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COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Assessing community assembly along a successional gradient in the North Adriatic Karst with functional and phylogenetic distances

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Abstract Recently, two approaches to account for ecological differences in community composition have been developed: one based on trait differences (functional diversity) and another based on evolutionary history (phylogenetic diversity). Combining them allows an integrated view of processes structuring communities. The North Adriatic Karst is covered by species-rich grasslands, but land abandonment has resulted in replacement by woodlands. This creates a successional gradient along which environmental conditions may change, and different community assembly rules may apply. We sampled 56 plant communities in the Karst and used functional-phylogenetic distances to assess assembly along a successional gradient, from grasslands to shrublands and woodlands. We found 146 species, for which we measured functional traits and built a phylogenetic tree. The three successional stages were floristically different, with grasslands having species that are typical of harsher soil conditions and woodlands with species preferring milder soil conditions. All communities had higher functional than phylogenetic distances, implying that closely related species tended to be phenotypically dissimilar. When more importance was given to functional distances, most grasslands and some shrublands were underdispersed; when more importance was given to phylogenetic distances, only one grassland was underdispersed and one woodland was overdispersed. Combining functional and phylogenetic distances provided us with better estimates of ecological differences in a successional gradient, where environmental filters seem to be the dominant force in early stages and competitive exclusion becomes more important in later stages. Taking into account that sucessional stages are assembled by different rules is essential to predicting their behaviour under future environmental scenarios.

Introduction

Understanding how communities are assembled has long been a central problem in ecology (Götzenberger et al. 2012). Previously, researchers sought to explain community assembly in terms of species number and abundance distribution (Cadotte et al. 2013); however, community assembly depends not only on species number and abundances per se, but also on their ecological differences (McGill et al. 2006). In the last 20 years, two approaches to account for ecological differences have been developed: one based on trait differences—i.e. functional diversity—and another based on evolutionary history—i.e. phylogenetic diversity (Pausas and Verdú 2010). Usually, these approaches have been taken separately but, as both have limitations (Cadotte et al. 2013), and since functional and phylogenetic diversity may be complementary, some studies have combined them

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to give new insights into community assembly (e.g., Jombart et al. 2010; Pavoine et al. 2010). Such methods consider co-occurrences, phenotype, phylogeny, and environment to obtain an integrated view of processes structuring communities (Pausas and Verdú 2010).

Following this reasoning, Cadotte et al. (2013) devised a method to consider both functional and phylogenetic differences at the same time to estimate species' pairwise distances in an ecologically meaningful way, while accounting for limitations of both approaches. In their method, distances between species are measured in the so-called "traitgram-space", weighting the contribution of functional and phylogenetic differences and calculating the "functional-phylogenetic distances" (FPDist; Cadotte et al. 2013). Functional-phylogenetic distances can be considered as either phylogenetic distances that take trait convergence or divergence into account or functional distances that take unmeasured phylogenetically correlated traits into account (Cadotte et al. 2013). As such, this method is thought to be a more accurate estimate of species differences than any functional or phylogenetic distance considered separately (Cadotte et al. 2013). When calculating functional-phylogenetic distances, the relative importance of trait and evolutionary differences can be tuned by a weighting parameter (Cadotte et al. 2013).

The North Adriatic Karst is traditionally known as a region covered by stony grasslands, which covered more than 80 % of the region in the late eighteenth century (Kaligarič and Ivajnšič 2014). However, land abandonment in the last decades has been driving the decline of these grasslands, being replaced by woodlands, which now cover more than 70 % of the region (Kaligarič and Ivajnšič 2014). Along this successional gradient, from grassland, through shrubland, to woodland, environmental conditions may change from harsher to milder conditions (Coiffait-Gombault et al. 2002). As they change, we may expect different community assembly rules (Webb et al. 2002). In early successional stages, harsher environmental conditions leads to habitat filtering as the dominant ecological force, which selects for species with attributes allowing them to cope with abiotic stresses, resulting in reduced trait range and functional underdispersion (Cadotte et al. 2013; Bhaskar et al. 2014). For example, shallower soils select shallow-rooted herbaceous species, which may have a suite of correlated attributes, such as low height, low specific leaf area, and high leaf dry-matter content, and thus may be functionally similar (Fujita et al. 2014). If these traits are conserved, that is, if species sharing similar attributes are closely related, then this functional underdispersion leads to phylogenetic underdispersion; if they are convergent, that is, if species sharing these attributes are distantly related, then it leads to phylogenetic overdispersion (Webb et al. 2002).

