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Effect of invasion by *Centaurea iberica* on community assembly of a mountain grassland of Kashmir Himalaya, India

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Abstract: Since the integrity of ecosystems is being challenged worldwide by invading species, there is a growing need to understand their effects on community assembly which is strongly related to community function. Null models, which are important quantitative tools in the search for ecological processes driving local diversity and species distributions, were used to determine whether or not the intact and invaded grassland communities differ from randomly created null communities in respect of species co-occurrence using four co-occurrence indices (C score; number of checkerboard units; number of species combinations and V ratio). In the intact grassland all the indices, except for the number of checkerboards, revealed significant species segregation as expected in competitively structured communities. In comparison, the invaded grassland showed random co-occurrence of species. Besides, decrease in the number of species in the invaded grassland and change in species diversity and dominance is also suggestive of disassembly of the grassland community by the invasive species.

Resumen: Debido a que la integridad de los ecosistemas está siendo amenazada en todo el mundo por las especies invasoras, hay una creciente necesidad de entender sus efectos en el ensamblaje de la comunidad, el cual está fuertemente relacionado con la función de la comunidad. Se utilizaron modelos nulos, que son herramientas cuantitativas importantes en la búsqueda de procesos ecológicos determinantes de la diversidad local y las distribuciones de las especies, para determinar si las comunidades de pastizal intactas y las invadidas difieren de comunidades creadas de manera aleatoria respecto a la presencia conjunta de especies, usando cuatro índices de coexistencia (el valor C; el número de unidades del tablero de ajedrez; el número de combinaciones de especies; y el cociente V). En el pastizal intacto todos los índices, excepto el número de unidades del tablero de ajedrez, revelaron una segregación significativa de las especies, como es de esperarse en comunidades estructuradas por la competencia. En contraste, el pastizal invadido mostró una coexistencia aleatoria de las especies. Además, el decremento en el número de especies en el pastizal invadido y el cambio en la diversidad de especies y la dominancia también sugieren que las especies invasoras afectan negativamente el ensamblaje de la comunidad de pastizal.

Resumo: Como a integridade dos ecossistemas vêm sendo desafiadas à escala mundial por espécies invasoras, existe uma necessidade crescente de compreender os seus efeitos no conjunto das comunidades e que estão fortemente relacionados com a função da comunidade. Modelos de hipótese nula, que são importantes ferramentas quantitativas na procura de processos ecológicos motores da diversidade local e a distribuição das espécies, foram utilizados para determinar se sim ou não as comunidades de pastagens intactas ou invadidas diferem das comunidades sem alteração casualmente criadas em relação a espécies co-ocorrendo usando

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índices de co-ocorrência (pontuação C; número de unidades de quadrícula; número de combinações de espécies e ratio V). Na pastagem intacta todos os índices, excepto para o número de quadrículas, revelou segregação significativa de espécies como expectável em comunidades competitivas estruturadas. Em comparação, as pastagens invadidas mostraram co-ocorrência casual. Além disso, o decréscimo do número de espécies nas pastagens invadidas e mudança na diversidade e dominância de espécies é também sugestiva da desmontagem da comunidade de pastagem pelas espécies invasivas.

Key words: Community assembly rules, null models, community invasion.

