

Inferences about nested subsets structure when not all species are detected

Emmanuelle Cam, James D. Nichols, James E. Hines and John R. Sauer

Cam, E., Nichols, J. D., Hines, J. E. and Sauer, J. R. 2000. Inferences about nested subsets structure when not all species are detected. – *Oikos* 91: 428–434.

Comparisons of species composition among isolated ecological communities of different size have often provided evidence that the species in communities with lower species richness form nested subsets of the species in larger communities. In the vast majority of studies, the question of nested subsets has been addressed using information on presence-absence, where a “0” is interpreted as the absence of a given species from a given location. Most of the methodological discussion in earlier studies investigating nestedness concerns the approach to generation of model-based matrices corresponding to the null hypothesis of a nonnested pattern. However, it is most likely that in many situations investigators cannot detect all the species present in the location sampled. The possibility that zeros in incidence matrices reflect nondetection rather than absence of species has not been considered in studies addressing nested subsets, even though the position of zeros in these matrices forms the basis of earlier inference methods. These sampling artifacts are likely to lead to erroneous conclusions about both variation over space in species richness, and the degree of similarity of the various locations. Here we propose an approach to investigation of nestedness, based on statistical inference methods explicitly incorporating species detection probability, that take into account the probabilistic nature of the sampling process. We use presence-absence data collected under Pollock’s robust capture-recapture design, and resort to an estimator of species richness originally developed for closed populations to assess the proportion of species shared by different locations. We develop testable predictions corresponding to the null hypothesis of a nonnested pattern, and an alternative hypothesis of perfect nestedness. We also present an index for assessing the degree of nestedness of a system of ecological communities. We illustrate our approach using avian data from the North American Breeding Bird Survey collected in Florida Keys.

E. Cam, J. D. Nichols, J. E. Hines and J. R. Sauer, U.S. Geological Survey, Biological Resources Div., Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, MD 20708-4019, USA (present address of EC: Laboratoire de Biologie, Université de Bretagne Occidentale, F-29285 Brest Cedex, France [ecam@univ-brest.fr]).

Many studies that have compared species composition among isolated communities of different size have provided evidence that these are “nested” (e.g., Patterson and Atmar 1986, Bolger et al. 1991, Wright et al. 1998, Fleishman and Murphy 1999). This particular pattern of species composition in islands or habitat isolates has recently received considerable attention. Systems of ecological communities are said to be nested if the species in smaller communities (i.e., with lower species

richness) form subsets of the species in larger communities (Patterson and Atmar 1986, Patterson 1987, Wright and Reeves 1992, Andrén 1994, Lomolino 1996). This pattern appears to be very common, and many efforts have been devoted to tests of hypotheses about ecological processes that may lead to nestedness (e.g., Cook and Quinn 1995, Lomolino 1996, Fleishman and Murphy 1999). Whittaker (1992) characterized the question of nestedness as relevant to a fundamental issue in

Accepted 14 June 2000

Copyright © OIKOS 2000

ISSN 0030-1299

Printed in Ireland – all rights reserved

ecology: whether the species composition of isolated communities is primarily the result of random processes, or is structured by ecological processes. The question of nestedness has also implications for conservation biology and the design of reserves (Patterson 1987, Cook 1995). In particular, the question of the proportion of species shared by communities of different size has revived the SLOSS debate (Patterson 1987, Simberloff and Martin 1991). The underlying reasoning is that a set of smaller reserves should harbor fewer species than a single larger reserve if smaller communities form nested subsets of larger ones (Patterson 1987).

