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Species richness and composition differ in response to landscape and biogeography

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Abstract

Context Understanding how landscape patterns affect species diversity is of great importance in the fields of biogeography, landscape ecology and conservation planning, but despite the rapid advance in biodiversity analysis, investigations of spatial effects on biodiversity are still largely focused on species richness.

Objectives We wanted to know if and how species richness and species composition are differentially driven by the spatial measures dominating studies in landscape ecology and biogeography. As both measures require the same limited presence/absence information, it is important to choose an appropriate diversity measure, as differing results could have important consequences for interpreting ecological processes.

Methods We recorded plant occurrences on 112 islands in the Baltic archipelago. Species richness and composition were calculated for each island, and the explanatory power of island area and habitat heterogeneity, distance to mainland and structural connectivity at three different landscape sizes were examined.

Results A total of 354 different plant species were recorded. The influence of landscape variables differed depending on which diversity measure was used. Island area and structural connectivity determined plant species richness, while species composition revealed a more complex pattern, being influenced by island area, habitat heterogeneity and structural connectivity.

Conclusions Although both measures require the same basic input data, species composition can reveal more about the ecological processes affecting plant communities in fragmented landscapes than species richness alone. Therefore, we recommend that species community composition should be used as an additional standard measure of diversity for biogeography, landscape ecology and conservation planning.

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Introduction

The relationship between biodiversity, local environment and landscape patterns has long occupied biologists and ecologists (Forster 1778; Watson 1835; Darwin 1859; Wallace 1880; Arrhenius 1921; MacArthur and Wilson 1967; Hanski 1999). Today this relationship marks the cornerstone of island biogeography and landscape ecology, the former being of renewed interest, 50 years after its conception (Patiño et al. 2017; Whittaker et al. 2017). A wide range of studies within these disciplines have identified associations between biodiversity and habitat patch area (Arrhenius 1921; Lindgren and Cousins 2017), shape (Aggemyr and Cousins 2012), quality (De Sanctis et al. 2010) and isolation (MacArthur and Wilson 1967; Lindgren and Cousins 2017), as well as habitat amount (Fahrig 2013), configuration and connectivity within a landscape (Haddad et al. 2017), and historical properties of the focal habitat or landscape (Helm et al. 2005). These examples show that the physical environment can shape diversity in different ways, but in the majority of cases, the measure of diversity used is species richness, i.e. the raw number of species counted in a particular patch. As habitat patches with the same species richness might have completely different sets of species, it is time to look beyond species richness in landscape ecology and biogeography (Patiño et al. 2017).

Although measures exist that reflect community structure and the abundance or evenness of species (Gotelli and Chao 2013), species richness remains the focus of biogeographical and landscape ecological studies (Whittaker and Fernandez-Palacios 2007). Richness is the easiest diversity measure to collect in the field (Purvis and Hector 2000; Gotelli and Chao 2013) and useful for comparison across datasets (Fahrig 2017) or between historical and modern inventories (Aggemyr and Cousins 2012). Measuring diversity using species richness has a long history in the species–area relationship (SAR), which is one of the most fundamental and well-studied associations in ecology and biology, with overwhelming evidence that it exists (Arrhenius 1921; Kohn and Walsh 1994; Drakare et al. 2006).

In community ecology, it is common to use a multivariate approach, including species diversity measures that account for the presence and abundance of individual species, which may reflect different biotic and abiotic factors that are not captured by measures of species richness (Purvis and Hector 2000; Chiarucci et al. 2011; Jenkins and Ricklefs 2011). These analyses are often performed in tandem with analyses of species richness, finding that different land use and management variables explain species richness and composition, or do so to varying extents (e.g. Klimek et al. 2007; Schmucki et al. 2012). If we are to accurately interpret how species richness and composition relate to one another and how they respond to environmental changes such as land-use change, climate change and shifts in management, it is important that we first understand how these common measures of diversity relate to the classic underlying biogeographical and landscape-ecological drivers of population and community patterns. However, this has not yet been explicitly explored.

