao's Q, and define a standardized ver-
246 sion of the BNI as:

$$248 \quad BNI_s = \frac{BNI}{RaoQ}$$

247 (Equation 4)

249 This standardized version is a proportion of Rao's Q, which can be described as the
250 proportion of functional diversity contributed by novel species pairs (for an applica-
251 tion, see the simulations below and in supplementary material S2). A detailed R
252 code, that helps the user to calculate the BNI and the BNIs, is provided in supple-
253 mentary material 3.

254 We purposely refer to the BNI as a framework because it is built upon the idea to
255 combine two relevant aspects into one measure, which can be easily adapted to the

256 needs of the user (e.g. by adding or replacing relevant components) depending on
257 the goal of the study. For example, the BNI as described above captures the func-
258 tional novelty of communities because it uses functional traits to calculate differences
259 between species. However, if the user aims to assess phylogenetic aspects of novel-
260 ty, or to compare phylogenetic aspects with functional aspects, then the functional
261 diversity component of the BNI may be replaced with a measurement of phylogenetic
262 distances between species (see case study 2 for an application). While phylogeny
263 has sometimes been used as a proxy for functional or ecological niche differences
264 between species (Webb *et al.* 2002; Helmus *et al.* 2007; Cadotte *et al.* 2009), it has
265 become clear that phylogenetic distances are, at best, an imperfect proxy (Emerson
266 & Gillespie 2008; Mason & Pavoine 2013). Calculating the BNI using phylogenetic
267 distances may be useful in cases when trait data are difficult to obtain or the evolu-
268 tionary history and relatedness of species are the focus of interest (Gerhold *et al.*
269 2015).

270 While the temporal component of the BNI was designed to use species residence
271 times as the most accurate way to weigh the novelty of species interactions, there will
272 often be situations where dates of first records are imprecise, incomplete or even en-
273 tirely missing. For these cases, we suggest the use of temporal categories to charac-
274 terize each species in the community. The generation of these categories, for exam-
275 ple, could be based on corresponding decades or centuries. Another approach would
276 be to adopt already existing temporal categorizations such as the three-level classifi-
277 cation scheme of European plant species by Schroeder (1968): non-native species
278 are classified according to their time of human introduction, either before Europe's
279 discovery of the New World in 1492 (archaeophytes or more generally archaeobiota)
280 or after 1492 (neophytes, neobiota). Species that colonized a given area after the

281 end of the last glacial period without human assistance are classified as native (see
282 case study 1 for an application). “Neonative” species could be added as another cat-
283 egory for species establishing due to climate change in the Anthropocene, i.e. since
284 the middle of the 20th century (Essl *et al.* 2019). If even these data are not available,
285 the user may opt for the most basic categorization method which classifies species
286 as either native or non-native (i.e. a binary categorization). In this case, the corre-
287 sponding temporal coexistence coefficient would be either 0 for pairs of native spe-
288 cies, or 1 for pairs involving at least one non-native species.

289 The BNI as described above is a multispecies approach since it captures the func-
290 tional novelty of communities and species assemblages. However, by modifying the
291 BNI equation, it is also possible to focus on the biotic novelty of particular novel target
292 species in relationship to the interacting resident species. A similar approach was
293 proposed by Saul & Jeschke (2015), which consider the implications of different de-
294 grees of eco-evolutionary experience of interacting resident and novel species.

295 **Simulations**

296 Simulations of plant communities were used to explore the behavior of the BNI in dif-
297 ferent scenarios of functional diversity and biological invasion. We randomly generat-
298 ed a regional pool of 250 species, with 70 % natives and 30 % non-natives. In order
299 to spread the simulated residence times realistically, we followed the three-level clas-
300 sification of European plant species described before, and separated non-natives into
301 long established non-natives (e.g. archaeophytes, 15 % of all simulated species) and
302 recently arrived non-natives (e.g. neophytes, 15 % of all species). We attributed
303 mean dates of arrival for each species based on these categories: 8518 years for
304 natives, 2786 years for archaeophytes, and a uniformly random generated year of
305 arrival since 1492 for the neophytes. The mean dates of arrival for natives and ar-

306 chaeophytes originate from the respective class limits of natives and archaeophytes
307 in the Berlin/Brandenburg area, i.e. around 10,000 BC (end of the last glacial period)
308 for natives and around 3,000 BC for the introduction of the first archaeophytes (Haas,
309 Giesecke, & Karg, 2003). Next, we randomly generated functional trait values for
310 each species. Three continuous traits were sampled from normal distributions, whose
311 mean and variance were determined according to one of four non-native trait scenar-
312 ios.

313 Since the BNI is designed to capture functional novelty, we explored scenarios where
314 neophyte species are bringing different functional trait values from the historical resi-
315 dent pool of species (i.e. natives and archaeophytes pooled together). We present
316 four trait scenarios: (1) traits for all species are sampled from the same distribution;
317 (2) traits of neophytes have on average higher values than the residents (i.e. different
318 mean); (3) traits of neophytes occupy a wider range of values than the other species
319 (i.e. different variance parameter); and (4) traits of neophytes have both a different
320 mean and a different variance than the traits of residents (cf. supplementary material
321 2 for additional scenarios). We then assembled 100 communities by sampling ran-
322 domly from the simulated species pool. The number of species sampled per commu-
323 nity was assigned randomly following a Poisson distribution ($\lambda = 25$). In order
324 to generate a gradient of increasing biological invasion for each simulation, the 100
325 communities were forced to integrate an increasing proportion of neophytes (0 %, 25
326 %, 50 %, 75 %, 100 %). Simulations were repeated 500 times, with incremental
327 changes in parameters for each scenarios every 20 simulations (cf. supplementary
328 material 2). We calculated Rao's Q, the BNI and the BNIs for each simulated com-
329 munity. All simulations and calculations were done in R version 3.6.0 (R Core Team
330 2019), and all code is included in supplementary material 3.