Many recent studies of nestedness have focused on how to test the hypothesis that a set of communities conforms to a nested pattern, and how to measure the degree of nestedness of systems of communities (e.g., Patterson and Atmar 1986, Hugueny 1997, Cook and Quinn 1998, Brualdi and Sanderson 1999). Addressing nestedness requires comparison of species composition in several locations, and estimation of the number of species present in smaller communities that also occur in larger communities (Andr n 1994). Species composition data are summarized in incidence matrices (i.e., presence-absence matrices where columns correspond to species and rows correspond to locations; Patterson and Atmar 1986). When data are sorted by species richness in the different sites, species found in smaller communities and in larger ones but not in intermediate ones correspond to “gaps” or “holes” in these matrices. This pattern is specifically relevant to most approaches to investigating nestedness (e.g., Andr n 1994, Brualdi and Sanderson 1999). Classic approaches to testing the hypothesis of a nested pattern, and to assessing the degree of nestedness of a system of communities, strongly rely on the position of zeros in incidence matrices, more precisely on “gaps”. There is very little discussion in the literature about the possibility that these zeros may sometimes correspond to sampling artifacts (but see Grayson and Livingston 1993, Kodric-Brown and Brown 1993); i.e., locations where species are present but not detected (Alpizar-Jara et al. unpubl.). There is growing awareness, however, that the number of species enumerated in a given location may be a biased estimate of the actual species richness in the location considered, unless species detection probability is equal to 1 (Burnham and Overton 1978, 1979, Nichols and Conroy 1996, Boulmier et al. 1998, Nichols et al. 1998a, b).

In fact, situations where investigators can enumerate all the species present in the area sampled are likely to be rare (Reed 1996, Lawlor 1998), particularly when focusing on animals (Nichols and Conroy 1996, Boulmier et al. 1998). Sober n and Llorente (1993), and Colwell and Coddington (1994) pointed out that new species are usually detected during later sampling sessions when the area of interest is sampled repeatedly within a short period of time. Similarly, Connor and

Simberloff (1978) pointed out that “collecting biases” may mask the phenomena of interest in studies of compositional similarity of fauna or flora. The fact that species may be missed by investigators during sampling efforts has direct implications regarding the approach to assessing nestedness (Patterson and Brown 1991, Kodric-Brown and Brown 1993). A zero in incidence matrices indicates that the species is actually absent from the site of interest only on condition that species detection probability is equal to one at that site. These sampling issues not only affect the validity of the inference about species richness in each of the various sites considered, but also about variation in species richness and species composition among sites. These issues are thus directly relevant to the question of nestedness (Patterson and Brown 1991, Kodric-Brown and Brown 1993, Cutler 1994, Cook 1995). However, we are not aware of any study on nestedness that incorporates the possibility that a zero in an incidence matrix is a nondetection rather than an absence.

There has been a recent renewed interest in use and development of statistical inference procedures based on capture-recapture models for addressing questions about variation over space in species richness, and for comparing species composition among communities in different locations (Nichols and Conroy 1996, Nichols et al. 1998a, b). These procedures are based on approaches to estimation of species richness explicitly incorporating species detection probability. They have been developed for handling situations where not all the species are detected during sampling sessions (Burnham and Overton 1978, Otis et al. 1978). Here we propose an approach to investigating nestedness based on these inference methods. We illustrate our approach using avian data from the BBS (Sauer et al. 1997) collected in Florida.

Approach to addressing nestedness based on capture-recapture models

Estimation

Our approach is based on estimators of the degree of similarity of the species composition of two communities proposed by Nichols et al. (1998b). This approach relies on sampling at two different spatial scales (i.e., sampling based on Pollock’s robust design; Pollock 1982, Nichols et al. 1998b), which are easy to identify in the case of archipelagos, for example. The first scale corresponds to the islands themselves (primary locations). These primary locations are then subdivided into a number of secondary sampling units (e.g., quadrats). These secondary samples are treated as replicate samples of the island community.

