

Multi-scale phylogenetic structure in coastal dune plant communities across the globe

Ane Kirstine Brunbjerg^{*,1,2}, Jeannine Cavender-Bares³,
Wolf L. Eiserhardt¹, Rasmus Ejrnæs², Lonnie W. Aarssen⁴,
Hannah L. Buckley⁵, Estelle Forey⁶, Florian Jansen⁷, Jens Kattge⁸,
Cynthia Lane⁹, Roy A. Lubke¹⁰, Angela T. Moles¹¹,
Ana Laura Monserrat¹², Robert K. Peet¹³, Julissa Roncal¹⁴,
Louise Wootton¹⁵ and Jens-Christian Svenning¹

¹ Ecoinformatics & Biodiversity Group, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C., Denmark

² Department of Bioscience, Aarhus University, Grenaavej 14, DK-8410 Rønde, Denmark

³ Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, Falcon Heights, MN 55108, USA

⁴ Department of Biology, Queens University, 116 Barrie Street, Kingston, Ontario K7L 3N6, Canada

⁵ Department of Ecology, Lincoln University, PO Box 84, Canterbury 7647, New Zealand

⁶ Laboratoire d'Ecologie, EA 1293 ECODIV, FED SCALE, UFR Sciences et Techniques, Université de Rouen, 76821 Mont Saint Aignan Cedex, France

⁷ Institute of Botany and Landscape Ecology, Soldmannstr. 15, 17487 Greifswald, Germany

⁸ Functional Biogeography Research Group, Max Planck Institute for Biogeochemistry, Hans Knoell Str. 10, 07745 Jena, Thuringia, Germany

⁹ Lake Lily Ecology, Ltd., PO Box 8455, Canmore, AB T1W 2V2, Canada

¹⁰ Department of Botany, Rhodes University, PO Box 94, Grahamstown, East Cape 6140, South Africa

¹¹ Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, The University of New South Wales, Botany Road, Kensington, Sydney, New South Wales 2034, Australia

¹² Grupo de Investigación en Sistemas Ambientales Complejos, Facultad de Ingeniería, Universidad de Flores, Pedernera 275, Ciudad de Buenos Aires, Argentina

¹³ Department of Biology, University of North Carolina, Chapel Hill, NC 27599-3280, USA

¹⁴ Department of Biology, Memorial University of Newfoundland, 232 Elizabeth Avenue, St. John's, NL A1B 3X9, Canada

¹⁵ Department of Biology, Georgian Court University, 900 Lakewood Avenue, Lakewood, NJ 08701, USA

*Correspondence address. Department of Bioscience, Aarhus University, Grenaavej 14, DK-8410 Rønde, Denmark. Tel: +45-8715-8865; Fax: +45-8715-4326; E-mail: akb@dmu.dk

Abstract

Aims

Studies integrating phylogenetic history and large-scale community assembly are few, and many questions remain unanswered. Here, we use a global coastal dune plant data set to uncover the important factors in community assembly across scales from the local filtering processes to the global long-term diversification and dispersal dynamics. Coastal dune plant communities occur worldwide under a wide range of climatic and geologic conditions as well as in all biogeographic regions. However, global patterns in the phylogenetic composition of coastal dune plant communities have not previously been studied.

Methods

The data set comprised vegetation data from 18 463 plots in New Zealand, South Africa, South America, North America and Europe. The phylogenetic tree comprised 2241 plant species from 149

families. We calculated phylogenetic clustering (Net Relatedness Index, NRI, and Nearest Taxon Index, NTI) of regional dune floras to estimate the amount of *in situ* diversification relative to the global dune species pool and evaluated the relative importance of land and climate barriers for these diversification patterns by geographic analyses of phylogenetic similarity. We then tested whether dune plant communities exhibit similar patterns of phylogenetic structure within regions. Finally, we calculated NRI for local communities relative to the regional species pool and tested for an association with functional traits (plant height and seed mass) thought to vary along sea–inland gradients.

Important Findings

Regional species pools were phylogenetically clustered relative to the global pool, indicating regional diversification. NTI showed

stronger clustering than NRI pointing to the importance of especially recent diversifications within regions. The species pools grouped phylogenetically into two clusters on either side of the tropics suggesting greater dispersal rates within hemispheres than between hemispheres. Local NRI plot values confirmed that most communities were also phylogenetically clustered within regions. NRI values decreased with increasing plant height and seed mass, indicating greater phylogenetic clustering in communities with short maximum height and good dispersers prone to wind and tidal disturbance as well as salt spray, consistent with environmental filtering along sea–inland gradients. Height and seed mass both showed significant phylogenetic signal, and NRI tended to correlate negatively with both at the plot level. Low

NRI plots tended to represent coastal scrub and forest, whereas high NRI plots tended to represent herb-dominated vegetation. We conclude that regional diversification processes play a role in dune plant community assembly, with convergence in local phylogenetic community structure and local variation in community structure probably reflecting consistent coastal–inland gradients. Our study contributes to a better understanding of the globally distributed dynamic coastal ecosystems and the structuring factors working on dune plant communities across spatial scales and regions.

Keywords: disturbance, phylogenetic community structure, plant functional traits, plant height, seed mass

INTRODUCTION

Different factors shape community structure and composition of biotic assemblages differently at different scales. At the same time, structuring factors at one scale are not independent of structuring factors at other scales (Ricklefs, 2004; Willis and Whittaker, 2002; Zobel, 1997). At global spatial extents, evolutionary and historical processes such as speciation, extinction, migration and plate tectonics may influence lineage distribution and local community structure (Kisling *et al.*, 2012; Ricklefs, 1987), notably through their effect on regional species pools from which species are filtered into local communities (Zobel, 1997). At local spatial extents, community structure may primarily be shaped by abiotic filtering and biotic interactions (Willis and Whittaker, 2002). Thus, integration of several spatial scales into a hierarchical framework has been proposed, e.g. in order to reveal the factors determining large-scale differences in species richness (Ricklefs, 2004; Willis and Whittaker, 2002). Only few studies have considered the importance of phylogenetic history for explaining community composition across large spatial extents (Cardillo, 2011). Although some recent studies (Barberán and Casamayor, 2010; Eiserhardt *et al.* 2013a; Kisling *et al.*, 2012) have focused on the determinants of phylogenetic community structure at continental and global scales, only a few taxonomic groups have been treated, and numerous questions on large-scale patterns remain unanswered. To the extent that diversification processes are important in community assembly, phylogenetic information is required to comprehend the interacting roles of ecology and evolution (Algar *et al.*, 2013, Cavender-Bares *et al.*, 2009, Emerson and Gillespie, 2008), and more studies are needed to understand the relative contributions of various mechanisms at different scales (Swenson, 2011). Here, we seek to uncover the important factors for community assembly across spatial scales from local filtering processes to global long-term diversification and dispersal dynamics.

