Drivers of species turnover vary with species commonness for native and alien plants with different residence times

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Abstract. Communities comprising alien species with different residence times are natural experiments allowing the assessment of drivers of community assembly over time. Stochastic processes (such as dispersal and fluctuating environments) should be the dominant factors structuring communities of exotic species with short residence times. In contrast, communities should become more similar, or systematically diverge, if they contain exotics with increasing resident times, due to the increasing importance of deterministic processes (such as environmental filtering). We use zeta diversity (the number of species shared by multiple assemblages) to explore the relationship between the turnover of native species and two categories of alien species with different residence times (archaeophytes [introduced between 4000 BC and 1500 AD] and neophytes [introduced after 1500 AD]) in a network of nature reserves in central Europe. By considering multiple assemblages simultaneously, zeta diversity allows us to determine the contribution of rare and widespread species to turnover. Specifically, we explore the relative effects of assembly processes representing isolation by distance, environmental filtering, and environmental stochasticity (fluctuating environments) on zeta diversity using Multi-Site Generalized Dissimilarity Modelling (MS-GDM). Four clusters of results emerged. First, stochastic processes for structuring plant assemblages decreased in importance with increasing residence time. Environmental stochasticity only affected species composition for neophytes, offering possibilities to predict the spread debt of recent invasions. Second, native species turnover was well explained by environmental filtering and isolation by distance, although these factors did not explain the turnover of archaeophytes and neophytes. Third, native and alien species compositions were only correlated for rare species, whereas turnover in widespread alien species was surprisingly unrelated to the composition of widespread native species. Site-specific approaches would therefore be more appropriate for the monitoring and management of rare alien species, whereas species-specific approaches would suit widespread species. Finally, the size difference of nature reserves influences not only native species richness, but also their richness-independent turnover. A network of reserves must therefore be designed and managed using a variety of approaches to enhance native diversity, while controlling alien species with different residence times and degrees of commonness.

Key words: biological invasions; compositional turnover; distance decay; environmental filtering; species commonness; species rarity; stochasticity; zeta diversity.

INTRODUCTION

Invasive alien species pose a major threat to biodiversity. A large proportion of research on biological invasions aims to understand how introduced species potentially spread and become assimilated in a novel environment, and to reduce both the impact of current invaders and the likelihood of new invasions (e.g. Crooks 2002, Hulme et al. 2009, Simberloff et al. 2013, Hui and Richardson 2017). In many parts of the world, invasions are relatively recent (starting after the 1800s), following the European emigration across the globe (Van Kleunen et al. 2015, Pyšek et al. 2017). Such movements of humans and commodities have introduced many alien species to central Europe over centuries (Pyšek et al. 2010, Essl et al. 2011), and the well-documented

records enable us to categorize these alien species according to their residence times as archaeophytes [introduced between 4000 BC and 1500 AD] and neophytes [introduced after 1500 AD]. The exceptional information on the residence time of regional alien and native species provides the opportunity to gain new insights on the mechanisms driving community assembly (Lodge 1993, Tilman 2004, Sax et al. 2007, Carlton 2009). In particular, we can infer the importance of different drivers of compositional diversity for categories of species with different residence times. We can thus potentially elucidate the spatially and temporally shifting processes that drive community assembly. Such insights are crucial for designing community-level strategies for managing invasions.

The Introduction-Naturalization-Invasion Continuum (INIC) conceptualizes the different barriers that alien species must overcome to establish sustainable populations in a novel environment (Richardson and Pyšek 2006, Blackburn et al. 2011). Different factors, such as propagule pressure,

dispersal strategies, reproductive traits and climate, affect the capacity of species to negotiate different barriers, and the importance of each factor varies along the INIC (Wilson et al. 2007, Richardson and Pyšek 2012). Consequently, species with similar residence times in a community or a region should have experienced similar sets of environmental barriers, but may have performed differently in negotiating the barriers along the INIC. Such differences in performance will be reflected by their presence and absence in certain communities, or regions, and thus by species turnover patterns.

As residence time increases, stochastic events should become less important overall, whereas deterministic processes (e.g. niche processes) should become more important as mediators of community composition (Stokes and Archer 2010, Hui et al. 2013, Måren et al. 2018). It is, however, important to note that there are two sources of stochasticity. Demographic stochasticity, as conceptualized in the neutral theory of biodiversity (Hubbell 2001), is the result of random birth, death and dispersal events. In contrast, environmental stochasticity corresponds to fluctuations in abiotic conditions and can profoundly affect local and regional persistence and thus invasion performance (Davis et al. 2000, Cuddington and Hastings 2016, Hui et al. 2017). In particular, communities driven by the same environmental factors (including synchronized environmental stochasticity) should display similar patterns of species turnover, signaling the predominant control of local community assemblages by environmental filtering (EF hereafter). On the other hand, different levels of demographic stochasticity, including dispersal, could drive the disparity in community assemblages and thus species turnover. This can result in a positive correlation between compositional similarities of two communities with their distance apart, hereafter isolation by distance (IBD). Although both EF and IBD can contribute to the ubiquitous distance decay of compositional similarities (Soininen et al. 2007, Morlon et al. 2008), we expect that IBD should generate more variability in species composition and thus a weaker correlation than EF. The interplay between these two sources of species turnover has rarely been explored in invasion science (but see Drake et al. 2006, Hui and Richardson 2017).

Alien species assemblages are embedded within native recipient communities (Shea and Chesson 2002); understanding the relationship between alien and native assemblages may thus provide crucial insights on both community assembly and the concept of invasibility (Hui and Richardson 2017). This could help in predicting which areas may be invaded in the future, i.e., the spread debt of invasion (Essl et al. 2011, Rouget et al. 2016). Different hypotheses have been advanced for explaining the relationship between alien and native assemblages (Rouget et al. 2016); some of these can be tested using such regional assemblages under different residence times. In particular, the correlation between the similarity of alien assemblages and the similarity of native assemblages across communities can be strong, as observed when comparing the South African native and alien biomes (Rouget et al. 2015), either due to similar abiotic selection (the "Goldilocks" hypothesis) or because of strong biotic interactions between alien and native species (the "Biome Decides" hypothesis). This correlation can also be weak, either because the distribution of alien species is largely idiosyncratic (the "Random Tessellation" hypothesis) or because the alien distribution predominantly reflects the imprint of particular invasion pathways (the "Something in the Way You Move" hypothesis).