Nichols et al. (1998b) developed a metric (“species co-occurrence”) that permits assessment of similarity of the species composition of two communities:

$$\hat{\phi}_i^{xy} = \frac{\hat{M}_i^{y(R_i^x)}}{R_i^x}, \quad (1)$$

where x and y are locations, and i the year. $\hat{M}_i^{y(R_i^x)}$ is the number of species detected in location x at time i (i.e., members of R_i^x) that are also present in location y at time i . $\hat{\phi}_i^{xy}$ (species co-occurrence) is the probability that a species present in location x at time i is also present in location y at that time (Nichols et al. 1998b). Another way of defining this quantity is the expected proportion of species at area x that are also present at area y (Nichols et al. 1998b). R_i^x is directly observed in location x , but $\hat{M}_i^{y(R_i^x)}$ (the number of species present in location x that are also present in location y) is estimated. Nichols et al. (1998b) recommended use of estimators of species richness from capture-recapture data developed for closed animal populations (e.g., Otis et al. 1978, Rexstad and Burnham 1991). These estimators can be used for data collected under a “quadrat-sampling” design (Nichols and Conroy 1996), such as the replicate samples collected in each island of an archipelago.

Predictions

To illustrate our approach, we consider a mainland or source pool area (denoted as area A) and two “islands”, the less distant of which (area B) lies between the source area A and the more distant island (area C). In the situation where the mainland is the “source” of all species found in the islands, species richness in the three areas should be ordered as $N_i^A \geq N_i^B \geq N_i^C$, where N_i^x denotes the number of species present at location x in year i . Here, we assume the situation in which all of the species on the islands (members of N_i^B, N_i^C) are also found on the mainland (are members of N_i^A).

If this is not the case, then it will frequently be reasonable to redefine N_i^B and N_i^C by restricting these species groups to members of N_i^A to insure the identification of a species pool that is relevant to considerations of nestedness. That is, it is desirable to place ourselves in a situation in which it is possible to specify and test hypotheses about processes that may lead to nested subsets. Hypotheses about potential processes generating nested patterns frequently involve differential immigration and extinction (e.g., Lomolino 1996), and rely on the existence of a specified species pool, either a source pool of potential colonists, or a common pool from which species may locally disappear.

A nested pattern corresponds to the existence of a hierarchy in the proportion of species shared among various communities, ranked by size for example. Under a nested pattern, the proportion of species in smaller communities also present in larger ones is expected to be higher than the proportion of species in larger communities also present in smaller ones. An

alternative pattern corresponds to the absence of such a hierarchy. The random sample hypothesis specified by Connor and McCoy (1979) can be viewed as an alternative hypothesis. Connor and McCoy described this hypothesis as follows: “species number is controlled by passive sampling from the species pool, larger areas receiving effectively larger samples than smaller ones”. Here we use this idea to specify our predictions for a situation where nesting does not occur.

Under our null hypothesis the probability of occurrence of a species in a location (e.g., an island) is proportional to the number of species in that location. If a location harbors twice as many species as another, then a given species in the pool has twice the probability of being in the location with higher species richness than in the other one. This null hypothesis can be used in situations where variation in species richness among locations is primarily linked to differences in island area for example, but other factors thought to influence species richness may also be considered. We stress the fact that our predictions concern patterns: they concern the relationship between sharing rates (the proportion of species that the communities have in common) that are expected if communities are composed of species randomly sampled from a specified pool. They do not depend on the potential processes leading to this pattern, such as random immigration from a source pool for example (e.g., Coleman et al. 1982, Cutler 1994; see also the discussion in Wright et al. 1998). Last, it is worth noting that the random sample hypothesis also relies on the existence of a specified species pool, which forms the basis for restriction of analysis to a subset of species (e.g., the mainland pool).

The only a priori restrictions are that $\phi_i^{CA} = \phi_i^{BA} = 1$. This equality is insured by our restriction to species that are members of N_i^A . Because of the ordering of species richness, $N_i^A \geq N_i^B \geq N_i^C$, we can also order the ϕ_i^{xy} as $\phi_i^{AC} \leq \phi_i^{AB}$. Beyond these relationships, additional predictions about the ϕ_i^{xy} depend on the hypothesis of interest, the nested subset hypothesis or a null hypothesis of a pattern based on random sampling.

