

Do species incidence matrices reflect different degrees of plant community integration?

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Background and aims – Assuming the asymmetrical hump model of the stress-gradient hypothesis, higher degree of species aggregation in floristically similar communities is expected under conditions of stronger environmental severity.

Methods – Several species incidence-based metrics were calculated for two large, homogeneous matrices pertaining to predefined community types: weed assemblage of trampled sites (S-P) and nutrient-rich pastures (F-A). For each metric and matrix, a standard effect size (SES) was estimated through a null model with fixed species frequencies and equiprobable sites.

Key results – All metrics related to co-occurrence, nestedness and clustering of species range boundaries have significant SES in both matrices, but they are all larger in S-P. No significant checkerboardness was detected in S-P, whereas F-A displays non-random segregation patterns that are exclusively due to species turnover. The core species effect is positive but not significant in S-P, and the between-site pairwise similarities present a monotonic distribution. The higher SES of coherence and the significant SES of homotoneity in F-A make it more clearly delineated as a syntaxon. In fact, between-site pairwise similarities are significantly higher in F-A and their distribution approaches a reversed J-shape.

Conclusions – The stronger species association and nestedness patterns revealed in weed assemblages are consistent with the hypothesis of higher community integration in harsh environments. However, the species-rich and productive grassland communities appear overall more structured. Regular and moderate disturbances produced by herbivores may be an important requisite for plant community organisation according to the core-satellite species hypothesis in fertile habitats. Although not a test for inferring underlying ecological processes, the joined use and comparison of complementary, species incidence-based metrics represents a useful exploratory tool for distinguishing between various patterns of species assembly, at least for relatively homogeneous, presence-absence matrices of different plant community types.

Key words – Checkerboardness, core-satellite species assembly, nestedness, null model, productive pastures, species co-occurrence, species turnover, stress-gradient hypothesis, weed communities.

INTRODUCTION

The degree of integration, as an intrinsic characteristic of plant communities, has been much overlooked since the quasi-unanimous acknowledgement of the individualistic response of species within communities, despite the evidence for positive interactions among plant species leading to multispecific vegetation clumps (Eccles et al. 1999, Callaway 2007). Lortie et al. (2004) advanced the concept of the integrated ecological community that accommodates a wide range of degree of integration, from highly individualistic to highly interdependent, thus reconciling the two traditional, opposing approaches. Apart from the interactions with other

organisms (e.g. herbivores, mycorrhizal fungi), the degree of coenotic integration depends on the interplay among: (i) stochastic processes (ii), abiotic tolerances of species, and (iii) positive and negative interactions among species (Lortie et al. 2004). Surely not by coincidence, the factors enumerated previously are generalisations and extensions of those used by Grime (2001) to build the trilateral plant strategy model, i.e. disturbance, stress-tolerance and competition, respectively.

Different intensities of disturbance and abiotic stress should bring about a differentiation in species assembly and integration within plant communities. In particular, the importance of direct facilitation in plant communities is likely

to increase with physical disturbance and environmental stress, but to level off or decline in extreme, very severe habitats (Michalet et al. 2006, Kawai & Tokeshi 2007, Brooker et al. 2008, Maestre et al. 2009, le Roux & McGeoch 2010). Similarly, indirect facilitation should increase along a biotic disturbance gradient due to associational defences against pest/herbivores (Bertness & Callaway 1994), but should be of little or no importance at high abiotic stress (Smit et al. 2009) and more common in species-rich communities developed on productive sites (Brooker et al. 2008). On the other hand, the importance of competition is expected to increase with site fertility (Brooker & Callaghan 1998, Grime 2001), but to drop when the abiotic disturbance and consumer pressure is high (Bertness & Callaway 1994). If not confounded or masked by other processes, the net effect of positive and negative interactions should be reflected in the patterns of species aggregation and segregation in natural assemblages. One way to assess empirically such relationships is to explore the properties of species incidence matrices in terms of checkerboardness (negative coherence), co-occurrence, nestedness, turnover and other patterns. The associated metrics are usually expressed as deviations from a statistical null model, which is generated by randomisation of an observed matrix, so that to mimic the stochastic assembly that is not constrained by species interactions (Gotelli 2001).

Pairwise checkerboardness corresponds to a cohabitation avoidance pattern, possibly determined by negative interspecific interactions or affinities for non-overlapping habitats (Götzenberger et al. 2012), so that the target species never coexist in the same assemblage. Co-occurrence is the opposite concept that fits, among others, into the positive interaction scenario and implies that two or more species share the same sites. Nestedness is a hierarchical, species loss pattern in which poor communities consist of nested subsets of more species-rich communities. Among other possible underlying processes, nestedness is promoted by the selective occupancy of sites according to species tolerance to environmental stress (Ulrich et al. 2009). Recent studies suggest that plant communities structured by positive interactions (e.g. facilitation) are likely to be assembled as networks with a significant nested structure (Verdú & Valiente Banuet 2008). Turnover is a species replacement pattern usually associated with ecological gradients or vicariant speciation caused by geographic barriers (Tuomisto 2010), but can be also shaped by negative interspecific interactions. Unlike nestedness, turnover implies checkerboardness in the paired distribution of species.

Homotoneity expresses the floristic uniformity of vegetation types ('plant associations'), which is proportional to frequencies of occurrence (constancies) of the prevalent species (Peet 1981). In floristically similar communities, a distinctive group of 'core' species that forms the 'normal specific assemblage' (*sensu* Guinochet 1973) is also predicted by the bimodal model of regional species distribution, i.e. the core-satellite species hypothesis (Hanski 1982). This model can be linked to Grime's (2001) classification of species as dominant, subordinate and transient. Thus, Gibson et al. (1999) showed that the core (character) and satellite (companion) species correspond to dominant and transient species, respectively. Finally, the subordinate species fit in the middle (hol-

low) of Hanski's distribution of frequencies. Several studies brought evidence for such a pattern of community organisation, i.e. dominant/core and subordinate/satellite species in productive, rich grasslands (Gotelli & Simberloff 1987, Collins & Glenn 1990, Olff & Bakker 1998). This suggests that plant community types from fertile sites that are presumably structured through competition and indirect facilitation have a higher homotoneity than those developed on infertile or frequently disturbed habitats and prevalently founded by positive interspecific interactions (e.g. direct facilitation).

Most studies aimed at revealing patterns in plant species co-occurrence are based on lists of taxa present in small-size plots that were located randomly in environmentally heterogeneous areas featuring some stress gradients (Weier et al. 1998, Dullinger et al. 2007, Bowker et al. 2010, Maltez-Mouro et al. 2010). The few studies that used samples at community scale placed within relatively homogeneous habitats (but from floristically different community types) revealed either random (Wolek 1997) or non-random patterns (Eccles et al. 1999). An important assumption in all these studies was that all plants from species pool had equal opportunities to reach any site within the study area, i.e. species matrices were not constrained by differences in dispersal success. For this reason, much of the recent research on species assembly have focused on the meta-community concept, i.e. a more or less heterogeneous set of local communities that are linked by dispersal of multiple, potentially interacting species (Presley et al. 2010).