Introduction

Community assembly provides a conceptual foundation for understanding the processes that determine which and how many species can occur in a particular community (Chase 2003a). However, the processes that determine the patterns of species co-occurrence have been controversial, and two main tradeoff-based theories of interspecific competition (Tilman 1988) and neutrality (Bell 2000; Hubbell 2001; McGill *et al.* 2006) have been advanced as potential explanations for the assembly, dynamics and structure of ecological communities (Tilman 2004). The two theories make markedly different predictions about community assembly processes. While the niche tradeoff models predict that resident species will most strongly inhibit establishment and growth of species similar to them, neutral models assume that all species are competitively identical and that regional abundances are determined by random forces driven by demographic stochasticity (Hubbell 2001). Though most investigators believe that neutral models predict random assembly of ecological communities independent of species traits (Fargione *et al.* 2003), few studies have shown that stochastic processes can also generate highly ordered systems (Ulrich 2004). Whether communities are assembled randomly or with a repeatable non-random process has wide implications for both basic and applied ecology. Thus, over the years many types of community assembly rule models like, body-size ratios (Dayan & Simberloff 1994), favoured states (Fox & Brown 1993), guild proportionality (Wilson 1989), species nestedness (Patterson & Atmar 1986; Ulrich & Gotelli 2007), and trait-environment association (Keddy & Weiher 1999) have been put forth. But the most influential model still remains the one proposed by Diamond (1975) who stated that community composition is characterized by a series of assembly rules, including forbidden species combinations, checkerboard distributions, and incidence functions which could be predicted by a few key variables, such as the size of the species pool, the abiotic environment, and interspecific interactions (Gotelli & McCabe 2002). Although Connor & Simberloff (1979) demonstrated that many of the patterns attributed by Diamond (1975) to interspecific competition could also arise in communities that were assembled by random colonization, meta-analysis of assembled data from 96 studies of species occurrences from scales of 1-10^{10} m^2 carried out by Gotelli & McCabe (2002) concluded that communities, in general, are assembled as a result of competitive interactions between species, and as predicted by Diamond's model, the observed communities show non-random co-occurrence pattern, fewer species combinations, and more checkerboard species pairs than is expected by chance. However, Connor & Simberloff (1979) pointed out that before discussing assembly rules it must be demonstrated that communities have species co-occurrence patterns different from null communities (randomly constructed communities). Consequently, null models have been developed and used widely to investigate patterns in species distributions and to identify possible mechanisms or assembly rules (Anderson *et al.* 2000; Peres-Neto *et al.* 2001). In fact, null models constitute a body of statistical methods to assess whether observed patterns in species distributions are distinct from arrangements of species taken at

random from the regional pool. Use of highly refined null models has also indicated involvement of non-random processes in community assembly (Gotelli 2000; Weiher & Clarke 1998; Zobel *et al.* 1993) as predicted by Diamond (1975). Besides, most studies suggest that community assembly often leads to a single stable equilibrium wherein the conditions of the environment and interspecific interactions determine which species will exist there. In such cases, regions of local communities with similar environmental conditions should have similar community composition (Law & Morton 1996; Sommer 1991; Tilman *et al.* 1986). However, others (Law 1999; Samuels & Drake 1997) suggest that community assembly can also lead to multiple stable equilibria and the resulting community depends on the assembly history, even when all species have access to the community. In these cases, a region of local communities with similar environmental conditions can be very dissimilar in their community composition.

While the effect of several regional and local factors on community assembly has been studied in great detail (Chase 2003a), yet the effect of non-native invasive species on the organization and structure of the invaded communities has been hardly considered (Sanders *et al.* 2003). Such studies have assumed urgency in view of ever increasing number of non-native invasive species and their role in reshaping the structure, dynamics and function of biological communities (Mack *et al.* 2000). Hence in the present study we used null model approach, as suggested by Gotelli (2000), and Gotelli & McCabe (2002), to find out whether or not the intact (un-invaded) and invaded grassland communities differ from randomly created null communities in respect of species co-occurrence patterns employing four co-occurrence indices (C score; number of checkerboard units; number of species combinations and V ratio). Second, we also examined whether invaded and intact sites differ from one another in competitive structure using guild structure algorithm of Gotelli & Entsminger (2001a). Also, we used the null model approach to assess the impact of *Centaurea iberica* on the structural organization of the invaded community. Finally, we compared the invaded and uninvaded grassland communities using commonly employed indices of species diversity and dominance.