We present a comparison of two biodiversity measures on 112 islands in the Baltic Sea in relation to classic biogeographical and landscape ecological variables, and we ask whether species richness and species composition respond differently to local, landscape and biogeographical factors. Combining extensive plant surveys with measures of island area, distance to mainland, amount of bare bedrock, open and forest habitats, and structural connectivity, we ask how plant richness and species composition differ in relation to the spatial environment. Islands are excellent model systems for investigating landscape effects on biodiversity (Wardle 2002; Whittaker et al. 2017), and our results are therefore of relevance to the understanding and management of other fragmented habitats or ecosystems.

Methods

Study area

The study area is situated in the outer archipelago of Stockholm, Sweden, in the Baltic Sea, covering

roughly 350 km^2, (midpoint 59°15′N, 18°50′E) (Fig. 1). Approximately 10,000 years ago, the Late Weichselian deglaciation started, with the enormous weight of the thick ice-sheet suppressing the land. When the ice retreated, the land started to rebound, and today the isostatic rebound in the area has still significant landscape effects, with islands rising by

approximately 4.6 mm per year (Auffret and Cousins 2018). The first islands in the study area started to appear c. 3000 years ago, and today the Stockholm archipelago consists of approximately 29,000 islands, ranging from smaller islets and skerries to larger islands with settlements. None of the islands included in this study have been connected to mainland by any
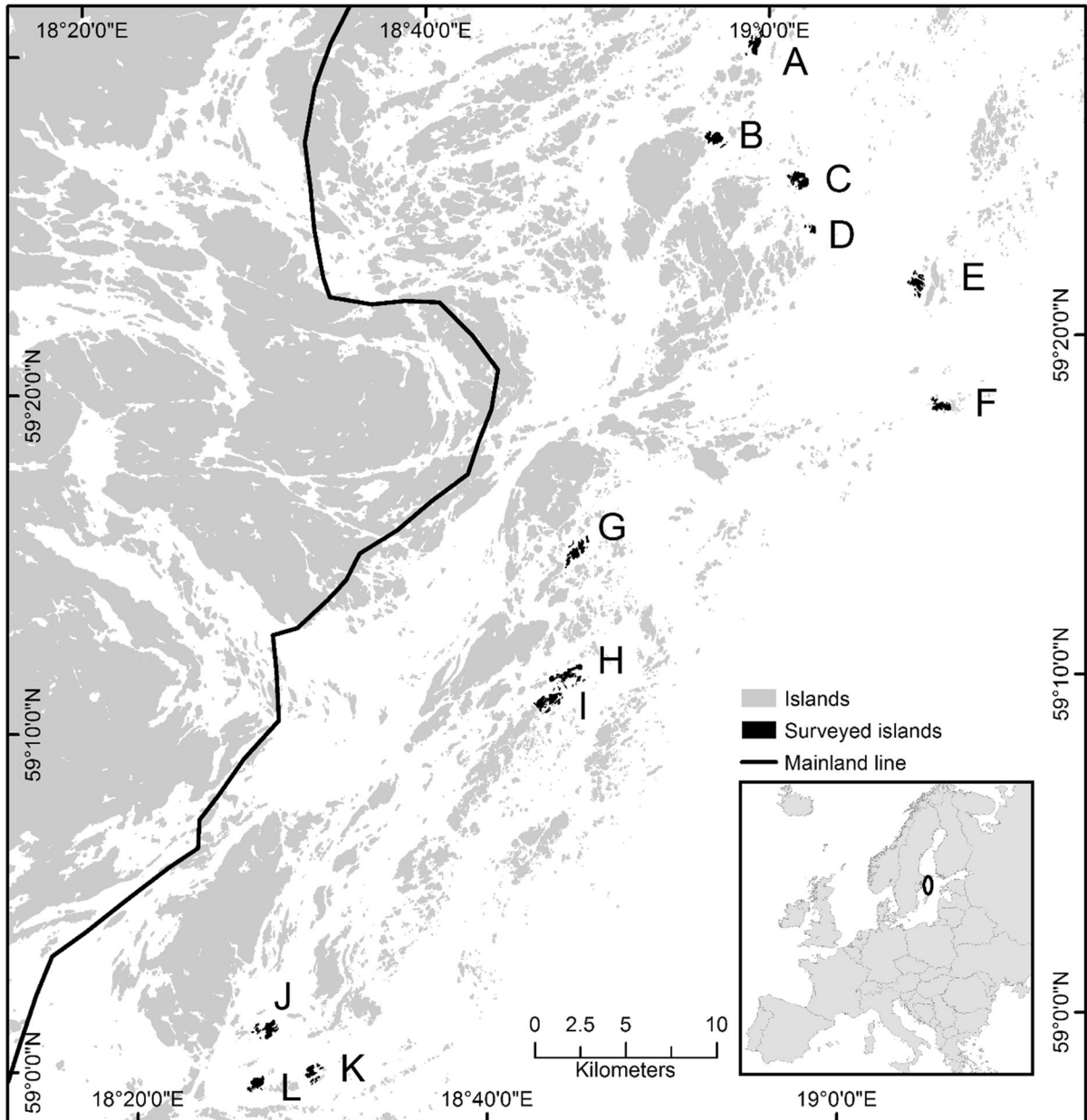