The aim of this study was to compare the structure of two species matrices circumscribed to well-defined plant community types developed within the same geographical region, but in different conditions of abiotic stress and disturbance. To this purpose, I used large floristic data sets that pertain to two community types: ruderal vegetation of trampled sites and managed grasslands on fertile soils. Such an approach has the potential to reveal fine patterns even within similar, recurring species assemblages that occupy ecologically equivalent habitats and, to show whether the floristic consistency of syntaxa depends on those factors that govern the plant species assembly.

According to the theory of integrated community, a higher degree of species integration in floristically similar communities is expected under conditions of higher environmental stress and disturbance. In particular, checkerboardness, turn-over and homotoneity should be lower, whilst species co-occurrence and nestedness should be larger in plant communities developed under environmental stress and disturbance. The reciprocal should hold for communities installed on fertile sites.

MATERIALS AND METHODS

Community type selection and model adaptation

To filter out the effects of regional species pool and habitat isolation on species co-occurrence patterns, the choice of plant community types to be contrasted was constrained by their distribution. Moreover, to avoid possible bias in the evaluation of non-random patterns of species incidence that could be induced by differences in plant community com-

plexity (vertical structure and successional maturity), the latter criteria were also taken into account. Consequently, two herbaceous, secondary community types with wide, continuous and largely overlapping distributions throughout the south-eastern Carpathian region were selected. The first one is assigned to the association *Sclerochloa dura* - *Polygonum arenastrum* Soó ex Bodrogekőzy 1966 corr. Borhidi 2003 (hereinafter named S-P), which encompasses weed assemblages developed in stressful and disturbed sites due to compact, trampled soils. The ecophysiological stress is related to the reduction in soil porosity, which induces temporary, oxygen or water (resource) deficit during rainy and drought periods, respectively. The S-P coenoses have low biomass, few species and are disturbed irregularly. The second one pertains to the association *Festuca rubra* - *Agrostietum capillaris* Horvat 1951 (hereinafter named F-A), which includes mesophilous, managed grasslands that are linked to moderately acidic but humus-rich soils. The F-A communities are species-rich, productive and regularly disturbed by (mostly sheep) grazing and mowing. By extending the scheme of models of plant community organisation proposed by Mirkin (1994), the S-P and F-A communities could be assigned to the R-S (ruderal-stress tolerant) and C-R (competitive-ruderal) coenotic strategy type, respectively.

The balance between negative and (indirect or direct) positive relationships in the two studied community types was theoretically predicted by using an adapted version of the asymmetrical hump model proposed by Michalet et al. (2006), in which plant species were assigned to either ‘com-

petitive’ or ‘stress tolerant-ruderal’ strategy (fig. 1). Due to differences in terms of environmental severity, the proportion of C and SR species in the floristic composition is assumed to be more or less balanced in F-A, but completely uneven (to the detriment of competitive species) in S-P. If such hypothesis holds true along a combined, stress - disturbance gradient, F-A should be positioned within the domain where both competition and indirect facilitation act jointly and species richness is high, whilst S-P should be located within the range of direct facilitation and low species richness (fig. 1). The previous predictions are based on Bertness & Callaway’s (1994) model and the review by Brooker et al. (2008). The net effect of species interactions at community level is then the sum of effects that operate on C and SR species.

Data collection and transformation

Two random sets of 145 relevés (floristic data samples) each pertaining to S-P and F-A were collected from literature and unpublished sources. All relevés were distributed within a convex hull whose major and minor axes measured about 550 km and 450 km along the NE-SW and NW-SE directions, respectively. The size of relevés varied from 9 to 25 m² in S-P and from 16 to 50 m² in F-A. Only the vascular species were considered in this study as the bryophytes and lichens were recorded only in few relevés. The names of all plant taxa were checked and, when appropriate, adjusted, for consistency with the current online version of Flora Europaea (<http://rbg-web2.rbge.org.uk/FE/fe.html>). Species cover scores were transformed in mid-cover class percentages with a view to assess the abundance-based resemblance between relevés.

In order to ascertain the compositional and structural homogeneity of relevés within each set (S-P and F-A), the two initial matrices were involved in an outlier analysis based on the box-and-whiskers plot rule. For this purpose, the pairwise floristic similarities between relevés were previously calculated using the transformed Horn index of overlap based on true diversities, as implemented in the R package ‘vegetarian’ by Charney & Record (2012). Such overlap measure is the only entropy-derived index that gives equal weights to common and rare species (Jost 2007). By using the end of the lower whisker in the corresponding box-plot as the cut-off value, two relevés from each data set displaying the smallest similarities with all the others were removed. The remaining pairwise similarities were all larger than 0.5. The trimmed presence-absence (binary) matrices of S-P and F-A, including 143 relevés each, were subsequently used as input in all species pattern analyses by assuming that the sites sampled were ecologically equivalent.

Metrics, null model and significance tests

A series of metrics, briefly presented in table 1, were used to explore different properties of species matrices. The statistical significance of the observed metrics in real data was expressed in terms of their standardised effect size (SES) by reference to the means of simulated indices drawn from 1000 random species assemblages: $SES = (\text{Observed metric} - \text{Mean of simulated metric}) / \text{Standard deviation of simulated}$

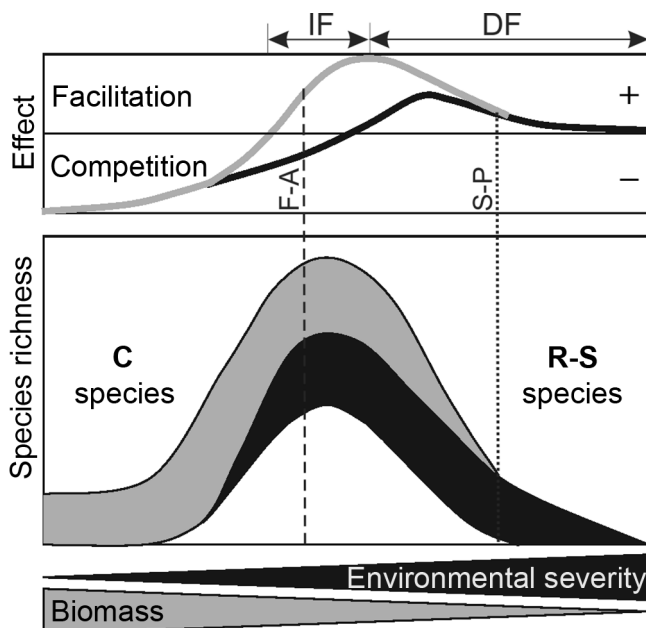


Figure 1 – Presumed location of the two plant community types considered within the conceptual model of asymmetric hump variation in the outcome of species interactions along an environmental severity gradient (F-A = *Festuca rubra* - *Agrostis tenuis* community; S-P = *Sclerochloa dura* - *Polygonum arenastrum* community; IF = indirect facilitation; DF = direct facilitation; C = competitive; RS = ruderal-stress tolerant). Adapted from Michalet et al. (2006).