331 **Case study 1: Biotic novelty of plant communities along an urbanization gradi-**
332 **ent**

333 To illustrate the strengths and weaknesses of the newly proposed measure, we ana-
334 lyzed changes in biotic novelty along an urbanization gradient in dry grassland com-
335 munities in Berlin, Germany. This vegetation type spans a range of near-natural to
336 strongly human-shaped sites throughout the city. For this reason, urban dry grass-
337 lands have been selected as a model ecosystem within the CityScapeLabs, an ex-
338 perimental platform with a network of 56 permanent plots, established for the evalua-
339 tion of biodiversity in urban environments. From April 18th to May 19th 2017, vegeta-
340 tion surveys were carried out in a 4 x 4 m plot within each of the 56 grasslands, re-
341 cording the abundance (percent cover) of 234 vascular plant species. Trait data for
342 the calculation of the BNI and Rao's Q were extracted from the TRY database
343 (Kattge *et al.* 2011) and the BioFlor database (Klotz *et al.* 2002). We used data for
344 twelve plant functional traits (plant height, specific leaf area, life form, flower color,
345 flower class, clonal growth organs, length of dispersal unit, seed mass, leaf area, leaf
346 nitrogen content, nitrogen fixation and mycorrhizal infection). Information on the first
347 record of neophytes is based on the atlas of the Berlin flora (Seitz *et al.* 2012). All
348 other species were classified as native or as archaeophytes (introduced by human
349 agency before 1492) according to the BioFlor database (Klotz *et al.* 2002). Note that
350 exact first record information (e.g. dates) were only available for neophytes, but not
351 for archaeophytes, nor native species, which is a typical situation of data availability
352 for plant species in Europe. Hence, we used for these two categories a mid-range
353 value for each species in the respective category and the exact first records for neo-
354 phytes only. The mid-range value for natives and archaeophytes was calculated from
355 the respective class limits in the focal area, i.e. around 10,000 BC (end of the last

356 glacial period) for natives and around 3,000 BC for the introduction of the first ar-
357 chaeophytes in the Berlin/Brandenburg region (Haas *et al.* 2003). This resulted in an
358 estimated residence time of 8518 years for natives and 2786 years for archaeo-
359 phytes.

360 To analyze the relationship between the biotic novelty of plant communities and the
361 level of urbanization (as a driver of ecological novelty), we applied a commonly used
362 indicator of urbanization: the percentage of sealed surfaces (i.e. impervious soils) in
363 the surrounding landscape (Lu & Weng 2006; Schwarz 2010). We calculated the
364 mean percentage of sealed surfaces in a 500 m buffer area around each of the 56
365 plots using publicly available urban habitat maps from the Berlin Senate Department
366 for Urban Development and Housing and QGIS 2.18.0 (QGIS Development Team
367 2016). Relationships of the BNI and the BNIs with the percentage of sealed surfaces,
368 Rao's Q and species richness were analyzed with linear models. All calculations
369 were carried out using R version 3.4.3 (R Core Team 2017).

370 **Case study 2: Biotic novelty of co-occurring vascular plants in Germany**

371 The second case study demonstrates the application of the BNI in conjunction with
372 big datasets. Here, we aimed to calculate the BNI for co-occurring vascular plants in
373 Germany and to evaluate how their biotic novelty is spatially related to the extent of
374 urban areas. It is a feature of this case study that it extensively used freely accessible
375 data from online databases. From the Global Biodiversity Information Facility (GBIF:
376 The Global Biodiversity Information Facility 2019) we downloaded the occurrence
377 dataset 'Flora von Deutschland (Phanerogamen)' which includes 9,577,887 records
378 of 5,721 vascular plant species in Germany (Bundesamt für Naturschutz / Netzwerk
379 Phytodiversität Deutschland 2018). These occurrence records are aggregated in 11 x
380 11 km grid cells of the grid of topographic maps (TK 25, scale 1:25000), which are

381 officially used for the design of species distribution maps in Germany. We used phy-
382 logenetic pairwise distances to calculate the BNI. In this case, the BNI thus captures
383 phylogenetic novelty rather than the functional novelty we calculated in our simula-
384 tions and in case study 1. To do so, we pruned the extensive phylogeny ‘Daphne’
385 (Durka & Michalski 2012) for our species set. Daphne is a dated phylogeny of a large
386 European flora for phylogenetically informed ecological analyses. Information wheth-
387 er a plant species is native or non-native in Germany plus information on first records
388 for neophytes were obtained from the BioFlor (Klotz *et al.* 2002) database. We calcu-
389 lated the BNI for each of the 3,003 grid cells and created a map using QGIS version
390 3.2.1 (QGIS Development Team 2018). A second layer, which indicates the extent of
391 urban areas based on MODIS satellite data (Schneider *et al.* 2009) was added to the
392 map. All calculations were carried out using R version 3.4.3 (R Core Team 2017) and
393 the R package ‘picante’ (Kembel *et al.* 2010) for phylogenetic tree pruning.

394 **Results**

395 **Simulations**

396 Simulations showed that the BNI varies broadly with the proportion of non-native
397 species and with the size of trait differences between species (Fig. 3). Overall, as
398 long as neophytes made up less than 50 % of the relative abundance of species in
399 the community, the BNI increased monotonously as more neophytes were added.
400 Beyond this point, however, the BNI did not always increase with the proportion of
401 neophytes. Its behavior depended on how much pairwise trait variance the neo-
402 phytes were bringing to the community, relative to the resident species.

403 In scenario 1, when neophytes were not on average functionally different from na-
404 tives, the BNI increased monotonously with the proportion of neophytes (Fig. 3a).
405 This is because, in this scenario, the mean pairwise trait differences (i.e. Rao’s Q)

406 remained constant, while the contribution of neophytes increased with their relative
407 abundance in the community. The BNI simulation curve tended to saturate at high
408 neophyte proportions as new neophyte species were less likely to add new trait dif-
409 ferences.

410 In scenario 2 and 4, when neophytes were on average functionally different from the
411 residents, the simulated BNI often showed a humped-shaped curve, with a maximum
412 at intermediate proportions of neophytes (Fig. 3c, g). This pattern is due to the fact
413 that the BNI is based on mean pairwise differences between species, which reaches
414 its maximum when one half (i.e. the neophytes) of the community is different from the
415 other (i.e. the resident species). A similar pattern could be observed for Rao's Q (de-
416 tails provided in supplementary material 2). Beyond this mid-point, the amount of trait
417 variance among the neophytes (SD_{neo}) determined the behavior of the BNI. As illus-
418 trated in scenario 3 and 4 (Fig 3e, g), as long as the trait values of the neophytes
419 were more variable than those of the resident species ($SD_{neo} > SD_{residents}$, with SD_{resi-
420 $dents} = 1$), the BNI increased monotonously with the proportion of neophytes and the
421 amount of variance in neophyte traits. On the other hand, if neophytes had a lower
422 trait variance (i.e. they were more similar amongst themselves) than the residents
423 ($SD_{neo} < SD_{residents}$), then the BNI tended to decrease with the proportion of neo-
424 phytes.