The community in island C is a perfect subset of the community in island B (in a given year i) if the probability that a species found in location C is also a member of the community in location B is equal to 1 ($\phi_i^{CB} = 1$). Under the null hypothesis, species at location C should be a random sample of species available in the pool (location A). Species at C also should represent a random sample of any subset of species from location A , and this forms the basis for the prediction that $\phi_i^{CB} = \phi_i^{AB}$. Species from location A appear in the subset of N_i^B (species of location B) with probability ϕ_i^{AB} ; hence, that should also be the probability that a member of N_i^C is also a member of N_i^B . So if area B contains only 25% of the species of source location A , and location C contains a random sample of species from location A , then we would expect 25% of those species to be common to location B .

In addition to the question of whether or not a system of communities is nested, one may want to assess the degree of nestedness of the system considered. Indeed, several hypotheses have been proposed concerning relationships between the degree of nestedness and ecological conditions such as oceanic islands versus land-bridge systems (e.g., Patterson and Atmar 1986), or the degree of isolation of habitat isolates or the size of patches resulting from habitat fragmentation (e.g., Bolger et al. 1991, Cook 1995). Perfect nestedness corresponds to the situation where $\varphi_i^{CB} = 1$. If the system is not nested at all, we expect that $\varphi_i^{CB} = \varphi_i^{AB}$. These expectations form a basis for specifying an index of nestedness:

$$\frac{\varphi_i^{CB} - \varphi_i^{AB}}{1 - \varphi_i^{AB}}$$

The expected value of this index is 0 if the system is consistent with the null hypothesis of a random sample, 1 if the system is perfectly nested, and an intermediate value if the system is consistent with a hypothesis between these two extremes. However we note that the value of this index is not always defined, and can be negative in certain situations. For example if $\varphi_i^{AB} = 1$ (i.e., if all the species of community *A* are estimated to be present in *B*), then the value of the index is undefined. Further, it may be possible for $\varphi_i^{CB} - \varphi_i^{AB}$ to be negative. This could occur if *B* and *C* represented very different habitats such that the species found at *B* were likely to be different from the species found at *C*. Biogeographic hypotheses have also been proposed to explain low sharing rates among locations (e.g., Patterson and Atmar 1986, Wright et al. 1998). This situation would correspond to a “nonoverlapping subset hypothesis”, leading to index value $-\varphi_i^{AB}/(1 - \varphi_i^{AB})$, when no species found at *C* were common to *B*. Negative values between this value and 0 would reflect less extreme situations of nonoverlapping subsets.

Example analysis

Methods

We used data from the Breeding Bird Survey to illustrate our approach (Sauer et al. 1997). The BBS is conducted every spring on permanent survey routes randomly located along secondary roads throughout the United States and southern Canada. There are approximately 2900 routes surveyed annually. Each route is 39.4 km long and consists of 50 stops spaced at 0.8-km intervals. An observer drives along the route and collects data during a 3-min observation period at each stop, recording all birds seen or heard within 0.40 km of the stop (Robbins et al. 1986). Our analysis included three routes located in the Florida Keys, plus

one route on the mainland (Fig. 1). We used data from 1987, when all of the four survey routes were run.

In order to place ourselves in a situation permitting investigation of nestedness, we specified a pool of species recorded on the route located on the mainland (location *A*) and estimated species co-occurrence among BBS routes by retaining the species in this pool exclusively. All the estimates of species richness we present are conditioned on the species list specified in the mainland location.