We explore the relationship between the turnover of native species and two categories of alien species with different residence times (archaeophytes and neophytes) in a network of nature reserves in the Czech Republic. Czech Republic has a long history of detailed studies of vascular plant invasions. The country hosts almost 1,500 alien taxa of vascular plants, making it an ideal context in which to explore this alien/native relationship in a temperate biome. To do so, we first calculate zeta diversity (the number of species shared by multiple assemblages; Hui and McGeoch 2014) and then explore the role of environmental and geographical factors in structuring assemblages using Generalized Dissimilarity Modelling (Ferrier et al. 2007) for multiple sites (Multi-Site Generalized Dissimilarity Modelling – MS-GDM; Latombe et al. 2017a). Zeta diversity offers a more complete description than traditional pairwise beta metrics of turnover in that it differentiates contributions from rare (shared by only few assemblages) and widespread (shared by many assemblages) species. We include environmental variables that affect species richness and composition to account for EF (i.e., deterministic species assembly), and distance between reserves to account for IBD (i.e., stochastic species assembly). To further explore the role of environmental stochasticity for structuring plant assemblages, we include temperature and precipitation seasonality as covariates in MS-GDM. We also assess the relationship between native and alien species assemblage composition, resulting either from direct biotic interactions between natives and aliens or from the influence of shared abiotic variables, by incorporating native zeta diversity as a covariate, i.e., computing the correlation between the similarity of alien assemblages from two (or more) communities and the similarity of native assemblages from the same communities. Finally, we disentangle the contribution of compositional differences and cross-assemblage compositional nestedness (necessary especially when the composition of a small site is a subset of the species present in a bigger and richer site) to observed turnover by calculating two new measures of zeta diversity corresponding to the Sørensen and the Simpson indices of diversity (Baselga 2010).

Using this method for examining species turnover across multiple sites, we explore a list of specific mutually non-exclusive propositions regarding processes that could mediate alien community assembly. First, since increasing residence time allows species to progress along the INIC, and therefore become more widespread and more spatially constrained by environmental variables (Pyšek and Jarošík 2005, Wilson et al. 2007, Richardson and Pyšek 2012, Hui et al. 2013), we expect the decline of zeta diversity to be steeper (i.e., less species shared by multiple assemblages, regardless of species richness) for neophytes than for native species, with archaeophytes showing intermediate values. Second, we expect native zeta diversity to be better explained by environmental variables than the zeta diversity of alien species. This is because the distributions of native species should become more influenced by environmental filters than the distributions of co-occurring alien species; this could lead to diminishing the importance of stochastic

processes with residence time in structuring communities. Third, if alien species are constrained by the same set of variables as native species in the long term (i.e., the Goldilocks or the Biome Decides hypotheses; Rouget et al. 2015), and if such constraints become more apparent with increasing residence time, we would then expect the turnover of native species to better explain the turnover of archaeophytes than the turnover of neophytes. The structure of neophyte communities, and therefore their turnover, should nonetheless be driven primarily by demographic stochasticity (i.e., the Random Tessellation or the Something in the Way You Move hypotheses). Finally, as an extension of the theory of island biogeography (MacArthur and Wilson 1967), variables typically related to species richness, such as reserve area, should generate turnover between sites as a result of compositional nestedness, i.e., by simply adding species to bigger and richer sites. Tests of these propositions provide the means for achieving a cohesive view of how alien species are integrated into regional meta-communities.

METHODS

Study area

The Czech Republic, located in Central Europe, is characterized by warm moist summers and mild winters corresponding to the temperate nemoral zonobiome (Breckle 2008), or humid temperate ecoregion (Bailey 1998). This seasonality has favoured the development of zonal temperate forests ecosystems dominated by deciduous trees with admixture of conifers (Bohn et al. 2004). Altitudinal, soil and hydrological variation resulted in forming extrazonal patchy habitats with coniferous and mixed forests, mires, dry grasslands, and azonal mountain and water-related habitats (Leuschner and Ellenberg 2017). In addition to species with evolutionary origin in the above zonobiomes, the habitats in the Czech Republic also harbor species that originated in the neighboring geographical regions, which makes the study area a floristically rich transitional zone among North European Boreal coniferous forest and South European Pannonic deciduous forest-steppe zones, and between Hercynian and Carpathian zones in the west and east, respectively (Chytrý 2012). Arctic, boreal, alpine, steppe and other relicts are relatively frequent in the Czech Republic and occur in both forest and non-forest habitats (Kaplan 2012). The localities of these relict taxa, as well as of other rare species, are covered by the network of nature reserves and protected areas, which is located within human-managed cultural landscape.

During the postglacial period, the altitudinal zonation with vegetation belts, typical of different forest types, has been formed (Abraham et al. 2016); at present they are more or less intensively managed or represent human-made stands. The landscape has been intensively used since the High Medieval deforestation of many areas. The key points in the development of the Czech flora and landscape occurred during the last two millennia along with the increasingly strong effects of human activity, as well as associated fragmentation and transformation of natural habitats (Chytrý 2012). The modern vegetation types formed by these processes, such as meadows or fishpond wetlands, still preserve a major proportion of unique biota (Michalcová et al. 2014). In total, the plant diversity is recorded using a system of 88 habitats (see Pyšek et al. 2012b for description).

The Czech Republic has a strong tradition of research on synanthropic and alien plants, both historically and recently; the alien flora and invasion patterns are therefore exceptionally well known. At present, there are 1454 alien taxa of vascular plants recorded in this country, among them 350 archaeophytes, introduced since the beginning of the Neolithic until the end of the Middle Ages, and 1104 neophytes, introduced in the Modern Period. Aliens make up 14.4% of the permanently present flora (Pyšek et al. 2012a). The highest levels of invasion of plant communities are recorded in cities and villages and their surroundings, floodplains of large rivers, disturbed landscapes in the north, and agricultural landscapes and forest plantations in the warm lowlands. The habitats and vegetation types harbouring the highest proportions of alien species in the Czech Republic are mostly those with a high level of disturbance or with generous supply of resources, especially nutrients, in some cases also water or light (Pyšek et al. 2012b).

Data

A database of presence-absence for vascular plant species in nature reserves throughout the Czech Republic has been collected by the Agency for Nature Conservation and Landscape Protection, Prague (Pyšek et al. 2002a, b, c). The database has information for 2,054 species in 302 reserves with richness ranging from 12 to 608 species and areas ranging from 0.17 to 4,279.79 ha. For each of the 302 nature reserves, species lists including all vascular plants were collected by using published records (see Pyšek et al. 2002a, b, c, 2003 for references to nature reserves and published species lists) or unpublished floristic inventories deposited at the Agency for Landscape Protection of the Czech Republic, Prague. These inventories were carried out regularly by professional botanists, using standardized procedures of recording all species occurring in a given reserve (Maršáková 1987).

