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

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Running head: A new framework for measuring biotic novelty

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Abstract

26   Anthropogenic changes in climate, land use and disturbance regimes, as well as in-

27   troductions of non-native species can lead to the transformation of many ecosystems.

28   The resulting novel ecosystems are usually characterized by species assemblages

29   that have not occurred previously in a given area. Quantifying the ecological novelty

30   of communities (i.e. biotic novelty) would enhance the understanding of environmen-

31   tal change. However, quantification remains challenging since current novelty met-

32   rics, such as the number and/or proportion of non-native species in a community, fall

33   short of considering both functional and evolutionary aspects of biotic novelty. Here,

34   we propose the Biotic Novelty Index (BNI), an intuitive and flexible multidimensional

35   measure that combines (1) functional differences between native and non-native in-

36   troduced species with (2) temporal dynamics of species introductions. We show that

37   the BNI is an additive partition of Rao's quadratic entropy, capturing the novel inter-

38   action component of the community's functional diversity. Simulations show that the

39   index varies predictably with the relative amount of functional novelty added by re-

40   cently arrived species, and they illustrate the need to provide an additional standard-

41   ized version of the index. We present a detailed R-code and two applications of the

42   BNI by (1) measuring changes of biotic novelty of dry grassland plant communities

43   along an urbanization gradient in a metropolitan region and (2) determining the biotic

44   novelty of plant species assemblages at a national scale. Results illustrate the ap-

45   plicability of the index across scales and its flexibility in the use of data of different

46   quality. Both case studies revealed strong connections between biotic novelty and

47   increasing urbanization, a measure of abiotic novelty. We conclude that the BNI

48   framework may help in building a basis for a better understanding of the ecological

49   and evolutionary consequences of global change.

Introduction

Ecological novelty has received growing attention in the recent literature (e.g. Hobbs *et al.* 2006; Heger *et al.* 2019) focusing on novel organisms (Jeschke *et al.* 2013), novel species interactions (Pearse & Altermatt 2013; Bezemer *et al.* 2014; Carthey & Banks 2014), novel communities (Lurgi *et al.* 2012) or novel ecosystems (Hobbs *et al.* 2009, 2013; Higgs 2017). 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 (Chapin & Starfield 1997; Williams & Jackson 2007; Bogan & Lytle 2011; Correa-Metrio *et al.* 2012), such as a when a reshuffling of species is induced by climate change (Williams & Jackson 2007) – and vice versa when introduced species, for example, strongly affect the nutrient cycling (Vilà *et al.* 2011; Jäger *et al.* 2013). 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).

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

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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.

Methods

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:

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

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

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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-

204   senckenberg.de/database/metacat/bikf.10029/bikf), regional databases (e.g. the Bi-

205   olFlor 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
$$r_i' = \frac{r_i - r_{min}}{r_{max} - r_{min}}$$

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

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

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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.

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
$$BNIs = \frac{BNI}{RaoQ}$$

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

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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.

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-

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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.

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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. This vegetation type spans a range of near-natural to strongly human-shaped sites throughout the city. For this reason, urban dry grasslands have been selected as a model ecosystem within the CityScapeLabs, an experimental platform with a network of 56 permanent plots, established for the evaluation of biodiversity in urban environments. From April 18th to May 19th 2017, vegetation surveys were carried out in a 4 x 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 twelve 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 (e.g. 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, 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

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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 BiolFlor (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.

Results

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)

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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.

17

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).

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.

18

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

19

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

480   supplementary material S4).

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).

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-

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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 tasets. 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

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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-

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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.

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.

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References

635 Alexander, J.M., Kueffer, C., Daehler, C.C., Edwards, P.J., Pauchard, A., Seipel, T.,

636 *et al.* (2011). Assembly of nonnative floras along elevational gradients explained

637 by directional ecological filtering. *Proc. Natl. Acad. Sci.*, 108, 656–661.

638 Alpert, P., Bone, E. & Holzapfel, C. (2000). Invasiveness, invasibility and the role of

639 environmental stress in the spread of non-native plants. *Perspect. Plant Ecol.*

640 *Evol. Syst.*, 3, 52–66.

641 Arévalo, J.R., Delgado, J.D., Otto, R., Naranjo, A., Salas, M. & Fernández-Palacios,

642 J.M. (2005). Distribution of alien vs. native plant species in roadside communities

643 along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands).

644 *Perspect. Plant Ecol. Evol. Syst.*, 7, 185–202.

645 Averett, J.P., McCune, B., Parks, C.G., Naylor, B.J., DelCurto, T. & Mata-González,

646 R. (2016). Non-native plant invasion along elevation and canopy closure

647 gradients in a middle rocky mountain ecosystem. *PLoS One*, 11, e0147826.

648 Baselga, A. (2010). Partitioning the turnover and nestedness components of beta

649 diversity. *Glob. Ecol. Biogeogr.*, 19, 134–143.

650   Bezemer, T.M., Harvey, J.A. & Cronin, J.T. (2014). Response of Native Insect

651   Communities to Invasive Plants. *Annu. Rev. Entomol.*, 59, 119–141.

652   Bogan, M.T. & Lytle, D.A. (2011). Severe drought drives novel community trajectories

653   in desert stream pools. *Freshw. Biol.*, 56, 2070–2081.

654   Botham, M.S., Rothery, P., Hulme, P.E., Hill, M.O., Preston, C.D. & Roy, D.B. (2009).

655   Do urban areas act as foci for the spread of alien plant species? An assessment

656   of temporal trends in the UK. *Divers. Distrib.*, 15, 338–345.

657   Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity

658   based on multiple traits. *J. Veg. Sci.*, 16, 533–540.