In late successional stages, milder environmental conditions leads to competition as the dominant ecological force,

which allows species presenting a wider range of attributes to potentially occur (Bhaskar et al. 2014). Coexistence in competitive communities is driven by the interaction of niche differences and competitive ability differences (Chesson 2000; Mayfield and Levine 2010). If competitive ability differences are higher than niche differences, competitive exclusion is promoted, resulting in functional overdispersion (Mayfield and Levine 2010). If niche differences are higher than competitive ability differences, either functional underdispersion or overdispersion is possible, depending on the magnitude of the differences (Mayfield and Levine 2010). If traits are conserved, functional and phylogenetic patterns are the same; if traits are convergent, these patterns are opposite (Mayfield and Levine 2010). In this sense, combining functional and phylogenetic distances for analysing patterns of community assembly may provide better estimates of ecological differences than either functional or phylogenetic distances alone (Cadotte et al. 2013).

We sampled plant communities in the Karst and used functional-phylogenetic distances to assess assembly along a successional gradient, from grasslands, through shrublands, to woodlands. We aimed to answer the following questions: (1) are successional stages related to different environmental variables? Since shrubs and trees decrease temperature and increase relative humidity (Vidrih et al. 2009), we expected woodlands to be related to milder conditions. (2) Are functional distances higher than phylogenetic distances? Since most of the traits do not present positive phylogenetic signal in Karst plant species (Pipenbaher et al. 2013), we expected functional distances to be higher (Cadotte et al. 2013). (3) Do functional-phylogenetic distances increase towards later successional stages? Since habitat filtering tends to be the dominant ecological force in early stages (Bhaskar et al. 2014), we expected them to increase. (4) Are functional-phylogenetic distances related to environmental variables? Since environmental gradients are important drivers of patterns of community diversity (Cadotte et al. 2013), we expected them to be related.

Materials and methods

Slovenia is located in central Europe, between the Julian Alps, the Dinaric Alps, the Mediterranean Plain, and the Pannonian Plain (Kaligaric et al. 2006). In Slovenia, the Karst, which covers about 43 % of the country, is developed wherever carbonate rocks are present, either on limestone or on dolomite (Hajna 2004). One of the regions that is covered by the Karst is the North Adriatic, in the southwestern portion of the country, between the Adriatic Sea and the Pre-Dinaric region (Pipenbaher et al. 2008). The North Adriatic Karst consists of calcareous limestone

Table 1 Functional traits used in analysis of community composition and their hypothesised relevance (from Pipenbaher et al. 2011, 2013)

Functional trait	Details (units)	Relevance
Life form	Categorical variable	Survival during unfavourable season
Growth form	Categorical variable	Resource acquisition
Plant height	Continuous variable (cm)	Competitive vigour, fecundity, and interval between disturbances
Spinescence	Binary variable	Defence against herbivores, heat, and water stress reduction
Trichomes	Ordinal variable	Defence against herbivores, heat, and drought stress reduction
Specific leaf area	Continuous variable ($mm^2\ mg^{-1}$)	Leaf lifespan, leaf defences, potential relative growth rate, and photosynthetic rate
Leaf dry matter content	Continuous variable ($mg\ g^{-1}$)	Density of leaf tissues, leaf lifespan, potential relative growth rate, and photosynthetic rate
Scleromorphy	Ordinal variable	Defence against herbivores, leaf lifespan, and water stress reduction
Leaf persistence	Categorical variable	Water and nutrient stress reduction, defence against herbivores
Leaf form	Categorical variable	Light interception and photosynthetic rate
Flowering start	Circular variable (°)	Reproductive success
Flowering length	Continuous variable (months)	Reproductive success
CSR strategy	Proportional variable	Unique combination of either high or low intensities of stress and disturbance

(Pipenbaher et al. 2008) and Rendzina soils (Repe 2004b). The climate is sub-Mediterranean, with annual rainfall around 1400 mm and mean annual temperature around 10.5 °C (Eler et al. 2013). Desiccation and erosion are caused by the so-called "bora wind" (Pipenbaher et al. 2008). The region was covered mostly by grasslands in the late eighteenth century, but since then abandonment and changed land-use have been driving woody plant encroachment (Kaligarič and Ivajnšič 2014). As a consequence, these grasslands have been replaced first by shrublands and later by woodlands (Kaligarič and Ivajnšič 2014).