Coastal dunes lend themselves to the study of community assembly across spatial scales. Coastal dunes are found on all continents and under a wide range of climatic and geologic conditions (Maun, 2009). Despite their worldwide distribution, dune ecosystems share universal sea–inland gradients in local environmental conditions with decreasing wind exposure, sand deposition, salt spray, pH and increasing soil organic matter and soil moisture from the sea and inland. As a consequence, a distinct coast–inland zonation of plant communities has long been acknowledged (Warming, 1909; Wilson and Sykes, 1999). This said, there are also strong geographic differences in the floristic composition of dune plant communities (Doing, 1985), likely reflecting climatic differences and regional scale processes such as speciation and extinction (Ricklefs, 1987). Thus, the make-up of local dune plant communities is likely affected by a variety of processes acting on widely different spatial scales. However, global patterns in the structure of coastal dune plant communities have not previously been studied quantitatively.

At a global scale, historical patterns in species origins may drive dune plant community composition and structure. However, these patterns may be blurred by a coastal dune environment offering excellent conditions for long-distance dispersal including wind dispersal along coast lines, water dispersal by sea currents and animal dispersal (especially by birds) (Maun, 2009). Of note, dune species are known to be adapted for water and wind dispersal (Maun, 2009). Thus, it is unclear how important *in situ* diversification is in dune plant communities. At regional and local scales, it has been demonstrated that the spatial distribution of plant species in coastal dunes is related to species sorting along environmental gradients (Brunbjerg *et al.*, 2012b; Gallego-Fernández and Martínez, 2011; Lane *et al.*, 2008) caused by the specific plant adaptations to this highly stressful and heterogeneous habitat (Maun, 2009). Moreover, phylogenetic community structure has been found to be related to disturbance and—to a lesser extent—competition at local and regional scales (Brunbjerg *et al.*, 2012a). This indicates that the evolutionary history of functional traits (any trait which

impacts fitness indirectly *via* its effects on growth, reproduction and survival as defined in [Violle *et al.*, 2007](#)) interacts with the strong local environmental gradients in dunes to shape plant communities ([Brunbjerg *et al.*, 2012a](#)).

At the global scale, we asked if the phylogenetic structure of regional dune floras reflects *in situ* diversification, and which barriers are limiting the exchange of lineages among regions. If long-distance dispersal is limited, closely related species would be expected to be geographically clustered according to historical places of clade diversification. Alternatively, if dune plant species are sufficiently vagile, lineage composition should be similar in different regions. We derived two hypotheses based on likely dispersal barriers for temperate and subtropical dune plants: (i) Land barriers may impede dispersal if dune plant species spread most readily with sea currents or along shorelines. In this case, we expected that regions bordering the same ocean, and thus sharing the same water currents and wind corridors, harbour phylogenetically similar floras. (ii) Tropical conditions may inhibit the spread of temperate dune species from the Northern to the Southern Hemisphere or *vice versa* due to climatic niche conservatism, i.e. the inability to evolve tolerance to tropical climates ([Wiens and Donoghue, 2004](#)), resulting in relatively strong differences in species composition between the two hemispheres. This is expected because tropical dunes are inhabited by different plant lineages relative to subtropical and temperate dunes ([Castillo *et al.*, 1991](#); [Lane *et al.*, 2008](#); [Maun, 2009](#)). We based our expectations on current geography since most of the well-represented lineages in this study diversified recently relative to the most important changes in dispersal corridors caused by continental drift ([Lomolino *et al.*, 2006](#)).

At a regional scale we asked if disturbance and other environmental factors that change consistently along the local sea–inland gradient have geographically consistent effects on community composition. If this environmental filtering is strong compared with other regional filtering processes, we expect local phylogenetic community structure to be qualitatively similar across the world despite different species pools. Environmental filtering of plant species based on their functional traits will cause a clustered phylogenetic community structure if traits are phylogenetically conserved ([Kraft *et al.*, 2007](#); [Webb *et al.*, 2002](#)). Plant height and seed mass are thought to be particularly important in reflecting species' ecological strategies related to disturbance ([Weiher *et al.*, 1999](#); [Westoby, 1998](#)). Smaller seeds pack fewer resources but are produced in greater number and have greater colonization and dispersal ability ([Aarssen and Jordan, 2001](#); [Henery and Westoby, 2001](#)) and may therefore be advantageous in disturbed environments. Taller plants compete more effectively for light ([Cavender-Bares *et al.*, 2004](#); [Tilman, 1982](#)), but shorter plants tend to be more resilient under high disturbance ([Weiher *et al.*, 1999](#); [Westoby, 1998](#)). Furthermore, smaller plants may be selected for in disturbed environments as energy is allocated to fast reproduction on the expense of competitive ability (e.g. plant height) because of the limited

time between disturbance events restricting time for vegetative growth ([Grime, 1979](#); [Westoby, 1998](#)). We hypothesize that significant environmental filtering will be associated with disturbed areas, as indicated by plots that contain species with short stature and low seed mass. If such disturbance-related traits are phylogenetically conserved, we expect a negative correlation between phylogenetic clustering in community structure and both seed mass and plant height.

Here, we addressed these questions using a large data set of vegetation plots from nine dune regions on five continents ([Fig. 1](#)). We hypothesized that (i) as a result of local diversification regional dune floras are phylogenetically clustered relative to the global dune species pool; (ii) regional dune floras bordering the same ocean basin are phylogenetically similar due to shared dispersal pathways; (iii) regional dune floras within hemispheres are phylogenetically similar due to the tropics acting as a barrier between the northern and southern temperate zone; (iv) local communities are phylogenetically clustered relative to the regional pool in all regions due to environmental filtering on phylogenetically conserved functional traits; and (v) local phylogenetic structure is correlated with disturbance-related plant traits reflecting environmental filtering along sea–inland gradients.

MATERIALS AND METHODS

Global scale analyses

Study sites and species data

The data set comprised species occurrence data from 18463 vegetation plots in natural coastal dune communities in North America, South America, Europe, Africa and Oceania ([Fig. 1](#); [Supplementary Table S1](#)) ranging from foredune to inland communities. We divided western North America and Europe into floristic subregions as these may host different regional species pools. Western North America was divided into Madrean (western Mexico and the southern California) and Vancouverian (North America from central California to Alaska) following [Cronquist \(1982\)](#), and Europe into North Atlantic region (western Denmark, Holland and Belgium), South Atlantic region (France) and Central European region (Germany and eastern Denmark) following [Frey and Lösch \(2010\)](#) ([Fig. 1](#)).