Species were classified into native species, archaeophytes and neophytes (Pyšek et al. 2002b, c). Archaeophytes are species that were introduced into Europe between ca. 4000 BC and ca. 1500 AD, between the initiation of agricultural activities during the Neolithic and the European exploration of the Americas. Neophytes are species that were introduced after 1500 AD (Pyšek et al. 2002b, c, 2004). Overall, native species form the majority of the species assemblages in nature reserves in the Czech Republic, with a richness ranging from 11 to 535 species (68.8 to 100% of the local species richness) (Fig. 1). Archaeophytes were present in 246 out of the 302 reserves, with richness ranging from 1 to 89 species (0.06 to 29.2% of the local species richness). Neophytes were present in 227 out of the 302 reserves, with richness ranging from 1 to 28 species (0.03 to 11.3% of the local species richness). Previous analyses using this database have focused on the relationship between native and alien species richness and the environment (Pyšek et al. 2002a, b, c), on the relationship between native and alien species richness and residence time category or the age of nature reserves (Pyšek et al. 2003), or on differentiating patterns of species

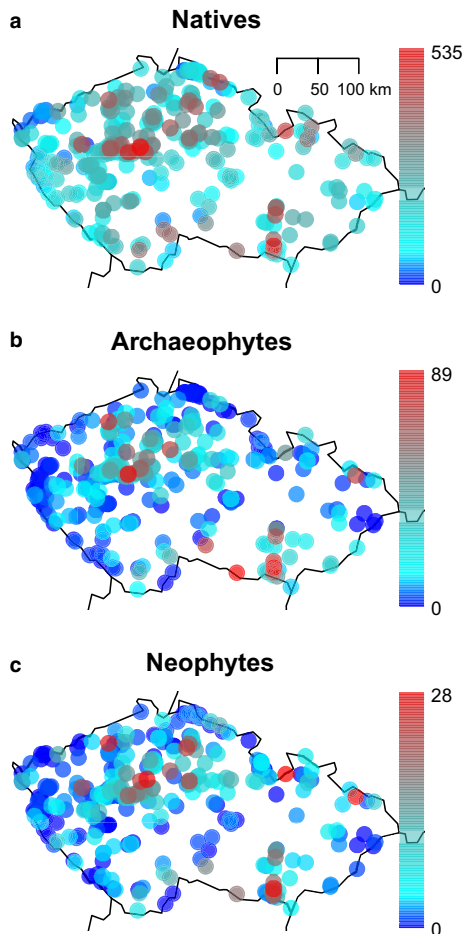**a Natives**

b Archaeophytes

c Neophytes

FIG. 1. Numbers of (a) native, (b) archaeophyte and (c) neophyte species richness in the 302 nature reserves in the Czech Republic.

composition for species within different residence time categories (Hui et al. 2013). These studies mainly found overall positive relationships between native and alien species richness (supporting the Goldilocks hypothesis), especially for neophytes (Pyšek et al. 2002a, b, c). Because neophyte richness is lower than expected from native richness in nature reserves, it has been argued that natural vegetation acts as an effective barrier to invasion (the Biome Decides hypothesis) (Pyšek et al. 2003). Alien species introduced more recently are nonetheless more likely to display more randomly assembled groups of species (the Random Tessellation or the Something in the Way You Move hypotheses) (Hui et al. 2013).

Six, independent, "static" environmental variables (number of habitats, average temperature in January, average precipitation in January, human density, area and year of reserve establishment) and spatial coordinates were used to characterize the nature reserves. Area and the number of habitats are typically related to species richness, as predicted by the Theory of Island Biogeography (MacArthur and Wilson 1967) and niche theory (Tilman 2004), respectively. The variables "year of reserve establishment" and "human density" were used as proxies of local residence time (as opposed to the overall residence time category of the species

in the Czech Republic) and the level of disturbance, respectively; these factors are known to be positively correlated with the extent of invasion (Hobbs and Huenneke 1992, Wilson et al. 2007). Temperature and precipitation are typically used as climate variables linked to niche selection. The spatial coordinates (latitude-longitude) were used to compute the orthodromic distance between reserves, to represent IBD. Human density and reserve area were log transformed to correct for skewness. Elevation was not included because it is highly correlated with temperature. Two variables representing environmental stochasticity (temperature and precipitation seasonality) were included, using data from the WorldClim database (Fick and Hijmans 2017). Both original seasonality values were correlated with January temperature and precipitation, and their residuals from linear regressions against these two January climatic variables were therefore used in the analyses.

Zeta diversity

Species diversity within and between nature reserves was assessed using zeta diversity, the number of species shared by any number of reserves (Hui and McGeoch 2014). ζ_1 is the average number of species per reserve (i.e., species richness, or alpha diversity), ζ_2 is the average number of species shared by any two reserves (i.e., the reverse of species turnover, or beta diversity), ζ_3 is the average number of species shared by any three reserves, and so on. The number of reserves is called the order of zeta. Since only widespread species can be shared by multiple reserves, whereas rare to common species can all be shared by two reserves, zeta diversity enables the differentiation between rare and common species to compositional turnover. As the order of zeta increases, the number of shared species across reserves necessarily decreases, hence the *zeta decline*. The zeta ratio ζ_i/ζ_{i-1} also informs on the rate at which species are retained as additional reserves are considered, and is called the retention rate (McGeoch et al. 2017). The retention rate can allow to distinguish apparently similar zeta declines, or to compare zeta declines with different richness values.

This zeta decline usually follows either an exponential or a power law parametric form (Hui and McGeoch 2014). An exponential decline means that the probability of retaining a species as the order increases is constant and independent of the species occupancy, therefore indicating random assemblages, whereas the power law is indicative of species with different site preferences. A more complex combination of both parametric forms has also been advocated to assess the relative contribution of stochasticity and deterministic assembly processes (Hui 2012, Kunin et al. 2018):

$$\zeta_i = a \times \exp(-b \times i) \times i^{-c} \qquad (1)$$

where a, b and c are positive numbers. In reality, the parametric form is piecewise and varies with the order of zeta, i. To identify the different pieces of the parametric form, we compare the values of the exponential and a power law parametric forms to the expected value of the $\log(\zeta_i)$ under both assumptions to determine their curvatures. If the value is greater (lower) than expected, the parametric form is concave (convex). Opposite signs of the curvature indicate a mix

of both parametric forms. If the signs of curvature are the same, the parametric form is the one with the lowest absolute curvature (see Appendix S1 for computational details).

The zeta decline and the retention rate were computed for native, archaeophyte and neophyte species, and the exponential, power law and combined parametric forms were fitted to compare the assemblages. For archaeophytes and neophytes, reserves with no species were excluded from the analyses.

Multi-site generalized dissimilarity modelling

Multi-Site Generalized Dissimilarity Modelling (MS-GDM; Latombe et al. 2017a) was used to evaluate how zeta diversity changed with environmental difference and distance between the nature reserves. MS-GDM requires the zeta values to be rescaled between [0,1]. This normalized ζ_n can be computed in different ways. Dividing the number of shared species across the n specific reserves by the overall richness γ of the n sites, ζ_n/γ, by the average richness of the n sites, ζ_n/ζ_1, or by the minimum richness across the n sites, $\zeta_n/\min(\zeta_1)$ corresponds to, respectively, the Jaccard, Sørensen or Simpson version of zeta. Considering the Sørensen version of turnover (and by extension the Jaccard version, since the relationship between the two measures is well established; Magurran and McGill 2011) may overemphasize the importance of difference in species richness (i.e., assemblage of one reserve is a subset of the one of another reserve, coined compositional nestedness) over "true", richness-independent turnover (Baselga 2010). We therefore calculated both the Sørensen and the Simpson versions of the normalized zeta for the following analyses. Variables typically strongly related to species richness should mostly generate turnover between sites as a result of compositional nestedness, and therefore contribute to the Sørensen version of zeta diversity, but not to the Simpson zeta diversity.