Table 1 – Brief description of some species incidence-based metrics and their expected effects in the two contrasted matrices (F-A versus S-P) with respect to the null model of random assembly of species.

Double versus single plus or minus sign stands for larger positive or negative effect, respectively. Abbreviations as in fig. 1.

Metric	Measure	Matrix ordering	Presumed effect in:		Application employed	References
			F-A	S-P		
Normalised checkerboardness within the turnover region (C-turn)	Normalised number of 2 x 2 checkerboard submatrices located inside the diagonal strip of the seriated matrix (true species turnover)	Reciprocal averaging	+	–	Turnover (Ulrich 2012)	Ulrich & Gotelli (2013)
Normalised checkerboardness independent of turnover (C-segr)	As above, but only cells located outside the diagonal strip of the seriated matrix were considered (diffuse segregation)	Reciprocal averaging	+	–	Turnover (Ulrich 2012)	Ulrich & Gotelli (2013)
Number of checkerboard species pairs (nCS)	Count of species pairs that never co-occur	Reciprocal averaging	+	–	EcoSim (Gotelli & Entsminger 2005)	Gotelli (2000)
Number of duplicate species (nDS)	Count of species pairs that always co-occur	Reciprocal averaging	+	++	Excel 2010 macro (this paper)	Pielou & Pielou (1968)
Togetherness (TGR)	Normalised number of paired 2 x 2 submatrices	Reciprocal averaging	+	++	Turnover (Ulrich 2012)	Ulrich & Gotelli (2013)
Clumping (CLP)	Normalised number of completely filled 2 x 2 submatrices	Reciprocal averaging	+	++	Turnover (Ulrich 2012)	Ulrich & Gotelli (2013)
Embedded absences (EA)	Coherence of species range	Reciprocal averaging	–	--	Turnover (Ulrich 2012)	Presley et al. (2010)
Morisita index (MI)	Clustering of species range boundaries	Reciprocal averaging	+	++	Turnover (Ulrich 2012)	Hoagland & Collins (1997)
Variance ratio (VR)	Species association and variability in species richness per site	Reciprocal averaging	+	++	EcoSim (Gotelli & Entsminger 2005)	Schluter (1984)
Standardised discrepancy (BR)	Minimum count of shifts in occurrences (standardised by matrix fill) to get a perfectly nested design	Row and column totals	–	--	Turnover (Ulrich 2012)	Brualdi & Sanderson (1999)
Nestedness based on overlap and decreasing fill (NODF)	Normalised count of species overlaps along the gradient of decreasing both species richness and frequency	Row and column totals	+	++	Turnover (Ulrich 2012)	Almeida-Neto et al. (2008)
Turnover component of beta diversity (β -sim)	Species turnover based on multi-site Sørensen dissimilarity	Reciprocal averaging	–	--	R packages ‘betapart’ (Baselga et al. 2013) and ‘vegan’ (Oksanen et al. 2013)	Baselga (2010)
Homotoneity (HMT)	Consistency in core species composition within a matrix circumscribed to a single community type	Reciprocal averaging	++	+	Excel 2010 macro (this paper)	Peet (1981)

ed metric (Gurevitch et al. 1992). Assuming a normal distribution of SES, values larger than 2 and lower than -2 are significantly different from zero, that is the null effect. The fixed-equiprobable (FE) algorithm was used to generate a null model of community assembly, in which each species occurrence was randomly re-shuffled within each row and all sites were treated as equally suitable and reachable. This null model preserves the differences between species but each

of them is equally likely to occur at all sites, irrespective of the presence of other species. The FE algorithm was recommended for analysing ‘sample lists’ (Gotelli 2000), i.e. lists of species taken from standardised samples within areas of relatively homogeneous habitat. In addition, under the null hypothesis of independent assembly of species (no effects of interspecific interactions) and the assumption of ecological equivalence of sites, the FE algorithm was empirically shown

to be robust, unbiased and powerful (Ladau & Ryan 2010). Because many metrics were particularly defined for matrices sorted by different criteria (Ulrich & Gotelli 2013), calculations were performed exclusively on matrices ordered by reciprocal averaging or according to row and column marginal totals (table 1). The visual inspection of species incidence patterns was done on matrices that were previously sorted by the application Binmatnest, so that to reach the configuration that is closest to perfect nestedness (Rodríguez-Gironés & Santamaría 2006).

The SES of homotoneity (*sensu* Peet 1981), could not be estimated because the permutation constraints led to identical expected and observed values. This problem was overcome by employing the mode and not mean species richness per site in its calculation.

The pairwise floristic similarities between communities within each binary matrix were calculated by means of Raup & Crick index, which is able to handle unknown and variable sample sizes by comparing the observed number of species that occur in both sites with the distribution of co-occurrences in random assemblages. These were generated through the FE algorithm using the function *raupcrick* in the R package ‘vegan’ (Oksanen et al. 2013). The significance of differences in location and shape between the distributions of pairwise similarities within each matrix was assessed through Wilcoxon-Mann-Whitney and Kolmogorov-Smirnov tests, respectively implemented in the R package ‘stats’ (R Development Core Team 2013).

Given the high floristic homogeneity of each matrix but the relative positioning of F-A and S-P along the environmental severity gradient (fig. 1), the effects to be estimated

for most metrics were predicted to have the same direction (sign) but different magnitude between the two matrices contrasted (table 1). Only the effects of patterns related to checkerboardness were expected to be opposite (positive and negative) in F-A and S-P matrix, respectively (table 1).

RESULTS

The effects of two checkerboard-based measures (C-turn and nCS) are significantly positive in F-A, indicating a sensible degree of species segregation (fig. 2). Conversely, the effects of the same metrics in S-P are not different from null and significantly negative, respectively (fig. 2). Outside the turnover region, the effect of checkerboard score (C-segr) is also trivial in S-P but, in contrast with C-turn, turns significantly negative in F-A (fig. 2).

The effects of β -sim are significantly negative in both matrices but the effect size is much stronger in S-P, which suggests less species segregation due to turnover than in F-A (fig. 2).