Fig. 1 The study area, situated in the outer archipelago of Stockholm, Sweden, in the Baltic Sea. Plant species richness and composition was surveyed on 112 islands (black) in 12 island

groups (**A–L**). The surrounding landscape is represented by islands in grey. The black line represents the border to inner archipelago, here used for measuring distance to mainland

land bridges (Fischer 2013), and the Baltic Sea is not influenced by tidal water. The mean precipitation is 600 mm per year, mean temperature in January is – 2 °C and in July 15 °C (Swedish Metrological and Hydrological Institute, SMHI 2016). The area belongs to the boreo-nemoral zone with a dominance of coniferous forests, although deciduous forests occur on many islands. However, on smaller skerries and islands in the outer archipelago the vegetation is sparse with few trees and no forest. When the islands rose above the sea most of the finer soil particles were washed away, leaving the islands with shallow soils, bare bedrock and pockets of deeper soils in sheltered positions. Soils are young and prone to drought thus the vegetation is often patchy. Most of the investigated islands are dominated by areas of low open vegetation with few trees and shrubs on thin soils and bare bedrock. Where the soils are deeper, conifers are found, mainly *Pinus sylvestris* and *Juniperus communis*, while broadleaf *Alnus glutinosa* is found on wetter soils. Beside junipers and alders, Rowans (*Sorbus aucuparia*) are among the first trees and shrubs to colonise the islands. We found a total number of 354 plant species on the 112 islands, with a mean of 58 (± 44 SD) species per island, (Table 1). The three most common species were *Allium schoenoprasum* (112 islands), *Sedum telephium* (106 islands), and *Rumex crispus* (103 islands). The most common species along the shoreline, reflecting the marine

influence, are *Phalaris arundinacea*, *Lythrum salicaria* and *Schoenoplectus maritimus*.

Species and landscape data

We surveyed plant species on 112 islands, 0.02–54.4 ha in size, distributed in 12 island groups in the outer Stockholm archipelago (Fig. 1). The 12 island groups were selected from islands in the outer archipelago, where their distinct grouping of islands facilitating fieldwork. Island groups ranged in size from three (groups B, D and F) to 19 (group I; Fig. 1) surveyed islands. All island groups contained additional skerries that were not included in the species inventories. Field surveys took place during two consecutive field seasons 2009–2010, from mid-June to mid-August. All islands were inventoried with equal sampling effort, approximately 45 min per hectare, walking back and forth across the whole of each island, observing the presence of plant species. Nomenclature followed Mossberg and Stenberg (2010). Plant species richness was calculated as number of species per island and plant species composition was represented in a binary matrix including species name and island and presence (1) or absence (0), without any information about abundance.