MS-GDM combines I-splines, a type of monotonic splines, and Generalized Linear Modelling (GLM) with a constraint on the sign of the parameters. It can be applied to specific orders of zeta (≥2) to assess if turnover in rare (low order of zeta) and widespread (high order of zeta) species is driven by different factors. MS-GDM follows three steps (see Latombe et al. 2017a for additional details). (1) Each environmental variable x is transformed into three I-splines $I_1(x)$, $I_2(x)$ and $I_3(x)$, which are non-linear, monotonic splines with values between [0,1] (more than three splines can be used, but may lead to overfitting). (2) For each combination of n reserves the normalized ζ_n is computed, as well as the average difference between the $I_i(x)$ of the n reserves and the average distance d between them. The average distance d is then also transformed into three I-splines $I_1(d)$, $I_2(d)$ and $I_3(d)$. (3) The relationship between normalized ζ_n and the differences is then computed using a GLM with a binomial distribution and a log link function:

$$\log(\zeta_n) \sim \sum_{k=1}^{3} \left(\sum_p \beta_{pk} g(\{I_{pk}(x_{pi}) - I_{pk}(x_{pj})\}_n) \atop + \beta_k g(\{I_{dk}(d_{ij})\}_n) \right) \quad (2)$$

where p is the ID of a continuous environmental variable x, i and j are two different reserves, $\{\cdot\}_n$ is a set of pairwise

combinations of the n reserves, $g(\cdot)$ is a function to combine the pairwise differences (the mean was used here, but other functions, such as the maximum, may be used; Latombe et al. 2017a), and β_{pk} is the coefficient associated with the spline k of variable x_p. Since it is assumed that the number of shared species must decrease with increasing environmental difference or distance, a negative constraint is imposed on the sign of the β_{pk} coefficients. For each environmental variable x, the total I-spline can then be computed as $I_T(x) = \sum_{k=1}^{3} \beta_i I_i(x)$. An I-spline I_T is monotonic and can be non-linear, with curve slope at a particular value x of the environmental variable representing the effect of the environmental variable on species turnover at this particular value. The relative total amplitude of the splines shows the relative effect of an environmental variable on zeta diversity compared to the other variables.

MS-GDM was applied for each category of species separately for ζ_2 to ζ_8, using first the six independent, static environmental variables described above, as well as distance between reserves, as predictors. The two seasonality variables were then included to assess the effect of environmental stochasticity. We also tested whether the composition of alien species was linked to the composition of native species (referred to as biotic MS-GDM, in contrast with the previous model referred to as abiotic MS-GDM hereafter or commodity despite the use of the number of habitat as a covariate). To do so, Eq. 1 was modified to incorporate $1-\zeta_n'$ as a measure of ecological distance between the native species composition of the reserves, ζ_n' being the normalized zeta diversity for the native species of the n same reserves as for the recently arrived species:

$$\log(\zeta_n) \sim \sum_{k=1}^{3} \left(\phi + \beta_k I_{\zeta'k}(1 - \zeta_n') \right) \quad (3)$$

where ϕ has the same formulation as in the brackets of Eq. 2. Two models (abiotic static and abiotic seasonality) were therefore computed for native species, and four models (abiotic static, abiotic seasonality, biotic static and biotic seasonality) for archaeophytes and neophytes. Finally, for each MS-GDM, we computed the predicted zeta values and calculated the Pearson R^2 between the observed and predicted zeta values to represent the explained variance of the model. To cross validate our results, we computed the abiotic/biotic, static/seasonality MS-GDMs for 202 out of the 302 reserves (randomly selected) and computed the variance between the zeta values predicted by the models and the observed zeta values for the remaining 100 reserves.

Species richness

As a baseline for comparison, Generalized Additive Models (GAM; Hastie and Tibshirani 1990) were used to assess the role of the environment in explaining species richness in the different nature reserves for the three categories of vascular plants. GAMs are a semi-parametric regression technique that accommodates non-linearities and non-monotonicity in the relationships. Due to the low number of unique values in the variable of the number of habitats and to avoid overfitting, the number of knots per spline was set
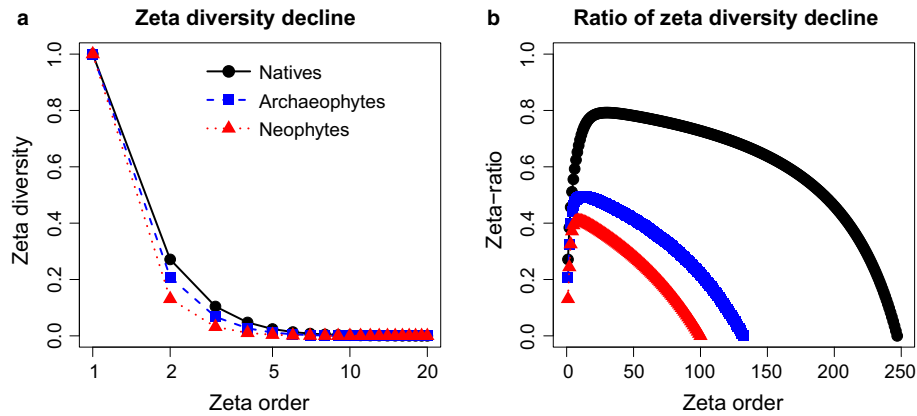
FIG. 2. Zeta diversity of native, archaeophyte and neophyte species. (a) Zeta decline (rescaled between 0 and 1 for comparison; the *x*-axis is on a log-scale and stops at order 20 to highlight differences between the three categories of assemblages), and (b) the corresponding zeta ratio computing the retention rate. The *x*-axis of the zeta decline is on a log-scale for clarity.

to 3. All analyses were performed in R (R Core Team 2018) using the R package *zetadiv* 1.1.1 (Latombe et al. 2017*b*) (the R scripts for performing all the analyses are available as online Supplementary Material).

RESULTS

Zeta diversity

The progressive shift in the community structure with the time of introduction of the three categories, from native to neophyte species, described by the shape of the *zeta decline* (Fig. 2)*,* is consistent with our hypothesis that communities are structured through time by the successive barriers along the INIC. The zeta declines rescaled between 0 and 1 are quite similar, but the decline of the neophytes is the sharpest (therefore having the lowest retention rate, which indicates that more species are lost as additional sites are considered in the computation of zeta), followed by the archaeophytes. This means that the proportion of rare to widespread species is inversely proportional to the residence time of the species category. The shape of the zeta ratio is also different between native species and the two categories of alien species. The retention rate of the archaeophytes and the neophytes shows a sharp initial increase (indicating that less species are lost as additional sites are considered in the computation of zeta, proportionally) followed by a relatively constant decrease. This suggests that the rate of the zeta decline initially decreases and then accelerates as the number of sites considered becomes higher than the occupancy of typical common species. The decline is slightly sharper for the neophytes. In contrast, after a sharp increase, the retention rate of the native species shows a shallow decline, followed by a sharp decline when considering more than 200 reserves. The shallow decline for intermediate orders of zeta suggests the presence of an intermediate class of species in terms of their occupancies. Because the concepts of species rarity and commonness are relative and context dependent (McGeoch and Latombe 2016), it appears that archaeophytes and neophytes may be separated into two classes of commonness, whereas three classes would be more appropriate for native species. This result illustrates the complexity

TABLE 1. Exponential and power law coefficients of the zeta decline parametric forms for native, archaeophyte and neophyte species in native reserves in the Czech Republic.