The study site, located near the settlement of Črnotiče, in the North Adriatic Karst (45°32–45°34′N and 13°52–13°54′E; Fig. A1 in the ESM), was covered by stony dry pasture grasslands from the *Satureion subspicataea* alliance. Encroachment occurs when abandoned grasslands are colonised by shrubs of early successional stages, such as *Cotinus coggygria* and *Juniperus communis*, and trees of mid- and late successional stages, such as *Ostrya carpinifolia* and *Quercus pubescens*. The outcome was an area covered by grasslands interspersed with shrublands and with woodlands of the *Ostryo-Quercetum pubescentis* association. In the summer of 2014, we placed 56 plots randomly in the study site, each plot with 10 m × 10 m, ending up with 20 plots in the grasslands, 17 in the shrublands, and 19 in the woodlands. In each plot, we sampled all vascular plants, identifying them to species level and then building a presence-absence community matrix. We also measured three soil variables that are important drivers of community assembly in the Karst (Vidrih et al. 2009)—temperature, moisture, and depth—with which we built an environmental matrix.

To assess community assembly in the Karst, we used the approach developed by Cadotte et al. (2013), in which functional and phylogenetic distances are taken into account simultaneously. To estimate functional distances, we used 13 functional traits (Table 1; Pipenbaher et al. 2011, 2013): life form, growth form, plant height, spinescence, trichomes, specific leaf area, leaf dry matter content, scleromorphy, leaf persistence, leaf form, flowering start, flowering length, and CSR strategy. Since we had binary, categorical, circular, continuous, ordinal, and proportional traits, we used a generalisation of Gower distances for mixed data (Pavoine et al. 2009) to convert the trait matrix into a functional distance matrix. To estimate phylogenetic distances, we built a phylogenetic tree based on Bell et al. (2010). We improved tree resolution by consulting references on specific clades, as recommended by Beaulieu et al. (2012), and placed the undated nodes in the tree evenly between the dated nodes (Webb et al. 2008). We calculated cophenetic distances to convert the tree into a phylogenetic distance matrix.

The functional-phylogenetic distance matrix was then computed using the functional distance matrix, the phylogenetic distance matrix, and two weighting parameters, a and p (Cadotte et al. 2013). Both pairwise distances are scaled to vary between 0 and 1 to standardise comparisons between functional and phylogenetic differences. The first parameter, a, goes from 0 to 1 and weights the contribution of functional and phylogenetic distances (Cadotte et al. 2013). For instance, when a is set 0, only functional distances are considered; when a is set 0.5, functional and phylogenetic distances are given equal weight; when a is set to 1, only phylogenetic distances are considered (Cadotte et al. 2013). The second parameter, p, needs to be equal to or higher than 1 to satisfy all mathematical requirements of a distance metric (Cadotte et al. 2013). Functional-phylogenetic distances have been shown to provide

better estimates of species' overall ecological differences and have greater power to detect community assembly patterns than either functional or phylogenetic distances alone (Cadotte et al. 2013).

To answer the first question, we did a canonical analysis of correspondence (Jongman et al. 1995), using the community and the environmental matrices. We grouped the communities according to the successional stage and tested whether the three stages presented different floristic compositions with a multivariate analysis of variance (Anderson 2001). We tested the significance of the first two axes and whether the soil variables were significantly related to these axes with 999 randomisations (Oksanen et al. 2013). To answer the second question, we plotted the mean pairwise functional-phylogenetic distances (MFPD) against the parameter a. The curves provide signatures of pairwise evolutionary relationships: when they are flat, evolutionary relationships are conserved; when they are increasing, evolutionary relationships are convergent; when they are decreasing, evolutionary relationships are divergent (Cadotte et al. 2013). We compared the observed curves with a null distribution generated with 4999 randomisations. The community is underdispersed when the observed curve is below the 2.5 % of the distribution and overdispersed when above the 97.5 %.

To answer the third question, we plotted MFPD against species richness (Cadotte et al. 2013). We compared the observed values with a null distribution generated with 4999 randomisations using all observed species. Again, the community is underdispersed when the observed curve is below 2.5 % and overdispersed when above 97.5 %. We used this procedure four times, setting a to 0, 0.2, 0.5, and 1 and, thus, giving progressively more importance to phylogenetic distances. To answer the fourth question, we did analyses of covariance, using MFPD as response variable and the two first canonical axes, successional stage, and the interaction terms as explanatory variables. We repeated this procedure, varying the phylogenetic-weighting parameter a from 0 to 1 and recording each time the value of the adjusted coefficient of determination (Cadotte et al. 2013). We carried out all analyses in R (R Development Core Team 2014), using the "ade4" (Dray and Dufour 2007) and "vegan" (Oksanen et al. 2013) packages, as well as the functions provided by Cadotte et al. (2013).