Candidate landscape variables consisted of island area, habitat heterogeneity, island height, distance to mainland, and structural connectivity (Table 1). Island area (hectare) was extracted from a digital terrain map from 2009 (1:50,000). Habitat heterogeneity on each island was calculated as the Shannon diversity of the three dominant land-cover types in the study area: open land, forest and bare rock, which were also extracted from the terrain map. Island height (m) was represented by the highest point of each island and extracted from a digital elevation model created from Lidar data from 2012, with a resolution of 1 m² or less. The geography of our study region dictates that there is no clear line that marks the boundary between mainland and archipelago, due to much of the inner archipelago being based on a mixture of large islands and mainland peninsulas. We therefore classified a border based on a shift in landscape character from larger more sheltered islands with denser deciduous and coniferous forest, human-populated areas, roads and other infrastructure to smaller islands exposed to the open sea and with sparse vegetation or smaller

Table 1 Summary data for all variables included in the study

	Mean	SD	Min	Max
Species richness	58	± 44	7	208
Island area	4.8	± 10.8	0.002	54.4
Island height	6.5	± 5.3	1.3	32.3
Distance to mainland	14.5	± 5.0	6.8	24.0
Habitat heterogeneity	0.222	± 0.240	0	1.04
Connectivity 100 m	4.7	± 8.2	0	41.7
Connectivity 1000 m	16.1	± 73.9	0.17	785.0
Connectivity 4000 m	81.8	± 137.4	0.94	744.5

Mean values (Mean), standard deviation (SD), minimum (Min), and maximum (Max) for species richness, island area (hectare), island height (metres), distance to mainland (kilometres), habitat heterogeneity, and structural connectivity (hectare) for the 112 islands in Stockholm archipelago, Baltic Sea

coniferous forest (see Fig. 1). Distance to mainland (km) was therefore measured as the Euclidean distance between island edge and this boundary. For structural connectivity we used a measure developed by Aggemyr and Cousins (2012) (Eq. 1), which is a non-species specific measure incorporating both habitat area and fragmentation. This means that a focal island surrounded by many small islands has a lower structural connectivity compared to an island that is surrounded by a few large islands encompassing the same area. This is to account for the fact that a larger island should contain more species that can disperse to the focal island. Connectivity measures such as this, that include information about size and distance of all potential source populations is especially desirable in highly fragmented habitats such as ours (Moilanen and Nieminen 2002). Three buffer distances were used to evaluate the effects of connectivity at local, landscape, and extended landscape scales on the diversity of each focal island. All islands within the buffer were included in the calculation, even those not surveyed for plant species.

$$C_i = \sum_{j \neq i} W_{A_j} W_{d_j} A_j \text{ where } W_{A_j} = \frac{A_j}{\sum_{l \neq i} A_l} \text{ and } W_{d_j} = k^{\frac{d_{ij}}{r}} \tag{1}$$

where A_j is the area of island j and $\sum_{l \neq i} A_l$ is the area of all surrounding islands within the buffer radius, r. For W_{A_j} applies $0 < W_{A_j} \leq 1$ and $\sum W_{A_j} = 1$. The exponential function, $k^{\frac{d_{ij}}{r}}$, was assigned to W_{d_j}. The Euclidean distance, d_{ij}, is the distance between island i and j, and r is the buffer radius and k is a constant scaling W_{d_j} which is equal to k when $d = r$. We set k to 0.01. Independent of the value of r we get $k \leq W_{d_j} < 1$. The combination of W_{A_j} and W_{d_j} gives $0 < W_{A_j} W_{d_j} \leq 1$. W_{d_j} gives less weight to islands further away from the focal island, but still within the buffer zone. The buffer distances (r) used were 100 m (local), 1000 m (landscape) and 4000 m (extended landscape). All landscape variables were calculated using ArcGIS 10.2.2 (ESRI, Redlands, CA, USA).

Statistical analysis

Two models were built to analyse plant species richness and plant species composition, both including

the full data set of 112 islands. To identify any collinearity between candidate environmental variables, Pearson product moment correlation coefficients were calculated for all variables: island area, island height (a proxy for island age), distance to mainland, habitat heterogeneity and structural connectivity. Strong correlations were identified between island area and island height (Pearson product moment correlation coefficient = 0.85), and between island area and habitat heterogeneity (Pearson product moment correlation coefficient = 0.78). We therefore removed island height from further analysis, but in order to retain a measure of habitat heterogeneity, we calculated the residuals of a regression between island area and habitat heterogeneity to remove the common variance between these two variables, and thus to include only the variance specific to habitat heterogeneity. This variable is hereafter referred to as habitat heterogeneity (residualized). All remaining variables has coefficients of less than 0.7 (Dormann et al. 2013; Online Resource Table 1). In addition to calculating correlation coefficients, we also examined explanatory variables using variance inflation factors (VIFs). Values greater than 10 indicate multicollinearity (Chatterjee and Hadi 2012), but to be conservative, VIFs of 3 or above should be excluded (Zuur et al. 2010). Our remaining variables of islands area, distance to mainland, habitat heterogeneity (residualized) and structural connectivity at the local, landscape and extended landscape scales all had VIFs below 2 (Online Resource Table 1). Prior to analysis, variables representing an area (island area and structural connectivity) were log10 transformed. All explanatory variables were rescaled to fit a scale between 0 and 1.