Species category	Exponential coefficient (b)	Power law coefficient (c)
Natives		
Order ≤ 29	0.1492 (*P*-value < 0.001)	2.1456 (*P*-value < 0.001)
Order > 29	0.4995 (*P*-value < 0.001)	0 (*P*-value = 1)
Archaeophytes		
Order ≤ 11	0.5321 (*P*-value < 0.001)	1.4189 (*P*-value < 0.001)
Order > 11	1.1940 (*P*-value < 0.001)	0 (*P*-value = 1)
Neophytes		
Order ≤ 8	0.5677 (*P*-value < 0.001)	2.0483 (*P*-value < 0.001)
Order > 8	1.4576 (*P*-value < 0.001)	0 (*P*-value = 1)

and the dynamic aspect of community assembly, as an intermediate class of species commonness only seems to appear after some time.

The parametric forms of the zeta declines indicate that for the three categories of native and alien species, the zeta decline is a combination of an exponential and a power law form for low orders (rare and common species). The power law component indicates some deterministic site preference by different species. In contrast, the zeta decline corresponds to an exponential decline for high orders (widespread species), i.e., more random spatial distributions (Table 1). The number of orders for which the zeta decline is better explained by the combined form is higher for the natives than for the other two categories, and this number corresponds to the start of the tail of the occupancy-frequency distributions (Appendix S2: Fig. S1). Nonetheless, the difference between the exponential and power law coefficients is higher for the native species than for the other two categories, with a strongly dominant power law decline (i.e., stronger deterministic site preference for natives).

Multi-site generalized dissimilarity modelling

The variance explained by the abiotic MS-GDM with the Sørensen ζ_n/ζ_1 (Simpson $\zeta_n/\min(\zeta_1)$) zeta for natives ranged from 0.094 (Simpson: 0.078) to 0.173 (Simpson: 0.127)

without the seasonality variables, and from 0.111 (Simpson: 0.085) to 0.185 (Simpson: 0.144) with the seasonality variables (Fig. 3a,c), but this small improvement was not significant, as shown by AIC values (Appendix S2: Tables S1, S2), indicating that environmental stochasticity has little impact on differences in native species composition. The explained variance was much lower for the other two categories, ranging from 0.009 (Simpson: 0.004) to 0.041 (Simpson: 0.030) for the archaeophytes, and from 0.006 (Simpson: 0.004) to 0.044 (Simpson: 0.044) for the neophytes without the seasonality variables, indicating that the variables used here have little predictive power for the change in species composition across nature reserves. Including the seasonality variables slightly improved the results of low (Simpson: all) orders for neophytes (ranging from 0.010 (Simpson: 0.009) to 0.062 (Simpson: 0.060)), suggesting that environmental stochasticity influences difference in species composition across nature reserves for neophytes, but not for archaeophytes (Fig. 3a,c; Appendix S2: Tables S1, S2).

The I-splines show that reserve area, January temperature and distance between reserves are the three main factors explaining native species turnover for the variables considered here, as shown by the relative amplitudes of the I-splines (Fig. 4). The non-linearities in the I-splines provide additional insights on the range of values over which variations

will have an important effect on turnover. Reserve area is the main factor for Sørensen ζ_2 (i.e., for ζ_2/ζ_1), and difference in area is especially important for small reserves (<10 ha; Appendix S2: Table S3), as shown by the initial steep slope of the spline. As the order increases, distance becomes the main predictor of species turnover, showing the effect of IBD and indicating that multiple reserves over a large area result in a greater diversity of species, but especially common species. As the order increases, January temperature also becomes as important as reserve area in explaining differences in species composition. The relatively linear I-splines for temperature indicate that difference in temperature is important over the whole range of values. In the context of climate change, changes in temperature would therefore affect the full spectrum of assemblages and have a substantial impact on their spatial distribution. Given the low variance explained by the abiotic MS-GDMs for archaeophytes and neophytes, the corresponding I-splines provide little information on the effect of abiotic variables on turnover. Using the Simpson zeta ($\zeta_n/\min(\zeta_1)$) in the abiotic MS-GDM generated similar splines (Appendix S2: Fig. S2), indicating that these relationships explain true turnover rather than nested species assemblages between reserves.

Adding the Sørensen or Simpson zeta diversity (ζ_n/ζ_1 or $\zeta_n/\min(\zeta_1)$) of native species as an additional predictor into
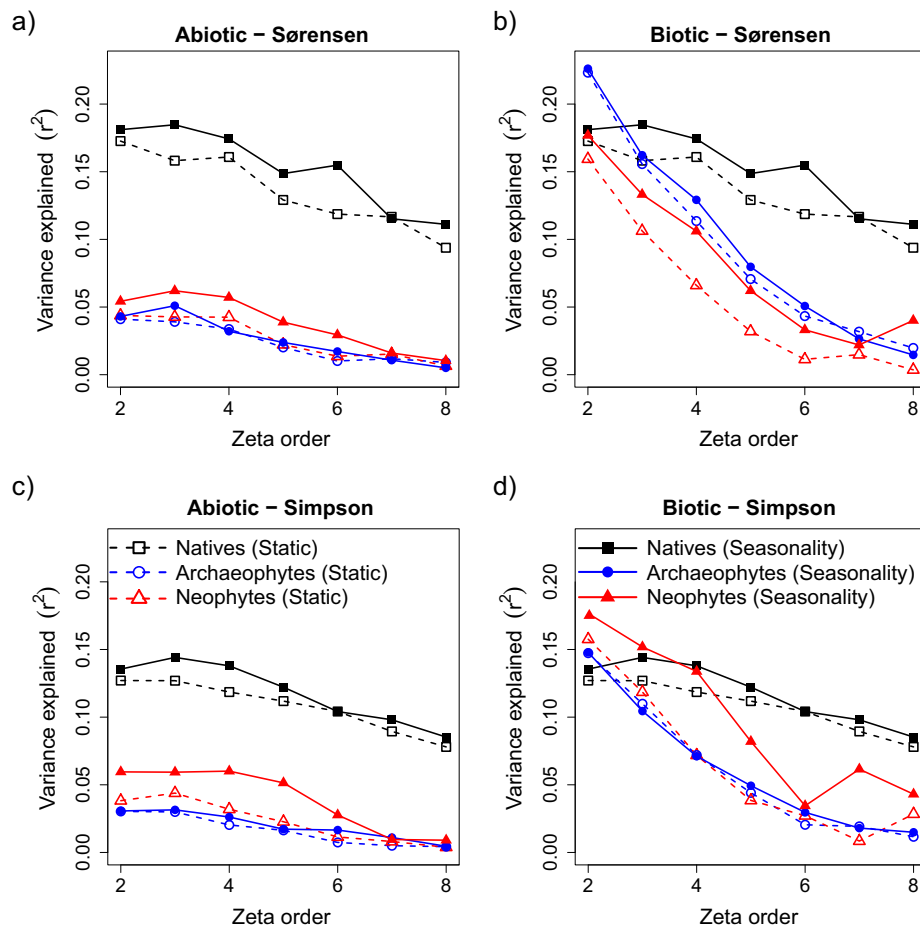

