Acta Zoologica Academiae Scientiarum Hungaricae 49 (3), pp. 159–165, 2003

EXTINCTION DISORDERS THE SPECIES COMPOSITION OF METACOMMUNITIES

A. BÁLDI

Animal Ecology Research Group of the Hungarian Academy of Sciences
Hungarian Natural History Museum, Ludovika tér 2, H-1083 Budapest, Hungary
E-mail: baldi@nhmus.hu

Nestedness is a common pattern in nature, where less species rich local communities are subsets from richer communities. Is this predictability of community composition holds after the loss of species? This problem was investigated by excluding the rarest species of four example metacommunities (collections of local communities within archipelagoes), and correlated the changes of nestedness with the loss of species and individuals. Rarest species is that with the least number of individuals. Nestedness declined after a small increase in two of the metacommunities with the exclusion of species, and reached random species composition in both metacommunities after the loss of 58–66% of species. The order of nested subset structure in the other two metacommunities increased until most of the species were excluded (76% and 92%). The loss of 7–30% of individuals from the rarest species in all metacommunities led to random compositions. Because the extinction of ca. half of the species has been observed in a variety of human disturbed communities, the loss of compositional predictability of metacommunities may be an important threat in the increasingly human dominated communities.

Key words: nested community structure, nestedness temperature calculator, birds, beetles, orthopterans, butterflies

INTRODUCTION

The loss of species is one of the key problems of nature conservation. Each extinction is irreversible, and depauperates biodiversity. In addition, the missing of a species from an ecosystem may have indirect effects on the entire system; these species are termed as keystone species, and got considerable interest in ecology and conservation (e.g., PAINE 1966, JORDÁN *et al.* 1999). In the present analysis I focus on rare species, which can be keystones (e.g., top predators or competitors) from an ecological point of view (GASTON 1994), but are inevitable "keystones" for nature conservation, because they are usually the most extinction prone species.

A community-based approach was used to assess the consequences of loss of rare species on community composition. Although there are still debates whether the species composition is random or not in metacommunities (e.g., WHITTAKER 1992), an increasing number of studies found nested community structure (COOK & QUINN 1995, WRIGHT *et al.* 1998). This is a deterministic pattern, where species in less species rich local communities are subsets from richer communities

(PATTERSON & ATMAR 1986), or, since island area and species numbers usually correlates (ROSENZWEIG 1995), species of smaller islands are subsets of large island communities. Nestedness is supposed to be a basic descriptor of communities (WORTHEN 1996), and widely used in conservation biology (e.g. CUTLER 1991, SIMBERLOFF & MARTIN 1991, BAZ & GARCIA-BOYERO 1996, HECNAR & M'CLOSKEY 1997, HANSSON 1998, CORNELIUS *et al.* 2000, GANZHORN & EISENBEIß 2001).

Nestedness analyses are based on the presence/absence matrix of species by islands or habitat patches. This means that species with least abundance has the same weight in the analyses as species with the most individuals. This is obviously not true in the real world, but efforts to include abundance data into nestedness analysis is missing, except ANDRÉN (1994). The problem is that few databases exist with abundance data per islands even on a local scale, and on large spatial scales only estimations possible (KUNIN 1998).

In this work a simple empirical approach was used to study the changes of community nestedness in relation to loss of rare species in four example communities, and the results were evaluated in the light of community ecology and the conservation of original community composition.

METHODS

I used the "Nestedness temperature calculator" (ATMAR & PATTERSON 1995) for measuring nestedness, which has a well documented theoretical basis (ATMAR & PATTERSON 1993), and performs well comparing with other nestedness measures (WRIGHT *et al.* 1998). The temperature T is a standardized measure of matrix disorder by assessing the deviation of the actual matrix from a similar rank, but perfectly nested matrix (ATMAR & PATTERSON 1993). T ranges from 0 (perfect nestedness) to 100 (complete disorder). However, this is true only for square matrices with equal number of rows and columns, and for 50% fill. In other cases, the actual matrix should be randomized, keeping the row and column numbers and the fill constant, to get the average T of the random matrices (which is less, sometimes considerable less than 100). ATMAR and PATTERSON (1995) suggest that already 50 random matrices give reliable measure of the random community. The actual matrices I used did not fulfill the criteria of square shape and 50% fill, therefore I did not use T directly. Instead, I used D, which was defined as:

$$D = (T_r - T_a) / SD_r$$

where T_r is the average temperature of 100 random matrices, T_a is the actual matrix temperature, and SD_r is the standard deviation of temperatures of the random matrices. The matrix was significantly nested if the chance to draw at least one matrix colder than the actual matrix was less than 0.05. D provides a reliable indication on whether the actual matrix is ordered or not, independently of shape and fill. D is a standardized effect size, analogous to that used by GUREVITCH *et al.* (1992). For the comparisons D was standardized ($D(st)=D/S$), where S is the species number of the metacommunity. The following procedures were used to study the effects of species loss on nestedness: after determining