425 These simulations illustrate how the BNI captures the absolute contribution of novel
426 species to functional diversity. As a consequence, communities composed of func-
427 tionally very similar non-natives will tend to have low functional diversity and a low
428 BNI. Interpretation of BNI values must therefore consider the relative abundance (or
429 proportion) of the non-native values in the community.

430 By contrast, the standardized value of the BNI (BNIs) showed no such changes in
431 behavior across scenarios. The BNIs increased monotonously with the proportion of
432 neophytes. The rate of increase was always higher than 1, with steeper curves gen-
433 erated by neophyte traits being different on average from residents (scenarios 2 and
434 4), or with higher variance than residents (scenarios 3 and 4).

435 **Case study 1: Biotic novelty of plant communities along an urbanization gradi-** 436 **ent**

437 The observed BNI values for the 56 Berlin grassland plots ranged from 0.002 to
438 0.092 and had a mean at 0.020 ± 0.016 SD. The plot with the lowest BNI value con-
439 tained 13 species of which 12 were native and 1 was non-native, specifically an ar-
440 chaeophyte species. The plot with the highest BNI value contained 32 species of
441 which 19, 6 and 7 were native, archaeophytes and neophytes, respectively. Statisti-
442 cal analyses of the BNI across the 56 plots indicated that the BNI was positively re-
443 lated to the urbanity indicator sealed surface area (Fig. 4). 15% of the variation in the
444 BNI was explained by the percentage of sealed surfaces around the plots ($P = 0.003$,
445 Fig. 4a). However, there were no significant relationships detectable between the
446 sealed surface area and traditional measures of biotic novelty, i.e. the number of non-
447 native species ($R^2 = 0.01$, $P = 0.443$, Fig. 4b) or their proportion ($R^2 = 0.04$, $P =$
448 0.130 , data not shown). Further, when considering total functional diversity (ex-
449 pressed as Rao's Q), we also identified a positive relationship with the sealed surface
450 area ($R^2 = 0.08$, $P = 0.040$, Fig. 4c), but less strong than the one for the BNI. Finally,
451 we investigated how the BNI varies independently of the variation in Rao's Q by cal-
452 culating the standardized version of the BNI. The standardized BNI (BNIs) showed a
453 similar relationship with the sealed surface area ($R^2 = 0.14$, $P = 0.004$, Fig. 4d) than
454 the non-standardized BNI.

455 We were also interested in how the BNI associates with community parameters such
456 as species richness and functional diversity. The BNI was not related to the total
457 number of species in the plots ($R^2 = 0.05$, $P = 0.103$, Fig. 5a), but showed a moder-
458 ately positive relationship with the number of non-native species ($R^2 = 0.23$, $P <$
459 0.001 , Fig. 5b). On the other hand, the BNI was strongly positively related with the
460 functional diversity (expressed as Rao's Q) of all species ($R^2 = 0.43$, $P < 0.001$, Fig.
461 5c), but weakly positively related to the functional diversity of the group of non-native
462 species ($R^2 = 0.09$, $P = 0.028$, Fig. 5d). The standardized version of the BNI (BNIs)
463 showed almost identical relationships to all four community parameters (Fig. S4.1 in
464 supplementary material S4).

465 **Case study 2: Biotic novelty of co-occurring vascular plant species in Germany**

466 The nationwide assessment of biotic phylogenetic novelty identified large areas with
467 high novelty in Germany, indicated by the distribution map and the slightly right-
468 skewed histogram of the BNI (Fig. 6). The BNI values ranged from 0 (at Zugspitze,
469 the highest mountain in Germany) to 64.18 (in Leipzig, the most populous city in the
470 German federal state of Saxony). Areas of very high novelty were clearly concentrat-
471 ed in and around urban areas: in addition to Leipzig, other areas of high novelty were
472 the cities Cologne (62.72), Bamberg (62.39) and Mülheim an der Ruhr (62.15). The
473 capital and largest city of Germany, Berlin, had the 9th highest BNI (61.06). That the
474 city surroundings also showed a higher extent in biotic novelty may be indicative for a
475 spatial spillover effect from cities to adjacent areas. However, this effect seemed to
476 be less pronounced in southern Germany. Areas of low novelty were visible predomi-
477 nantly in southern and partly in central Germany, presumably due to the ranges of
478 the Alps and the central uplands, respectively, in these regions. The standardized

479 version of the BNI (BNIs) showed an almost identical distribution map (Fig. S4.2 in
480 supplementary material S4).

481 Discussion

482 This study introduced the Biotic Novelty Index (BNI) and demonstrated its applicabil-
483 ity as a framework to measure the ecological novelty of communities at different spa-
484 tial scales. We regard ecological novelty as a continuous gradient ranging from his-
485 toric or analog to novel (Heger *et al.* 2019) rather than a binary classification. Accord-
486 ingly, we have designed the BNI to be able to gradually measure ecological novelty.
487 More specifically, the BNI focuses on the biotic rather than abiotic component of eco-
488 logical novelty (i.e. biotic novelty). It measures the extent of trait differences among
489 novel and non-novel species and, simultaneously, takes temporal dynamics into ac-
490 count. Arithmetically, the BNI represents the expected functional novelty between two
491 randomly picked individuals in the community. Further, we refer to the BNI as a
492 framework because it is built upon the idea of combining two relevant aspects of a
493 research field into one formula, which can be easily adapted to the needs of the user
494 (e.g. by adding or replacing relevant components).