659   Bundesamt für Naturschutz / Netzwerk Phytodiversität Deutschland. (2018). Flora

660   von Deutschland (Phanerogamen).

661   Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009). Using

662   phylogenetic, functional and trait diversity to understand patterns of plant

663   community productivity. *PLoS One*, 4, e5695.

664   Carthey, A.J.R. & Banks, P.B. (2012). When Does an Alien Become a Native

665   Species? A Vulnerable Native Mammal Recognizes and Responds to Its Long-

666   Term Alien Predator. *PLoS One*, 7, e31804.

667   Carthey, A.J.R. & Banks, P.B. (2014). Naïveté in novel ecological interactions:

668   Lessons from theory and experimental evidence. *Biol. Rev.*, 89, 932–949.

669   Castro-Díez, P., Pauchard, A., Traveset, A. & Vilà, M. (2016). Linking the impacts of

670   plant invasion on community functional structure and ecosystem properties. *J.*

671   *Veg. Sci.*, 27, 1233–1242.

672   Catford, J.A., Vesk, P.A., Richardson, D.M. & Pyšek, P. (2012). Quantifying levels of

673   biological invasion: towards the objective classification of invaded and invasible

674   ecosystems. *Glob. Chang. Biol.*, 18, 44–62.

675   Chapin, F.S. & Starfield, A.M. (1997). Time lags and novel ecosystems in response

676   to transient climatic change in arctic Alaska. *Clim. Change*, 35, 449–461.

677   Chocholoušková, Z. & Pyšek, P. (2003). Changes in composition and structure of

678   urban flora over 120 years: a case study of the city of Plzeň. *Flora - Morphol.*

679   *Distrib. Funct. Ecol. Plants*, 198, 366–376.

680   Correa-Metrio, A., Bush, M.B., Cabrera, K.R., Sully, S., Brenner, M., Hodell, D.A., *et*

681   *al.* (2012). Rapid climate change and no-analog vegetation in lowland Central

682   America during the last 86,000 years. *Quat. Sci. Rev.*, 38, 63–75.

683   DeCandido, R., Muir, A.A. & Gargiullo, M.B. (2004). A First Approximation of the

684   Historical and Extant Vascular Flora of New York City: Implications for Native

685   Plant Species Conservation. *J. Torrey Bot. Soc.*, 131, 243–251.

686   Durka, W. & Michalski, S.G. (2012). Daphne: a dated phylogeny of a large European

687   flora for phylogenetically informed ecological analyses. *Ecology*, 93, 2297–2297.

688   Emerson, B.C. & Gillespie, R.G. (2008). Phylogenetic analysis of community

689   assembly and structure over space and time. *Trends Ecol. Evol.*, 23, 619–630.

690   Essl, F., Dullinger, S., Genovesi, P., Hulme, P.E., Jeschke, J.M., Katsanevakis, S., *et*

691   *al.* (2019). A Conceptual Framework for Range-Expanding Species that Track

692   Human-Induced Environmental Change. *Bioscience*.

693   Garcia, R.A., Cabeza, M., Rahbek, C. & Araújo, M.B. (2014). Multiple dimensions of

694   climate change and their implications for biodiversity. *Science*, 344, 1247579.

695   Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., *et al.*

696   (2004). Plant functional markers capture ecosystem properties during secondary

697   succession. *Ecology*, 85, 2630–2637.

698   GBIF: The Global Biodiversity Information Facility. (2019). *What is GBIF?* Available

699   at: https://www.gbif.org/what-is-gbif. Last accessed 26 August 2019.

700   Gerhold, P., Cahill, J.F., Winter, M., Bartish, I. V. & Prinzing, A. (2015). Phylogenetic

701   patterns are not proxies of community assembly mechanisms (they are far

702   better). *Funct. Ecol.*, 29, 600–614.

703   Godefroid, S. & Koedam, N. (2007). Urban plant species patterns are highly driven by

704   density and function of built-up areas. *Landsc. Ecol.*, 22, 1227–1239.

705   Gower, J.C. (1971). A General Coefficient of Similarity and Some of Its Properties.

706   *Biometrics*, 27, 857–871.

707   Haas, J.N., Giesecke, T. & Karg, S. (2003). Die mitteleuropäische

708   Subsistenzwirtschaft des 3. bis 2. Jahrtausends v.Chr. aus paläoökologischer

709   Sicht. *J. Neolit. Archaeol.*, 5, 1–8.

710   Heger, T., Bernard-Verdier, M., Gessler, A., Greenwood, A.D., Grossart, H.-P.,

711   Hilker, M., *et al.* (2019). Towards an Integrative, Eco-Evolutionary Understanding

712   of Ecological Novelty: Studying and Communicating Interlinked Effects of Global

713   Change. *Bioscience.*

714   Helm, A., Zobel, M., Moles, A.T., Szava-Kovats, R. & Pärtel, M. (2015). Characteristic

715   and derived diversity: Implementing the species pool concept to quantify

716   conservation condition of habitats. *Divers. Distrib.*, 21, 711–721.

717   Helmus, M.R., Bland, T.J., Williams, C.K. & Ives, A.R. (2007). Phylogenetic

29

718   measures of biodiversity. *Am. Nat.*, 169, E68–83.

719   Higgs, E. (2017). Novel and designed ecosystems. *Restor. Ecol.*, 25, 8–13.

720   Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., *et al.*

721   (2006). Novel ecosystems: theoretical and management aspects of the new

722   ecological world order. *Glob. Ecol. Biogeogr.*, 15, 1–7.

723   Hobbs, R.J., Higgs, E. & Harris, J.A. (2009). Novel ecosystems: implications for

724   conservation and restoration. *Trends Ecol. Evol.*, 24, 599–605.