Since the data for species *richness* were overdispersed with a mean of 58 and variance of 1956, a generalized linear mixed model (GLMM) with a negative binomial distribution was built, with the above explanatory variables, while island group was included as a random factor to eliminate the effect of islands being geographically grouped (Fig. 1). ANOVA was used to test whether this random factor was significant, comparing the full model with and without it. To estimate the relative quality of the models we used Akaike information criterion (AIC) and stepwise backwards selection (Akaike 1974; Aho et al. 2014). When the best model was found, each variable within this model (island area, local

connectivity, and extended landscape connectivity) was excluded one at a time and the significant contribution of each variable was tested using ANOVA at α = 0.05. We also created single-predictor models explaining species richness with each of these variables, plus island group as a random factor. Finally, plant species were also divided into four groups depending on life form: forbs, graminoids (families Poaceae, Juncaceae, and Cyperaceae), shrubs, and trees. Each group was analysed separately with GLMM to identify patterns for each species group separately, with island group as random factor. We used stepwise backward selection as method and the relative quality of the models was estimated using AIC (Online Resource Table 2). Statistical analysis was carried out using R 3.3.3 (R Core Team 2017), package usdm, function: *vifstep* (Naimi 2015), package lme4: function *glmer.nb* (Bates et al. 2014), package MASS: function *glm.nb* (Venables and Ripley 2002), and package vegan, function: *diversity* (Oksanen et al. 2018).

Plant species *composition* was analysed using partial canonical correspondence analysis (pCCA) to assess the effect of landscape variables on species composition. In the partial CCA, the variability in the species composition explained by island group was first subtracted and then a CCA was performed on the residual variability (Borcard et al. 1992; Lepš and Šmilauer 2003). All variables, i.e. island area, distance to mainland, habitat heterogeneity (residualized), structural connectivity at 100, 1000, and 4000 metres buffer radii were included. We also analysed the effect of each explanatory variable when no other was included (Lambda-1) and how much each explanatory variable contribute to the additional variance explained when included in the model (Lambda-A). Using automatic selection with Monte Carlo 499 permutations and α = 0.05, significant variables for species composition were analysed. As with species richness, we also analysed the data in groups according to life form. By analysing each group with only one significant variable at a time in a pCCA, the species scores indicate how the species are arranged along that variable (Online Resource Table 3). The pCCA was performed in CANOCO 4.5 (CANOCO for Windows Version 4.56, Biometris-Plant Research International, Wageningen, The Netherlands). Data have been deposited at the Figshare data repository:

http://dx.doi.org/10.17045/sthlmuni.5607112 (Aggemyr et al. 2018).

Results

A total of 354 species were found on the 112 islands. Of these, 242 species were classified as forbs, 66 as graminoids, 30 as shrubs, and 16 as trees.

Plant species richness

Three variables were found to have significant effects in explaining species richness on the 112 islands after controlling for island group. By far the most important factor was island area, with more species being found on larger islands (estimate = 3.99, standard error = 0.15, p < 0.000). Structural connectivity also had a positive effect on species richness, with higher connectivity at both at the local scale (buffer radius 100 m; estimate = 0.24, standard error = 0.11, p = 0.026) and the extended landscape scale (buffer radius 4000 m; estimate = 0.81, standard error = 0.32, p = 0.012) resulting in more species-rich island communities, with a stronger positive effect of connectivity in the extended landscape (Table 2). Although the above three variables were all significant in the final model and made significant contributions to the final model (ANOVA: island area p < 0.000, local-scale connectivity p = 0.026 and extended landscape-scale connectivity p = 0.021; Table 2), single-predictor models (also including island group as a random factor) showed only island size to have a significant (positive) effect on species richness. Nonetheless, the final model containing all three variables fits the data better than the single-predictor island area model, as shown by the models' AIC (Table 2). The random factor island group was significant (p = 0.015). Variables not significant (p > 0.05) were distance to mainland, habitat heterogeneity (residualized), and landscape-scale structural connectivity. Patterns of species richness across species life forms were similar to those of the whole community, especially evident for forbs, the largest group (Online Resource Table 2).