495 **The BNI captures novelty in both functional diversity and introduction history**

496 We designed the BNI to combine two aspects of ecological novelty: historical novelty,
497 captured by the sequence of arrivals of new species in a given region, and functional
498 novelty contributed by the new species (Heger *et al.* 2019). Simulations show that the
499 BNI does capture the latter aspect in a predictable manner: for a given proportion of
500 non-native species, increasing trait differences between species increases the func-
501 tional novelty of the community, and the BNI increases accordingly. However, the
502 behavior of the BNI is not always linear in response to the first aspect, i.e. the propor-
503 tion of non-native species. The BNI may be maximized at intermediate proportions of

504 non-native species, when the most functionally different pairs of species (in our case
505 the resident species vs. the neobiota) are also the most heavily weighted in the cal-
506 culation, both by their relative abundances and by the temporal coefficient. This be-
507 havior of the BNI demonstrates its similarities with Rao's quadratic entropy as a di-
508 versity measure. The following applies to Rao's Q: when a new species is added to a
509 given community and this species is functionally very similar or identical to the resi-
510 dent species, the addition of this new species results in a lower functional diversity of
511 the community. Rao's Q is thus maximized when the most different species in the
512 community are in high abundance. To the BNI, this property translates in the follow-
513 ing manner: when a non-native species is added to a given community and this spe-
514 cies is very similar or identical to the other pre-existing non-natives in the considered
515 traits, the addition of this non-native species may result in a lower BNI for the com-
516 munity. This behavior might be counterintuitive depending on the goal of the study
517 and the user's viewpoint on biotic novelty, which is why we also recommend calculat-
518 ing the standardized BNI values (BNIs).

519 The BNIs offers an additional description of biotic functional novelty of the community
520 by quantifying the proportion of functional diversity (measured as Rao's Q) that is
521 contributed by novel species interactions in the community. The advantage of this
522 standardization is that, by construction, it is monotonous with regard to increasing
523 proportions of non-native species, and the size of trait differences. This standardized
524 version may therefore provide a more objective measure to compare the level of bio-
525 tic novelty between communities with different levels of functional diversity, or as-
526 sembled from a different species pool. Nevertheless, the untransformed value of the
527 BNI remains a valuable measurement when the goal is to quantify the absolute
528 amounts of functional diversity contributed by novel species in a community. Depend-

529 ing on a study's goal, we would recommend to use either of the two or both versions
530 of the index in combination; the latter gives a fuller picture of variation in novelty
531 across communities.

532 **Case studies**

533 Both case studies revealed strong connections of biotic novelty, as measured with
534 the BNI or BNIs, with abiotic novelty. The first study showed that the BNI of 56 dry
535 grassland plant communities in Berlin was positively related to the observed urbanity
536 indicator (i.e. percentage of sealed surfaces). This is not surprising, as previous stud-
537 ies demonstrated that the construction and expansion of towns and cities promote
538 the loss of native species and their replacement by non-native species
539 (Chocholoušková & Pyšek 2003; Standley 2003; DeCandido *et al.* 2004; Tait *et al.*
540 2005; Knapp *et al.* 2010). Further, spatial analyses often show that, for many taxa,
541 increasing intensity of urban activity causes non-native species to increase in abun-
542 dance and species richness while native species decline (McKinney 2001, 2006;
543 Godefroid & Koedam 2007; Kowarik 2008). For example, in rural floras around Berlin,
544 there are less than 20 % non-native plant species, but from the outskirts to the city
545 center of Berlin, the percentage of non-native species increases from about 30 to
546 50 % of all species (Kowarik 2008). The high non-native species richness of urban
547 floras has often been explained by increasing importation of non-native individuals
548 and favorable habitat for the establishment of non-native species (McKinney 2006).
549 However, in the present study system, this relationship between increasing urbanity
550 and non-native species richness was not supported since we found no relationship
551 between the sealed surface area and non-native species richness (nor their propor-
552 tion on total species richness). This finding underlines that the BNI captures different

553 aspects of biotic novelty than the plain number and/or proportion of non-native spe-
554 cies.

555 Our analyses also showed a strong relationship of the BNI with Rao's Q. This was
556 expected, given that the BNI is actually an additive partition of Rao's Q (see supple-
557 mentary material 1 for details). Several recent studies also examined whether inva-
558 sions of non-native species change the structure of native communities by increasing
559 or decreasing functional diversity (Castro-Díez *et al.* 2016; Loiola *et al.* 2018; de la
560 Riva *et al.* 2019). These measures that compare invaded and uninvaded communi-
561 ties functionally and calculate the magnitude of change share a similar basis with the
562 BNI. However, the BNI includes all possible species pairings weighted by the tem-
563 poral coexistence coefficient rather than a comparison of categories (which Castro-
564 Díez *et al.* 2016; Loiola *et al.* 2018 and de la Riva *et al.* 2019 do). These conceptual
565 differences in how biotic novelty is assessed were reflected in the result that the BNI
566 was only weakly positively related to the functional diversity of the group of non-
567 native species (Fig. 5d).

568 Further, by applying the standardization of the BNI (the BNI in proportion to Rao's Q),
569 we showed in the first case study that the BNI was not driven by the inherent varia-
570 tion in functional diversity along the urbanity gradient (since BNI and BNIs varied to a
571 very similar extent along the gradient). As shown in our methods section, this stand-
572 ardization of the BNI can be easily applied by the user for a validation of the BNI re-
573 sults.

574 The second case study demonstrated the applicability of the BNI to nationwide da-
575 taset. The grid-cell map showed that areas of very high novelty of vascular plant
576 species were predominantly concentrated in and around urban areas in Germany,
577 which is partially in line with former nationwide assessments of vascular plants in

578 Germany (Kühn *et al.* 2004) and the UK (Botham *et al.* 2009). These studies de-
579 scribed that neophytes were very strongly associated with urban land cover, but do
580 not appear to be spreading out of urban habitats into the wider countryside. Our find-
581 ing that the BNI is also higher around urban areas might be due to spread of novel
582 species along transportation pathways, such as roads (von der Lippe & Kowarik
583 2008) and rivers (Maskell *et al.* 2006), which connect cities and are located in corre-
584 sponding grid cells in the map.