Results

In the 56 plots, we found 146 species, belonging to 44 families and 23 orders, for which we measured functional traits (Table A1 in the ESM) and built a phylogenetic tree (Fig. A2 in the ESM). Out of the 146 species, 85 occurred in the grasslands, 98 in the shrublands, and 87 in the woodlands.
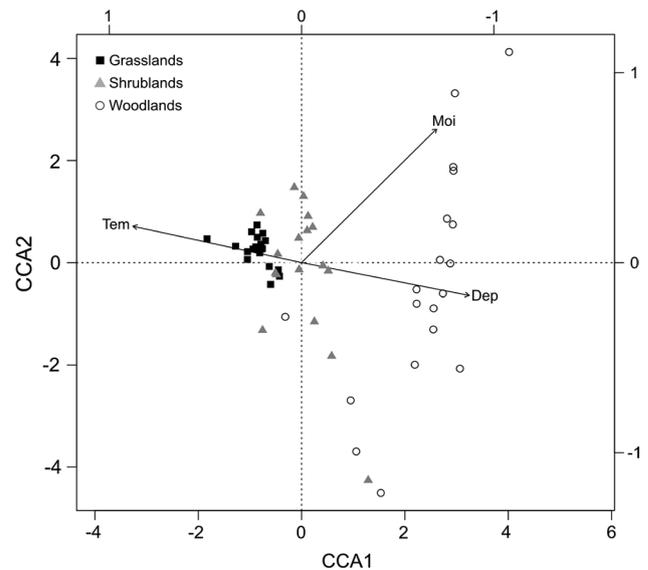

Fig. 1 Canonical correspondence analysis of the floristic composition of 56 communities in the North Adriatic Karst. Soil variables related to these areas are indicated: *Dep* soil depth, *Moi* soil moisture, *Tem* soil temperature

Considering floristic composition, each successional stage was different from the others ($P < 0.001$ in all cases). The first two axes of the canonical correspondence analysis explained only 10 % of the variation, but they were significant ($P = 0.001$ for the first axis and $P = 0.008$ for the second axis). The first axis was related positively to depth and moisture and negatively to temperature, whereas the second axis was related positively to moisture and temperature and negatively to depth (Fig. 1). All three environmental variables were significantly related to the first two axes (depth: $R^2_{adj} = 0.50$, moisture: $R^2_{adj} = 0.65$, temperature: $R^2_{adj} = 0.51$; $P < 0.001$ in all cases). The first axis separated the three successional stages, with grasslands with negative scores, shrublands with scores close to 0, and woodlands with positive scores (Fig. 1).

When we plotted the functional-phylogenetic distances against the parameter a, all 56 communities exhibited decreasing curves (Figs. A3–5 in the ESM), indicating that functional distances were higher than phylogenetic distances. We highlighted two communities of each successional stages, representative of the patterns found (Fig. 2). Of the 56 communities, 19 were significantly under- or overdispersed for at least some values of a (Fig. 3). When we set a to 0 and to 0.2, 14 grasslands and four shrublands were undispersed; when we set it to 0.5, 12 grasslands and four shrublands were undispersed; and when we set it to 1, one grassland was underdispersed and one woodland was overdispersed (Fig. 3). Even though six grasslands were always within the null distribution (Figs. 2a, 3), most of them were underdispersed when a was lower (Figs. 2b,