Materials and methods

Study site

The present investigation was undertaken at two adjacent sites, separated by a seasonal stream, within a grassland spread over an area of 5 km^2 near Dignibal, located 21 km north-east of Srinagar city in the state of Jammu and Kashmir, India. The study area is a part of the Great Zanaskar range of Trans-Himalayas, and lies between 34° 04´ to 34° 14´ N latitude and 74° 48´ to 75° 85´ E longitude. The grassland has a well-drained gentle slope topography. The climate is of sub-Mediterranean type with four distinct seasons, *viz.*, spring (March-May), summer (June-August), autumn (September-November) and winter (December-February). Grasslands in this area represent the last abode of threatened Kashmir Stag (*Cervus elaphus hanglu*).

The intact site (uninvaded) was dominated by *Themeda anathera* Hack., in association with other herbs and few shrubs whereas the invaded site was dominated by *Centaurea iberica* Trev. ex Spreng., and other, mostly unpalatable herbs and thorny shrubs. Both the sites are located at the same elevation of 1950 m (a.m.s.l.), on a similar aspect. The intact site has been protected from anthropogenic disturbance, chiefly livestock grazing, by barbed wire fencing for the last 20 years. The invaded site has no such protection and road alignment and livestock grazing in this site are the main factors of disturbance.

Co-occurrence pattern

To ascertain whether or not the intact and invaded sites within the grassland show assembly rules, species presence-absence matrices were generated by laying randomly 50 quadrats, each of 1 m^2, in the two sites of the grassland during summer (June-August). Four statistical indices: C-score (Stone & Roberts 1990), number of checkerboard pairs (Diamond 1975), Combo - the number of species combinations (Pielou & Pielou 1968), and V-ratio (Robson 1972; Schluter 1984) were calculated following Gotelli & Entsminger (2001a). The C-score index quantifies the average amount of co-occurrence among all unique pairs of species in the assemblage. In a competitively structured community, the observed C-score should be significantly larger than expected by

chance. The number of checkerboard species pairs (CHECKER), i.e., the number of species combinations that never occur, should be significantly larger in a competitively structured community. The number of species combinations (COMBO) in a competitively structured community should be significantly smaller than expected by chance because competition leads to "forbidden" combinations that will not be found. The V-ratio measures the variance in the number of species per site and in a competitively structured community, the observed V ratio should be significantly smaller than expected by chance. These indices were computed not only for observed presence-absence matrices but also for null communities generated using following null model algorithms.

Null model algorithms

The probability of each index listed above was determined using Monte Carlo randomizations of the original presence-absence matrix. The original matrices were permuted 10,000 times and the statistical significance of the observed values was determined by comparing the indices of the original matrix to the distribution of randomly generated indices (Manly 1995). Three null models, used in the present study to randomize each matrix using "swap" and "independent" algorithm (Gotelli & Entsminger 2001 b) were: (i) Fixed-fixed in which the row and column sums of the original matrix are retained which preserves differences in species richness among sites (column totals) and differences in occurrence frequencies among species (row totals). Though, some authors have argued that such an algorithm is prone to Type II error (Alatalo 1982; Gilpin & Diamond 1984), Gotelli (2000) pointed out that it has good statistical properties when tested against random and structured matrices. The V-ratio cannot be used with this algorithm, as it does not generate any variation in row and column sums; (ii) Fixed-equiprobable in which only the row sums are fixed, and the columns (= sites) are treated as equiprobable. Thus, the number of species in a site (column total) is allowed to vary, but all sites have the same average number of species. This null model is useful where sites are of similar size and quality (as in quadrat samples); and (iii) Fixed-proportional which is a compromise algorithm between fixed column totals and equiprobable columns and makes the probabilities of species placement proportional to the observed column totals. With this option, the observed row totals are maintained in the simulation but the column totals are not fixed. On average, however, the rank order of sites based on species richness in the null assemblages matches the rank order of sites in the original matrix.