585 We observed on the grid-cell map that areas of low novelty were visible predominant-
586 ly in southern Germany and partly in central Germany, which coincidences with
587 mountain ranges in Germany. Previous studies also showed that non-native species
588 richness typically declines along elevational gradients (Alexander *et al.* 2011; Seipel
589 *et al.* 2012; Averett *et al.* 2016). This pattern has been explained by two factors: (1)
590 special adaptations are required to invade extreme environments (Alpert *et al.* 2000;
591 Pauchard *et al.* 2009; Alexander *et al.* 2011), making mountains inherently resistant
592 to invasions; and (2) anthropogenic disturbance decreases with increasing elevation,
593 leading to fewer species introductions (i.e. lower propagule pressure) and also higher
594 resistance to invasions (Arévalo *et al.* 2005; Averett *et al.* 2016).

595 We are aware that analyzing a dataset with the extent of our second case study is
596 not free of concerns. For example, the large grid-cell size (11 x 11 km) and the spa-
597 tial autocorrelation of grid cells (Kühn *et al.* 2004) may be problematic sources of er-
598 ror. Sampling bias (i.e. there are more botanical institutes and experts in urbanized
599 areas than in less urbanized areas) and other potential explanatory variables (e.g.
600 geological types of grid cells) may play important roles for such an analysis as well.
601 However, since it is the scope of this paper to demonstrate possible applications of
602 the BNI rather than disentangling various factors that structure biotic novelty, we re-

603 frained to perform complex statistical analysis and chose to present a map without
604 underlying models. Therefore, it is up to future studies to focus on this demanding
605 task.

606 **Conclusions**

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

623

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633

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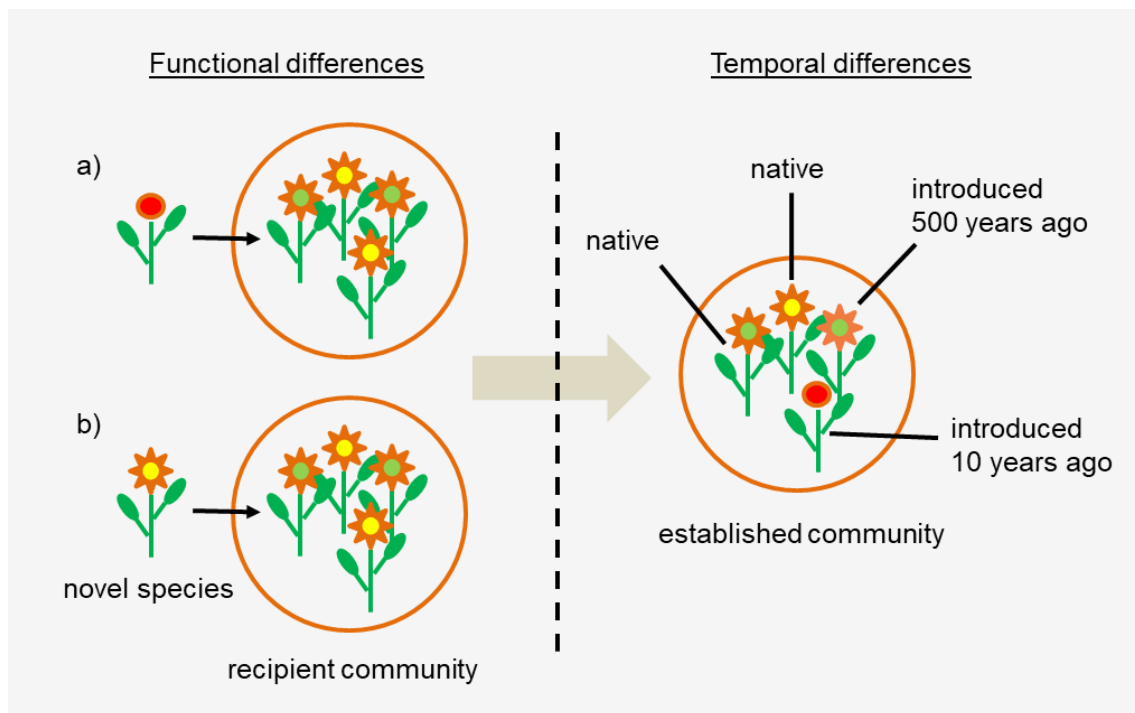
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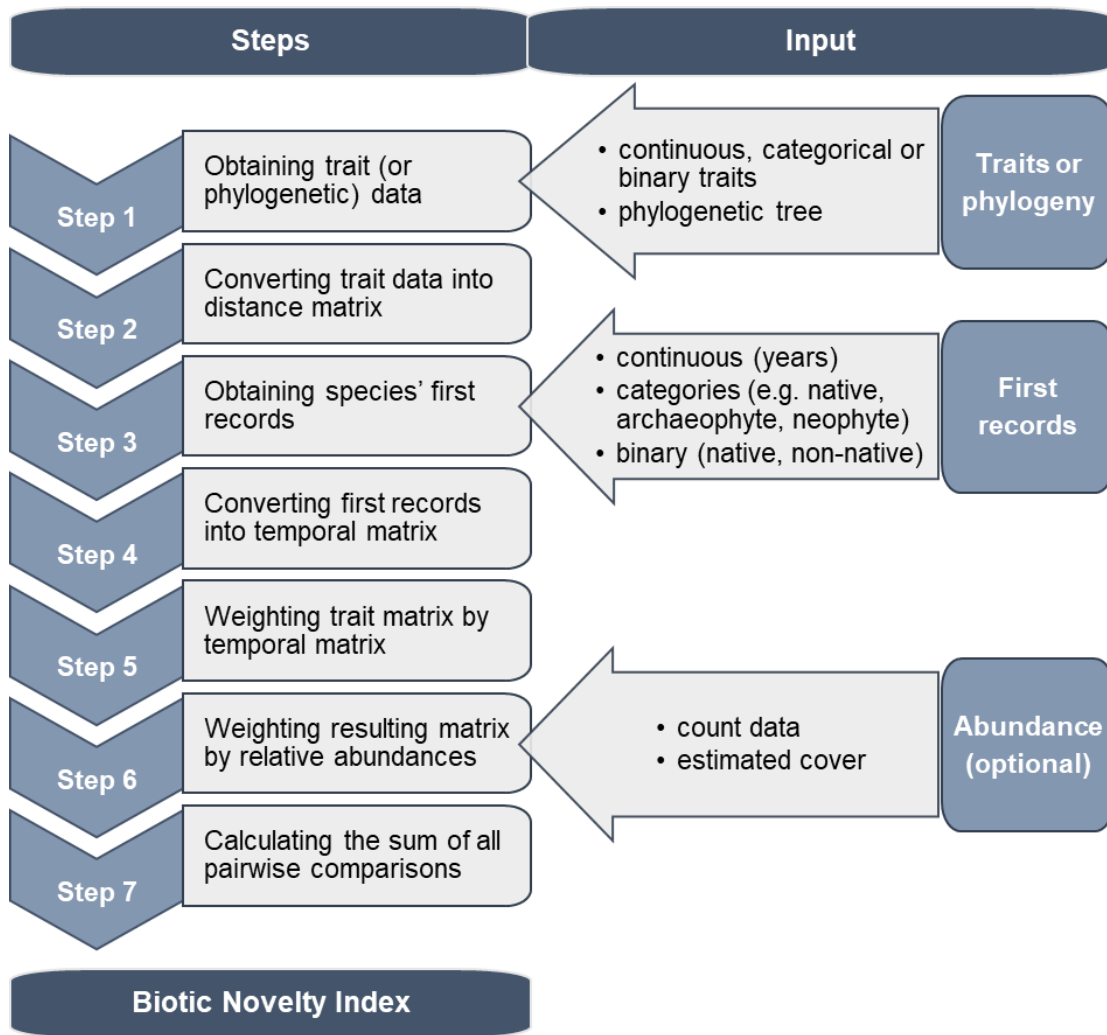
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859 **Figures**