Table 2 Variables explaining plant species richness on 112 islands in a Baltic Sea archipelago. GLMM shows the fixed predictors present in the final generalized linear mixed-effects model that also contained island group as a random factor

	Estimate	GLMM			ANOVA		AIC
		Standard error	Residual deviance	p Value	Chi square	p Value	
Full model							
Island area	3.99	0.29		< 0.001	216.2	< 0.001	1105.3
Conn 100	0.24	0.11		0.03	4.9	0.03	894.1
Conn 4000	0.81	0.32		0.01	5.3	0.02	894.5
Single variable							
Island area	3.98	0.16	889.4	< 0.001			897.4
Conn 100	− 0.03	0.29	1097.8	0.93			1105.8
Conn 4000	1.12	0.71	1095.3	0.12			1103.3

ANOVA and AIC show the effect of removing each predictor from the full model containing all predictors. AIC of the full model was 891.1, residual deviance for the full model was 879.1, and residual deviance for the null model was 1097.8 with island group as random factor. A GLMM with island group as random factor was also performed for each single variable. Random factor was significant (p = 0.015)

Plant species composition

Species composition on the 112 islands revealed a more complex pattern, with island area and structural connectivity at a landscape scale the most important variables for species composition, controlling for the effect of island group. Habitat heterogeneity (residualized) followed by extended landscape and local connectivity, which were also significant predictors ($\alpha < 0.05$) of plant community composition on the islands. Island area had the highest effect on species composition, both when no other variable was included (Lambda-1) and in the full model (Lambda-A). Since we used residualized habitat heterogeneity, the Lambda-1 of 0.07 was the variance explained when the correlation effect between island area and habitat heterogeneity was removed. Distance to mainland had no effect on species composition ($p > 0.05$), however tree species were negatively influences by distance to mainland (Online Resource Table 3). The sum of all canonical eigenvalues was 0.419 and total inertia was 3.448, which means that 12% of the variation in species composition could be explained by the environmental variables used in this analysis after the effect of island group was removed. Axis 1 explained 63.8% (eigenvalue 0.267) of the total explainable variance (the species-environment relation) of the data, and the cumulative percentage explained for axis one and two was 74.5% (eigenvalue

for Axis 2 was 0.045). As with species richness, species composition showed generally the same trends when comparing species groups separately, although there was some variation in the effect of local-scale connectivity (Online Resource Table 3).

Discussion

We have demonstrated that plant species richness and composition differ significantly in their responses to local, landscape and biogeographical variables, with species composition showing the potential to offer additional insights to ecological processes when combined with the commonly-used measure of species richness. Island size was the dominant driver of both species richness and composition, following the species–area relationship and patch area's well-known effects on species richness (Arrhenius 1921; Drakare et al. 2006), turnover (Auffret et al. 2017a) and composition (Negoita et al. 2016). However, ecological processes are driven by factors relating to different elements of the landscape and at different scales, all of which can affect species occurrences in a focal patch (Plue and Cousins 2018). Indeed, we showed that species richness and composition responded to habitat heterogeneity and landscape connectivity at different spatial scales (Tables 2 and 3), while further patterns emerged when focussing on specific life forms (Online

Table 3 Variables explaining ($\alpha = 0.05$) plant species composition on 112 islands in the Baltic Sea archipelago

Variable	Lambda-1	Lambda-A	p Value
Island area	0.26	0.26	0.002
Connectivity 1000 m	0.09	0.04	0.006
Habitat heterogeneity (residualized)	0.07	0.05	0.002
Connectivity 4000 m	0.04	0.04	0.026
Connectivity 100 m	0.03	0.03	0.028

The variables are presented in inclusion order explaining plant species composition on the 112 islands included in the study. Lambda-1 gives explained variance for the single variable model. Lambda-A gives the additional variance the variable explains, given the variables already included. Distance to mainland was not significant p > 0.05

Resource Table 3). Such additional landscape effects can for example give valuable guidance for conservation strategies, even when habitat area is known to be the strongest driver of biodiversity patterns (Sullivan et al. 2017).