A global species list was constructed by combining the regional species lists. We used species as the taxonomic level; information on subspecies and variants was not used. Furthermore, hybrids and observations not identified to species level were omitted. The species list was checked for synonyms according to the taxonomy from Taxonomic Name Resolution Service ([Boyle *et al.*, 2013](#); <http://tnrs.iplantcollaborative.org/>). We did not discriminate between native and introduced species.

Phylogeny

An initial phylogenetic tree was constructed in Phylomatic ([Webb and Donoghue, 2005](#)) using the Phylomatic tree



Figure 1: world map showing data location and the nine regions. Region acronyms: Vancouverian North America (V.N.A), Madrean North America (M.N.A), Eastern North America (E.N.A), South America (S.Am), Central Europe (C.EU), North Atlantic European coast (N.Atl.EU), South Atlantic European coast (S.Atl.EU), South Africa (S.Af) and New Zealand (NZ).

R20100701 for plants, which is based on the APG III system (Bremer *et al.*, 2009). Six species were not recognized by Phylomatic (Selaginellaceae (one species), Lycopodiaceae (four species), Cupressaceae (one species)), and these were manually placed in the tree according to Wikström and Kenrick (2001) and Ran *et al.* (2010). This initial tree was resolved as far as possible according to available literature (see Supplementary Table S2a). Three phylogenetic trees were constructed: (i) a ‘minimal conflict tree’, which included only well-supported and non-conflicting relationships from the literature, (ii) a ‘highly resolved tree’, which included both well-supported and less well-supported nodes, and (iii) a ‘fully resolved tree’ where all polytomies in the highly resolved tree were resolved randomly (for details, see Supplementary Data S2b). In the minimal conflict and highly resolved trees, species not found in literature were placed unresolved in the tribe/subfamily/genus they were known to belong to based on relevant taxonomic literature (see Supplementary Table S2a).

We approximated divergence times in Phylocom v. 4.1 (Webb *et al.*, 2008) using the branch length adjustment (BLADJ) function and an age file based on estimated ages from recent literature, mainly Bell *et al.* 2010 (see Supplementary

Table S3 for full details). The dated tree consisted of 2307 species from 171 families and 969 genera; however, for the analyses, a reduced tree with only angiosperms was used to avoid outlier effects on community phylogenetic structure by the very few ($n = 65$) gymnosperms and pteridophytes in the data set. The tree used for the analyses consisted of 2241 species from 149 families and 940 genera.

Local scale analyses

Species occurrence data

Because of variable plot sizes, we divided the data set into two groups: small plots (1–4 m²) and large plots (70–100 m²). This permitted comparison of phylogenetic community structure among regions and variation due to differences in plot size could be accounted for (Supplementary Table S4).

Trait data

We used two traits from the TRY database (Kattge *et al.*, 2011, see Supplementary Table S5 for details) thought to be particularly important for species’ ecological strategies related to disturbance: plant height and seed mass. We used maximum plant height to avoid measurements of seedlings and

juveniles registered in the trait data set (Moles et al., 2009). An additional maximum plant height data set was provided by Angela Moles (Moles et al., 2009). For each species, the maximum height was used if values from several data contributors were found in the combined TRY and Moles data set. For seed mass, mean trait values were calculated for each species if values from several data contributors were found in the database. Seed mass data were obtained for 50% and maximum plant height for 68.4% of the species corresponding to 88.9 and 93.1% of the species occurrence in the whole data set.

Statistical analyses

Global scale analyses

First, we tested if the species co-occurring in any of the nine regions (New Zealand, South Africa, South American, Eastern North America, Vancouverian North America and Madrean North America, North Atlantic Europe, South Atlantic Europe and Central Europe) were more (or less) closely related phylogenetically than expected from random assembly of the global species pool. This was done using both the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI; Webb et al., 2002) to be able to compare phylogenetic community structure at different phylogenetic levels. These indices are defined as standardized effect sizes, quantifying how strongly the phylogenetic relatedness of a set of co-occurring species deviates from a null expectation. They are calculated as $-1 \times [(r_{\text{obs}} - \text{mean}(r_{\text{rand}}))/\text{sd}(r_{\text{rand}})]$, where r_{obs} is the observed phylogenetic relatedness and r_{rand} is the distribution of phylogenetic relatedness expected from random assembly (the null model). NRI and NTI differ only in the way r is calculated: NRI uses the mean pairwise divergence time among co-occurring species, whereas NTI uses the mean of the divergence times between each species and its closest co-occurring relative. Positive values of NRI and NTI indicate phylogenetic clustering (i.e. co-occurring species are more closely related than expected from the null model); negative values indicate phylogenetic overdispersion (i.e. co-occurring species are more distantly related than expected). Calculations were done in R v. 2.12 (R development core team, 2008) using R package Picante (Kembel et al., 2010). We used a null model in which species names were randomly swapped 999 times across the phylogenetic tree (null model 'taxa.labels' in Picante), holding species richness of regions and the species turnover among them constant. The calculation was performed for all three phylogenetic trees (minimal conflict, highly resolved and fully resolved).

Second, we tested if regions were phylogenetically more similar within the same ocean (due to land barriers) or hemisphere (due to climate barriers) than expected at random. To this end, we calculated the phylogenetic turnover among regions using the `comdistnt` and `comdist` function in Picante. For each pair of regions A and B, `comdist` quantifies the mean of all phylogenetic distances (i.e. time since divergence) separating species occurring in A from species occurring in B. `Comdistnt` quantifies the average of the phylogenetic distance

between each species in A and its closest relative in B. To test the dispersal hypotheses, we used a permutational multivariate analysis of variance (adonis) in the Vegan package in R, as recommended by Oksanen (2009). Clustering of regions according to hemisphere (Southern Hemisphere: New Zealand, South Africa, South America versus Northern Hemisphere: North America and Europe) would suggest a tropical dispersal barrier, whereas clustering according to shared sea ways (Atlantic Ocean: Europe, South America, South Africa and Eastern North America versus Pacific: Western North America and New Zealand) would indicate importance of long-distance dispersal *via* sea ways.

The `Nodesig` function in Phylocom (Webb et al., 2008) was used on relative abundance within each region (number of occurrences per species standardized with the total number of occurrences in the region) to identify the clades that were significantly over- or under-represented in the Northern and Southern Hemisphere regions, respectively. Relative abundance was used to minimize the effect of presence of few individuals of, e.g. introduced species occurring in an area by 'accident'. `Nodesig` compares the number of descendent taxa from a given node in each sample with the number of descendent taxa from a given node in a random sample with the same number of taxa (Webb et al., 2008).