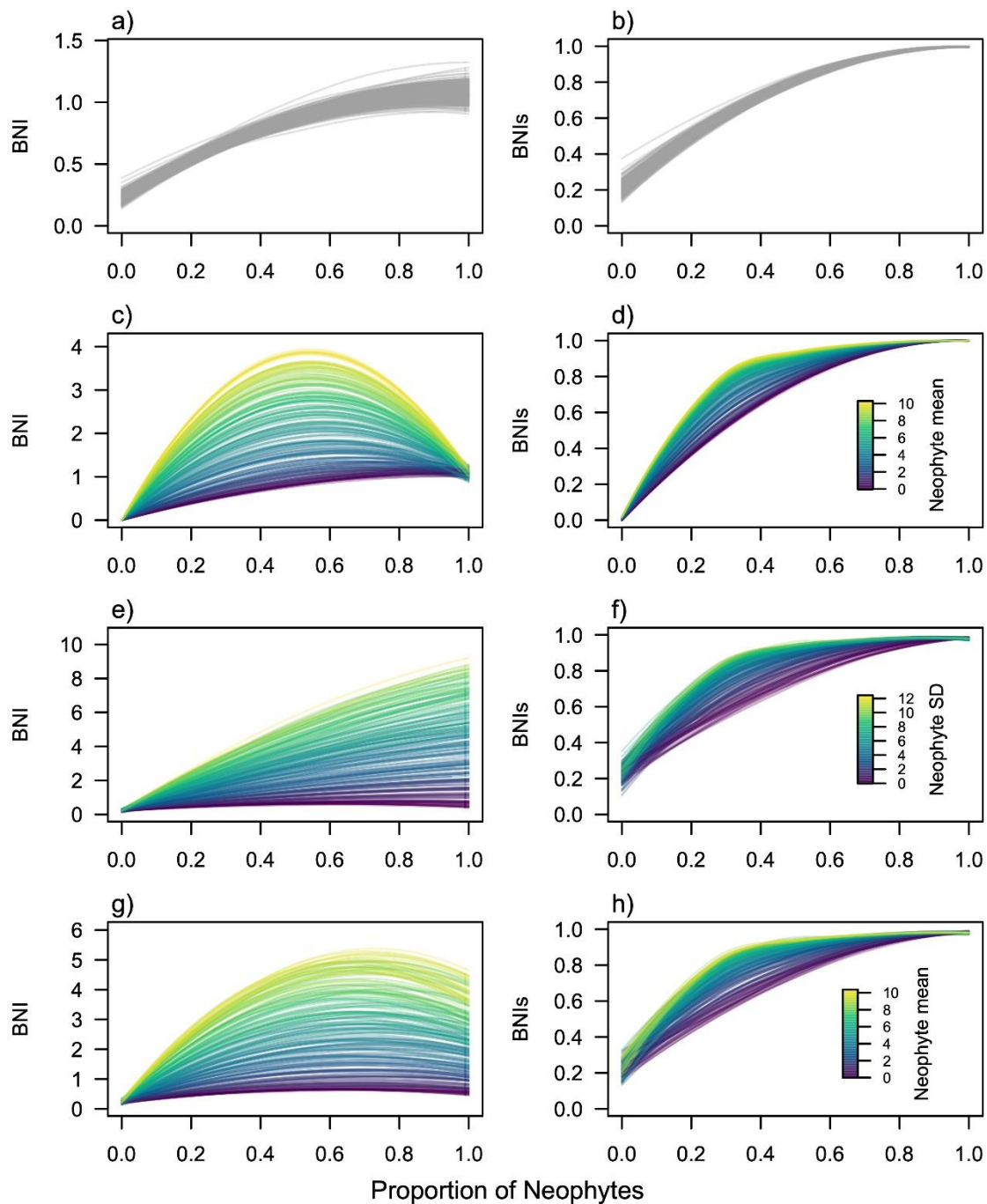
860

861 **Figure 1:** Scheme of two aspects of biotic novelty in a hypothetical plant community that are
862 both captured by the BNI. Left side: A novel species that enters a community of resident
863 species may be functionally different (scenario a) or similar (scenario b) compared to the
864 resident species. Right side: In a given community, there is typically not only one non-
865 resident species, but multiple species that may have arrived at different points in time in the
866 focal region.



