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A comparative analysis of nested subset patterns of species composition

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Abstract We present a broad comparative assessment of nested subsets in species composition among ecological communities. We assembled presence-absence data from a broad range of taxa, geographic regions, and spatial scales; and subjected this collection of datasets to common analyses, including a variety of metrics for measuring nestedness and null hypotheses against which to evaluate them. Here we identify ecological patterns in the prevalence and strength of nested subset structure, and assess differences and biases among the available methodologies. In all, we compiled 279 presence-absence matrices, of which 163 do not overlap in their coverage of species and sites. The survey includes studies on vertebrates, arthropods, mollusks, plants, and other taxa; from north temperate, tropical, and south temperate latitudes. Our results were as follows. Statistically significant nestedness was common. Assemblages from landbridge archipelagos were strongly nested, and immigration experiments were least nested. This adds further empirical support to the hypothesis that extinction plays a major role in producing nested structure. Nest-

edness was positively correlated with the ratio of the areas of the largest and smallest sites, suggesting that the range in area of sites affects nestedness. Taxonomic differences in nestedness were weak. Higher taxonomic levels showed stronger nesting than their constituent lower taxa. We observed no effect of distance of isolation on nestedness; nor any effects of latitude. With regard to methodology, the metrics N_c and U_t yielded similar results, although N_c proved slightly more flexible in use, and deals differently with tied sites. Similarities also exist in the behavior of N_0 (“ N ”) and U_p , and between N_1 and U_a . Standardized nestedness metrics were mostly insensitive to matrix size, and were useful in comparative analyses among presence-absence matrices. Most metrics were affected by the proportion of presences in the matrix. All analyses of nestedness, therefore, should test for bias due to matrix fill. We suggest that the factors controlling nested subset structure can be thought of as four filters that species pass to occur at a site: a sampling filter, a distance filter, a habitat filter, and an area filter – and three constraints on community homogeneity: evolutionary history, recent history, and spatial variation in the environment. The scale of examination can also have important effects on the degree of nestedness observed.

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Introduction

Recording the occurrence of a species at a given place and time is at once an elementary and an integrative ecological observation. At minimum, noting the existence of a species precedes any other biological knowledge about it. For the vast majority of species worldwide, and especially for vascular plants and invertebrates, we have only isolated records of occurrence and brief characterizations of morphology. In some

cases, we have enough information to describe a “distribution” – where a species does and does not occur. Distributional information is integrative: it represents the expression of a species’ ecology and history across a complex and varying environment. The outwardly simple information in species distributional patterns contains clues that can help us understand complex ecological relationships. Presence/absence matrices – tables of sites versus species recording which species occurred at each site and which did not – are examples of commonly recorded and potentially valuable distributional information about species, communities, and environments.

Nested subsets constitute a special kind of distribution pattern that is observed in presence-absence matrices and that carries unique information. A group of species assemblages is said to be nested when the species making up smaller biotas are also found in all larger ones. When a number of such biotas are ranked by species richness, they present a nested series. In a presence/absence matrix where sites are arranged in order of decreasing species richness and species are ranked in order of decreasing number of occurrences, species presences in a strongly nested set of communities will fill the upper left of the matrix in a roughly triangular shape. Nested subsets can only be observed at and above the level of a single community or assemblage, and in this sense nestedness is a meta-community or landscape pattern.

The quantitative measurement of nestedness is relatively new, and several metrics for measuring nestedness have recently been proposed (Patterson and Atmar 1986; Cutler 1991; Simberloff and Martin 1991; Wright and Reeves 1992; Atmar and Patterson 1993). Nestedness as measured by these metrics has been detected in a variety of systems, though most studies have been of vertebrates – particularly birds and mammals in habitat fragments (Whittaker 1992). A variety of factors are thought to contribute to nested patterns, including extinction, colonization, habitat structure, niche structure, and passive sampling. However, to date there is no consensus among ecologists regarding methodologies or hypotheses, and extensions of nested subset analysis to other taxa, regions, and spatial scales are just beginning (Patterson 1990; Simberloff and Martin 1991; Wright and Reeves 1992; Cook 1995; Cook and Quinn 1995; Lomolino 1996; Worthen et al. 1996).

To address these deficiencies, we began a broad comparative assessment of nested-subset patterns. Our objectives have been: (1) to assemble presence-absence data from as broad a range of taxa, geographic regions, and spatial scales as possible; (2) to subject this collection of datasets to common analyses, including most of the available metrics for measuring nestedness and various null hypotheses against which to evaluate them; (3) to assess differences and biases among the available methodologies; and (4) to identify biological patterns in the prevalence and strength of nested subset structure.