We used the class of estimators of species richness integrating species detection probability recommended by Nichols et al. (1998a, b). Previous work on the BBS has provided strong evidence of heterogeneity in detection probability among species (Boulinier et al. 1998). Consequently we used the capture-recapture model *M*(h), which permits variation in detection probability among species. We used the jackknife estimator for model *M*(h) developed by Burnham and Overton (1978, 1979). Detailed information on the approach to estimation of species richness using the BBS data is provided in Boulinier et al. (1998) and Nichols et al. (1998a, b). We estimated species co-occurrence using program COMDYN (Hines et al. 1999).

Results

The estimated number of species in the pool that were present on the Keys decreased as the distance from mainland increased. For the species pool specified on the mainland (BBS route *A*; Fig. 1), the estimate of species richness is equal to 48.20, estimated standard error: $\hat{SE} = 9.37$ (observed species richness: $S = 40$). For the three other routes, observed and estimated richness are respectively: route *B*: 22.03, $\hat{SE} = 6.58$ ($S = 18$), route *C*: 18.70, $\hat{SE} = 2.38$ ($S = 18$), and route *D*: 17.50, $\hat{SE} = 2.43$ ($S = 15$). In all cases, the proportion of species in a smaller community that are also present in a community of intermediate size (i.e.,

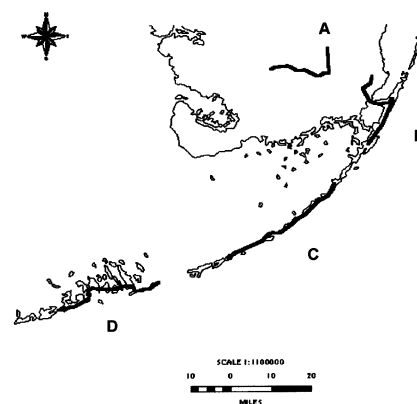


Fig. 1. Location of the BBS routes in the Florida Keys.

Table 1. Estimates of species co-occurrence (the probability that a member of the community in location 1 is also a member of the community in location 2).

Location 1	Location 2			
	(A) ¥	B	C	D
A	***	0.55 (0.18)	0.47 (0.11)	0.44 (0.09)
B	(1)	***	0.92 (0.12)	0.86 (0.15)
C	(1)	0.92 (0.12)	***	0.87 (0.11)
D	(1)	1.00 (0.07)	1.00 (0.05)	***

¥ As location A was used to specify the species pool, the communities found in locations B, C and D are necessarily subsets of the community in A. Consequently, the proportion of species in smaller communities also member of larger community in A cannot be used to draw inference about nestedness. In brackets: estimated standard errors.

$\phi_{i^{xy}}$, with $N^x < N^y$) is higher than the proportion of species present in a larger community that are also members of the community of intermediate size ($\phi_{i^{xy}}$, with $N^y < N^z$) (Tables 1 and 2). For example, $\hat{\phi}_{87}^{CB} > \hat{\phi}_{87}^{AB}$ (0.92, $\hat{SE} = 0.12$ vs 0.55, $\hat{SE} = 0.18$), $\hat{\phi}_{87}^{DB} > \hat{\phi}_{87}^{AB}$ (1.00, $\hat{SE} = 0.07$ vs 0.55, $\hat{SE} = 0.18$), and $\hat{\phi}_{87}^{DC} > \hat{\phi}_{87}^{BC}$ (1.00, $\hat{SE} = 0.05$ vs 0.92, $\hat{SE} = 0.12$). These results indicate some degree of nestedness in this system of communities. In addition, the community in location D appears to be a perfect subset of communities in location B and C (i.e., $\hat{\phi}_{87}^{DC} = \hat{\phi}_{87}^{DB} = 1.00$). All the indices of nestedness are very high (Table 2) and indicate perfect nestedness in most systems of three locations.

Discussion

The results of our example analysis are consistent with several studies that have compared the species composition among communities in archipelagos (e.g., Patterson and Atmar 1986). We found evidence that the number of species in the pool decreases as distance from the mainland increases. In addition, the expected proportion of species in more distant communities also present in communities in intermediate position is higher than the expected proportion of species in communities closer to the mainland that are also present in communities in intermediate position. This supports the hypothesis of nested subsets. Last, the most distant location appears to be a perfect subset of the two other insular communities (closer to the mainland). Importantly, the approach we used for addressing nestedness

Table 2. Indices of nestedness for all sets of three locations ordered from the mainland to the most distant from the mainland.