To further describe the phylogenetic differences among regions, we identified specific indicator clades for each region using an indicator species analysis (Dufrene and Legendre, 1997) on a node \times site matrix in the `labdsv` package in R. To avoid identifying a large number of small nodes, a significance level of 0.001 was used. The node \times site matrix was derived from a node-as-factor matrix (computed in Phylocom) containing the abundance of certain nodes in a given region from the species phylogeny. The node-as-factor algorithm assesses for each node in the phylogeny whether one or more of its descendent species are found in a given species assemblage (here region), resulting in a node \times site matrix equivalent to the species \times site matrix normally used in community ecology (Webb et al., 2008).

Local scale analyses

Within each region, we used NRI to determine local phylogenetic community structure for each plot (both small: 1–4 m² and large: 70–100 m²) relative to the regional species pool. To allow interpretation of the NRI results, we calculated the phylogenetic signal of each trait (maximum plant height and seed mass). To this end, we used the 'phylosignal' function in Picante and the highly resolved tree to calculate Blomberg's K (Blomberg et al., 2003). P values were based on the variance of the phylogenetically independent contrasts relative to a null model that randomly reshuffled the trait values 1000 times on the phylogenetic tree.

To quantify functional variance among communities, we calculated mean seed mass and maximum plant height for each plot. Mean seed mass was calculated based on \log_{10} seed mass values. We used the maximum height of the tallest

species in each plot, assuming that tall individuals are particularly important for community structure *via* size-asymmetric competition for light (Tilman, 1982). As very tall growing species may have a dominant influence on the outcome of competition for light, height was not log transformed as is otherwise common for continuous trait variables (Moles *et al.* 2004, 2009). Mean plot seed mass and maximum height were only calculated for plots with three or more species with known trait values. We built a linear Ordinary Least Squares (OLS) regression model using NRI as response variable and maximum plant height, mean seed mass, the 14 combinations of region and plot size as well as all interactions (region \times seed mass \times plant height) as explanatory variables. Mean seed mass and maximum plant height were centered and standardized before analyses. The full model was reduced to the best nested model based on the Akaike Information Criterion (AIC). Only plots having mean trait values for both traits were used ($n = 8344$). To assess spatial non-independence of plots within regions, we calculated Moran's I (Legendre and Legendre, 1998) for the residuals of the final model separately for each combination of region and plot size using the Spatial Analysis in Macroecology software (SAM; Rangel *et al.*, 2010). Only plots having geographic coordinates were used ($n = 7599$).

To further describe the ecological difference between more-clustered and less-clustered plots, we calculated the relative proportion of tree-shrub-liana species vs. herb-graminoid-vine species in the 10 plots with highest and lowest NRI values, respectively, for each region. Growth form data (for the 513 species in the selected plots) were compiled from TRY (Kattge *et al.*, 2011, <http://www.try-db.org>) ($n = 411$), and for species not found in these sources ($n = 102$), we used Wikipedia (<http://en.wikipedia.org>) and other web sources. An independent *t*-test was used to assess whether the amount of tree, shrub and liana species differed between plots having high and low NRI values.

Scale dependence of local NRI

Because of the differences in sampling methods (plot size, regional extent and regional habitat heterogeneity) across regions, we assessed the robustness of the phylogenetic community structure analyses. We tested the effect of plot size on NRI values as we expected clustering to be stronger in small plots compared with large plots because larger plots encompass greater environmental heterogeneity and thereby less similar plant species—decreasing clustering (Cavender-Bares *et al.*, 2006; Willis *et al.*, 2010). Difference in mean NRI values in small and large plots was assessed using an independent *t*-test. Furthermore, the effect of differences in regional species pools in terms of regional extent and regional habitat heterogeneity on mean plot NRI was assessed. Latitudinal extent was used as a proxy for regional extent, whereas habitat heterogeneity was estimated by the length of the first axis in a Detrended Correspondence Analysis (DCA) on species presence-absence in plots for each region. We expected mean plot NRI to increase with both regional extent and habitat heterogeneity as environmental filtering should be stronger across larger gradients

(Cavender-Bares *et al.*, 2009). To test the hypothesis, we built OLS models using mean NRI values for small and large regions as response variables and regional habitat heterogeneity and regional extent as explanatory variables, respectively.

RESULTS

Global scale analyses

Of the nine geographic regions, South America, New Zealand and Western North America showed significant clustering based on the NRI. Based on the NTI, all regions except for Eastern North America and South Africa were significantly clustered (Fig. 2; Supplementary Table S6). Because results were consistent regardless of the phylogenetic tree used, only results for the highly resolved tree are reported hereafter.

Calculating the significance of clustering due to a tropical climate barrier or land barriers using *adonis* (R package 'Vegan') and based on phylogenetic similarity, we found the grouping of regions based on climatic barriers to be highly significant in an *F*-test. Regions on the same side of the tropical climate barrier were significantly clustered together based on mean nearest taxon distances (comdistnt, $F = 1.81$, $P = 0.016$) but not based on mean pairwise distances (comdist). Regions sharing water-dispersal ways did not cluster together based on either of the phylogenetic turnover metrics. Over-represented lineages in the Southern Hemisphere included clades within Aizoaceae, Gnaphalioideae, Senecio, Vernoniaceae, Santalales and Celastrales, whereas under-represented lineages were Lamiaceae, Rosaceae, Fagales, Salicaceae, Violaceae and *Carex* (Supplementary Fig. S1; Supplementary Table S7). Most clades had the opposite relationship to the Northern Hemisphere.

The Species Indicator Analysis yielded 986 significant nodes using a 0.001 significance level. The number of clades for which a given region was a significant indicator for more than 50% of the clade's descendants ranged from 0 to 12 clades. Specifically, the North Atlantic European region and South Africa were significant indicator regions for more than 50% of the species in 12 and 11 clades, respectively, whereas New Zealand and South Atlantic European regions were indicator region for less than 50% of the descendant species in clades (Supplementary Table S8).

Local scale analyses

Intra-regional NRI values were positive in 11 of 14 regions and most (9 of 14) were significantly different from the null model in which species were randomly swapped across the phylogeny. Only the Madrean North American region showed significantly negative NRI values and only for small plots (Table 1). To emphasize the areas with strong phylogenetic community structure, only the regions in which NRI was significant in more than 10% of the plots were used for further analysis (South Africa, North Atlantic European region (large and small plots), Central European region (large and small plots), Madrean North America (large plots) and Eastern North America (large plots)) (Table 1).