725   Hobbs, R.J., Higgs, E.S. & Hall, C.M. (2013). Introduction: Why Novel Ecosystems?

726   In: *Novel Ecosystems* (eds. Hobbs, R.J., Higgs, E.S. & Hall, C.M.). John Wiley &

727   Sons, Ltd, Chichester, UK, pp. 1–8.

728   Hulme, P.E. & Bernard-Verdier, M. (2018). Comparing traits of native and alien

729   plants: Can we do better? *Funct. Ecol.*, 32, 117–125.

730   Jäger, H., Alencastro, M.J., Kaupenjohann, M. & Kowarik, I. (2013). Ecosystem

731   changes in Galápagos highlands by the invasive tree *Cinchona pubescens*.

732   *Plant Soil*, 371, 629–640.

733   Jeschke, J.M., Keesing, F. & Ostfeld, R.S. (2013). Novel organisms: Comparing

734   invasive species, GMOs, and emerging pathogens. *Ambio*, 42, 541–548.

735   Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., *et al.* (2011).

736   TRY - a global database of plant traits. *Glob. Chang. Biol.*, 17, 2905–2935.

737   Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly,

738   D.D., *et al.* (2010). Picante: R tools for integrating phylogenies and ecology.

739   *Bioinformatics*, 26, 1463–1464.

740 Klotz, S., Kühn, I. & Durka, W. (2002). *BIOLFLOR – Eine Datenbank zu biologisch-*

741 *ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenr. für Veg.*

742 BfN-Schriftenvertrieb im Landwirtschaftsverl., Hiltrup, Münster, Bonn-Bad

743 Godesberg (Germany).

744 Knapp, S., Kühn, I., Stolle, J. & Klotz, S. (2010). Changes in the functional

745 composition of a Central European urban flora over three centuries. *Perspect.*

746 *Plant Ecol. Evol. Syst.*, 12, 235–244.

747 Korell, L., Schmidt, R., Bruelheide, H., Hensen, I. & Auge, H. (2016). Mechanisms

748 driving diversity–productivity relationships differ between exotic and native

749 communities and are affected by gastropod herbivory. *Oecologia*, 180, 1025–

750 1036.

751 Kowarik, I. (2008). On the role of alien species in urban flora and vegetation. In:

752 *Urban Ecology: An International Perspective on the Interaction Between Humans*

753 *and Nature* (eds. Marzluff, J.M., Shulenberger, E., Endlicher, W., Alberti, M.,

754 Bradley, G., Ryan, C., et al.). Springer US, New York, pp. 321–338.

755 Kühn, I., Brandl, R. & Klotz, S. (2004). The flora of German cities is naturally species

756 rich. *Evol. Ecol. Res.*, 6, 749–764.

757 de la Riva, E.G., Godoy, O., Castro-Díez, P., Gutiérrez-Cánovas, C. & Vilà, M.

758 (2019). Functional and phylogenetic consequences of plant invasion for coastal

759 native communities. *J. Veg. Sci.*, 30, 510–520.

760 Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring

761 functional diversity from multiple traits. *Ecology*, 91, 299–305.

762 von der Lippe, M. & Kowarik, I. (2008). Do cities export biodiversity? Traffic as

763   dispersal vector across urban-rural gradients. *Divers. Distrib.*, 14, 18–25.

764   Loiola, P.P., de Bello, F., Chytrý, M., Götzenberger, L., Carmona, C.P., Pyšek, P., *et*

765   *al.* (2018). Invaders among locals: Alien species decrease phylogenetic and

766   functional diversity while increasing dissimilarity among native community

767   members. *J. Ecol.*, 106, 2230–2241.

768   Lu, D. & Weng, Q. (2006). Use of impervious surface in urban land-use classification.

769   *Remote Sens. Environ.*, 102, 146–160.

770   Lurgi, M., López, B.C. & Montoya, J.M. (2012). Novel communities from climate

771   change. *Philos. Trans. R. Soc. B Biol. Sci.*, 367, 2913–2922.

772   Maskell, L.C., Bullock, J.M., Smart, S.M., Thompson, K. & Hulme, P.E. (2006). The

773   distribution and habitat associations of non- native plant species in urban

774   riparian habitats. *J. Veg. Sci.*, 17, 499–508.

775   Mason, N.W.H. & Pavoine, S. (2013). Does trait conservatism guarantee that

776   indicators of phylogenetic community structure will reveal niche-based assembly

777   processes along stress gradients? *J. Veg. Sci.*, 24, 820–833.

778   McKinney, M.L. (2001). Effects of human population, area, and time on non-native

779   plant and fish diversity in the United States. *Biol. Conserv.*, 100, 243–252.

780   McKinney, M.L. (2006). Urbanization as a major cause of biotic homogenization. *Biol.*

781   *Conserv.*, 127, 247–260.

782   Mora, C., Frazier, A.G., Longman, R.J., Dacks, R.S., Walton, M.M., Tong, E.J., *et al.*

783   (2013). The projected timing of climate departure from recent variability. *Nature*,

784   502, 183–187.

785   Parker, J.D., Burkepile, D.E. & Hayt, M.E. (2006). Opposing effects of native and

786   exotic herbivores on plant invasions. *Science*, 311, 1459–1461.

787   Pauchard, A., Kueffer, C., Dietz, H., Daehler, C.C., Alexander, J., Edwards, P.J., *et*

788   *al.* (2009). Ain't no mountain high enough: plant invasions reaching new

789   elevations. *Front. Ecol. Environ.*, 7, 479–486.

790   Pearse, I.S. & Altermatt, F. (2013). Predicting novel trophic interactions in a non-

791   native world. *Ecol. Lett.*, 16, 1088–1094.