Species richness

In accordance with studies from other island systems and fragmented terrestrial habitats, species richness on our 112 islands increased with increasing island area (MacArthur and Wilson 1967; Lindgren and Cousins 2017) (Table 2). We also found a positive effect on species richness with increasing structural connectivity at the local scale (buffer radius 100 m) and at the extended landscape scale (buffer radius 4000 m). At the local scale, nearby islands may function as source populations contributing to source-sink dynamics or by the rescue-effect, preventing species from going extinct (Brown and Kodric-Brown 1977; Piessens et al. 2004), or they might even act as extensions of the focal island itself and therefore allow the island to support a higher species richness. At the extended landscape scale, high values of connectivity indicate that there is simply more land surrounding the focal island that can host a larger species pool, which can then be reflected in the species richness of the focal island (Pärtel et al. 1996). Surprisingly, our results did not show a negative effect of distance to mainland on species richness, which alongside island size is a fundamental part of island biogeography theory (MacArthur and Wilson 1967). This could be explained by the islands' geographical position relatively far out into the archipelago relative to the common dispersal distances of most plant species

(Bullock et al. 2017). In previous work, we have shown that distance to mainland is an important predictor of plant species richness and immigration (Aggemyr and Cousins 2012; Auffret et al. 2017a), but these studies were carried out in a less isolated part of the Stockholm archipelago, closer to the mainland. In the current case, it could be that the connectivity at the wider landscape has replaced distance to mainland as a factor explaining species richness, being more appropriate to the dispersal ability of the taxonomic group studied here. Furthermore, the configuration of the surrounding landscape might have a positive effect with islands acting as stepping stones, an effect not captured by Euclidean measures such as distance to mainland. Other studies have also stressed the importance of the landscape configuration and its influence on plant species richness (Hernandez-Stefanoni 2005), with more fragmented landscapes often having lower species richness (Collinge 1996; Turner 1996; Laurance 2008; Cousins 2009).

Species composition

In contrast to species richness, plant species composition on an island was determined by habitat heterogeneity and structural connectivity at multiple scales alongside island area (Table 3). Not surprisingly, islands with more habitat types and a more heterogeneous distribution of these habitats were found to support different sets of plant species than islands with more homogeneous land cover. Elsewhere in the literature, habitat heterogeneity has been shown to be reflected in island height (Panitsa et al. 2008; Kougioumoutzis and Tiniakou 2015) We found that heterogeneity was highly correlated with both island

height and island size (Online Resource Table 1), meaning that either could be used as a proxy in areas where land-use maps are unavailable. In our study system, island height is strongly related to island age as a result of isostatic land uplift, and hence soil development and successional stage. This itself can also be related to biodiversity in coastal habitats (Auffret and Cousins 2018). Habitat heterogeneity has also been found to be strongly linked to plant species richness (Stein et al. 2014), but habitat heterogeneity was only significant in determining species composition in our case. This could be because in our system, the strong effect of island area on species richness overrides all variables that occur within the island itself and that these only affect species composition to a significant extent. This illustrates that in other isolated and/or strongly fragmented systems, the use of species composition can be used to identify how additional patch-level variables drive variation in plant communities.