Set of locations	Index of nestedness
ABC	0.82
BCD	1
ABD	1
ACD	1

relies on estimators of species richness and species co-occurrence that explicitly account for species detection probability, more precisely for variation in detection probability among species.

The main methodological debate about approaches to addressing nestedness concerns specification of null hypotheses, the corresponding manner of generating incidence matrices using randomization, and appropriate tests to compare observed matrices and model-based expectations (Andr en 1994, Hugu eny 1997, Cook and Quinn 1998, Brualdi and Sanderson 1999; see Ryt i and Gilpin 1987 and Atmar and Patterson 1993 for different approaches). There is also debate concerning measurement of the degree of nestedness (e.g., Wright and Reeves 1992, Atmar and Patterson 1993; review by Cutler 1994, Cook 1995). That is, in most studies the methodological issues raised assume the existence of a known incidence matrix and do not deal with the possibility of imperfect knowledge of the communities.

In many cases this assumption may not be realistic. Sampling communities for the purpose of enumerating species is obviously a probabilistic process. The fact that species may be missed by investigators during sampling sessions has long been recognized (Burnham and Overton 1979, Preston 1979). However, we are not aware of studies of nestedness that have used a probabilistic approach to estimation of species richness and of the proportion of species shared by the various sites considered. In previous studies, as emphasized by Cook (1995), ‘‘any measure of nestedness must depend on the confidence (often a function of sampling effort) in producing a complete species list for each site’’.

Variation in detection probability among species results not only from differences in species characteristics such as behavior or size, but also from variation in the number of individuals in each species in the area sampled (i.e., abundance, density and spatial distribution of the individuals in each species; Alpizar-Jara et al. unpubl.). The second component is likely to have implications for analyses of nested subsets. Metapopulation models predict that under certain conditions, there should be a positive relationship between local abundance and the proportion of ‘‘patches’’ where the species is present (Hanski et al. 1993). This prediction has received empirical support (Hanski et al. 1993). Under this view, at the level of systems of ecological communities, we might expect that abundance (in the different species) influences the proportion of species that the various isolated communities have in common (i.e., species co-occurrence; Nichols et al. 1998b). This prediction is based on an analogy between ‘‘patches’’ sensu Hanski et al. (1993) and isolated communities. As abundance may influence species detection probability and the proportion of species shared by the various locations, species detection probability and sharing rate may covary (Nichols et al. 1998a, Alpizar-Jara et al. unpubl.).

This is likely to have direct implications for studies of nestedness based on observed proportions of species present in different locations (Patterson and Brown 1991, Alpizar-Jara et al. unpubl.). Indeed, the species most likely to be missed (not detected even though they are present, because of low detection probabilities) could also be least likely to be shared by two locations. These species may be less likely to be present in several “patches” sensu Hanski et al. (1993), or in several islands or habitat isolates in studies of nestedness. This could result in an apparent higher degree of nestedness of the system of communities than actually exists in studies where species detection probability is not taken into account. Observed sharing rates could be higher than the actual proportion of species shared by locations, because investigators may detect a higher proportion of species that are shared by the various locations, and miss a higher proportion of species that are not.

Because of the particular importance of the interpretation of “gaps” in species presence-absence data in investigations of nestedness, we recommend use of probabilistic approaches to estimation of species co-occurrence (Nichols et al. 1998b). It is desirable to use inference methods explicitly incorporating species detection probability for addressing questions involving community-level parameters in situations where not all the species are detected during sampling efforts, which is the case with the Breeding Bird Survey (Boulinier et al. 1998). Resorting to such approaches may be particularly important in studies of nestedness, where investigators are dealing with community level rates that may covary with species detection probability. Alpizar-Jara et al. (unpubl.) assessed the performance of the estimator of the metric describing variation over space in species composition used in the present study (eq. 1), in the presence of heterogeneity in species detection probability. They concluded that this estimator is a reasonable choice for studies based on BBS data.