792   Poos, M.S., Walker, S.C. & Jackson, D.A. (2009). Functional-diversity indices can be

793   driven by methodological choices and species richness. *Ecology*, 90, 341–347.

794   QGIS Development Team. (2016). QGIS Geographic Information System. Open

795   Source Geospatial Foundation Project.

796   QGIS Development Team. (2018). QGIS Geographic Information System. Open

797   Source Geospatial Foundation Project.

798   Qian, H. & Ricklefs, R.E. (2006). The role of exotic species in homogenizing the north

799   American flora. *Ecol. Lett.*, 9, 1293–1298.

800   R Core Team. (2017). R: A language and environment for statistical computing.

801   R Core Team. (2019). R: A language and environment for statistical computing.

802   Radeloff, V.C., Williams, J.W., Bateman, B.L., Burke, K.D., Carter, S.K., Childress,

803   E.S., *et al.* (2015). The rise of novelty in ecosystems. *Ecol. Appl.*, 25, 2051–

804   2068.

805   Rao, C.R. (1982). Diversity and dissimilarity coefficients: A unified approach. *Theor.*

806   *Popul. Biol.*, 21, 24–43.

807 Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B.E.L. & Pavoine, S.

808   (2016). Measuring the functional redundancy of biological communities: a

809   quantitative guide. *Methods Ecol. Evol.*, 7, 1386–1395.

810 Saul, W.-C. & Jeschke, J.M. (2015). Eco-evolutionary experience in novel species

811   interactions. *Ecol. Lett.*, 18, 236–245.

812 Saul, W.-C., Jeschke, J.M. & Heger, T. (2013). The role of eco-evolutionary

813   experience in invasion success. *NeoBiota*, 17, 57–74.

814 Schleuter, D., Daufresne, M., Massol, F. & Argillier, C. (2010). A user's guide to

815   functional diversity indices. *Ecol. Monogr.*, 80, 469–484.

816 Schneider, A., Friedl, M.A. & Potere, D. (2009). A new map of global urban extent

817   from MODIS satellite data. *Environ. Res. Lett.*, 4, 044003.

818 Schroeder, F.G. (1968). Zur Klassifizierung der Anthropochoren. *Veg. Acta Geobot.*,

819   16, 225–238.

820 Schwarz, N. (2010). Urban form revisited-Selecting indicators for characterising

821   European cities. *Landsc. Urban Plan.*, 96, 29–47.

822 Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M.,

823   *et al.* (2017). No saturation in the accumulation of alien species worldwide. *Nat.*

824   *Commun.*, 8, 14435.

825 Seipel, T., Kueffer, C., Rew, L.J., Daehler, C.C., Pauchard, A., Naylor, B.J., *et al.*

826   (2012). Processes at multiple scales affect richness and similarity of non-native

827   plant species in mountains around the world. *Glob. Ecol. Biogeogr.*, 21, 236–

828   246.

829   Seitz, B., Ristow, M., Prasse, R., Machatzi, B., Klemm, G., Böcker, R., *et al.* (2012).

830   Der Berliner Florenatlas. *Verh. Bot. Ver. Berlin Brandenburg*, 7, 1–533.

831   Shimadzu, H., Dornelas, M. & Magurran, A.E. (2015). Measuring temporal turnover in

832   ecological communities. *Methods Ecol. Evol.*, 6, 1384–1394.

833   Standley, L.A. (2003). Flora of Needham, Massachusetts - 100 Years of floristic

834   change. *Rhodora*, 105, 354–378.

835   Strauss, S.Y., Lau, J.A. & Carroll, S.P. (2006). Evolutionary responses of natives to

836   introduced species: what do introductions tell us about natural communities?

837   *Ecol. Lett.*, 9, 357–374.

838   Tait, C.J., Daniels, C.B. & Hill, R.S. (2005). Changes in species assemblages within

839   the Adelaide metropolitan area, Australia, 1836-2002. *Ecol. Appl.*, 15, 346–359.

840   Verhoeven, K.J.F., Biere, A., Harvey, J.A. & van der Putten, W.H. (2009). Plant

841   invaders and their novel natural enemies: who is naïve? *Ecol. Lett.*, 12, 107–

842   117.

843   Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., *et al.* (2011).

844   Ecological impacts of invasive alien plants: a meta-analysis of their effects on

845   species, communities and ecosystems. *Ecol. Lett.*, 14, 702–8.

846   Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002). Phylogenies and

847   community ecology. *Annu. Rev. Ecol. Syst.*, 33, 475–505.

848   Williams, J.W. & Jackson, S.T. (2007). Novel climates, no-analog communities, and

849   ecological surprises. *Front. Ecol. Environ.*, 5, 475–482.

850   Williams, J.W., Jackson, S.T. & Kutzbach, J.E. (2007). Projected distributions of

851   novel and disappearing climates by 2100 AD. *Proc. Natl. Acad. Sci.*, 104, 5738–

852   5742.

853   Wilsey, B.J., Teaschner, T.B., Daneshgar, P.P., Isbell, F.I. & Polley, H.W. (2009).

854   Biodiversity maintenance mechanisms differ between native and novel exotic-

855   dominated communities. *Ecol. Lett.*, 12, 432–442.

856   Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., *et al.*

857   (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.