Materials and methods

The survey

We began our survey by compiling species compositions for archipelagos surveyed by Connor and McCoy (1979). Because a minority of their sources reported species composition at individual sites, this pool was supplemented by other studies. We used the expanded pool, containing some 150 “archipelagos”, to identify poorly represented taxa (many invertebrate groups), life-zones (aquatic and marine systems), and geographic locations (the tropics). We then made an effort to find additional studies covering these poorly represented conditions.

The end product of these efforts was 279 presence-absence matrices, listed in Table 1, and associated information. We subdivided some complex data sets for our analyses; these instances are indicated in the table as not being independent of other data sets. We performed statistical comparisons only on independent studies.

Metrics of nestedness

N0

N0 was proposed (as “*N*”) by Patterson and Atmar (1986) and referred to as “*N0*” by Wright and Reeves (1992). For each species, *N0* counts the number of absences from biotas richer than the most depauperate site on which it occurs, and sums these counts across all species. *N0* decreases with increasing nestedness, reaching zero when nesting is perfect, and tends to increase as numbers of sites and species increase. Wright and Reeves showed that the statistical significance of *N0* under a simple null hypothesis can be evaluated analytically. More complex null models are evaluated by simulation.

N1

Presented by Cutler (1991, as “*N2*”) and Wright and Reeves (1992), *N1* is in a sense the complement of *N0*. It is a count of the number of presences of a species at sites more impoverished than the richest one from which it is absent, summed over species. Like *N0*, *N1* decreases with increasing nestedness, and tends to increase with increasing matrix rank. The statistical significance of *N1* is assessed in the same manner as *N0*.

Ua, *Up*, and *Ut*

Developed by Cutler (1991), the metric *Ut* is a minimized count of species’ unexpected absences from larger biotas (*Ua*) and unexpected presences in smaller biotas (*Up*). The metric *Ut* can be visualized as the minimum number of steps (“holes” filled or “outliers” erased) required to transform a given distribution into a perfectly nested one, summed across species in the matrix. In cases where there is more than one way to minimize *Ut*, *Ua* and *Up* can be assigned fractional values. The *U* metrics decrease with increasing nestedness and tend to increase with matrix rank. At present, the statistical significance of the *U* statistics is assessed by simulation.

Nc

Proposed by Wright and Reeves (1992), *Nc* counts the number of times a species’ presence at a site correctly predicts its presence at equally rich or richer sites, summing these counts across sites and species. *Nc* also equals the sum of the number of species shared over all pairs of sites. Unlike *N0* and *N1*, which ignore ties between sites in species richness, *Nc* includes such cases in assessing nestedness. *Nc* increases with increasing nestedness, and with matrix rank. The statistical significance of *Nc* under a simple null hypothesis can be calculated analytically. As with the other metrics,

the significance of N_c relative to more complex null hypotheses can be evaluated by Monte Carlo simulation (see section on null hypotheses).

T

Proposed by Atmar and Patterson (1993), *T* provides a standardized measure of matrix disorder (matrix “temperature”) by assessing the deviation of an observed matrix from one of the same rank and fill that is perfectly nested (see also “Nestedness Calculator” at <http://www.bvis.uic.edu/museum/science/science.html>; reviewed by Kelt 1997). The observed matrix is first “packed”, reordering rows and columns so as to concentrate presences in the upper left corner of the matrix. The packed matrix of the observed distributions is then compared to a maximally nested matrix, and presences and absences that differ from the maximally nested state are identified. The relative distances of these presences and absences along the skew-diagonal (i.e., across both rows and columns, rather than solely across rows as in other metrics) are measured, squared and summed. Matrix temperature *T* equals the ratio of this sum of squared deviations to its maximum value (estimated by simulation), multiplied by 100. *T* thus ranges from 0 for a perfectly nested matrix to 100 for one that is completely disordered. The statistical significance of an observed matrix’s *T* value is assessed by simulation.