Comparison between intact and invaded communities

To test for differences in species co-occurrence between intact and invaded communities, a partition test was used following Sanders *et al.* (2003). The data from both the communities were organized as a single matrix in which each row represented a species and each column (=region) represented a sample (invaded or un-invaded) followed by reshuffling of the sample labels of "invaded" and "un-invaded" among the different columns. Above-mentioned indices of community structure (C-score, number of checkerboard pairs, number of species combinations and V-ratio) were then calculated for the invaded and un-invaded matrices. Finally, the variance of the above mentioned indices was calculated for each random partition. The larger this variance, more different the invaded and un-invaded communities. All null model analyses were conducted with ECOSIM 7.0 software.

Species diversity

We calculated the Shannon-Wiener diversity index ($H' = -\Sigma p_i \ln p_i$, where, p_i is the proportion of individuals of the *i*th species). For the purpose of comparison H_{max} was also determined assuming that all the species are equally abundant.

Simpson's (inverse) diversity index (1/D) was also calculated as it is most commonly used. Since this index has the disadvantage of being heavily weighted towards the most abundant species and addition of a few rare species will fail to change it, the index proposed by Berger & Parker (1970) was used, although it is also influenced by sample size. While no perfect index of diversity is available, May (1975) concluded that Berger-Parker index (D) is one of the most satisfactory measures available and the same was also used in the present investigation:

$$D = \frac{N_{max}}{N}$$

Where, N_{max} is the number of individuals in the most abundant species and N is the total number of individuals.

Results

Community composition

The intact part of the grassland supported 21 plant species with *Themeda anathera*, *Lespedeza elegans* and *Trifolium pratense* being the most frequent species (Table 1). In comparison, vegetation in the invaded area of the grassland comprised only 7 species; *Centurea iberica* was the most frequent species, which incidentally is also a non-native invasive species (Table 1).

Species co-occurrence

Tables 2 and 3 illustrate the results of testing the original presence-absence matrices of constituent plant species in the intact and invaded sites of the grassland using three algorithms and four co-occurrence indices. In respect of intact grassland, the C score was statistically significant with two algorithms (fixed-fixed; fixed-proportional). The CHECKER was not statistically significant with any of the null models used. Forty nine species combinations were observed in the matrix, which was statistically significant for all the used null model algorithms. The V-ratio was statistically significant when used with the fixed-proportional null model. Data reveal that the co-

Table 1. Frequency of plant species in the intact and invaded sites of the grassland.

Name of taxa	Family	Intact site	Invaded site	Frequency (%)
Androsace rotundifolia Hardw.	Primulaceae	+	-	42
Artemesia annua L.	Asteraceae	+	-	66
Asparagus filicinus Ham.	Liliaceae	+	-	20
Bothriochloa ischaemum Keng	Poaceae	-	+	70
Bupleurum hoffmiestri L.	Apiaceae	+	-	50
Carex nubigena D.Don.	Cyperaceae	+	-	28
Centaurea iberica Trev. Ex Spreng	Asteraceae	-	+	100
Cichorium intybus L.	Asteraceae	-	+	10
Clinopodium vulgare L.	Lamiaceae	+	-	56
Cynodon dactylon Pers.	Poaceae	-	+	24
Dactylis glomerata L.	Poaceae	+	-	32
Erigeron multicaulis Wall. Ex DC.	Asteraceae	+	-	50
Euphorbia wallichi Hook.f.	Euphorbiaceae	+	-	26
Hieracium umbellatum L.	Asteraceae	+	-	18
Hypericum perforatum L.	Hypericaceae	+	-	56
Indigofera heterantha Wall. Ex Brand	Fabaceae	+	-	72
Leonurus cardiaca L.	Lamiaceae	+	-	22
Lespedeza cuneata G.Don	Fabaceae	-	+	28
Lespedeza elegans Camb.	Fabaceae	+	-	58
Lespedeza tomentosa Sieb. Ex Mexim	Fabaceae	+	-	52
Lithospermum arvense L.	Boraginaceae	+	-	42
Origanum vulgare L.	Lamiaceae	+	-	56
Plantago lanceolata L.	Plantaginaceae	-	+	10
Silene vulgaris Garcke	Caryophyllaceae	+	-	42
Themeda anathera Hack.	Poaceae	+	-	100
Thymus serpyllum L.	Lamiaceae	-	+	36
Trifolium pratense L.	Fabaceae	+	-	64

+ = present; - = absent

occurrence of the plant species in the intact grassland is determined by competitive interactions between the species (Table 2). In comparison, none of the indices was significant with any used null model algorithm in the *Centaurea* invaded part of the grassland thus tending to indicate disassembly of the community structure.