858
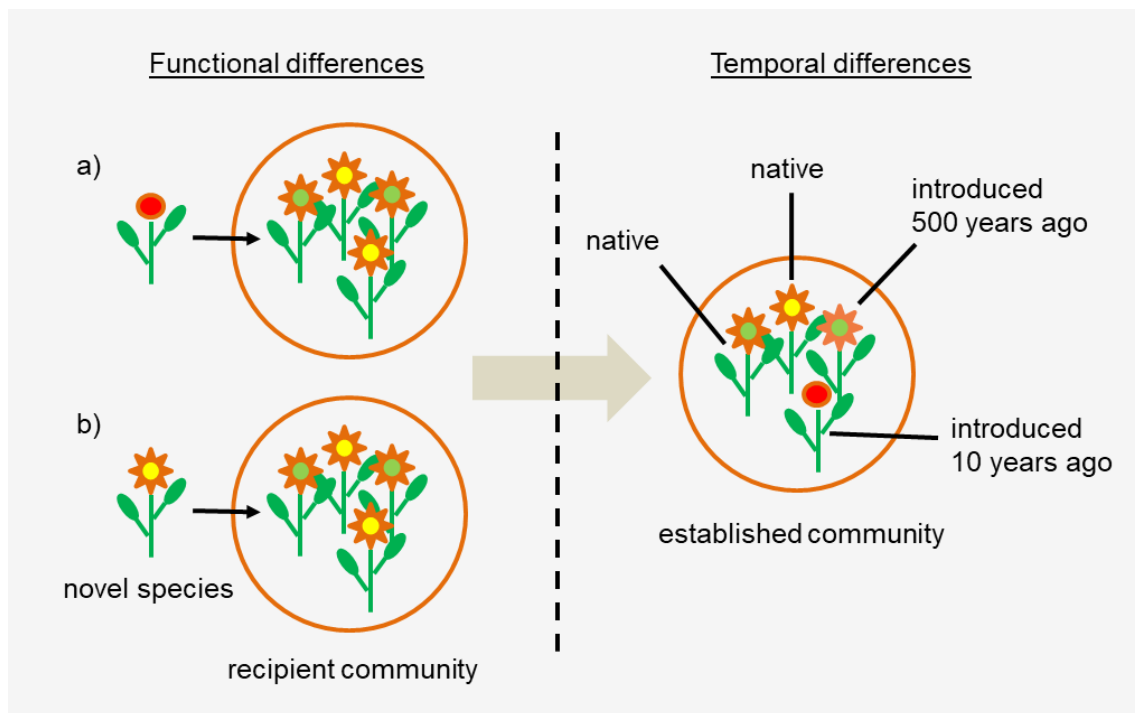
Figures

Figure 1: Scheme of two aspects of biotic novelty in a hypothetical plant community that are both captured by the BNI. Left side: A novel species that enters a community of resident species may be functionally different (scenario a) or similar (scenario b) compared to the resident species. Right side: In a given community, there is typically not only one non-resident species, but multiple species that may have arrived at different points in time in the focal region.
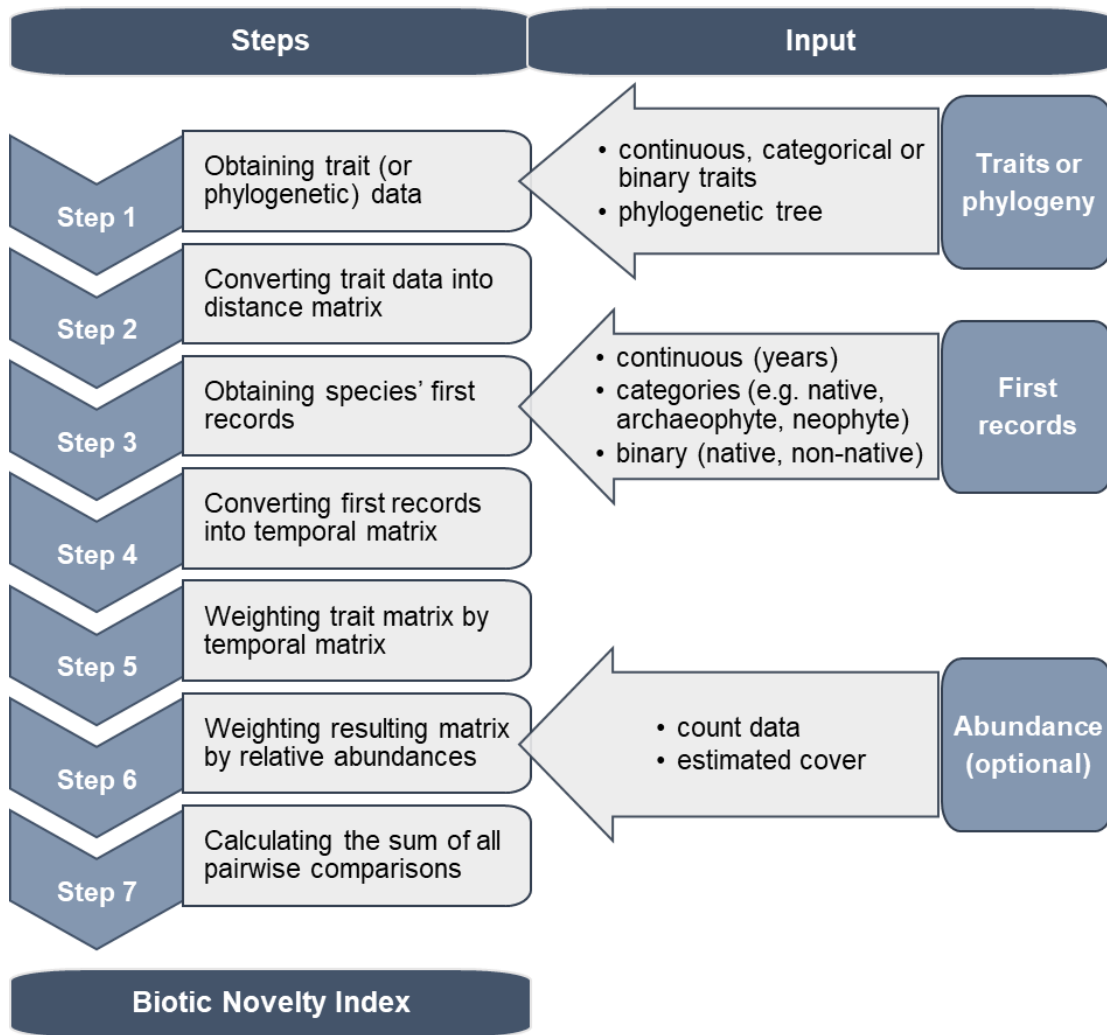
Figure 2: Standardized procedure for calculating the biotic novelty of a community with the Biotic Novelty Index (BNI).