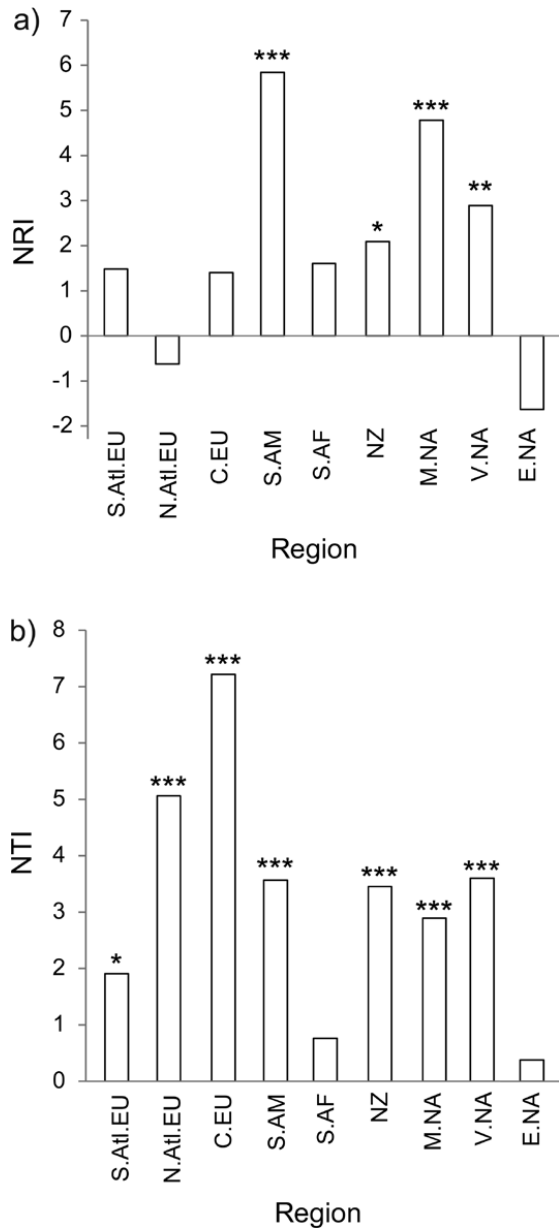


Figure 2: (a) NRI and (b) NTI for each of the nine regions (see Fig. 1 for abbreviations). Negative NRI/NTI values indicate phylogenetic overdispersion, whereas positive NRI/NTI values indicate phylogenetic clustering. Significance is indicated with asterisk: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Blomberg’s K for both plant height and seed mass indicated significantly greater signal than the random model, but less than expected based on Brownian motion evolution (Table 2) as is commonly found in plant trait studies (Eaton et al., 2012; Knapp et al., 2012). Plant height was more strongly phylogenetically conserved than seed mass.

The best OLS model of NRI included region, maximum plant height, mean seed mass and their interaction terms

when using plots holding three or more species for which we had trait values (8344 plots; Table 3; Fig. 3). We found significant differences in NRI between regions. Except for South Africa and Madrean North America, maximum plant height and mean seed mass significantly affected NRI with maximum plant height showing the most consistent pattern among regions (Table 3; Fig. 3; Supplementary Table S9). In general, NRI decreased with increasing maximum plant height (except for North Atlantic European region (small)), whereas NRI increased with mean seed mass for some regions (North Atlantic European region (small), Central European region (small)) and decreased with mean seed mass for other regions (North Atlantic European region (large), Central European region (large) and Eastern North America (large)) (Fig. 3). The results showed significant but weak spatial autocorrelation (Moran’s $I < 0.1$) when calculating Moran’s I on residuals from the full model (Supplementary Table S10). Using all plots (including the plots with less than three species with trait values; 8694 plots) gave similar results ($R^2 = 0.11$, $P < 0.001$).

In all of the five regions containing large plots (and meeting the 10% NRI-criteria), the proportion of trees, shrubs and lianas was higher in plots with low NRI values. However, the trend was only significant in North Atlantic Europe (t -test, $P = 0.013$, mean %high NRI = 0.007, mean %low NRI = 0.072), Central Europe (t -test, $P = 0.001$, mean %high NRI = 0.049, mean %low NRI = 0.260) and Eastern North America (t -test, $P < 0.001$, mean %high NRI = 0.085, mean %low NRI = 0.650), while South Africa was marginally significant (t -test, $P = 0.099$, mean %high NRI = 0.226, mean %low NRI = 0.348), and Madrean North America non-significant (Fig. 4).

Scale dependence of local NRI

When testing the effect of plot size on local plot NRI values in regions for which we had data from both large and small plots, we found a consistent pattern of lower NRI values in small plots (Fig. 5). All, but one region (Vancouverian North America), showed a significant difference in mean NRI between large and small plots. Vancouverian North America was the only region for which the 10% criterion was not met, which might explain the non-significant result for this region.

The effect of regional habitat heterogeneity (as indicated by length of DCA axis 1) on plot NRI was small and not significant for neither small nor large plots. Furthermore, the effect of regional extent (as measured by the latitudinal extent of the region) on plot NRI was small and not significant for neither small nor large plots.

DISCUSSION

In this global study of dune plant communities, we found a cross-scale pattern of phylogenetic clustering, i.e. of regional scale assemblages relative to the global species pool and of plot-scale assemblages relative to the regional species pool. The clustering of regional scale assemblages indicates that dune floras have at least partly assembled *via* regional diversification.

Table 1: mean local phylogenetic community structure represented by NRI for small and large plots in the nine regions

Region	Number of plots	Plot area (m ²)	Mean NRI	<i>P</i> (NRI ≠ 0)	Number of NRI+ (%)	Number of NRI- (%)	Regional extent (km)	Habitat heterogeneity
S.Af	151	100	1.184	<0.001	26 (17.2)	0 (0.0)	168.83	5.40
S.Am	230	100	0.087	0.123	3 (1.3)	4 (1.7)	523.41	6.11
NZ	411	4	0.087	0.103	9 (2.2)	0 (0.0)	675.57	4.50
S.Atl.EU	129	1	0.209	0.008	1 (0.8)	0 (0.0)	224.16	4.01
M.NA	142	1–4	–0.645	<0.001	1 (0.7)	12 (8.5)	1676.10	1.05
M.NA	102	70–100	0.857	<0.001	17 (16.7)	0 (0.0)	1676.10	1.05
V.NA	17	1–4	–0.158	0.572	0 (0.0)	0 (0.0)	3254.15	13.20
V.NA	82	70–100	–0.001	0.992	2 (2.4)	0 (0.0)	3254.15	13.20
N.Atl.EU	1896	1–4	1.193	<0.001	286 (15.1)	1 (0.1)	709.60	9.41
N.Atl.EU	4585	70–100	1.540	<0.001	1001 (21.8)	2 (0.0)	709.60	9.41
E.NA	1015	1–4	0.182	<0.001	53 (5.2)	0 (0.0)	253.05	6.27
E.NA	495	70–100	0.012	0.836	18 (3.6)	48 (9.7)	253.05	6.27
C.EU	675	1–4	0.817	<0.001	92 (13.6)	8 (1.2)	240.18	9.04
C.EU	834	70–100	1.392	<0.001	179 (21.5)	0 (0.0)	240.18	9.04

P values for *t*-test (mean NRI different from zero) and the number and fraction of significant positive (NRI+) and negative (NRI-) NRI plot values using rank significance are given. The regions holding more than 10% significant NRI plot values are marked in bold. Regional extent is measured as latitudinal extent. Habitat heterogeneity within regions is measured as length of axis one of the detrended correspondence analysis. For region acronyms, see Fig. 1.