Comparison between intact and invaded communities

Data show that the observed C-score, Checker and Combo are larger for the intact grassland than the invaded grassland while marginal difference is seen in the simulated data set pointing towards differences in the community structure of the two grasslands (Table 4). In order to find out whether or not the two grassland areas are significantly different, we calculated the variance in the co-occurrence index across the two community types. Among the four indices, C-score and Combo only showed significant differences between un-invaded and invaded grassland sites. The observed variance in C-score (2233.67) was significantly larger than the simulated value (p=0.000), and likewise the observed variance in Combo (480.50) was significantly larger than the simulated value (p=0.000), suggesting a significant influence of invasion by *C. iberica* on community assembly.

Table 2. Results of null model analyses of the co-occurrence matrix of the intact site. (SS expected score generated using sequential swap algorithm, IS expected score generated using the independent swap algorithm).

Index	Row constraint	Column constraint	Observed index	Simulated index (SS)	Simulated index (IS)
C-score	Fixed	Fixed	112.12	111.49*	111.48*
	Fixed	Equiprobable	112.12	110.89	110.95
	Fixed	Proportional	112.12	106.33*	106.36*
Checker	Fixed	Fixed	2.00	0.67	0.68
	Fixed	Equiprobable	2.00	0.69	0.69
	Fixed	Proportional	2.00	0.60	0.59
Combo	Fixed	Fixed	49.00	49.97*	49.99*
	Fixed	Equiprobable	49.00	49.99*	49.99*
	Fixed	Proportional	49.00	49.99*	49.99*
V-ratio	Fixed	Equipropable	0.96	1.00	0.99
	Fixed	Proportional	0.96	1.35*	1.35*

*Observed score is significantly (p<0.05) different from the expected score

Table 3. Results of null model analyses of the co-occurrence matrix of the invaded site. (SS expected score generated using sequential swap algorithm, IS expected score generated using the independent swap algorithm).

Index	Row constraint	Column constraint	Observed index	Simulated index (SS)	Simulated index (IS)
C-score	Fixed	Fixed	45.29	43.93	43.92
	Fixed	Equiprobable	45.29	44.62	44.62
	Fixed	Proportional	45.29	41.16	41.02
Checker	Fixed	Fixed	0.00	0.63	0.60
	Fixed	Equiprobable	0.00	1.17	1.17
	Fixed	Proportional	0.00	1.01	1.03
Combo	Fixed	Fixed	18.00	18.82	18.81
	Fixed	Equiprobable	18.00	19.09	19.11
	Fixed	Proportional	18.00	19.07	19.09
V-ratio	Fixed	Equipropable	1.08	0.99	0.99
	Fixed	Proportional	1.08	1.12	1.13

Table 4. Co-occurrence structure in intact vs. invaded sites.

Index	Observed value		Mean simulated value	
	Intact site	Invaded site	Intact site	Invaded site
C-score	112.12	45.29	67.79	65.02
Checker	2.00	0.00	155.24	154.87
Combo	49.00	18.00	37.29	36.44
V-ratio	0.96	1.08	2.96	2.94

Table 5. Comparison of species diversity and dominance in intact and invaded sites.

Index	Intact site	Invaded site
Shannon-Weiner Diversity Index (H')	2.95	1.66
Shannon H_{max}	3.05	1.95
Simpson Diversity	0.05	0.22
Simpson Diversity (1/d)	18.37	4.46
Beger-Parker Domiance (D)	0.10	0.36
Berger-Parker Dominance (1/D)	9.80	2.78

Perusal of the data reveals that Shannon-Weiner Index (H') was lower in invaded site compared to intact site (Table 5). Likewise, for the invaded site H_{max} was only 1.95 while the same for the intact site was 3.05. Dominance, whether computed using Simpson's or Berger-Parker index, was higher for the invaded site.