Fig. 2 Mean pairwise functional-phylogenetic distances (MFPD) as a function of the weighting parameter *a* for six communities in the North Adriatic Karst. *Dotted lines* Observed mean pairwise distances. The *dark grey*, *grey*, and *light grey* shading represents 50, 90, and 95 % confidence intervals, respectively, of the null distributions, with their averages indicated by the *solid lines*. The *curves* for all 56 communities are presented in Figs. A3–5 in the ESM
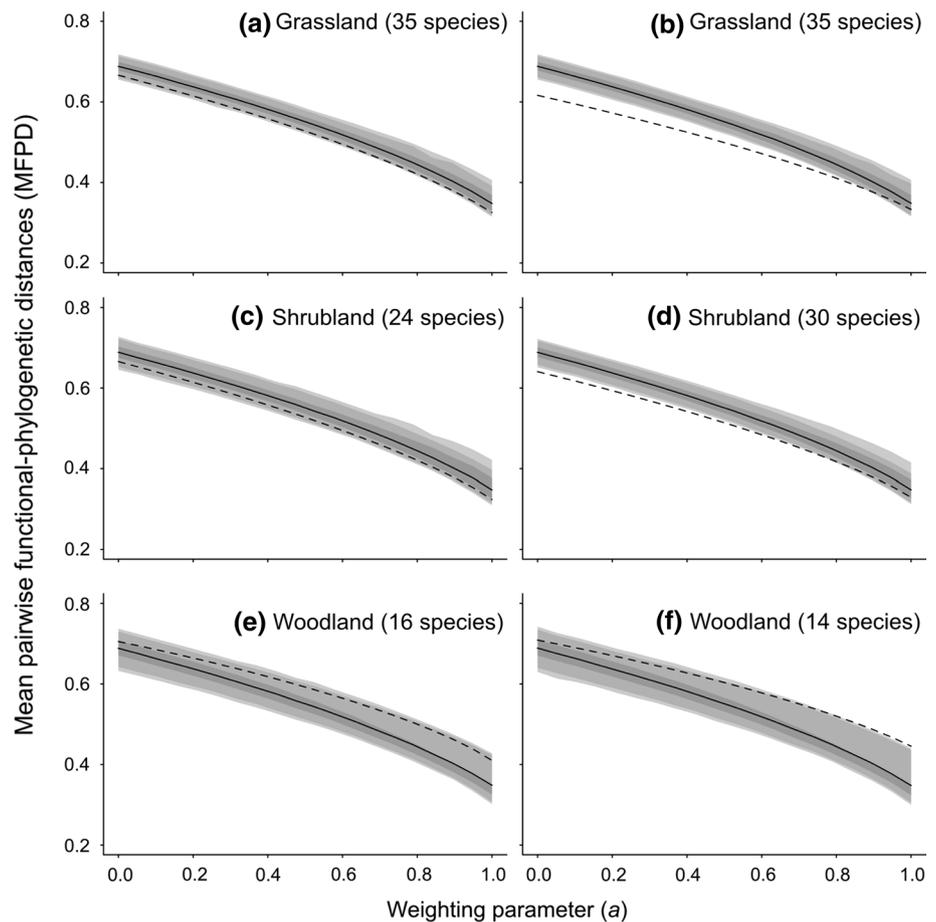
3). Most of the shrublands were always within the null distribution (Figs. 2c, 3), but four of them were underdispersed when *a* was lower (Figs. 2d, 3). The woodlands were usually always within the null distribution (Figs. 2e, 3), except one that was overdispersed when *a* was closer to 1 (Figs. 2f, 3).
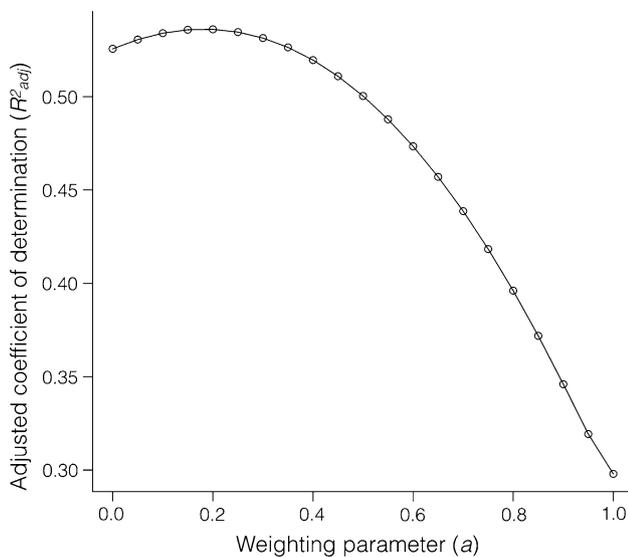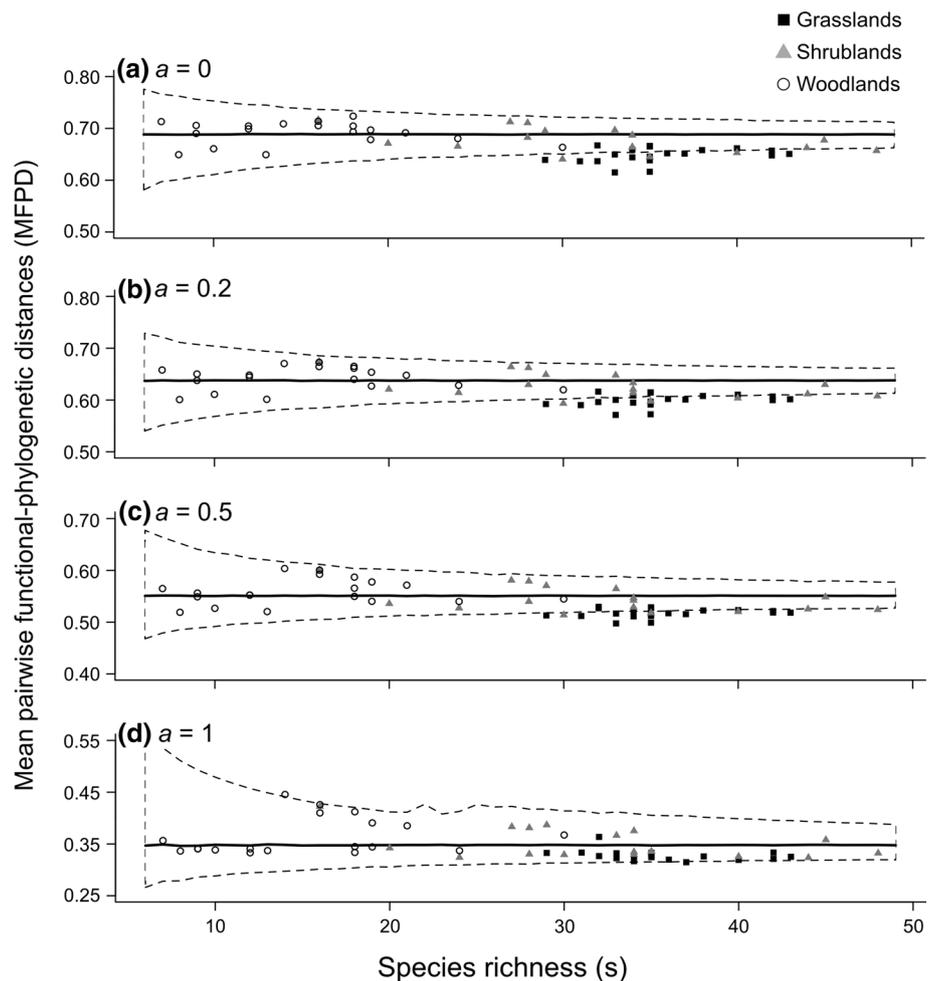
In the analyses of covariance of MFPD as a function of the first two canonical axes, successional stage, and the interaction terms, values of the adjusted coefficient of determination were higher when *a* was close to 0, going from 0.527 when *a* was set to 0, peaking at 0.536 when *a* was set to 0.2, and decreasing to 0.298 when *a* was set to 1 (Fig. 4). MFPD increased from grasslands, through shrublands, to woodlands for any value of *a* (Fig. 5, Table 2). When *a* was 0 ($R^2_{adj} = 0.527$) and 0.2 ($R^2_{adj} = 0.536$), MPFD values were related positively to the first axis (Fig. 5a, c; Table 2) and negatively to the second axis (Fig. 5b, d; Table 2). In both cases, the magnitude of change did not depend on the successional stage (Table 2). When *a* was 0.5 ($R^2_{adj} = 0.500$), MPFD were related positively to the first axis (Fig. 5e; Table 2), but only for the shrublands, and negatively to the second axis (Fig. 5f; Table 2). When *a* was 1 ($R^2_{adj} = 0.298$), MPFD were related positively to the