Table 2: phylogenetic signal of two functional traits (maximum plant height for 1532 species and seed mass for 1121 species) as measured by Blomberg's *K* relative to two null models: random (species randomized 999 times across the tips of the phylogeny) and Brownian motion trait evolution

Null model	Functional traits	Kobs	K.mean.null	Sim > obs	K.ses	<i>P</i>
Random	Plant height	0.57	0.09	0	26.85	0.001
	Seed mass	0.35	0.11	0	1.68	0.001
Brownian motion	Plant height	0.57	1.00	983	–1.35	0.984
	Seed mass	0.35	1.00	999	–2.04	1.000

Observed phylogenetic signal (Kobs), mean value of null model (K.mean.null), number of simulated observations greater than the observed (Sim > obs), standardized effect size (K.ses) and *P* values (*P*) are given.

Table 3: Anova table for the best ordinary least square model for NRI as a function of region, maximum plant height (*H*) and mean seed mass (*SM*) and interactions between them

	Df	Sum sq	Mean sq	<i>F</i> value	<i>P</i>
Region	6	1279.3	213.2	131.55	<0.001
<i>H</i>	1	92.7	92.7	57.17	<0.001
<i>SM</i>	1	9.2	9.2	5.69	0.017
Region: <i>H</i>	6	224.9	37.5	23.13	<0.001
Region: <i>SM</i>	6	190.4	31.7	19.58	<0.001
<i>H</i> : <i>SM</i>	1	5.7	5.7	3.52	0.061
Region: <i>H</i> : <i>SM</i>	6	61.0	10.2	6.27	<0.001
Residuals	8316	13478.7	1.6		

The model is based on 8344 plots holding at least three species with trait values in the seven regions with significant NRI values based on the 10% criteria. Degrees of freedom (Df), sum of squares (Sum sq), mean sum of squares (Mean sq), *F* and *P* values are given.

In particular, a tropical climate barrier appears to separate two 'evolutionary arenas' (Jetz and Fine, 2012) for temperate and subtropical dune plant communities, resulting in phylogenetically distinct groups in the Northern and Southern Hemisphere. Within regions, significant phylogenetic clustering appears to reflect strong environmental filtering along sea–inland gradients, as evidenced by the link to disturbance-related plant functional traits (maximum plant height, mean seed mass).

Global scale

Our study showed regional dune plant communities to be clustered compared to the global species pool, indicating the importance of regional diversification (hypothesis 1; Crisp *et al.*, 2009). Some regions were inhabited by more phylogenetically distinct groups of species than others. NTI showed stronger clustering than NRI, indicating that especially recent

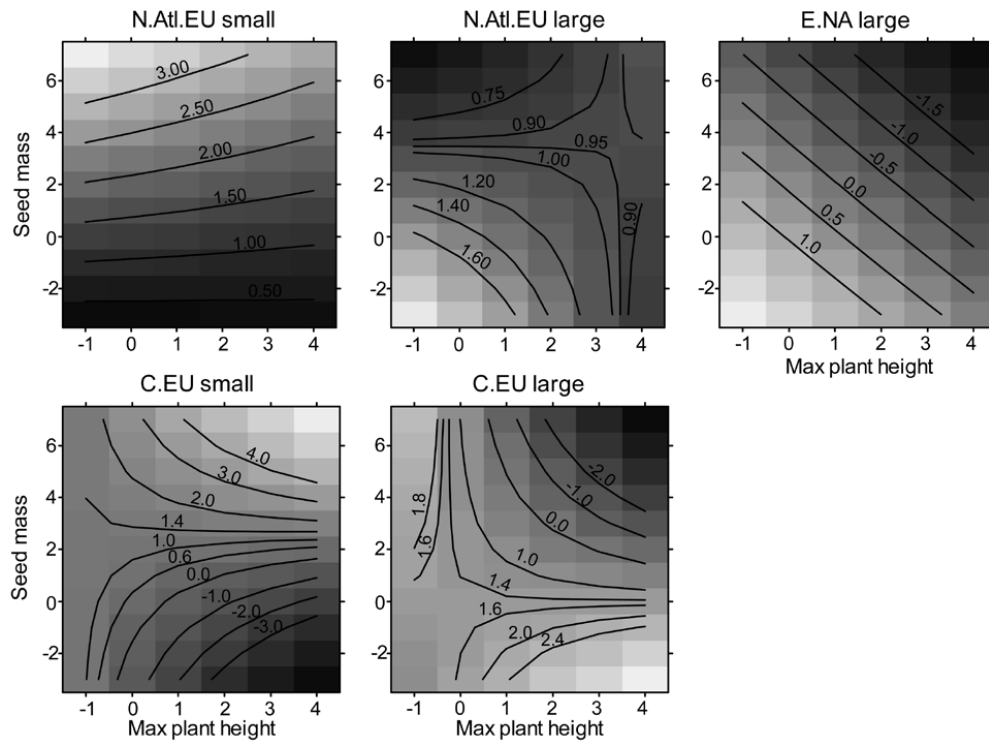


Figure 3: contour plots showing predicted NRI from the OLS regression of NRI on maximum plant height and mean seed mass for each of the five regions for which significant NRI values were obtained (according to the 10% criteria). Only the five regions for which the OLS were significant are shown. Plant height and seed mass are standardized by subtracting the mean and dividing by the standard deviation. Darker grey represents lower NRI values. Standardized coefficients from OLS models are reported in [Supplementary Table S9](#).