Discussion

Our study reveals that invasion of the grassland by exotic invasive *C. iberica* not only reduces the number of species but also alters the species co-occurrence and species diversity patterns. In intact part of the grassland, observed C-score obtained by using two null model algorithms was significantly higher than the simulated value. It is indicative of competitively structured co-occurrence pattern among the species. However, the observed C-score value when calculated by the fixed-equiprobable null model was not statistically significant. This model treats all the sites as equally suitable for all species (Haukisalmi & Henttonen 1998), which may not be the case with our grassland in view of spatial heterogeneity reported by a number of workers in different communities (McNaughton 1983; Collins *et al.* 1998; Olff & Ritchie 1998). In the invaded area of the grassland none of the null models yielded a significantly higher observed C-score value than expected by chance which indicates disorganization of the community assembly by invasion.

The second index used for studying the community organization in intact and invaded parts of the grassland was the number of species pairs that never co-occur, forming "checkerboard" distributions (Diamond 1975). The competitively structured communities should contain more checkerboard pairs than randomly assembled communities (Gotelli & McCabe 2002) but in neither of the present sites, the metric was statistically significant. This measure, according to Gotelli (2000), is more sensitive to random error, which is common in presence-absence matrices as used in the present study, and may not always detect patterns of negative co-occurrence. The number of species combinations (Pielou & Pielou 1968) in the intact site in our study was significantly smaller than expected by chance irrespective of the null model algorithm used. Such was not the case with the invaded site. This observation lends further support to our earlier conclusion of community disorganization by the invasive *C. iberica*. The smaller number of species combinations in the intact community is presumably due to competitive species interactions, which structure the community and lead to "forbidden" combinations that will not be found (Diamond 1975). The observed V-ratio of the intact grassland when computed with the fixed-proportional null model was significantly lower than the simulated value, while the same was not true for the invaded grassland. *C. iberica* not only reduces species diversity but also changes species composition. In addition, its invasion also disrupts community assembly which becomes evident when co-occurrence pattern of observed and null matrices of intact and invaded sites is compared. These conclusions are further strengthened when the species co-occurrence structure of invaded community is compared with the intact community, using C-score and Combo in particular. Although previous studies have also documented the effects of invasive species on native community structure (Gotelli & Arnett 2000), the present study stands out in that the invaded and intact grassland sites are part of the same grassland and the chances of difference

between the sites, other than variation in the extent of invasibility, are minimal. Also it is easy to comprehend that the two sites must not have differed in respect of species community and organization prior to invasion. But how to account for development of different communities under otherwise similar environmental conditions? Many controlled laboratory experiments (Drake *et al.* 1993; Gilpin *et al.* 1986; Lawler 1993), field experiments (Chase 2003b; Jenkins & Buikema 1998) and observations of natural systems (Cole 1983; Petraitis & Latham 1999) have indicated that under similar environmental conditions, very different communities can develop as a result of variation in the timing and sequence of species invasions (Chase 2003a). However, it remains to be seen whether or not the entire grassland would be invaded by *C. iberica* in the course of time. Besides, understanding of ecological processes structuring a community, such as competition (Law & Morton 1996), disturbance (Burke & Grime 1996), fluctuating resources (Davis *et al.* 2000), or growth rate of species (Rejmánek & Richardson 1996) can also shed light on as to why a species establishes and then spreads in a particular community (Elton 1958; Shea & Chesson 2002).

In conclusion, it may be stated that the invasion of the grassland by *C. iberica* leads to change in community composition, increase in number and abundance of non-palatable weedy species at the expense of palatable species, decrease in diversity and disorganization of community structure with serious implications for functional integrity and suitability of such grasslands as foraging grounds for the threatened Kashmir Stag (*Cervus elaphus hanglu*).