The index of togetherness (TGR) shows positive, larger effects in S-P than in F-A, which provides evidence for stronger patterns of species co-occurrence in the former community type (fig. 2). The other two relating metrics, clumping score (CLP) and number of duplicate species (nDS), have almost equal effect sizes in the two matrices contrasted (fig. 2). The positive effect size of Morisita index (MI) is more than four times larger in S-P than in F-A, meaning more clustered occurrence boundaries in the former matrix (figs 2 & 3). The effects of the embedded absences (EA) are significantly negative in both community matrices but in F-A

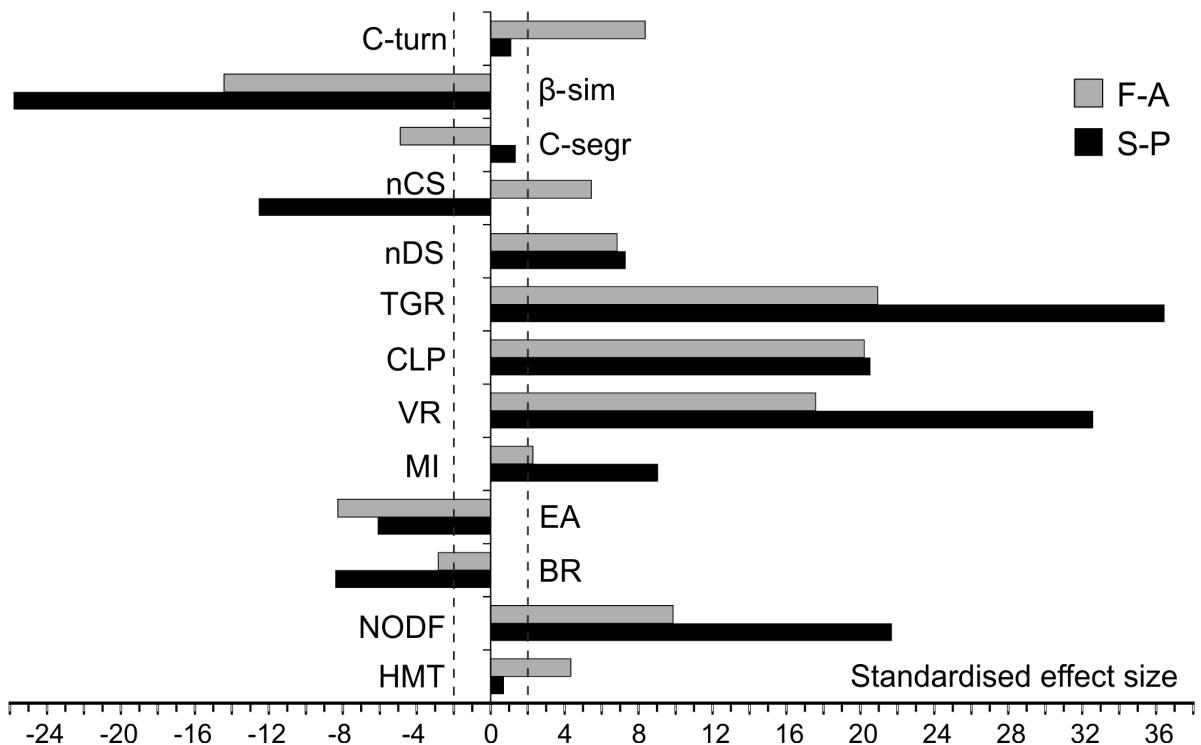


Figure 2 – Standardised effect size of species incidence-based metrics in the two contrasted community matrices (the two dashed reference lines mark the interval of non-significant effect size at 5% alpha probability). Abbreviations as in table 1.

the absolute magnitude is larger, which implies more coherence in species ranges (fig. 2).

The variance ratio (VR) has positive, significant effects in both matrices, which reveals positive covariance between species pairs. Nevertheless, the sensible larger effect size in S-P also indicates a higher variability in species richness per site than in F-A (figs 2 & 3). A similar pattern is revealed by the two measures of nestedness (NODF and BR) whose effects are all significant but larger in S-P matrix, which appears more nested than its counterpart (figs 2 & 3).

The effect of homotoneity is positive in both observed matrices but in S-P its size is not significantly different from

null (fig. 2). This means the prevalent species in S-P matrix display a distribution of constancies that is similar in location to those obtained in the random matrices generated. The higher floristic homogeneity of F-A matrix is also proved by the significantly larger pairwise similarities as compared to those in S-P matrix (Wilcoxon-Mann-Whitney test: $z = 11.232$; $p < 0.0001$). In addition, there is a significant difference in shape between the distributions of pairwise similarities (Kolmogorov-Smirnov test: $KSa = 9.046$; $p < 0.0001$), the one corresponding to F-A matching a reversed J-shaped model (fig. 4A) and that of S-P approaching a monotonically decreasing model (fig. 4B).