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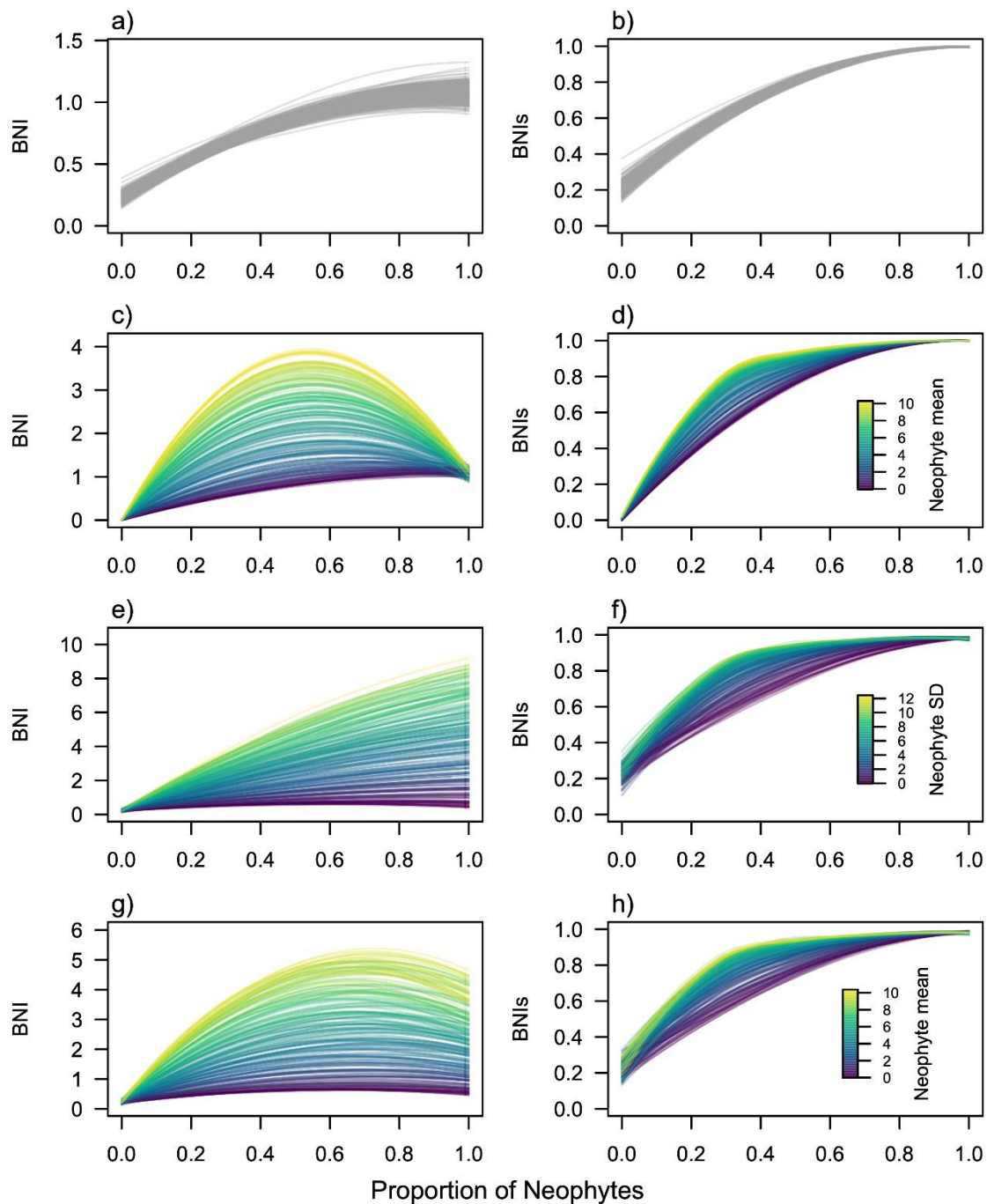
Figure 3: Variation of the Biotic Novelty Index (BNI) and its standardized value (BNIs) in four simulation scenarios. Communities were simulated with an increasing proportion of recently introduced non-native plants (neophytes). Scenarios explore different parameters (mean and SD) of the normal distribution from which species traits for neophytes were sampled. In the first scenario (a, b), traits of native and non-native species follow the same normal distribution (trait mean = 0, SD = 1). In scenario 2 (c, d), the mean trait values of neophytes are increasingly different from the natives (colors represent variation in neophyte trait mean from 0 to 10; SD = 1). In the third scenario (e, f), natives and neophytes have the same trait mean (mean = 0), but neophyte trait SD increases from 0 to 10. In the fourth scenario (g, h), both the mean and SD of neophyte trait distributions increase together from 0 to 10 and 0 to 5, respectively. Lines represent LOESS regressions fitted on the 100 simulated points corresponding to one simulation run.
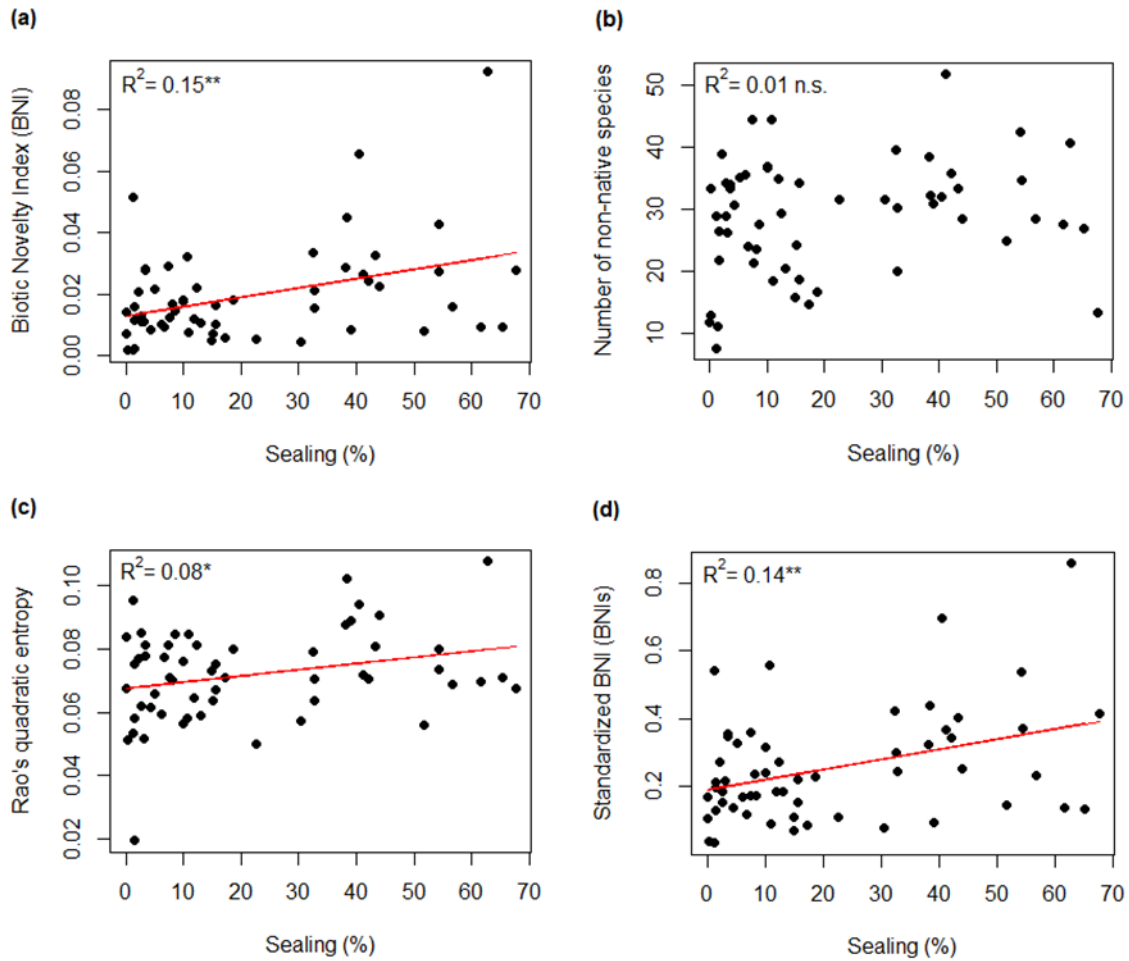
Figure 4: Case study 1 – relationships between the percentage of sealed surface area in a 500 m buffer zone around the 56 urban grassland plots and (a) the BNI, (b) the number of non-native species, (c) Rao's Q as a measure of functional diversity, and (d) the standardized BNI. Asterisks indicate statistical significance using linear models ('***' = $P < 0.001$, '**' = $P < 0.01$, '*' = $P < 0.05$, 'n.s.' = $P \geq 0.05$).