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References

Alatalo, R.V. 1982. Bird species distributions in the Galapagos and other archipelagoes: competition or chance? *Ecology* **63**: 881-887.

Anderson, D.R., K.P. Burnham & W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence and an alternative. *Journal of Wildlife Management* **64**: 912-923.

Bell, G. 2000. The distribution of abundance in neutral communities. *American Naturalist* **155:** 606-617.

Berger, W.H. & F.L. Parker. 1970. Diversity of planktonic foraminifera in deep sea sediments. *Science* **168**: 1345-1357.

Burke, M.J.W. & J.P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* **77**: 776-790.

Chase, J. M. 2003a. Community assembly: when should history matter? *Oecologia* **136**: 489-498.

Chase, J.M. 2003b. Experimental evidence for alternative stable equilibria in a benthic pond food web. *Ecology Letters* **6**: 733-741.

Cole, B.J. 1983. Assembly of mangrove ant communities: patterns of geographical distribution. *Journal of Animal Ecology* **52**: 397-347.

Collins, S.L., A.K. Knapp, J.M. Briggs, J.M. Blair & E.M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* **280**: 745-747.

Connor, E.F. & D. Simberloff. 1979. The assembly of species communities: chance or competition. *Ecology* **60**: 1132-1140.

Davis, M.A., J.P. Grime & K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**: 528-534.

Dayan, T. & D. Simberloff. 1994. Morphological relationships among coexisting heteromyids: an incisive dental character. *American Naturalist* **143**: 462-477.

Diamond, J.M. 1975. Assembly of species communities. pp. 342-444. *In*: M.L. Cody & J.M. Diamond (eds.) *Ecology and Evolution of Communities*. Harvard University Press, Cambridge.

Drake, J.A., T.E. Flum, G.J. Witteman, J. Voskuil, A.M. Hoylman, C. Creason, D.A. Kenny, G.R. Huxel, C.S. Larue & J.R. Duncan. 1993. The construction and assembly of an ecological landscape. *Journal of Animal Ecology* **62**: 117-130.

Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen, London, UK.

Fargione, J., C.S. Brown & D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences*, *USA* **100**: 8916-8920.

Fox, B.J. & J.H. Brown. 1993. Assembly rules for functional groups in North American desert rodent communities. *Oikos* **67**: 358-370.

Gilpin, M.E., M.P. Carpenter & M.J. Pomerantz. 1986. The assembly of a laboratory community: multi-species competition in *Drosophila*. pp. 23-40. *In*: J. Diamond & T.J. Case (eds.) *Community Ecology*. Harper and Row, New York.

Gilpin, M.E. & J.M. Diamond. 1984. Are species co-occurrences on islands nonrandom, and are null hypotheses useful in community ecology? pp. 297-315. *In:* D.R. Strong, Jr., D. Simberloff, L.G. Abele & A.B. Thistle (eds.) *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton.

Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**: 2606-2621.

Gotelli, N.J. & A.E. Arnett. 2000. Biogeographic effects of red fire ant invasion. *Ecology Letters* **3**: 257-261.

Gotelli, N.J. & G.L. Entsminger. 2001a. EcoSim: null models software for ecology. Version 6.0. Acquired Intelligence Inc. and Kesey-Bear. http://homepages.together.net/gentsmin/ecosim.htm.

Gotelli, N.J. & G.L. Entsminger. 2001b. Swap and fill algorithms in null model analysis: rethinking the Knight's Tour. *Oecologia* **129**: 281-291.

Gotelli, N.J. & D.J. McCabe. 2002. Species co-occurrences: a meta-analysis of J.M. Diamond's assembly rule model. *Ecology* **83**: 2091-2096.

Haukisalmi, V. & H. Henttonen. 1998. Analyzing interspecific associations in parasites: alternative methods and effects of sampling heterogeneity. *Oecologia* **116**: 565-574.

Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.