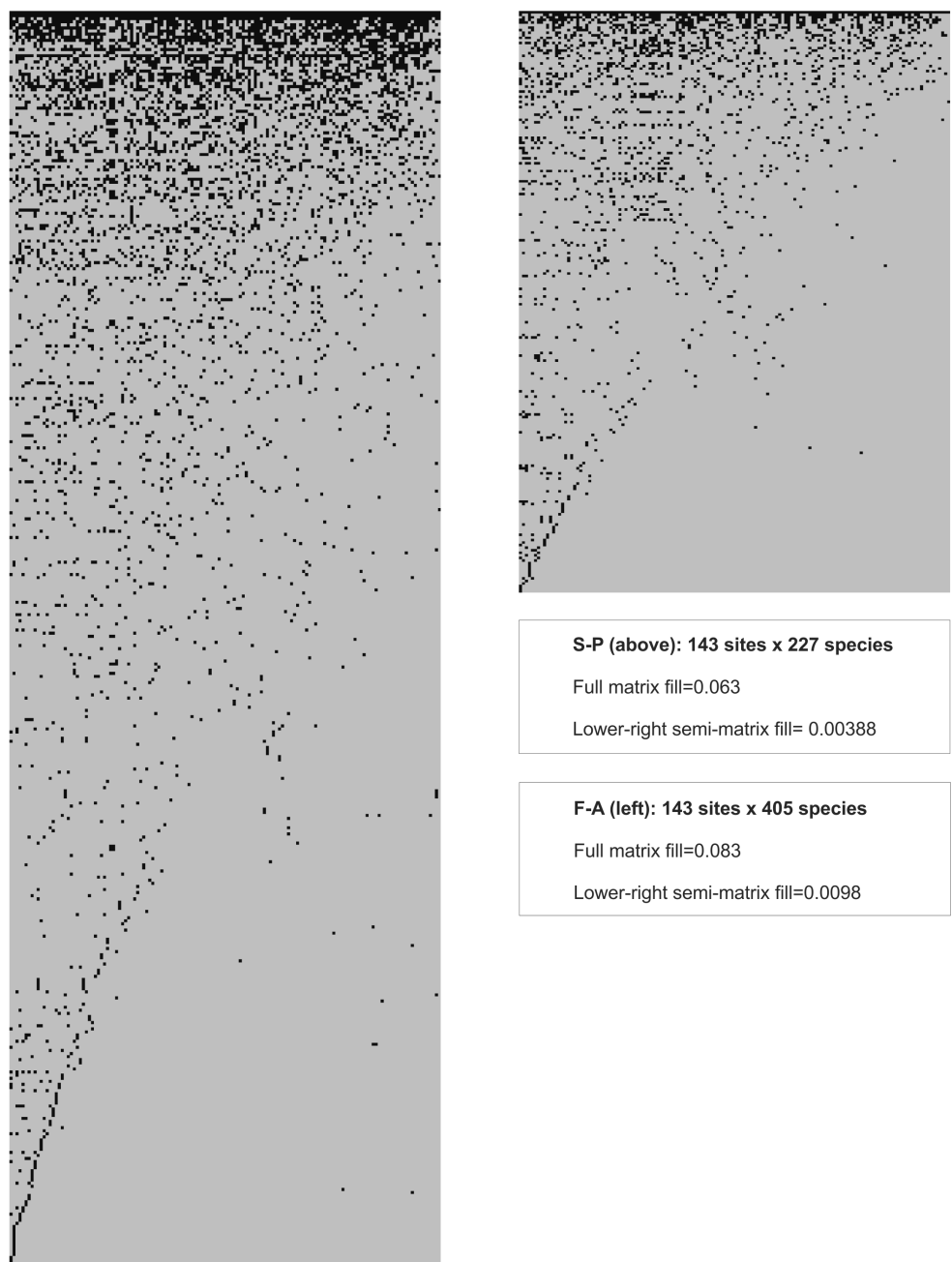


Figure 3 – Sorted matrices of F-A and S-P according to nestedness maximisation criterion (black and grey dots correspond to species presences and absences, respectively).

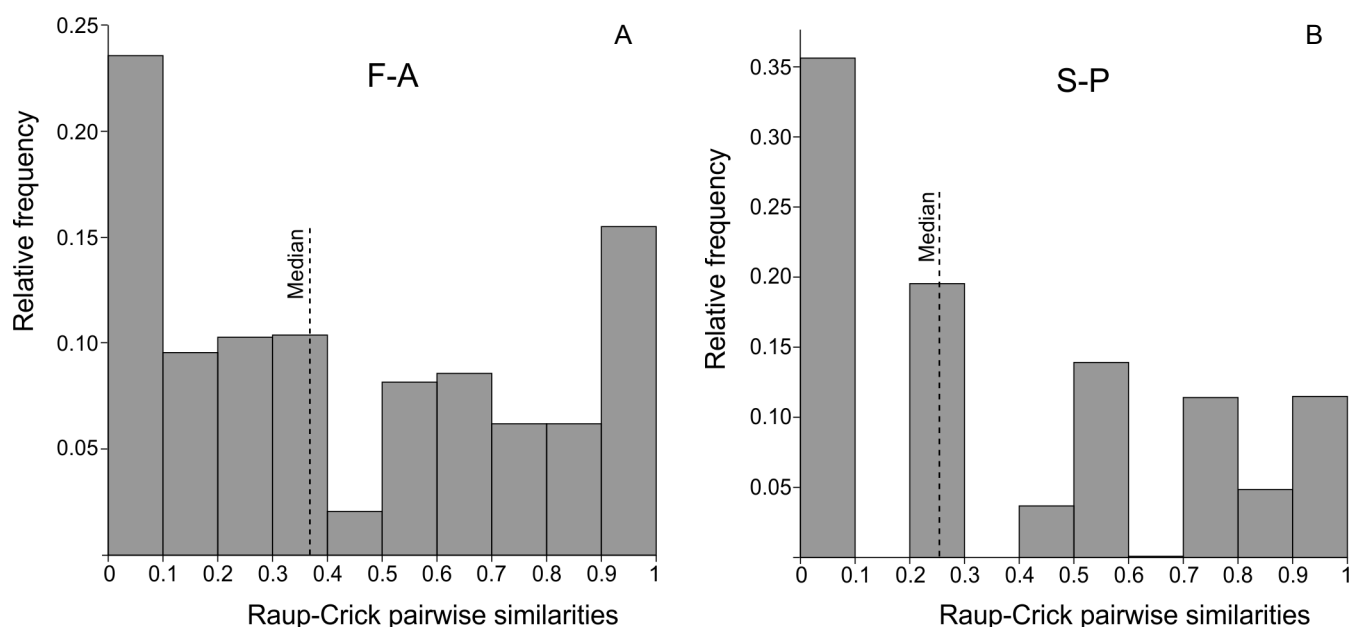


Figure 4 – Distribution of the pairwise Raup-Crick similarities between sites within F-A (A) and S-P (B) matrices. There are statistically significant differences in location and shape between the two distributions (see the Results section).

DISCUSSION

Effect size of species incidence patterns

All metrics revealing checkerboardness and co-occurrence patterns in species incidence give consistent results in the sense that they all indicate the S-P communities as being more aggregated than the F-A communities by reference to the random assemblages of the same set of species. This outcome is consistent with, but not a proof of, the stress-gradient hypothesis (Bertness & Callaway 1994, Maestre et al. 2009) according to which, higher frequency of positive interactions between species is expected in stressful and frequently disturbed habitats. As the importance of regional factors (species pool richness and biogeographic barriers) was roughly uniformised across the two data sets, the stronger patterns detected in the S-P matrix provide evidence for a deterministic community assembling by environmental filtering and species assembly rules that often lead to a relatively stable equilibrium (Weiher & Keddy 1995, Wilson 1999, Lortie et al. 2004).

The most unexpected outcome is the negative, strong effect of C-segr in the F-A matrix coupled with a slightly positive, even though not significant, effect in S-P. That means that the checkerboard pattern detected in the F-A matrix by the nCS index is exclusively due to pure species turnover (as shown by C-turn), and not also to diffuse segregation as originally predicted. The latter inference conforms with the findings of Ulrich & Gotelli (2013) who pointed to turnover as the dominant pattern of species segregation in empirical presence-absence matrices.

By reference to the scheme of twelve coherent meta-community structures defined by combining different patterns of species boundary clumping and turnover (Presley et al. 2010), the two community matrices (F-A and S-P) display

Clementsian and Quasi-Clementsian structures, respectively. That is not at all surprising, given the high resemblance of relevés within each matrix that encompasses only a single community type. The difference between the two matrices in terms of dispersion of the filled cell is more visible after their ordering according to row and column marginal totals, as there is a lower concentration of species presences in the F-A matrix than in the S-P counterpart, which makes the latter appear more aggregated.

The effect size and direction of all metrics discussed so far suggest that both segregation and aggregation patterns are present in F-A matrix, and that the latter is overwhelmingly prevalent in S-P. Such an outcome was predicted by the rough positioning of the two community types within the Michalet's et al. (2006) model of the net effect of species interactions along an environmental severity gradient. However, the aggregation and segregation patterns detected in the two community matrices cannot provide by themselves evidence about the nature of and the balance between positive and negative species interactions.