first axis (Fig. 5g; Table 2), also only for the shrublands, and were not related to the second axis (Fig. 5h; Table 2).

Discussion

The combination of functional and phylogenetic distances was useful in giving better estimates of ecological differences along a successional gradient, in which different stages seem to be assembled by different rules. Being semi-natural, the grasslands in the North Adriatic Karst need to be actively managed to persist or, once abandoned, they are colonised by shrubs and trees, having their floristic compositions changed and becoming shrublands in about 5 years and woodlands in about 10 years (Kaligarič et al. 2006; Diacon-Bolli et al. 2012). As a matter of fact, we found different floristic compositions in the three stages, even between the two extremes and the shrublands, which are usually recognised as a transition zone between grasslands and woodlands (Sutherland 2002). Not only were the three stages floristically different, but they occurred under different soil conditions, with grasslands related to warmer soils and woodlands related to deeper and wetter soils. The

Fig. 4 Results of the relationships between MFPD and the first two canonical axes, successional stage, and the interaction terms as a function of the weighting parameter *a*. Values are the adjusted coefficient of determination

occurrence of woodlands in milder conditions could be both cause and consequence, since soil heterogeneity, such as local deep-soil patches, supports woody species invasion on the one hand, and the woody species themselves also make the soils more favourable on the other (Pärtel and Helm 2007).

The decreasing curves we found when we plotted MFPD against the parameter *a* were a signature of divergent pairwise evolutionary relationships. Most of the traits in Karst plant species present a negative phylogenetic signal (Pipenbaher et al. 2013), implying convergent evolution, i.e. the independent evolution of similar attributes (Rosemblum et al. 2014). Similar attributes may evolve repeatedly, because different lineages experience similar environments that favour similar adaptive solutions (Rosemblum et al. 2014). Convergent evolution leads then to divergent pairwise relationships, that is, closely related species tend to be functionally dissimilar (Webb et al. 2002). Thus, the divergent pairwise evolutionary relationships in the North Adriatic Karst flora resulted in high values of functional distances for small values of phylogenetic distances, which