Fig. 3. Variance explained (R^2 between observed and predicted zeta values) by abiotic (a, c) and biotic (b,d) MS-GDM considering static and seasonality environmental variables, distance and the native zeta diversity for (a, b) Sørensen zeta and (c, d) Simpson zeta.
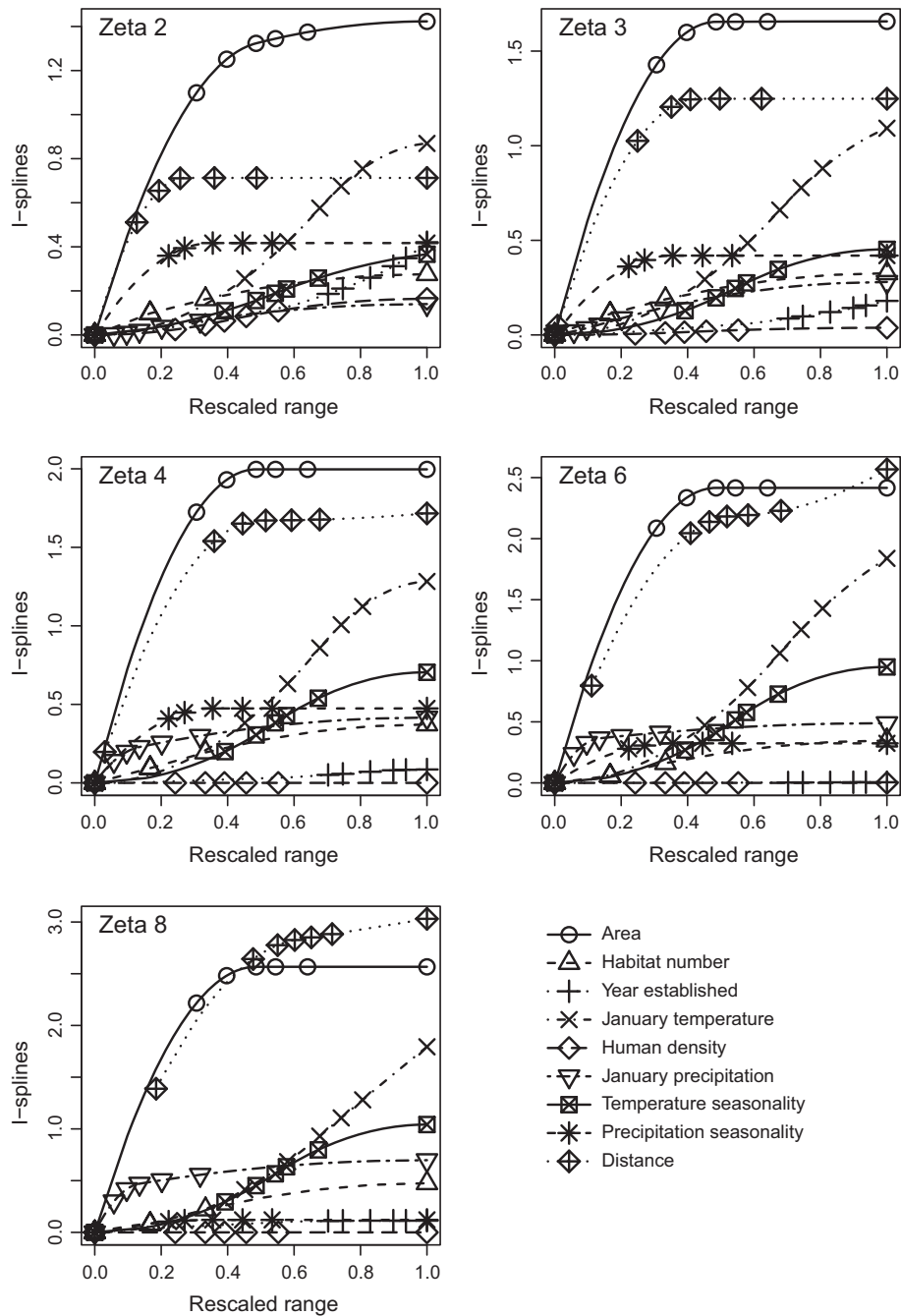
FIG. 4. I-splines generated by abiotic MS-GDM considering static and seasonality environmental variables using Sørensen zeta diversity on native species, showing the effect of environmental variables and distance on zeta diversity. The symbols indicate quantiles for each variable. For distance, the *y*-axis should be interpreted as $1-\zeta$.

the static biotic MS-GDM increased greatly and significantly the variance explained of the zeta diversity of archaeophytes and neophytes especially for low orders of zeta (Fig. 3b,d; Appendix S2: Tables S1, S2). The variance explained ranged from 0.020 (0.012) to 0.223 (0.147) for archaeophytes and from 0.004 (0.008) to 0.159 (0.158) for neophytes. The effect was therefore more important on archaeophytes for the Sørensen zeta diversity, but similar for the Simpson zeta diversity. It indicates a relatively stronger correlation between the compositional nestedness of natives

with archaeophytes, but not with neophytes (Fig. 3b, d). Including the seasonality variables produced similar results for the archaeophytes for both the Sørensen and Simpson zeta diversity, but, as for the static MS-GDM, increased the variance explained for the neophytes, which was even higher than for archaeophytes for the Simpson zeta diversity, showing the importance of environmental stochasticity in structuring neophyte communities.

The I-splines of native zeta diversity as a predictor had a greater amplitude than the I-splines of the other

variables, indicating the importance of native turnover for explaining archaeophyte and neophyte turnover in the regression (causing the splines of the other variables to overlap; Fig. 5, Appendix S2: Fig. S3). The effect of native zeta diversity was especially high for high values of $1-\zeta_n'$ (Eq. 3), as indicated by the increasing slope of the spline. This means that changes in native zeta for low values have a disproportionate effect on changes in low zeta values of archaeophytes and neophytes. In other words, a small increase in similarity of native flora between reserves translates into a larger increase in similarity for alien flora.