Taking into consideration the possible causes of nested subset patterns as listed by Ulrich et al. (2009), it is likely that the nestedness patterns detected in both community matrices are related to the selective occupancy of sites according to species tolerance to grazing and mowing (in F-A) and, to soil compaction and plant trampling (in S-P). As the pattern of species loss is a consequence of any factor that promotes the orderly disaggregation or aggregation of assemblages, the communities within the two matrices could represent slightly different dynamic stages, from species-poorer assemblages established in recently disturbed environments to gradually richer assemblages developed in ecologically more favourable habitats, partly recovered from the last disturbance event. Since high levels of nestedness are intrinsically associated with strong species aggregation (Ulrich & Gotelli 2007, Ul-

rich et al. 2009), the larger nestedness effect observed within S-P matrix is probably due to the ecologically more severe habitats.

The high degree of S-P community integration does not necessarily imply high consistency in its species composition, as this syntaxon is loosely defined in terms of species constancy (homotoneity). This is due in part to stronger pattern of species loss and higher uncertainty in the species richness of S-P communities, which consist of many opportunistic species whose establishment in or exclusion from trampled sites is also governed by casual disturbances. On the contrary, the less aggregated F-A matrix is more coherent (fewer embedded absences), homotonous (higher proportion of prevalent species) and floristically homogeneous (larger pairwise similarities), which makes it more clearly delineated as a syntaxon. Unlike the monotonic distribution corresponding to S-P, the reversed J-shaped distribution of the pairwise similarities in F-A matrix recalls the Raunkiaer's law of frequency, which was formerly used to assess the degree of uniformity (homotoneity) of vegetation units (McIntosh 1962). The differences between the distributions of similarities within S-P and F-A matrices may be related to the contrasting floristic distinctiveness of the corresponding high-rank syntaxa. For instance, the ruderal vegetation order (*Polygono arenastri* - *Poetalia annuae* Tüxen in Géhu et al. 1972 corr. Rivas-Martínez et al. 1991) circumscribed to the S-P community type is much poorer in character (high fidelity) species than the order *Arrhenatheretalia* Tüxen 1931, which encompasses the F-A grasslands. The previous considerations suggest that regular and moderate disturbances due to herbivores (like in F-A grasslands) may be an important requisite for plant community organisation according to the dominant/core-subordinate/satellite species hypothesis in productive habitats (Gotelli & Simberloff 1987, Collins & Glenn 1990).

Although S-P matrix is more aggregated and consequently, the weed communities seem more integrated, F-A matrix appears more structured as all metrics taken into consideration showed significant effects with respect to randomly assembled communities. This confirms how intimately linked the segregated and aggregated patterns are in empirical matrices and that a single matrix can display different kinds of non-random patterns (Gotelli & Ulrich 2012, Ulrich & Gotelli 2013). Overall, F-A grassland communities have a higher floristic distinctiveness, given the constancy of the core species and the higher stability in species richness. The differences in environmental conditions should have promoted different mechanisms of species co-existence at community level (see Wilson 2011 for a review). In particular, the allogenic disturbance and alpha-niche differentiation/grazer pressure may be the dominant stabilising mechanisms in S-P and F-A communities, respectively.

Performance of metrics

Generally, the effects of the metrics employed were consistent with the theoretical predictions and agreed among them in indicating similar or opposite species patterns. The difference in matrix fill between F-A and S-P was most likely too small (i.e. 2%) to affect perceptibly the comparisons based

on these indices. Yet, there are some differences in their performance.

First, the number of checkerboard species pairs (nCS) was the only measure that distinguished very sharply (via opposite effects) between the two community type matrices, but without filtering out the diffuse segregation and species turnover. Conversely, the two main components of the checkerboard score (C-turn and C-segr) indicated a less crisp distinction, probably because the matrix-wide checkerboardness was shared between turnover-dependent and independent segregation (Ulrich & Gotelli 2013). Second, the number of duplicate species (nDS) and the clumping score (CLP) seem to have less discriminant power than togetherness (TGR) and variance ratio (VR) in discerning the strength of species association.

On my knowledge β -sim and HMT have never been employed in species co-occurrence analysis based on simulation of null communities. The first index was inversely related to C-turn, which may appear illogical. However, as Baselga (2012) pointed out, β -sim is the turnover component of a multi-site dissimilarity, which is conceptually different from the species replacement pattern based on checkerboard units. Therefore, β -sim should be probably regarded more as a matrix-wide segregation index (derived from the dissimilarity due to species replacement) than a plain turnover measure. The performance of the HMT index was good judging from its consistency with respect to EA metric and its ability to discriminate between the F-A and S-P matrices.

Limitations and prospects

The analysis of species incidence patterns can provide valuable insights into the patterns of plant community structuring and organisation that are dependent, among other factors, on the environmental severity (mainly abiotic stress and disturbance). Although the present results suggest a link between species matrix structure and community integration, the observed non-random patterns do not necessarily imply any direct relationship with the strength, direction or net effect of species interactions within plant assemblages. For instance, the observed species co-occurrence patterns could have been generated by other processes than species interactions, like common ecological response and tolerance of species to abiotic stress and disturbance. Another limitation of the current approach is that one could expect different level of community integration even in very similar environments because of the absence/presence of certain key species. This is because positive interactions emerging through facilitation are species-specific (Callaway 2007). Finally, some metrics need further refinement and testing for a full understanding of their behaviour and meaning when applied to differently structured matrices.

The ecological equivalence of sites, assumed on the basis of floristic compositional homogeneity, did not exclude some environmental variation among sites (i.e. mesoclimatic gradients) that counterbalanced each other to a large extent. However, unknown environmental changes or anthropogenic influences could have exerted confounding or noise effects on the estimates of the strength of non-random species patterns. Another possible source of bias is related to sampling

grain (Reitalu et al. 2008), as the relevé size cannot fit for the whole range of possible spatial patterns. In particular, the relatively large size of relevés with respect to the scale at which herbaceous plants usually interact might have partially obscured the patterns of species segregation, but enhanced the detection of positive associations (Crawley 1997).

A peculiarity of the present study is its confinement to predefined, Braun-Blanquetian ‘plant associations’, represented by ecologically and floristically similar coenoses spread throughout a large territory, in contrast to analogous studies performed within the framework of more or less heterogeneous metacommunities. Such difference in geographic extension and homogeneity of community matrices could be crucial for the ability of different metrics to reveal patterns that are dependent on spatial scale. As a matter of fact, Ulrich & Gotelli (2013) found greater frequencies of nested, turnover and segregated/aggregated patterns for matrices assembled at the biogeographic scale versus the local scale. Consequently, the inferences pertaining to single community types with large regional distribution may not be extrapolated to metacommunities and vice versa.

Another important issue to be considered is the herein use of the fixed row - equiprobable column randomisation that is generally regarded as rather liberal, but which actually generated quite low variance in species richness per site. In any case, the comparison of the present results with those based on the commonly used fixed - fixed algorithm must be done with caution. For example, Götzenberger et al. (2012) demonstrated, by employing numerous empirical matrices, that the standardised effect size (SES) values of the number of checkerboard species pairs (nCS) were higher for null models that kept the row and column marginals constant, compared with those that constrained only the species frequencies.