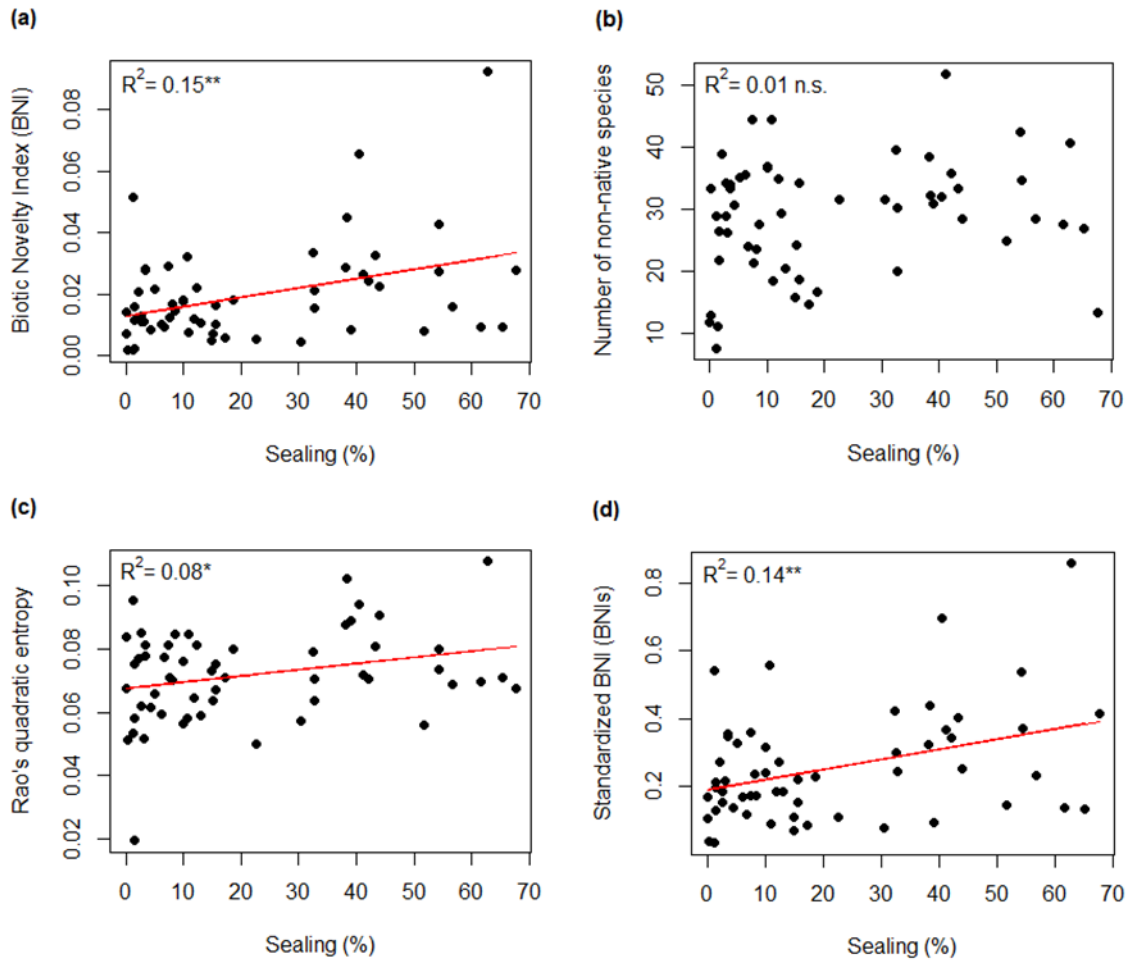
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868 **Figure 2:** Standardized procedure for calculating the biotic novelty of a community with the
869 Biotic Novelty Index (BNI).



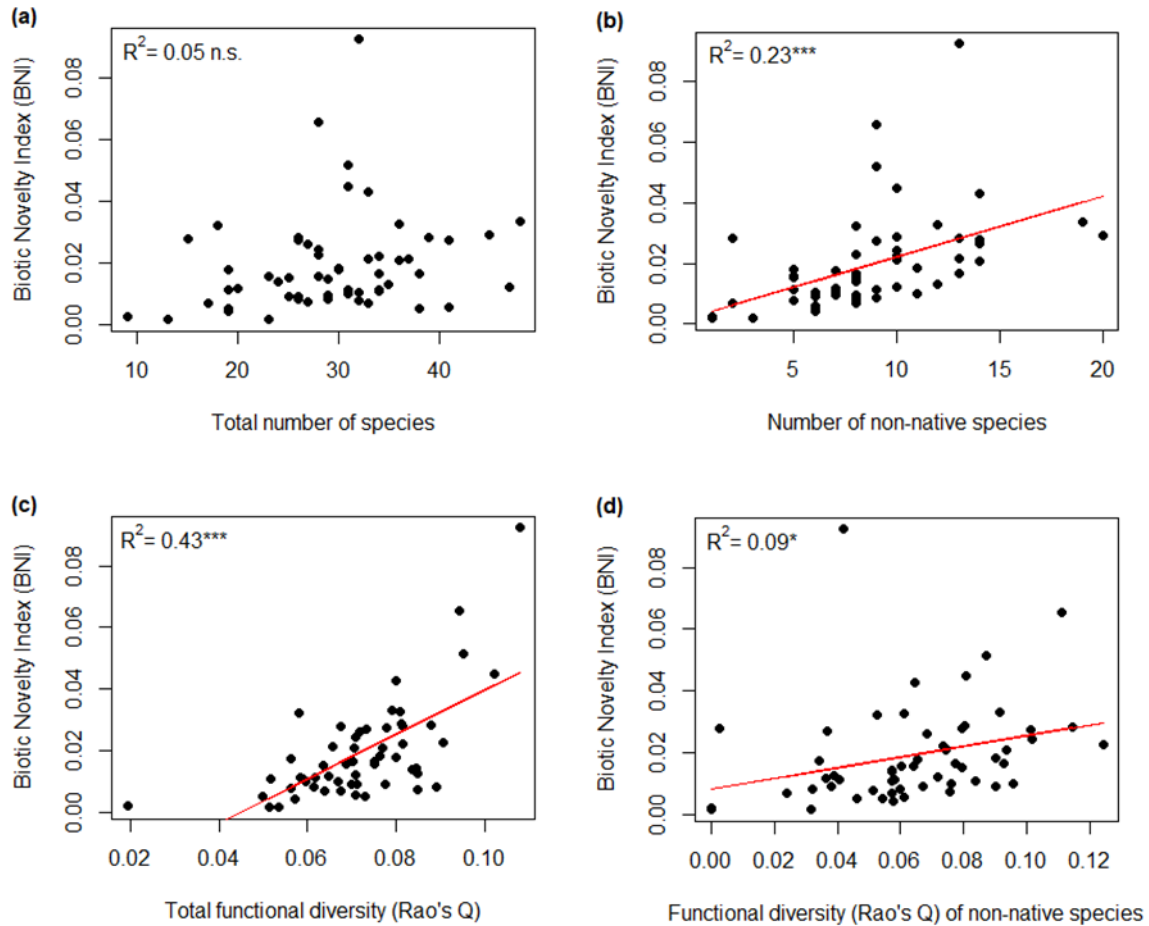
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871 **Figure 3:** Variation of the Biotic Novelty Index (BNI) and its standardized value (BNIs) in four
872 simulation scenarios. Communities were simulated with an increasing proportion of recently
873 introduced non-native plants (neophytes). Scenarios explore different parameters (mean and
874 SD) of the normal distribution from which species traits for neophytes were sampled. In the
875 first scenario (a, b), traits of native and non-native species follow the same normal distribu-
876 tion (trait mean = 0, SD = 1). In scenario 2 (c, d), the mean trait values of neophytes are in-
877 creasingly different from the natives (colors represent variation in neophyte trait mean from 0
878 to 10; SD = 1). In the third scenario (e, f), natives and neophytes have the same trait mean
879 (mean = 0), but neophyte trait SD increases from 0 to 10. In the fourth scenario (g, h), both
880 the mean and SD of neophyte trait distributions increase together from 0 to 10 and 0 to 5,
881 respectively. Lines represent LOESS regressions fitted on the 100 simulated points corre-
882 sponding to one simulation run.