Jenkins, D.G. & A.L. Buikema. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecological Monographs* **68**: 421-443.

Keddy, P. & E. Weiher. 1999. The scope and goals of research on assembly rules. pp. 1-20. *In*: E. Weiher & P. Keddy (eds.) *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge, UK.

Law, R. 1999. Community assembly. pp. 143-171. *In*: J.M. McGlade (ed.) *Advanced Ecological Theory*. Blackwell Science, Oxford, UK.

Law, R. & R.D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* **77**: 762-775.

Lawler, S.P. 1993. Direct and indirect effects in microcosm communities of protists. *Oecologia* **93**: 184-190.

Mack, R.N., D. Simberloff, W.M. Lonsdale, J. Evans, M. Clout & F.A. Bazzaz. 2000. Biotic invasion: causes, epidemiology, global consequences and control. *Ecological Applications* **10**: 689-710.

Manly, B.F.J. 1995. A note on the analysis of species co-occurrences. *Ecology* **76**: 1109-1115.

May, R.M. 1975. Patterns of species abundance and diversity. *In*: M.L. Cody & J.M. Diamond (eds.) *Ecology and Evolution of Communities*. Harvard University Press.

McGill, B.J., B.A. Maurer & M.D. Weiser. 2006. Empirical evaluation of neutral theory. *Ecology* **87**: 1411-1423.

McNaughton, S.J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* **53**: 291-320.

Olff, H. & M.E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* **13**: 261-265.

Patterson, B.D. & W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagoes. *Biological Journal of the Linnean Society* **28**: 65-82.

Peres-Neto, P. R., J.D. Olden & D.A. Jackson. 2001. Environmentally constrained null models: site suitability as occupancy criterion. *Oikos* **93**: 110-120.

Petraitis, P.S. & R.E. Latham. 1999. The importance of scale in testing the origins of alternative community states. *Ecology* **80**: 429-442.

Pielou, D.P. & E.C. Pielou. 1968. Association among species of infrequent occurrence: the insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. *Journal of Theoretical Biology* **21**: 202-216.

Rejmánek, M. & D.M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* **77**: 1655-1661.

Robson, D.S. 1972. Appendix: statistical tests of significance. *Journal of Theoretical Biology* **34**: 350-352.

Samuels, C.L. & J.A. Drake. 1997. Divergent perspectives on community convergence. *Trends in Ecology and Evolution* **12**: 427-432.

Sanders, N.J., N.J. Gotelli, N.E. Heller & D.M. Gordon. 2003. Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences, USA* **100**: 2474-2477.

Schluter, D. 1984. A variance test for detecting species associations, with some example applications. *Ecology* **65**: 998-1005.

Shea, K. & P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* **17**: 170-176.

Sommer, U. 1991. Convergent succession of phytoplankton in microcosms with different inoculum species composition. *Oecologia* **87**: 171-179.

Stone, L. & A. Roberts. 1990. The checkerboard score and species distributions. *Oecologia* **85**: 74-79.

Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences*, *USA* **101**: 10854-10861.

Tilman, D., R. Kiesling, R. Sterner, S. Kilham & F.A. Johnson. 1986. Green, bluegreen and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon, and nitrogen. *Arch Hydrobiologia* **106**: 473-485.

Ulrich, W. 2004. Species co-occurrences and neutral models: reassessing J.M. Diamond's assembly rules. *Oikos* **107**: 603-609.

Ulrich, W. & N.J. Gotelli. 2007. Null model analysis of species nestedness patterns. *Ecology* **88**: 1842.

Weiher, E. & P.G.D. Clarke. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* **81**: 309-322.

Wilson, J.B. 1989. A null model of guild proportionality, applied to stratification of a New Zealand temperate rain forest. *Oecologia* **80**: 263-267.

Zobel, K., M. Zobel & R.K. Peet. 1993. Changes in pattern diversity during secondary succession in Estonian forests. *Journal of Vegetation Science* **4**: 489-498.