Since field experiments aimed at validating complex relationships at geographic scales are challenging, the analysis of community matrices is promising for relating species patterns, environmental constraints and community properties. The use of multiple metrics represents a useful exploratory tool for distinguishing between various patterns of species assembly, especially when applied to relatively homogeneous matrices of different community types developed under contrasting environmental conditions. For instance, the consideration of two distinct checkerboard components (C-turn and C-segr) appears to be useful for differentiating between interaction-independent segregation (i.e. pure species replacement) and turnover-independent (diffuse) segregation (Ulrich & Gotelli 2013). The same authors suggested a pairwise analysis of species for matrix-wide pattern validation but such an approach doesn't seem feasible for matrices composed of several hundreds of species and, in addition, may be misleading if based on (dis)similarity measures (Baselga 2013). Finally, it must be stressed that an informative comparison of effect sizes of species patterns can be only made between matrices pertaining to communities that are similar in terms of plant density, vertical structure as well as evolutionary temporal scale. For instance, the degree of community integration may be higher in primary (climax) communities than in secondary assemblages, as a longer species co-evolution could have led to increased specialisation.

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REFERENCES

- Almeida-Neto M., Guimarães P., Guimarães Jr P.R., Loyola R.D., Ulrich W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and quantification. *Oikos* 117: 1227–1239. <http://dx.doi.org/10.1111/j.0030-1299.2008.16644.x>
- Baselga A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19: 134–143. <http://dx.doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga A. (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* 21: 1223–1232. <http://dx.doi.org/10.1111/j.1466-8238.2011.00756.x>
- Baselga A. (2013) Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography* 36: 124–128. <http://dx.doi.org/10.1111/j.1600-0587.2012.00124.x>
- Baselga A., Orme D., Vileger S. (2013) Betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.2 [online]. Available from <http://CRAN.R-project.org/package=betapart> [accessed 25 Nov. 2013]
- Bertness M., Callaway R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution* 9: 191–193. [http://dx.doi.org/10.1016/0169-5347\(94\)90088-4](http://dx.doi.org/10.1016/0169-5347(94)90088-4)
- Bowker M.A., Soliveres S., Maestre F.T. (2010) Competition increases with abiotic stress and regulates the diversity of biological soil crusts. *Journal of Ecology* 98: 551–560. <http://dx.doi.org/10.1111/j.1365-2745.2010.01647.x>
- Brooker R.W., Callaghan T.V. (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* 81: 196–207. <http://dx.doi.org/10.2307/3546481>
- Brooker R.W., Maestre F.T., Callaway R.M., Lortie C.L., Cavieses L.A., Kunstler G., Liancourt P., Tielbörger K., Travis J.M.J., Anthelme F., Armas C., Coll L., Corcket E., Delzon S., Forey E., Kikvidze Z., Olofsson J., Pugnaire F., Quiroz C.L., Saccone P., Schiffrers K., Seifan M., Touzard B., Michalet R. (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96: 18–34. <http://dx.doi.org/10.1111/j.1365-2745.2007.01295.x>
- Brualdi R.A., Sanderson J.G. (1999) Nested species subsets, gaps, and discrepancy. *Oecologia* 119: 256–264. <http://dx.doi.org/10.1007/s004420050784>
- Callaway R.M. (2007) Positive Interactions and Interdependence in Plant Communities. Dordrecht, Springer.
- Charney N., Record S. (2012) vegetarian: Jost Diversity Measures for Community Data. R package version 1.2 [online]. Available from <http://CRAN.R-project.org/package=vegetarian> [accessed 20 Mar. 2013]
- Collins S.L., Glenn S.M. (1990) A hierarchical analysis of species abundance patterns in grassland vegetation. *The American Naturalist* 135: 633–648. <http://dx.doi.org/10.1086/285066>
- Crawley M.J. (1997) The structure of plant communities. In: Crawley M.J. (ed.) *Plant Ecology*: 475–531. Oxford, Blackwell Science.