Species richness

The relationships between species richness and the environmental variables were very similar for the three categories of species, and the correlations between the richness of the three categories were high (native-archaeophyte: $R = 0.77$; native-neophyte: $R = 0.73$; archaeophyte - neophyte: $R = 0.84$; all P-values < 0.001), although the GAM explained better native richness than for archaeophytes and neophytes (deviance explained = 47.7%, 30% and 30.5%, respectively). For the three categories, richness was positively associated with the area, the number of habitats, the
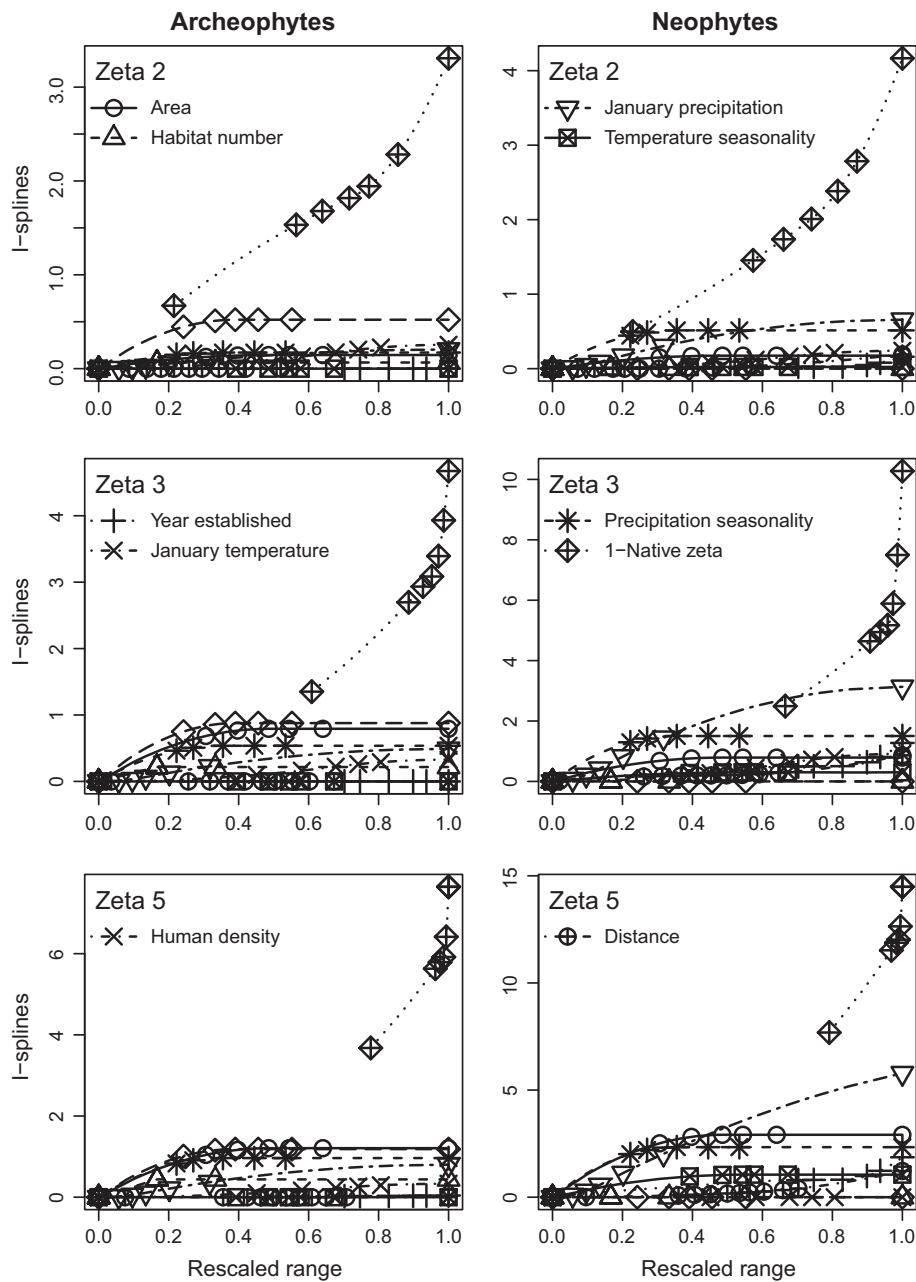

FIG. 5. I-splines generated by biotic MS-GDM considering static and seasonality environmental variables, distance and the Sorensen zeta diversity of native species. Note that the I-spline for native zeta represents $1-\zeta'$, as in Eq. 3. As a result, there are no low values (no combination of sites shared all species). For distance and native zeta, the y-axis should be interpreted as $1-\zeta$.

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January temperature and the human density of the reserves (P-values < 0.05; Appendix S2: Fig. S4). The year of reserve establishment had no impact on richness.

Discussion

The analyses presented in this paper provide novel insights on the mechanisms that mediate how alien species assemblages with different residence times are incorporated into regional species pools in temperate biomes. We accounted for the different levels of rarity and commonness of the native and alien taxa, using an invaded plant meta-community of nature reserves in the Czech Republic. The profile of species turnover is consistent with the residence time of the assemblages, with the species belonging to the more recent category (neophytes) having not only lower richness, but also a lower retention rate (Fig. 2). This is consistent with the fact that more species should become widespread with longer residence times (Pyšek and Jarošík 2005, Wilson et al. 2007, McGeoch and Latombe 2016). In addition, the zeta decline of native species showed a stronger agreement with a power law parametric form, which suggests that native vascular plant assemblages are more driven by deterministic assembly processes (Hui and McGeoch 2014). This is consistent with the higher percentage of variance explained for abiotic MS-GDM applied to native species compared to archaeophytes and neophytes (Fig. 3), indicating that the structure of native vascular plant assemblages is more constrained by environmental factors, as we expected. Similar to our results, Hui et al. (2013) observed a progressive level of compartmentalization and functional distinctiveness between modules with the residence time of the categories on the same data, indicating diminishing stochasticity relative to deterministic processes. However, our results show that not all patterns change at the same rate over time. Although the differences in zeta diversity (Fig. 2) show a gradual change, there is a large difference between natives and the two types of alien vascular plant species; the variance explained by abiotic static MS-GDM for archaeophytes and neophytes was equally low. Association between a species assemblage and these environmental variables therefore appears to require longer residence time than experienced by archaeophytes in the region.

Moreover, contrary to our expectations, including seasonality of temperature and precipitation in MS-GDM improved the variance explained for neophytes but not for archaeophytes (and not significantly for natives), for both the abiotic and biotic analyses (Fig. 3). Environmental stochasticity therefore appears to enable neophyte vascular plant species to colonize nature reserves due to short-term but recurrent changes in abiotic conditions providing temporary establishment opportunities (Davis et al. 2000, Cuddington and Hastings 2016). The ephemeral and local aspect of environmental variability should, by definition, have a stronger effect on rare species; this is also supported by the fact that the effect of seasonality variables disappears as the order of zeta increases for the static MS-GDM (Fig. 3a,c). The effect of environmental stochasticity on rare neophyte species is therefore likely to emerge because there has been insufficient time for selection to occur and to exclude poorly performing species. In contrast, the lack of correlation between turnover in common native and alien vascular plant species in the biotic MS-GDM may be explained by demographic stochasticity, if alien species become common because of positive feedbacks on propagule pressure, as part of the regime shift in invaded ecosystems (Gaertner et al. 2014). There are nonetheless many ways of becoming common (McGeoch and Latombe 2016); other typical causes include high levels of propagule pressure through multiple human-mediated introductions of alien species, for example related to trade (Dlugosch and Parker 2008, Westphal et al. 2008) or widespread planting (Donaldson et al. 2014). The spread debt of invasion, representing the additional areas that may be invaded in the future (Rouget et al. 2016), is therefore more likely to be predicted by potential local environmental variation for neophytes than for archaeophytes.