Fig. 5 MFPD as a function of the first two canonical axes (CCA1 and CCA2) when the weighting parameter *a* was set to **a**, **b** 0, **c**, **d** 0.2, **e**, **f** 0.5, and **g**, **h** 1 for 56 communities in the North Adriatic Karst. Only slopes significant according to the analyses of covariance are drawn
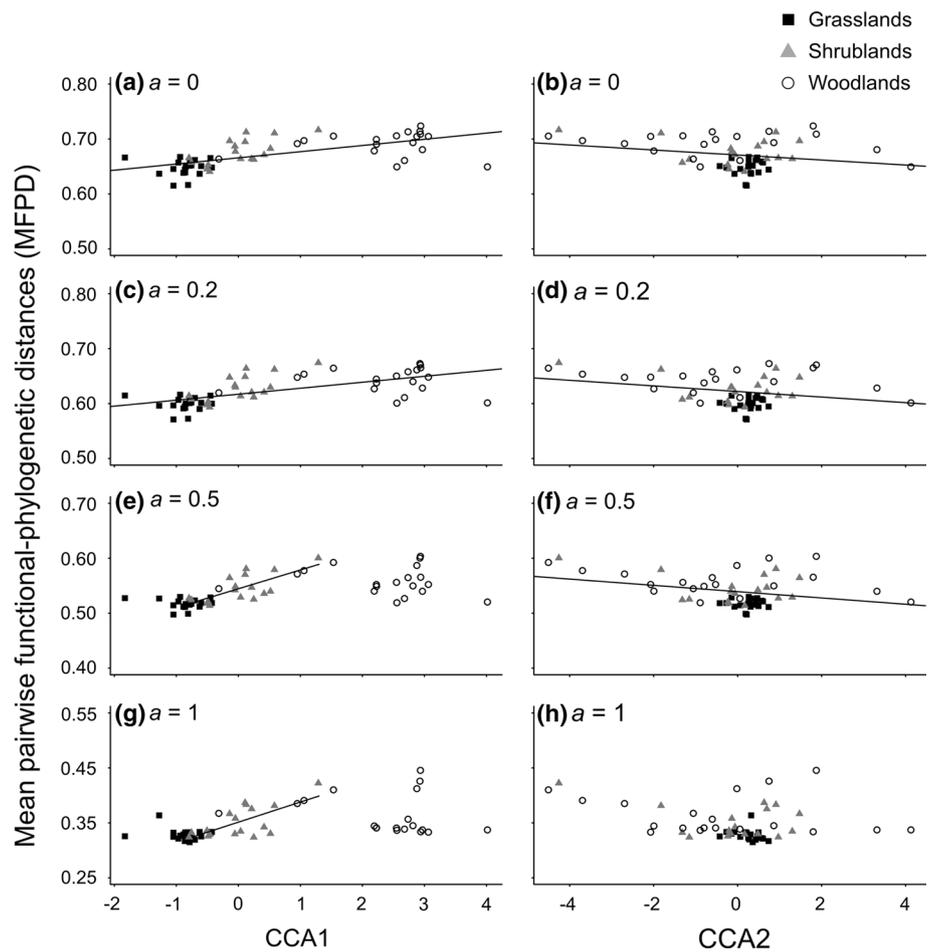
Table 2 Results from the analyses of covariance between mean pairwise functional-phylogenetic distances (MFPD) as a function of the first two canonical axes (CCA1 and CCA2), successional stage (stage), and the interaction terms for four values of the phylogenetic-weighting parameter *a*

| | *a* | | | |
	0	0.2	0.5	1
CCA1	<0.001*	<0.001*	<0.001*	<0.001*
CCA2	0.009*	0.006*	0.006*	0.067
Stage	0.033*	0.017*	0.012*	0.048*
CCA1: stage	0.112	0.055	0.026*	0.046*
CCA2: stage	0.372	0.477	0.720	0.847

* Significant *P* values

is an indication of high rates of evolution of the measured traits (Cadotte et al. 2013). If functional distances are higher than phylogenetic distances in the Karst flora, then the former tends to be more informative than the latter to detect community assembly rules.

Indeed, we found more communities different from the null expectation when we gave more importance to functional distances. When *a* was lower, most of the grasslands and some of the shrublands were underdispersed, suggesting that environmental filter was the dominant ecological force in early successional stages. Warmer, drier, and shallower soils may filter the species pool, allowing only those species able to cope with less water and nutrient availability to persist (Eler et al. 2013). In the grasslands, functional underdispersion may also be due to habitat management, especially grazing, which alters small-scale conditions by creating patches of bare soil, reducing competitive exclusion due to biomass removal (Jacquemyn et al. 2011; Gazol et al. 2012). Functional-phylogenetic distances better represent true functional distances when only subsets of ecologically relevant traits are measured (Cadotte et al. 2013). The same traits we measured here were useful to compare community assembly rules in pastures and meadows in the North Adriatic Karst and thus are thought to be ecologically relevant (Pipenbaher et al. 2013).