Acknowledgements – Emmanuelle Cam was supported by a Cooperative Agreement between the United States Dept of Agriculture’s Forest Service and North Carolina State University’s Dept of Forestry. We are most grateful to Jane Fallon for her help with GIS, and to B. D. Patterson for providing constructive comments on this manuscript.

References

Andr n, H. 1994. Can one use nested subset patterns to reject the random sample hypothesis? Examples from boreal bird communities. – *Oikos* 70: 489–491.

Atmar, W. and Patterson, B. D. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. – *Oecologia* 96: 373–382.

Bolger, D. T., Albert, A. C. and Soul , M. E. 1991. Occurrence patterns of birds species in habitat fragments: sampling, extinction, and nested subsets. – *Am. Nat.* 137: 155–166.

Boulinier, T., Nichols, J. D., Sauer, J. R. et al. 1998. Estimating species richness to make inferences in community ecology: the importance of heterogeneity in species detectability. – *Ecology* 79: 1018–1028.

Brualdi, A. R. and Sanderson, J. G. 1999. Nested species subsets, gaps, and discrepancy. – *Oecologia* 119: 256–264.

Burnham, K. P. and Overton, W. S. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. – *Biometrika* 65: 625–633.

Burnham, K. P. and Overton, W. S. 1979. Robust estimation of population size when capture probabilities vary among animals. – *Ecology* 60: 927–936.

Coleman, B. D., Mares, M. A., Willig, M. R. and Hsieh, Y.-H. 1982. Randomness, area, and species richness. – *Ecology* 63: 1121–1133.

Colwell, R. K. and Coddington, J. A. 1994. Estimating terrestrial biodiversity through extrapolation. – *Philos. Trans. R. Soc. Lond. B.* 345: 101–118.

Connor, E. F. and Simberloff, D. 1978. Species number and compositional similarity of the Galapagos flora and avifauna. – *Ecol. Monogr.* 48: 219–248.

Connor, E. F. and McCoy, E. D. 1979. The statistics and biology of the species-area relationship. – *Am. Nat.* 113: 791–833.

Cook, R. R. 1995. The relationship between nested subsets, habitat subdivision, and species diversity. – *Oecologia* 101: 204–210.

Cook, R. R. and Quinn, J. F. 1995. The influence of colonization in nested subsets. – *Oecologia* 102: 413–424.

Cook, R. R. and Quinn, J. F. 1998. An evaluation of randomization models for nested subsets analysis. – *Oecologia* 113: 584–592.

Cutler, A. H. 1994. Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. – *Landscape Urban Planning* 28: 73–82.

Fleishman, E. and Murphy, D. D. 1999. Patterns and processes of nestedness in a Great Basin butterfly community. – *Oecologia* 119: 133–139.

Grayson, D. K. and Livingston, S. D. 1993. Missing mammals on Great Basin Mountains: Holocene extinctions and inadequate knowledge. – *Conserv. Biol.* 7: 527–532.

Hanski, I., Kouki, J. and Halka, A. 1993. Three explanations of the positive relationship between distribution and abundance of species. – In: Ricklefs, R.E. and Schluter, D. (eds), *Species diversity in ecological communities. Historical and geographical perspectives*. Univ. of Chicago Press, pp. 108–116.

Hines, J. E., Boulinier, T., Nichols, J. D. et al. 1999. COM-DYN: software to study the dynamics of animal communities using a capture-recapture approach. – *Bird Study* 46: 209–217.