In addition to how island characteristics differed in determining species richness and composition, the scale at which structural connectivity determined community patterns also varied. For species composition, structural connectivity at the landscape scale (buffer 1000 m) rather than at the local or extended landscape scale was the most important (Fig. 2). This might be because at this intermediate scale the landscape is more heterogeneous compared to the local scale but the dispersal distances required to reach the focal island are shorter compared to the largest
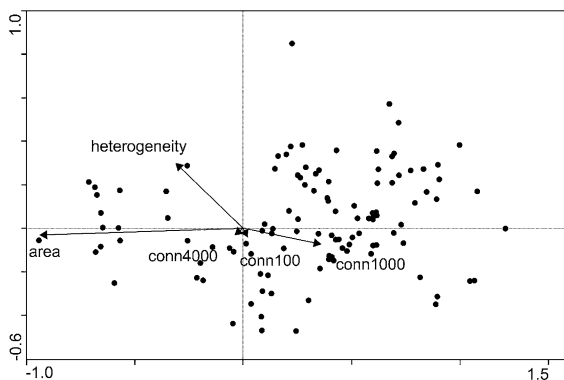
scale. Although seed dispersal usually occurs at local scales, distances of hundreds of metres to kilometres are not uncommon (Bullock et al. 2017), and can be important for colonizing new areas (Cain et al. 2000). Therefore, whereas connectivity at the local scale and extended landscape scale can explain species richness through the maintenance of individual populations and through a larger available species pool, respectively, having a number of different islands within plausible dispersal distances at the landscape scale can influence the identity of plant species present on the focal island.

Differences in species composition across islands with different local and landscape characteristics are almost certainly driven to some extent by species' functional traits. Species with different traits will be more or less abundant in the three main habitats identified on our study islands, with for example more drought-tolerant plants being more adapted to rocky areas and taller species with larger leaves are more likely to occupy forested habitats (Kimberley et al. 2014; Copeland et al. 2016). Seed dispersal, which is also strongly related to plant functional traits (Thomson et al. 2011; Tamme et al. 2014), will also determine which species disperse and how long it may take, while both structural connectivity and the plant species' ability to disperse and establish are important to understand how plant populations are connected in space (Negoita et al. 2016; Auffret et al. 2017b). Indeed, we have previously shown that plant functional traits and biogeographical and landscape variables interact to drive community turnover in the Stockholm archipelago, with for example good dispersal ability combining with proximity to mainland to increase immigration, and seed banking more likely to promote species persistence on larger islands (Auffret et al. 2017a). Interactions between functional traits and landscape parameters have been found elsewhere (Lindborg et al. 2012), and give valuable context to differences in plant species composition across environmental gradients.

Outlook

Although species richness can be an informative measure of diversity, plant communities are dynamic systems under constant change due to local extinction and immigration. As discussed above, community assembly and turnover are determined by the interactions between spatial structure and plant functional

Fig. 2 A pCCA (the effect of island group partialled out) biplot for plant species composition on all 112 islands (dots) and significant explanatory variables (arrows); island area (area), habitat heterogeneity residualized (heterogeneity), and structural connectivity (conn), each number represent a buffer radius (100, 1000, and 4000 m)

traits (Negoita et al. 2016; Auffret et al. 2017a), resulting in divergent species compositions while species richness remains tied to island size (Aggemyr and Cousins 2012). Our analyses show that using species richness alone can fail to capture both how within-patch environmental variation and key ecological processes such as immigration and extinction driving changes in community composition in time and space (Kadmon and Pulliam 1993; Wilsey et al. 2005; Morris et al. 2014). Therefore, it is clearly valuable to include species composition as a response variable in landscape ecological and biogeographical analyses.

In a world with continuing habitat destruction and fragmentation (Foley et al. 2005; Kuemmerle et al. 2016; Watson et al. 2016) it is essential for both researchers and practitioners to understand patterns of biodiversity in an area and how it is influenced by local and landscape conditions. Measurements of biodiversity therefore need to be efficient regarding the use of limited resources to investigate large areas but also to be comparable over time and between regions. While techniques to analyse biodiversity data are advancing rapidly (La Salle et al. 2016), investigations of spatial effects on biodiversity are still largely focused on species richness (Haddad et al. 2017; Whittaker et al. 2017). By using a comprehensive data set of plant species occurrences from 112 islands, we show that the inclusion of a measure of species composition can give a greater insight into the ecological processes occurring in a fragmented landscape than the number of species present. As only presence/absence data are required, we recommend that species community composition should be used as a standard and informative measure of diversity for biogeography, landscape ecology and conservation planning.

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