Succession can be viewed as community assembly in progress, and different assembly rules seem to apply throughout it (Bhaskar et al. 2014). When *a* was lower, most shrublands and all woodlands did not depart from the null expectation, which may be due to the influence of

stochastic factors (Bhaskar et al. 2014). Since an increase in the intensity of competition occurs when there is an increase in the biomass of competitors, such as in late successional stages (Rees 2013), it is possible that both opposing patterns, environmental filter and competitive exclusion, act on the communities in late successional stages, cancelling out their effects (Cadotte et al. 2013). It is also possible that competitive ability differences—for example, difference in height—and niche differences—for example, difference in preference for soil— cancel each other out, leading to a random pattern (Mayfield and Levine 2010). Thus, in the North Adriatic Karst, different community assembly rules seems to apply throughout the successional gradient, with the importance of environmental filter decreasing and the importance of competitive exclusion increasing from grasslands to woodlands.

When we gave more importance to phylogenetic distances and set a to 1, except for one grassland that was underdispersed and one woodland that was overdispersed, no other communities departed from the null expectation. When the traits relevant to community assembly are conserved, the phylogeny contains important ecological information, which increases the chances of detecting community patterns for high values of a (Cadotte et al. 2013). In such case, a congruence between functional- and phylogenetic-based patterns of community structure is expected (Kraft et al. 2007). However, when traits are convergent, as in Karst plant species (Pipenbaher et al. 2013), overdispersion is expected when the dominant ecological force is environmental filter and randomness is expected when it is competitive exclusion (Webb et al. 2002). If so, we should have found overdispersion in early successional stages when a was higher. Phylogenetic randomness in this case could be due to an inability to detect overdispersion (Kraft et al. 2007) or to transhumance, which brought species with different origins and evolutionary history to the Karst (Kaligarič et al. 2006).

Regressing MFPD against elevation for subalpine grasslands, Cadotte et al. (2013) found higher amounts of variance explained when a was set to 0.35, suggesting that, for those communities, the combination of functional and phylogenetic information could better reveal community assembly rules. In the Karst, similarly, the variance explained by the first two canonical axes, successional stage, and interaction terms was higher when a was set to 0.2, suggesting that, even if functional distances were more informative than phylogenetic ones, the latter also contributed to unravel community assembly rules, because both measured and unmeasured traits were influencing species coexistence across the successional gradient and the functional and the phylogenetic distance matrices differed in some way (Cadotte et al. 2013). We used the collective knowledge available in the systematics literature to improve the resolution of the reference phylogenetic tree, which otherwise would have many polytomies (Beaulieu et al. 2012). An improvement in the quality of the phylogeny, though, may increase the importance of phylogenetic distances.

Regardless of value of a, MFPD increased from grasslands, through shrublands, to woodlands. Moreover, when we gave more importance to functional distances or when a was lower, we found positive relationships between MFPD and the first canonical axis, along which soil conditions get milder, that is, moisture and depth increase and temperature decreases. Thus, the milder the environment, the higher the distances, increasing from grasslands to woodlands, suggesting once more that the importance of environmental filters is higher in early successional stages and lower in late ones. When we gave more importance to phylogenetic distances, that is, when a was higher, we found positive relationships between MFPD and the first canonical axis only for the shrublands, which could be due to the colonisation of highly original species, such as *Juniperus communis*. Except when a was 1, we found negative relationships between MFPD and the second canonical axis, though they were less obvious in relation to the successional stages, since moisture increased along this axis but depth decreased.

For centuries, grasslands were part of the landscape identity in the North Adriatic Karst (Kaligarič and Ivajnšič 2014). Abandonment and changed land-use, however, have caused their decline (Kaligarič and Ivajnšič 2014). With woody plant encroachment, not only are grasslands disappearing, but so are cultural landscapes, threatening many areas of the Karst with the loss of their traditional appearance (Repe 2004a; Kaligarič and Ivajnšič 2014). This traditional appearance comprises not only aesthetic values, but also different ecological functions. Even though functional distances were more informative, combining functional and phylogenetic distances provided us with better estimates of species' ecological differences in a successional gradient in the Karst, where environmental filter seems to be the dominant force in early stages and competitive exclusion seems to become more important toward late stages. Taking into account that grasslands, shrublands, and woodlands are assembled by different rules is essential if one wants to conserve them (Keddy 1999) and to predict how they will behave under future environmental scenarios (Götzenberger et al. 2012).

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