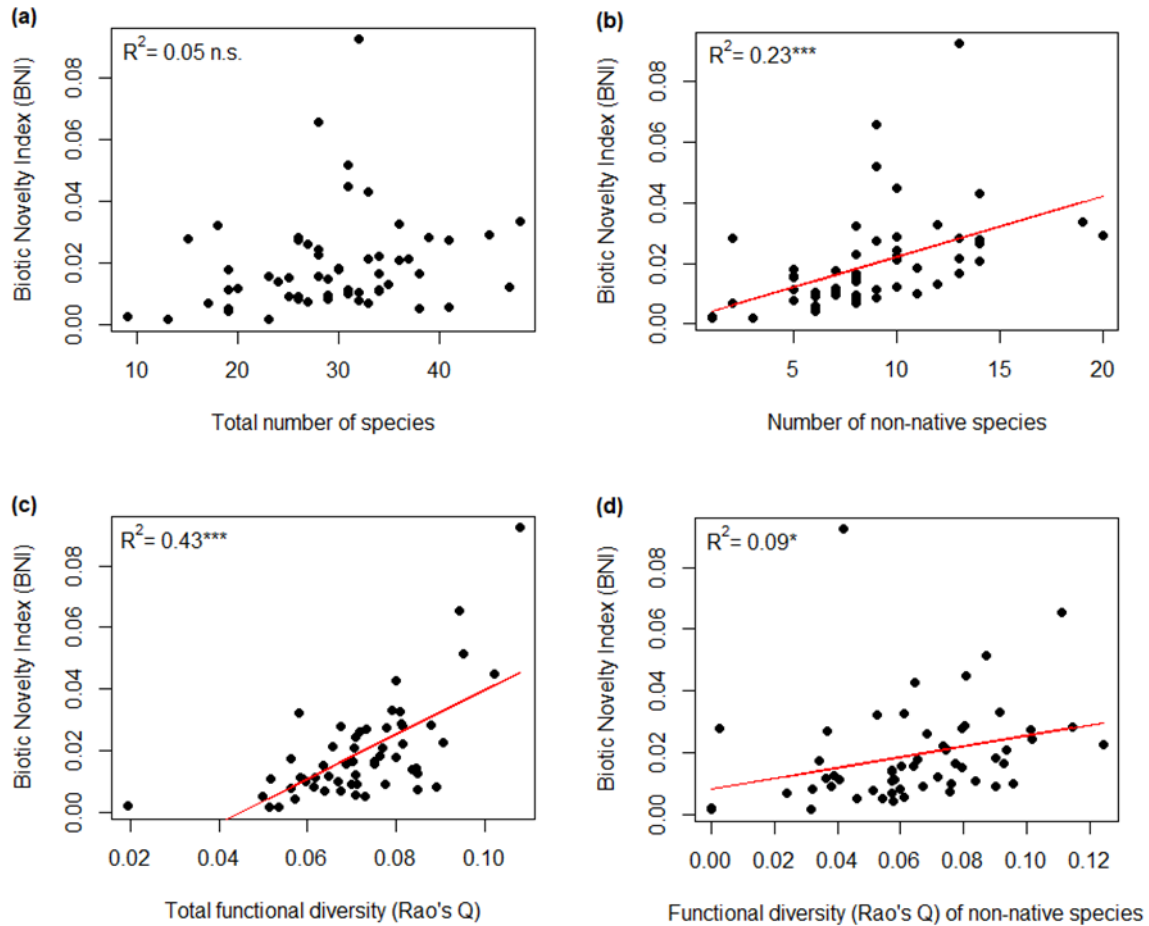
Figure 5: Case study 1 – relationships between the BNI and (a) the total number of species, (b) the number of non-native species, (c) Rao's Q as a measure of functional diversity, and (d) the functional diversity of non-native species in the 56 urban grassland plots. Asterisks indicate statistical significance using linear models ('***' = $P < 0.001$, '**' = $P < 0.01$, '*' = $P < 0.05$, 'n.s.' = $P \geq 0.05$).
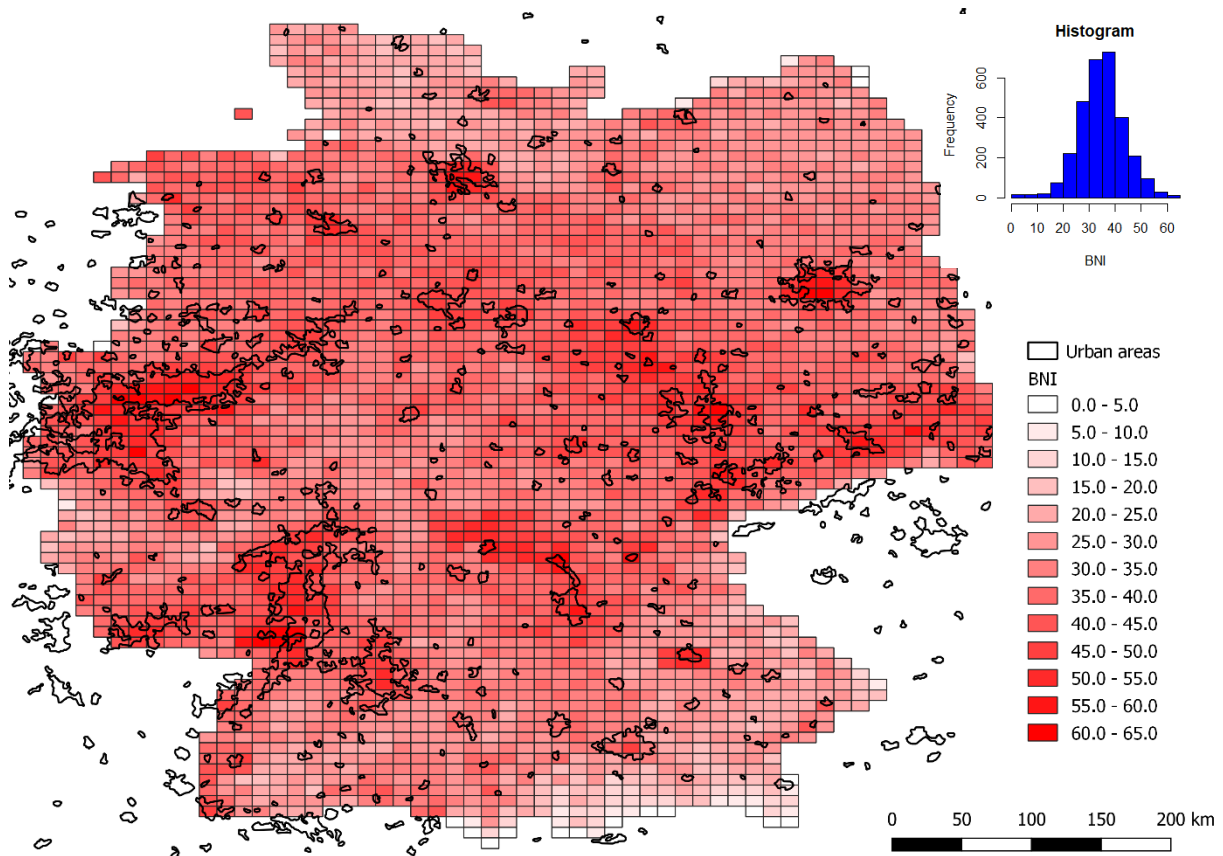
Figure 6: Case study 2 – biotic novelty of co-occurring vascular plants in Germany aggregated in 11 x 11 km grid cells calculated with the BNI. Areas outlined in black indicate the extent of urban areas based on MODIS satellite data (Schneider *et al.* 2009).