Hugueny, B. 1997. Community nestedness and the proper way to assess statistical significance by Monte-Carlo tests: some comments on Worthen and Rohde’s (1996) paper. – *Oikos* 80: 572–574.

Kodric-Brown, A. and Brown, J. H. 1993. Incomplete data sets in community ecology and biogeography: a cautionary tale. – *Ecol. Appl.* 3: 736–742.

Lawlor, T. E. 1998. Biogeography of great Basin mammals: paradigm lost? – *J. Mammal.* 79: 1111–1130.

Lomolino, M. V. 1996. Investigating causality of nestedness of insular communities: selective immigrations or extinctions? – *J. Biogeogr.* 23: 699–703.

Nichols, J. D. and Conroy, M. J. 1996. Estimation of species richness. – In: Wilson, D. E., Cole, F. R., Nichols, J. D. et al. (eds), *Measuring and monitoring biological diversity. Standard methods for mammals*. Smithsonian Inst. Press, pp. 226–234.

Nichols, J. D., Boulinier, T., Hines, J. E. et al. 1998a. Estimating rates of local extinction, colonization and turnover in animal communities. – *Ecol. Appl.* 8: 1213–1225.

Nichols, J. D., Boulinier, T., Hines, J. E. et al. 1998b. Inference methods for spatial variation in species richness and community composition when not all species are detected. – *Conserv. Biol.* 6: 1390–1398.

Otis, D. L., Burnham, K. P., White, G. C. and Anderson, D. R. 1978. Statistical inference from capture data on closed animal populations. – *Wild. Monogr.* 62.

- Patterson, B. D. 1987. The principle of nested subsets and its implications for biological conservation. – *Conserv. Biol.* 1: 323–334.
- Patterson, B. D. and Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. – *Biol. J. Linn. Soc.* 28: 65–82.
- Patterson, B. D. and Brown, J. H. 1991. Regionally nested patterns of species composition in granivorous rodent assemblages. – *J. Biogeogr.* 18: 395–402.
- Pollock, K. H. 1982. A capture-recapture sampling design robust to unequal catchability. – *J. Wildl. Manage.* 46: 752–757.
- Preston, F. W. 1979. The invisible birds. – *Ecology* 60: 451–454.
- Reed, J. M. 1996. Using statistical probability to increase confidence of inferring species extinction. – *Conserv. Biol.* 10: 1283–1285.
- Rexstad, E. and Burnham, K. P. 1991. User's guide for interactive program CAPTURE. Abundance estimation of closed animal populations. – Colorado State Univ., Fort Collins, CO.
- Robbins, C. S., Bistrak, D. and Sauer, J. R. 1986. The breeding bird survey: its first fifteen years, 1965–1979. – U.S. Fish Wildl. Serv. Resour. Publ. 157.
- Ryti, T. M. and Gilpin, M. E. 1987. The comparative analysis of species occurrence patterns in archipelagos. – *Oecologia* 73: 282–287.
- Sauer, J. R., Hines, J. E., Gough, G. et al. 1997. The North American Breeding Bird Survey Results and Analysis. Version 96.4. – Patuxent Wildlife Research Center, Laurel, MD. Available at <www.mbr-pwrc.usgs.gov/bbs/bbs.html>.
- Simberloff, D. and Martin, J. L. 1991. Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. – *Ornis Fenn.* 68: 178–192.
- Soberón, J. M. and Llorente, J. B. 1993. The use of species accumulation functions for the prediction of species richness. – *Conserv. Biol.* 7: 480–488.
- Whittaker, R. J. 1992. Stochasticism and determination in island ecology. – *J. Biogeogr.* 19: 587–591.
- Wright, D. H. and Reeves, J. H. 1992. On the meaning and measurement of nestedness of species assemblages. – *Oecologia* 92: 416–428.
- Wright, D. H., Patterson, B. D., Mikkelsen, G. M. et al. 1998. A comparative analysis of nested subset patterns of species composition. – *Oecologia* 113: 1–20.