- Dullinger S., Kleinbauer I., Pauli H., Gottfried M., Brooker R., Nagy L., Theurillat J.P., Holten J.I., Abdaladze O., Benito J.L., Borel J.L., Coldea G., Ghosn D., Kanka R., Merzouki A., Klettner C., Moiseev P., Molau U., Reiter K., Rossi G., Stanisci A., Tomaselli M., Unterlugauer P., Vittoz P., Grabherr G. (2007) Weak and variable relationships between environmental severity and small-scale co-occurrence in alpine plant communities. *Journal of Ecology* 95: 1284–1295. <http://dx.doi.org/10.1111/j.1365-2745.2007.01288.x>
- Eccles N.S., Esler K.J., Cowling R.M. (1999) Spatial pattern analysis in Namaqualand desert plant communities: evidence for general positive interactions. *Plant Ecology* 142: 71–85. <http://dx.doi.org/10.1023/A:1009857824912>
- Gibson D.J., Ely J.S., Collins S.L. (1999) The core-satellite species hypothesis provides a theoretical basis for Grime's classification of dominant, subordinate, and transient species. *Journal of Ecology* 87: 1064–1067. <http://dx.doi.org/10.1046/j.1365-2745.1999.00424.x>
- Gotelli N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606–2621. [http://dx.doi.org/10.1890/0012-9658\(2000\)081](http://dx.doi.org/10.1890/0012-9658(2000)081)
- Gotelli N.J. (2001) Research frontiers in null model analysis. *Global Ecology and Biogeography* 10: 337–343. <http://dx.doi.org/10.1046/j.1466-822X.2001.00249.x>
- Gotelli N.J., Entsminger G.L. (2005) EcoSim: Null Models Software for Ecology, version 7.71 [online]. Available from <http://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html> [accessed 29 Mar. 2012]
- Gotelli N.J., Simberloff D. (1987) The distribution and abundance of tallgrass prairie plants: a test of the core-satellite hypothesis. *The American Naturalist* 130: 18–35. <http://dx.doi.org/10.1086/284695>
- Gotelli N.J., Ulrich W. (2012) Statistical challenges in null model analysis. *Oikos* 121: 171–180. <http://dx.doi.org/10.1111/j.1600-0706.2011.20301.x>
- Götzenberger L., de Bello F., Bräthen K.A., Davison J., Dubuis A., Guisan A., Lepš J., Lindborg R., Moora M., Pärtel M., Pellissier L., Pottier J., Vittoz P., Zobel K., Zobel M. (2012) Ecological assembly rules in plant communities - approaches, patterns and prospects. *Biological Reviews* 87: 111–127. <http://dx.doi.org/10.1111/j.1469-185X.2011.00187.x>
- Grime J.P. (2001) Plant strategies, vegetation processes, and ecosystem properties. Chichester, Wiley.
- Guinocet M. (1973) La phytosociologie. Collection d'écologie. Paris, Masson.
- Gurevitch J., Morrow L.L., Wallace A., Walsh J.S. (1992) A meta-analysis of competition in field experiments. *The American Naturalist* 140: 539–572. <http://dx.doi.org/10.1086/285428>
- Hanski I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38: 210–221. <http://dx.doi.org/10.2307/3544021>
- Hoagland B.W., Collins S.L. (1997) Gradient models, gradient analyses, and hierarchical structure in plant communities. *Oikos* 78: 23–30. <http://dx.doi.org/10.2307/3545796>
- Jost L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology* 88: 2427–2439. <http://dx.doi.org/10.1890/06-1736.1>
- Kawai T., Tokeshi M. (2007) Testing the facilitation–competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proceedings of the Royal Society B* 274: 2503–2508. <http://dx.doi.org/10.1098/rspb.2007.0871>
- Ladau J., Ryan S.J. (2010) MPowering ecologists: community assembly tools for community assembly rules. *Oikos* 119: 1064–1069. <http://dx.doi.org/10.1111/j.1600-0706.2009.17574.x>
- le Roux P.C., McGeoch M.A. (2010) Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162: 733–745. <http://dx.doi.org/10.1007/s00442-009-1484-9>
- Lortie C.J., Brooker R.W., Choler P., Kikvidze Z., Michalet R., Pugnaire F.I., Callaway R.M. (2004) Rethinking plant community theory. *Oikos* 107: 433–438. <http://dx.doi.org/10.1111/j.0030-1299.2004.13250.x>
- Maestre F.T., Callaway R.M., Valladares F., Lortie C. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97: 199–205. <http://dx.doi.org/10.1111/j.1365-2745.2008.01476.x>
- Maltez-Mouro S., Maestre F.T., Freitas H. (2010) Co-occurrence patterns and abiotic stress in sand-dune communities: their relationship varies with spatial scale and the stress estimator. *Acta Oecologica* 36: 80–84. <http://dx.doi.org/10.1016/j.actao.2009.10.003>
- McIntosh R.P. (1962) Raunkiaer's law of frequency. *Ecology* 43: 533–535. <http://dx.doi.org/10.2307/1933384>
- Michalet R., Brooker R.W., Cavieres L.A., Kikvidze Z., Lortie C.J., Pugnaire F.I., Valiente-Banuet A., Callaway R.M. (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* 9: 767–773. <http://dx.doi.org/10.1111/j.1461-0248.2006.00935.x>
- Mirkin B.M. (1994) Which plant communities do exist? *Journal of Vegetation Science* 5: 283–284. <http://dx.doi.org/10.2307/3236163>
- Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Wagner H. (2013) Vegan: Community Ecology Package. R package version 2.0-9 [online]. Available from <http://CRAN.R-project.org/package=vegan> [accessed 18 Nov. 2013]
- Ollf H., Bakker J.P. (1998) Do intrinsically dominant and subordinate species exist? A test statistic for field data. *Applied Vegetation Science* 1: 15–20. <http://dx.doi.org/10.2307/1479081>
- Peet R.K. (1981) Forest vegetation of the Colorado Front Range. *Vegetatio* 45: 3–75. <http://dx.doi.org/10.1007/BF00240202>
- Pielou D.P., Pielou E.C. (1968) Association among species of infrequent occurrence: the insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. *Journal of Theoretical Biology* 21: 202–216. [http://dx.doi.org/10.1016/0022-5193\(68\)90070-2](http://dx.doi.org/10.1016/0022-5193(68)90070-2)
- Presley S.J., Higgins C.L., Willig M.R. (2010) A comprehensive framework for the evaluation of metacommunity structure. *Oikos* 119: 908–917. <http://dx.doi.org/10.1111/j.1600-0706.2010.18544.x>
- R Development Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria [online]. Available from <http://www.R-project.org/> [accessed 11 Nov. 2013]
- Reitalu T., Prentice H.C., Sykes M.T., Lonn M., Johansson L.J., Hall K. (2008) Plant species segregation on different spatial scales in semi-natural grasslands. *Journal of Vegetation Science* 19: 407–416. <http://dx.doi.org/10.3170/2008-8-18381>
- Rodríguez-Gironés M.A., Santamaría L. (2006) A new algorithm to calculate the nestedness temperature of presence-absence matrices. *Journal of Biogeography* 33: 924–935. <http://dx.doi.org/10.1111/j.1365-2699.2006.01444.x>
- Schluter D. (1984) A variance test for detecting species associations, with some example applications. *Ecology* 65: 998–1005. <http://dx.doi.org/10.2307/1938071>

- Smit C., Rietkerk M., Wassen M.J. (2009) Inclusion of biotic stress (consumer pressure) alters predictions from the stress gradient hypothesis. *Journal of Ecology* 97: 1215–1219. <http://dx.doi.org/10.1111/j.1365-2745.2009.01555.x>
- Tuomisto H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33: 2–22. <http://dx.doi.org/10.1111/j.1600-0587.2009.05880.x>
- Ulrich W. (2012) Turnover – a FORTRAN program for analysis of species associations, version 1.1 [online]. Available from www.home.umk.pl/~ulrichw/ [accessed 15 Nov. 2013]
- Ulrich W., Almeida-Neto M., Gotelli N.J. (2009) A consumer's guide to nestedness analysis. *Oikos* 118: 3–17. <http://dx.doi.org/10.1111/j.1600-0706.2008.17053.x>
- Ulrich W., Gotelli N.J. (2007) Disentangling community patterns of nestedness and species co-occurrence. *Oikos* 116: 2053–2061. <http://dx.doi.org/10.1111/j.2007.0030-1299.16173.x>
- Ulrich W., Gotelli N.J. (2013) Pattern detection in null model analysis. *Oikos* 122: 2–18. <http://dx.doi.org/10.1111/j.1600-0706.2012.20325.x>
- Verdú M., Valiente-Banuet A. (2008) The nested assembly of plant facilitation networks prevents species extinctions. *The American Naturalist* 172: 751–760. <http://dx.doi.org/10.1086/593003>
- Weiher E., Clarke G.D.P., Keddy P.A. (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81: 309–321. <http://dx.doi.org/10.2307/3547051>
- Weiher E., Keddy P. (1995) The assembly of experimental wetland plant communities. *Oikos* 73: 323–335. <http://dx.doi.org/10.2307/3545956>
- Wilson J.B. (1999) Assembly rules in plant communities. In: Weiher E., Keddy P. (eds) *Ecological Assembly: advances, perspectives, retreats*: 130–164. Cambridge, Cambridge University Press.
- Wilson J.B. (2011) The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored. *Journal of Vegetation Science* 22: 184–195. <http://dx.doi.org/10.1111/j.1654-1103.2010.01226.x>
- Wolek J. (1997) Species co-occurrence patterns in pleustonic plant communities (class Lemnetaea). *Fragmenta Floristica et Geobotanica*, suppl. 5: 3–100.

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