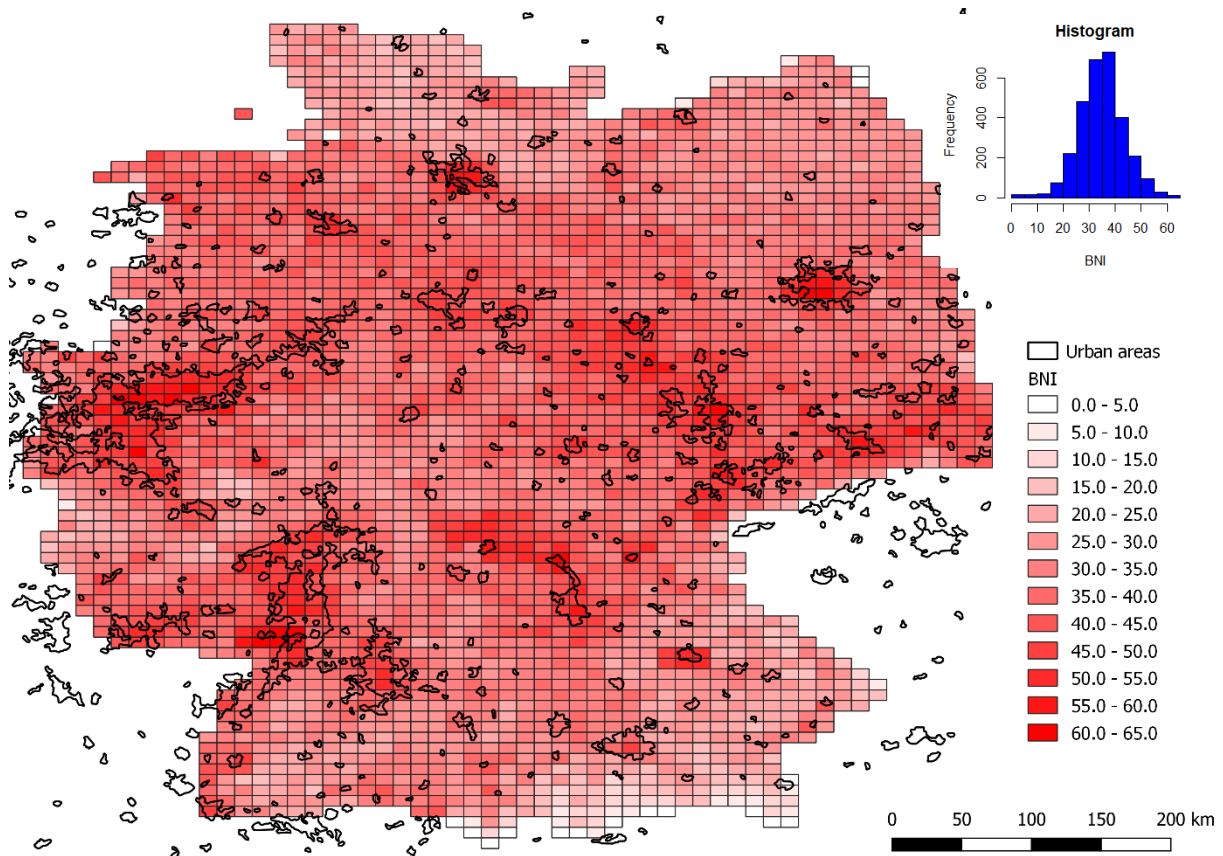
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884 **Figure 4:** Case study 1 – relationships between the percentage of sealed surface area in a
885 500 m buffer zone around the 56 urban grassland plots and (a) the BNI, (b) the number of
886 non-native species, (c) Rao's Q as a measure of functional diversity, and (d) the standard-
887 ized BNI. Asterisks indicate statistical significance using linear models ('***' = $P < 0.001$, '**' =
888 $P < 0.01$, '*' = $P < 0.05$, 'n.s.' = $P \geq 0.05$).



889

890 **Figure 5:** Case study 1 – relationships between the BNI and (a) the total number of species,
891 (b) the number of non-native species, (c) Rao's Q as a measure of functional diversity, and
892 (d) the functional diversity of non-native species in the 56 urban grassland plots. Asterisks
893 indicate statistical significance using linear models (**** = $P < 0.001$, *** = $P < 0.01$, ** = $P <$
894 0.05 , 'n.s.' = $P \geq 0.05$).



895

896 **Figure 6:** Case study 2 – biotic novelty of co-occurring vascular plants in Germany
897 aggregated in 11 x 11 km grid cells calculated with the BNI. Areas outlined in black indicate
898 the extent of urban areas based on MODIS satellite data (Schneider *et al.* 2009).