Table 1. Description of the four studied archipelagos

Taxon	Habitat	No. patches	No. species	Individuals	Source
Orthopterans	steppe patches in forest (range: 0.02–40 ha)	27	32	692	BÁLDI & KISBENEDEK 1999
Butterflies	forest patches in agricultural (?) landscape (range: 3.6–2115 ha)	13	81	2259	BAZ & GARCIA-BOYERO 1996
Carabid beetles	Baltic islands with forests, bogs, meadows, fields (range: 0.5-c7000 ha)	24	61	16073	KOTZE *et al.* 2000
Birds	reed islands in a lake (range: 0.0025–2.5 ha)	75	17	522	BÁLDI unpubl. data

the temperature of the actual matrix, the rarest species (i.e. with the least number of individuals) was excluded from the metacommunity: that is a column, or more columns, if there were more species with the same number of individuals, was excluded from the matrix. Then the temperature was determined again, followed by the exclusion of the next rarest species, and so on. The procedures were terminated, when the matrix reached disorder. This procedure modified the abundance relations of the archipelago's metacommunity in a controlled way, therefore it was possible to correlate species loss and nestedness.

Three published and one unpublished datasets were used in the analysis (Table 1): orthopterans (Orthoptera) in steppe patches of the Buda-hills, Central Hungary (BÁLDI & KISBENEDEK 1999), butterflies (Lepidoptera) in forest fragments of Central Spain (BAZ & GARCIA-BOYERO 1996), carabid beetles on real islands in the Baltic (KOTZE *et al.* 2000), and birds on small reed islands of Lake Velence, Hungary (unpubl. data, see details on the study in BÁLDI & KISBENEDEK 2000). The four matrices were different in size, shape, fill, organisms, and location.

RESULTS

The four metacommunities sampled showed different changes of *D(st)* when the rarest species were excluded (Fig. 1). *D* first increased, then decreased in orthopterans and butterflies, but increased in beetles and birds for most steps. Both orthopteran and butterfly metacommunities reached random structure after the exclusion of ca. 60% of species, but more then three-quarters of the species had to be taken off from the beetle and bird metacommunities to reach $\alpha = 0.05$ significance level (Table 2).

Regarding the number of excluded individuals that belonged to the rarest species, the loss of 7–30% of individuals resulted in random communities in all the four taxa (Table 2).

Table 2. Number of excluded species and excluded individuals from the metacommunities, necessary to reach random community composition

	Orthopterans	Butterflies	Beetles	Birds
Number of excluded rare species	19–21 (59–66%)	47 (58%)	56 (92%)	13 (76%)
Number of excluded individuals of rare species	45–66 (7–10%)	186 (8%)	4791 (30%)	117 (22%)

DISCUSSION

The gradual exclusion of the rarest species from four metacommunities (birds, carabid beetles, butterflies and orthopterans) showed different changes in the nested subset structure. There are several possible mechanisms to explain the differences, including the evenness (partitioning of individuals among species) of communities, life history and landscape characteristics. However, the important point for nature protection is that there may be metacommunities, where species