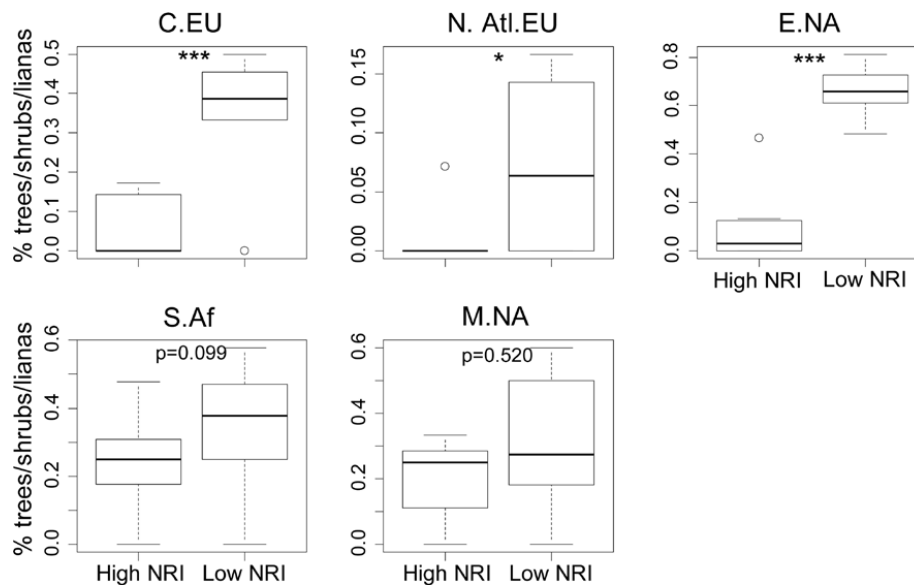


Figure 4: box plot showing percent of trees, shrubs and lianas in the 10 plots with highest and lowest NRI values, respectively, within each of the five regions for which data for large plots were available. Significance is indicated with asterisk: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. P values are given where there were insignificant differences in mean percentage of trees, shrubs and lianas between plots with high and low NRI.

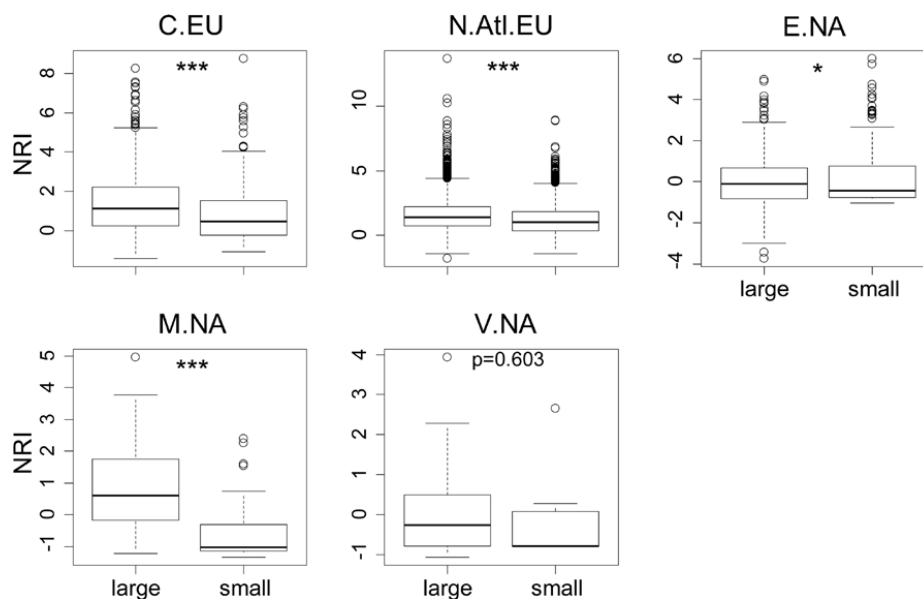


Figure 5: box plot showing local plot NRI values for large and small plots in the five regions for which data on both large and small plots were available (see Fig. 1 for abbreviations). Significant difference between mean NRI values is indicated with asterisk: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. P values are given where there were insignificant differences in mean NRI values between small and large plots.

diversification has happened within regions rather than across regions (NTI quantifies the distance among tips rather than the total mean distance between all species in a region; Webb *et al.*, 2002). Hence, recent clustering (NTI) was significant in all but two regions suggesting that, despite the fact that most deep lineages occur on every continent and both hemispheres, specific sub-lineages have evolved in every region. Most likely, the coastal dune flora in these regions has not evolved from clades that are shared among the world dunes but are derived from the respective regional inland floras with subsequent *in situ* diversification. However, our results do not show if the clustering is actually due to diversification within the dune habitat (of each region), due to certain clades of each region's adjacent inland flora being more prone to developing dune lineages (clade-level preadaptation) or due to stochastic recruitment to the dune flora from regionally diversified lineages. Furthermore, there may be a general tendency of phylogenetic community structure being scale-sensitive, with increasing clustering when using larger species pools (Swenson *et al.*, 2006).

Because dune species are known to be adapted to water and wind dispersal (Maun, 2009), we expected similarities among regions sharing the same water current and wind corridors; in other words, we expected regions to be grouped into Pacific and Atlantic super regions (hypothesis 2). This was not the case, indicating that dispersal across landmasses (e.g. North America) is no more limited than dispersal across oceans or along shorelines, at least not on evolutionary timescales (Crisp *et al.*, 2009). Alternatively, a land barrier effect may be counteracted by an effect of shared continental

species pool, i.e. dune communities on the same landmass or the same biome are phylogenetically similar because they contain lineages that are derived from the same flora (Crisp *et al.*, 2009). Lacking separation between Pacific and Atlantic dune plant communities may also be explained by efficient long-distance dispersal by wind in the Southern Hemisphere. This phenomenon is known as a strong driver of floristic connectivity among Southern Hemisphere regions, at least for cryptogam species (Muñoz *et al.*, 2004). The observed lack of separation between groups across landmasses could also be a recent phenomenon related to human transport of propagules and introduction of invasive species influencing species distribution and plant community composition. Since the Columbian Exchange (*sensu* Mann, 2006) initiated in the 16th century, the cross-scale distribution of plant species has also been affected by humans. Especially across coastal regions, human movement of plant species has occurred by introducing non-native species to new areas both unintentionally over major trade routes, and intentionally, e.g. to prevent sand drift (Martínez and García-Franco, 2004) or to establish edible or ornamental plants (Pimentel *et al.*, 2000). Human settlement and development alters coastal dune environments, which may indirectly have influenced migration and colonization of plant species (Provoost *et al.*, 2011). Current species composition at both local and regional scales is therefore likely to be affected by these anthropogenic mechanisms (Ellis *et al.*, 2012). Thus, if no introduction of non-natives had occurred, the observed clustering within regions probably would have been even stronger. However, it is hard to make a clear-cut separation of native

and non-native dune plant species given their likely long history of human introductions and other human effects.

In contrast to the hypothesized land barriers, the tropics appear to be a strong climatic dispersal barrier for temperate dune plants, causing separate diversifications in the Northern and Southern Hemisphere (hypothesis 3, discussed in [Wiens and Graham, 2005](#)). Since only the phylogenetic turnover metric based on nearest neighbour distances (comdistnt) yielded a significant result, this seems to be true only for relatively recent diversification; deeper divergences of clades are apparently found across the globe. This finding indicates that dune plants cannot readily disperse over long distances *via* water currents, but ecological connectivity in terms of suitable climate is required. Again, this result is not necessarily limited to dune plants, since the clustered dune plant lineages in each hemisphere may derive from preadapted clades that are restricted to either South or North.