Considering dissimilarity in native species composition improved the capacity of MS-GDM to explain turnover of both archaeophytes and neophytes, especially for low orders of zeta, i.e., mostly for rare species (Fig. 3). As for other studies (Rouget et al. 2015), it is not clear whether the composition of alien vascular plant assemblages in Czech reserves is driven by similar environmental variables that were not considered in our analyses, such as soil composition, or by positive or negative biotic interactions (the "Goldilocks" or the "Biome Decides" hypotheses, respectively). The percentage of variance explained decreased with the order of zeta for both types of species implies that the distribution of widespread alien species is independent of the distribution of native widespread species. In contrast, the correlation between native, archaeophyte and neophyte richness implies that native richness can explain between 53 and 60% of alien richness variance using a simple linear regression, more than doubling the variance explained by biotic MS-GDM for ζ_2. Taken together, the even lower variance explained for higher order zeta shows the decline of predictive power of species turnover (from ζ_1 [species richness] to higher orders of zeta) with species commonness. This decline in explanatory power also highlights the conundrum facing predictions of compositional turnover vs. richness for vascular plants in this network of nature reserves, as the predictive power of turnover will drop by more than half compared to richness.

The fact that turnover in widespread alien species is not driven by the same factors as widespread native species has important implications for the management of vascular plants in Czech nature reserves. Based on the spatial correlation between native and alien biomes, Rouget et al. (2015) concluded that management of alien species should be biome-specific. However, our results show that this is only true for relatively rare species. The impact of alien species is hypothesized to be proportional to the abundance, the occupancy and the per capita effect of species (Parker et al. 1999). Widespread species are therefore likely to have greater impacts than rare ones. Such species should therefore be managed on a species-by-species basis (Crawley 1987, Van Wilgen et al. 2011, Sun et al. 2013). Nonetheless, alien species that are rare may be so because of specific habitat constraints (Rabinowitz 1981), but many may also be on a trajectory to becoming common (McGeoch and Latombe 2016). There is therefore much uncertainty about the potential of rare alien species to generate major impacts in native communities, and species-by-species management has also been advocated for such

species (Wilson et al. 2013). The management of alien species is therefore a complex issue, which must be addressed using a combination of strategies to improve its efficiency.

Using both the Sørensen and the Simpson versions of zeta diversity provides further insights for the interpretation of similarity in turnover of native and alien species. As expected, the zeta diversity of native species was better related to the zeta diversity of archaeophytes than neophytes for the static variables (Fig. 3). However, the difference of explained variance between the biotic MS-GDM (Eq. 3) of archaeophytes and neophytes was higher using Sørensen than using Simpson zeta diversity, especially after incorporating seasonality variables. Compositional nestedness will generate lower zeta values for the Sørensen formula, whereas it will have no impact when using the Simpson formula, because the latter computes "true" turnover (different reserves are different if they all contain different species) (Baselga 2010). Nestedness in native species composition therefore better explains the nestedness of archaeophyte composition than that of neophytes. It implies that reserves whose composition encompasses the native composition of other reserves also do so for archaeophytes, but not for neophytes. The other scenario explaining the correlation between Sørensen zeta diversities, that reserves with higher native richness have lower archaeophyte richness, i.e., inverse compositional nestedness, can be discarded since the richness of the three types of species are highly correlated.

Finally, we expected differences in reserve area to be a better predictor of Sørensen than Simpson zeta diversity, since Sørensen zeta diversity is influenced by compositional nestedness. However, the relative importance of differences in reserve area for explaining native turnover was similarly high for both Sørensen and Simpson zeta diversity, indicating that reserve area influences not only species richness, but also species composition. Interestingly, the shapes of the splines for richness and species turnover differed. An increase in reserve area impacts plant species richness more for big reserves than for small ones, as shown by the initial shallow slope of the GAM spline, which increases with species area (Appendix S2: Fig. S4). In contrast, an increase in reserve area impacts species composition for small reserves, as shown by the initial steep slope of the I-splines (Fig. 4, Appendix S2: Fig. S2), which plateau at approximately the same value at which the slope of the GAM spline increases (~10 ha; Appendix S2: Table S3). The effect of reserve area on species composition when accounting for richness may be due to a correlation with other variables not included in the data (including abiotic variables, visitor numbers, etc.), or to biotic interactions resulting from differences in species richness, or a mix of both. The design of networks of protected areas usually focusses on the number of sites, their locations, and the total area (e.g. Cabeza and Moilanen 2001, Camm et al. 2002, Rodrigues et al. 2004), but variation in area is usually overlooked. Our results show that this characteristic may be critical to enhance species diversity at the regional scale.

Conclusions

The Czech Republic has a long history of research and excellent data on vascular plant invasions. This provides a unique opportunity to study how plant assemblages with different residence times are structured by different factors in temperate biomes using a meta-community of nature reserves. Comparing turnover in native, archaeophyte and neophyte species in regional assemblages using zeta diversity and Multi-Site Generalized Dissimilarity Modelling confirms the decrease in importance of stochastic factors with residence time as mediators of plant assemblage structure across the meta-community (as previously observed in Hui et al. 2013), while providing novel insights about the assembly process. These analyses enable us to account for the role of commonness and rarity of species in the relationship between the compositions of vascular plant assemblages with different residence times. Using native species turnover as a predictor of the turnover of alien species indeed shows that the positive correlation between native and alien species composition at the regional scale that has been observed in other studies (Rouget et al. 2015) is only valid for rare species, whereas turnover in widespread alien species is independent of native composition. An important implication of this is that different monitoring approaches are required for alien species with different levels of commonness when choosing sites for a monitoring program, especially in early stages of such a program when the number of sites is limited (Latombe et al. 2017c). If the program targets rare species in early stages of invasion, a site-specific approach based on the presence of native species would be appropriate. For more common species further on the INIC, a species-specific approach would be more suitable. Also, environmental stochasticity was found to have an effect on species composition only for neophytes, but not for archaeophytes, offering possibilities to predict the spread debt of invasion for neophytes in such environments (Essl et al. 2011, Rouget et al. 2016). Finally, differences in the size of nature reserves influence not only native species richness, but also the richness-independent turnover of native species (i.e., species replacement). Networks of reserves in temperate biomes must therefore be designed and managed using a variety of approaches to enhance native plant diversity, including increasing the size difference between reserves, while controlling alien species with different residence times and degrees of commonness. Since this study focuses on a plant meta-community in a temperate biome, it is difficult to predict how these relationships would be conserved in other biomes, such as tropical ones. Although we may expect the qualitative relationships to be maintained, performing such analyses for a variety of climates would shed additional insights on the fundamental mechanisms structuring plant community assembly.

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Supporting Information