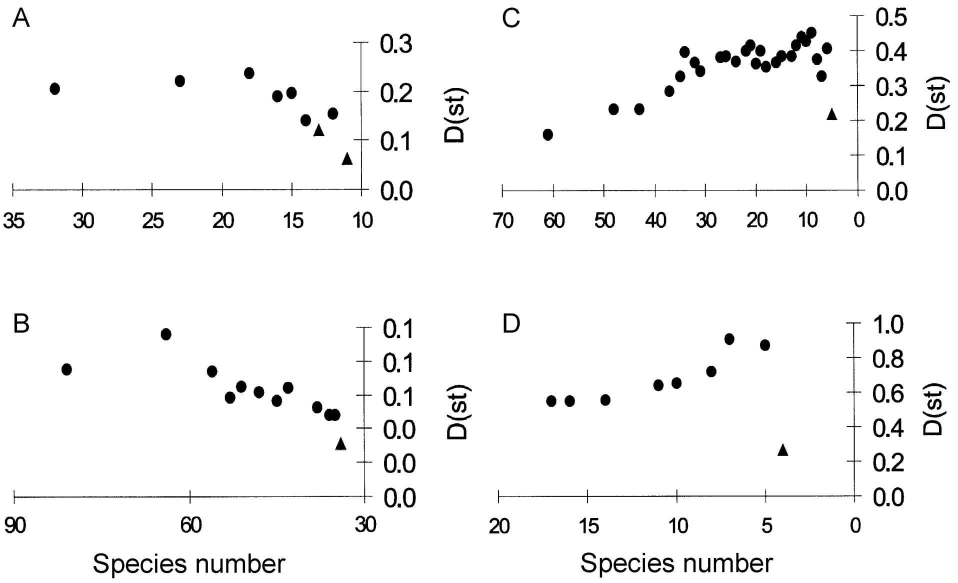

Fig. 1. Changes of nestedness in relation to the exclusion of the rarest species from the metacommunity. A = orthopterans, B = butterflies, C = beetles, D = birds, D(st) is the standardized difference between the average temperature of 100 random matrices and the actual matrix temperature, divided by the standard deviation of the random matrices. Triangles indicate non-significant nestedness at α=0.05

loss immediately decrease predictability of species composition. This degradation may be present soon, even if at the first extinctions the ordered structure is increasing, as in the orthopteran and butterfly metacommunities in this work, or ANDRÉN (1994).

The definition of rarity was based on the number of individuals in this study. However, rarity can be defined based on distribution, as well, i.e., the rarest species is that with the least number of occurrences on islands. Presumbaly, the results would be similar, if the latter definition had been used, because abundance (number of individuals) and distribution (number of occupied islands) are usually correlates (e.g., HE & GASTON 2000), as was found for the bird data (BÁLDI unpubl. result).

The results have important conservation message. Species extinctions are sadly common and widespread both globally and locally (LAWTON & MAY 1995, REAKA-KUDLA *et al.* 1997). The extinction of rare species is widely documented, there are several examples, when even half of the species gone extinct within a few decades. For example, ROONEY and DRESS (1997) observed 80% and 59% loss in herb and shrub species after 66 years in hemlock-beech and hemlock stands, respectively. Species losses are well documented for Singapore: 51% of plant species, and 32% of diurnal bird species were lost during the last century (TURNER *et al.* 1996, CASTELLATTA *et al.* 2000). Estimated species loss rate of beetles from 1-ha tropical forest fragments was 49.8% (DIDHAM *et al.* 1998). DRAYTON and PRIMACK (1996) observed the loss of 37% of original plant species from a Boston park in the last century. Nine percent of the native flora of 1159 taxa is already extinct, and 52.5% are at risk of extinction of Hawaiian flora (SAKAI *et al.* 2002). Therefore, there are several observations, when extinctions are already matched the 50–60% loss of species threshold found in the present analysis, indicating the actuality of the problem.

Nestedness is recently a popular subject of community ecology investigations. I should make the methodological note that the changing of nested subset structure with the loss of species highlights the problem of comparing nestedness of communities: differences may be simply the consequence of different level of human impact, i.e. different level of species loss. The more species were lost the smaller is the order of metacommunities. In the present study all the four metacommunities are considered as natural ones. This is supported by the fact that the habitats were not disturbed for decades, the age of patches was at least >100 years for orthopterans (BÁLDI & KISBENEDEK 1997), >150 years for birds (BÁLDI & KISBENEDEK 2000), and seems to be similar for the butterflies (BAZ & GARCIA-BOYERO 1996) (and obviously much more for the real islands of the beetle study).

*

Acknowledgements – I thank the stimulating discussions with F. JORDÁN, and the comments of two reviewers. The study was supported by the Hungarian Scientific Research Fund (OTKA F/29242), a Bolyai Research Fellowship, and a Junior Fellowship from the Central European University.

REFERENCES

ANDRÉN, H. (1994) Can one use nested subset pattern to reject the random sample hypothesis? Examples from boreal bird communities. *Oikos* **70**: 489–491.

ATMAR, W. & PATTERSON, B. D. (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* **96**: 373–382.

ATMAR, W. & PATTERSON, B. D. (1995) *The nestedness temperature calculator: a visual basic program, including 294 presence-absence matrices*. AICS Research Inc., University Park, NM USA and The Field Museum, Chicago, IL USA.

BÁLDI, A. & KISBENEDEK, T. (1997) Orthopteran assemblages as indicators of grassland naturalness in Hungary. *Agric. Ecosyst. & Environ.* **66**: 121–129.

BÁLDI, A. & KISBENEDEK, T. (1999) Orthopterans in small steppe patches: an investigation for the best-fit model of the species-area curve and evidences for their non-random distribution in the patches. *Acta Oecol.* **20**: 125–132.

BÁLDI, A. & KISBENEDEK, T. (2000) Bird species numbers in an archipelago of reeds at Lake Velence, Hungary. *Global Ecol. & Biogeogr.* **9**: 451–462.

BAZ, A. & GARCIA-BOYERO, A. (1996) The SLOSS dilemma: a butterfly case study. *Biodivers. & Conserv.* **5**: 493–502.