The hemisphere affiliation (from indicator clade analyses) of clades responsible for the significant difference between Northern and Southern Hemisphere dune regions was consistent with knowledge of the current distribution of clades ([Mabberley, 1997](#)) and, to some degree, with knowledge of place of origin (e.g. Aizoaceae over-represented in the Southern Hemisphere and originated in South Africa; Salicaceae and Fagales over-represented in the Northern Hemisphere and originated in Laurasia ([Raven and Axelrod 1974](#))). Therefore, although exotic species have been introduced to new areas and dunes have been degraded, this have not disrupted the general floristic distribution patterns at least at the scale of this analysis (in some areas invasive species have out-competed native species and changed the local dune communities as discussed in [Maun \(2009\)](#)). Also clades characteristic for each region reflected the current distribution of species. Large clades holding widely distributed species (e.g. Pooideae, *Cyperus* complex; [Maun, 2009](#)) were significantly indicated by most of the nine regions ([Supplementary Table S8](#)), whereas specific regions were indicators of smaller clades, again in accordance with occurrence of characteristic clades found in the respective regions (Aizoaceae (e.g. *Carpobrotus* spp.) and Anacardiaceae (e.g. *Rhus* spp.) in South Africa ([van der Maarel, 1993a](#)); Arecaceae (e.g. *Sabal* spp.) and Cactaceae (e.g. *Opuntia* spp.) in Eastern North America ([van der Maarel, 1993a](#)); Salicaceae (*Salix arenaria*), Ericaceae (*Calluna vulgaris*, *Erica tetralix*), Rubiaceae (*Galium* spp.) and Adoxaceae (*Sambucus nigra*) in North Atlantic Europe ([van der Maarel, 1993b](#))).

In a global perspective, tropical dunes are still under-represented within the available data sets, and further meta-analyses should be performed to obtain a more complete picture of the relations among dune plants and community composition.

Local scale

The local analyses showed a predominantly clustered pattern within dune communities in all regions, indicating ubiquitous importance of environmental filtering (hypothesis 4). This

pattern was expected based on earlier results for Danish dunes ([Brunbjerg et al., 2012a](#)) and the hypothesis of similarly strong sea-inland environmental gradients in dune systems worldwide. Our results of consistent clustering in phylogenetic community structure across regions confirm the observations of [Doing \(1985\)](#) who described the similarities in community structure for foredune plant communities across continents.

Both plant height and seed mass showed a stronger phylogenetic signal than random. Thus, closely related species have more similar seed mass and plant height than expected by chance, supporting the idea that phylogenetic community structure may indeed be related to these two traits. From well-known ecological theories of disturbance adaptation and plant traits ([Grime, 1979](#); [Westoby, 1998](#)) and results from studies on coastal dunes ([Brunbjerg et al., 2012a](#)), we expected to find NRI relations to disturbance-related plant traits (hypothesis 5). Maximum plant height is assumed to decrease with increasing disturbance at the plot level because of the trade-off between vegetative growth and fast reproduction ([Grime, 1979](#); [Westoby, 1998](#)). Seed mass is also expected to decrease with increasing disturbance within the dune complex as seed mass is lower in open and light habitats compared with closed and low-light habitats ([Mazer, 1990](#)). However, it has been found that species growing in areas of persistent and strong natural disturbance (beaches) have larger seeds ([Maun, 2009](#)). The relationship of NRI to both functional trait variables indicates that disturbed areas harbour more closely related species. This seems to be a pattern not only in Danish dunes ([Brunbjerg et al., 2012a](#)) but also at a global scale. However, the effect differed among regions. One of the reasons why seed mass did not show a more consistent correlation with NRI may be that species in disturbed dune areas may disperse by rhizomes as well as by seeds. A species' dispersal ability is therefore not fully described by seed mass (as noted in [Feagin and Wu, 2007](#)). Furthermore, seed dispersal distance has been found to be more strongly related to plant height than seed mass ([Thomson et al., 2011](#)) potentially weakening the hypothesized relationship between seed mass and disturbance. Recently, it has been discussed whether mean plant trait values are useful in community studies as intraspecific variation in trait values due to, e.g. plasticity or genetic variability may also be important for some traits ([Auger and Shipley, 2013](#); [Violle et al., 2012](#)). The importance of accounting for intraspecific variation has been demonstrated ([Albert et al., 2010](#); [Messier et al., 2010](#)), but the documented effect differs among traits and spatial scale of the study ([Albert et al., 2010](#); [Auger and Shipley, 2013](#)). However, at global scale and different plant growth forms interspecific variation dominates intraspecific variation ([Kattge et al., 2011](#)). Working on this large, global scale, using average plant trait values calculated from the TRY database was inevitable and seems justified.

Using all plots (not only the ones for which we have trait data) to calculate the relative amount of trees/shrubs/lianas vs. herbs/graminoids/vines further improved our ecological

understanding of phylogenetic clustering: plots with high clustering are the plots with greater numbers of herbs and grasses, whereas plots with lower clustering contain forest and scrub-like vegetation (Fig. 4). This is in accordance with the disturbance hypothesis outlined above. Furthermore, the results indicate that phylogenetic clustering decreases along a successional gradient from more disturbed to more stable conditions. This pattern also holds true in tropical forests (Norden *et al.*, 2012; Whitfeld *et al.*, 2012) but has been found to vary among taxonomic groups in boreal forest (Zhang *et al.*, 2014).

Surprisingly, there was no effect of the methodological inconsistencies among the plot data sets in two of three analyses. Scaling of the species pool has been found to affect phylogenetic clustering (Eiserhardt *et al.*, 2013b), but in our study, only plot size (and neither regional extent nor regional habitat heterogeneity) affected clustering, with large plots (70–100 m²) tending to have higher NRI values. Therefore, our results may suggest that small plots (1–4 m²) are too small to show a pattern in phylogenetic community structure relative to the regional species pool or that communities in small plots are assembled more by chance or competitive interactions and less by environmental filtering.

For the first time, coastal dune community data from five continents have been assembled and quantitatively analysed. Our findings point to the existence of two distinct ‘evolutionary arenas’ (the Northern and Southern Hemisphere), in which *in situ* diversification is an important component of the regional community assembly process. At local scale, similar environmental mechanisms driving the plant community structure were related to maximum plant height and mean seed mass, lending support to the importance of filtering along the sea-land environmental gradient for dune vegetation across the world. Our study adds on to seminal, descriptive studies by Cowles (1899); Warming (1909) and later by van der Maarel (1993a, 1993b) on dune ecosystems and contributes to a better understanding of the structuring factors working on dune plant communities across spatial scales and regions.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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