CASTELLETTA, M., SODHI, N. S. & SUBARAJ, R. (2000) Heavy extinctions of forest avifauna in Singapore: Lessons for biodiversity conservation in Southeast Asia. *Conserv. Biol.* **14**: 1870–1880.

COOK, R. R. & QUINN, J. F. (1995) The influence of colonization in nested species subsets. *Oecologia* **102**: 413–424.

CORNELIUS, C., COFRÉ, H. & MARQUET, P. A. (2000) Effects of habitat fragmentation on bird species in a relict temperate forest in semiarid Chile. *Conserv. Biol.* **14**: 534–543.

CUTLER, A. (1991) Nested faunas and extinction in fragmented habitats. *Conserv. Biol.* **5**: 496–505.

DIDHAM, R. K., HAMMOND, P. M., LAWTON, J. H., EGGLETON, P. & STORK, N. E. (1998) Beetle species responses to tropical forest fragmentation. *Ecol. Monogr.* **68**: 295–323.

DRAYTON, B. & PRIMACK, R. B. (1996) Plant species lost in an isolated conservation area in Metropolitan Boston from 1894 to 1993. *Conserv. Biol.* **10**: 30–39.

GANZHORN, J. U. & EISENBEIβ, B. (2001) The concept of nested species assemblages and its utility for understanding effects of habitat fragmentation. *Basic & Appl. Ecol.* **2**: 87–95.

GASTON, K. J. (1994) *Rarity*. Chapman and Hall, UK, 205 pp.

GUREVITCH, J., MORROW, L. L., WALLACE, A. & WALSH, J. S. (1992) A meta-analysis of field experiments on competition. *Am. Nat.* **140**: 539–572.

HANSSON, L. (1998) Nestedness as a conservation tool: plants and birds of oak-hazel woodland in Sweden. *Ecol. Letters* **1**: 142–145.

HE, F. & GASTON, K. (2000) Occupancy-abundance relationships and sampling scales. *Ecography* **23**: 503–511.

HECNAR, S. J. & M'CLOSKEY, R. T. (1997) Patterns of nestedness and species association in a pond-dwelling amphibian fauna. *Oikos* **80**: 371–381.

JORDÁN, F., TAKÁCS-SÁNTA, A. & MOLNÁR, I. (1999) A reliability theoretical quest for keystones. *Oikos* **86**: 453–462.

KOTZE, D. J., NIEMELÄ, J. & NIEMINEN, M. (2000) Colonization success of carabid beetles on Baltic islands. *J. Biogeogr.* **27**: 807–819.

KUNIN, W. E. (1998) Extrapolating species abundance across spatial scales. *Science* **281**: 1513–1515.

LAWTON, J. H. & MAY, R. M. (1995) *Extinction rates*. Oxford Univ. Press, Oxford, 233 pp.

PAINE, R. T. (1966) Food web complexity and species diversity. *Am. Nat.* **100**: 65–75.

PATTERSON, B. D. & ATMAR, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linnean Soc.* **28**: 65–82.

REAKA-KUDLA, M. L., WILSON, D. E. & WILSON, E. O. (1997) *Biodiversity II*. Joseph Henry Press, Washington, D.C., 549 pp.

ROONEY, T. P. & DRESS, W. J. (1997) Species loss over sixty-six years in the ground-layer vegetation of Heart's Content, an old-growth forest in Pennsylvania USA. *Nat. Areas J.* **17**: 297–305.

ROSENZWEIG, M. L. (1995) *Species diversity in space and time*. Cambridge Univ. Press, Cambridge, 436 pp.

SAKAI, A. K., WAGNER, W. L. & MEHRHOFF, L. A. (2002) Patterns of endangerment in the Hawaiian flora. *Systematic Biology* **51**: 276–302.

SIMBERLOFF, D. & MARTIN, J.-L. (1991) Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. *Ornis Fenn.* **68**: 178–192.

TURNER, I. M., CHUA, K. S., ONG, J. S. Y., SOONG, B. C. & TAN, H. T. W. (1996) A century of plant species loss from an isolated fragment of lowland tropical rain forest. *Conserv. Biol.* **10**: 1229–1244.

WHITTAKER, R. J. (1992) Stochasticism and determinism in island ecology. *J. Biogeogr.* **19**: 587–591.

WORTHEN, W. B. (1996) Community composition and nested-subset analyses: basic descriptors for community ecology. *Oikos* **76**: 417–426.

WRIGHT, D. H., PATTERSON, B. D., MIKKELSON, G. M., CUTLER, A. & ATMAR, W. (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia* **113**: 1–20.

Revised version received September 3, 2003, accepted October 22, 2003, published November 30, 2003