All of the metrics above except *T* suffer from strong dependence on matrix size, which makes comparisons of nestedness between matrices difficult. Wright and Reeves (1992) proposed a transformation of N_c that avoided this problem (“*C*”), and here we generalize their procedure to standardize the size-dependent metrics above. The resulting metrics, which, following Lomolino (1996), we call percent nested (PN) metrics, are calculated:

$$PN_x = 100 \times (X_{obs} - X_{exp}) / (X_{perf} - X_{exp}),$$

where PN_x is the percent nested value corresponding to raw metric X , X_{obs} is the observed value of X , X_{exp} is the expected value of X , and X_{perf} is the value X would take if the matrix were perfectly nested. The value of N_0 , N_1 , and the U metrics under perfect nesting is zero. The value of N_c under perfect nesting is its maximum value: the sum over all pairs of sites of the most species that could be shared given the observed site richnesses (Wright and Reeves 1992). The expected value (X_{exp}) depends on what null hypothesis you use, and is either calculated analytically or estimated as the mean of simulated values. Unlike *T*, the PN indices increase with increasing nestedness, from 0%, indicating complete disorder, to 100%, indicating perfect nesting. Below we examine the behavior of the percent nestedness indices PN_0 , PN_1 , PN_c , PN_{Ua} , PN_{Up} , and PN_{Ut} , and of *T*, and use some of these standardized metrics to explore taxonomic and geographic patterns in nestedness.

The null hypotheses

Null hypotheses in biogeography are used to relate observed species distributions to the patterns generated by a particular model of the world (Colwell and Winkler 1984). Choice of model is therefore of great importance. In this study, we evaluated nestedness relative to three different null hypotheses, denoted R_0 , R_1 , and R_2 , which correspond to a progressively graded series of constraints. For each data set and under the constraints of each of these null hypotheses, we generated 1000 random matrices and calculated the metrics above (excluding *T*) for each. We then compared the values of these metrics for the observed matrix to the distributions of values from the randomized matrices in order to evaluate their statistical likelihoods.

R_0

For each island or site in a random matrix, species were drawn from a uniform probability distribution until its species richness

equalled that observed. R_0 corresponds to the RANDOM0 constraints presented and evaluated by Patterson and Atmar (1986), and described by Wright and Reeves (1992) as the “equiprobable species” null hypothesis. Random matrices generated under R_0 have little nested structure. However, R_0 -generated matrices differ greatly from natural ones in having few broadly or narrowly distributed species.

R_1

For each simulated site, species were drawn with probabilities weighted by their observed incidence values, until the number of species drawn equalled the observed richness. This null hypothesis corresponds to the RANDOM1 constraints of Patterson and Atmar (1986). In R_1 simulations, a species found on ten islands is twice as likely to be picked in any given draw as a species found on only five islands. Mathematically, the probability of drawing species i , $p_i = J_i / J_T$, where J_i is the incidence of species i and J_T is the sum of the incidence values over all species not yet drawn to the site. (This weighting is not equivalent to the fraction of sites occupied, but those values are difficult to work into a simulation because they do not sum to 1 across species.) Because R_1 incorporates information on differences in incidence among species, R_1 -generated random biotas are more nested than R_0 biotas.

R_2

This null hypothesis was newly fashioned for the present study in order to address observations that the incidence totals of matrices generated by R_1 do not closely approximate those of the observed matrix (Simberloff and Martin 1991; Wright and Reeves 1992; Cook and Quinn 1998). Rather, widespread species are under-represented in matrices assembled by R_1 , while narrowly distributed species are over-represented. By a trial and error process in which the incidence vectors used in R_1 trials were raised to exponents ranging from 1.1 to 3.0 (in increments of 0.1), we found, over a variety of matrix ranks and fills, that using squared incidence values divided by the sum of the squared values to produce p_i values generated random matrices with incidence values that resembled observed ones. Thus, our R_2 algorithm is similar to R_1 but uses probabilities derived from squared incidence values in drawing species to fill sites. As a null hypothesis, R_2 suffers from being purely phenomenological, but has the advantage of mimicking the incidence structure of real matrices without the difficulties encountered under even more rigid incidence constraints (Diamond and Gilpin 1982).

R_{00}

The foregoing null hypotheses constrain row totals (species richnesses) to equal those observed, and place increasing constraint on the values taken by column totals (species incidence), producing progressively greater nested structure in simulated assemblages. However, these constraints do not fit well with the thermodynamic perspective taken by Atmar and Patterson (1993) in constructing their “temperature” metric, *T*. Their program (Atmar and Patterson 1995) generates simulated null matrices without either row or column constraints (hence “00”); only the total number of presences is fixed at the observed value. We used R_{00} , only, as the null hypothesis for calculating and testing values of *T*.

All four null hypotheses assume that sites are independent of one another. This assumption is likely to be violated where species can reliably move between sites, or where substantial environmental differences exist between sites.

Figure 1 depicts a sample matrix created under each null hypothesis, together with the actual distribution of frogs in Amazonian forest fragments (“amazfrog” in Table 1). Simulations under R_0 , R_1 , and R_2 produce matrices packed successively more tightly into the upper-left corner, and hence which are increasingly nested.

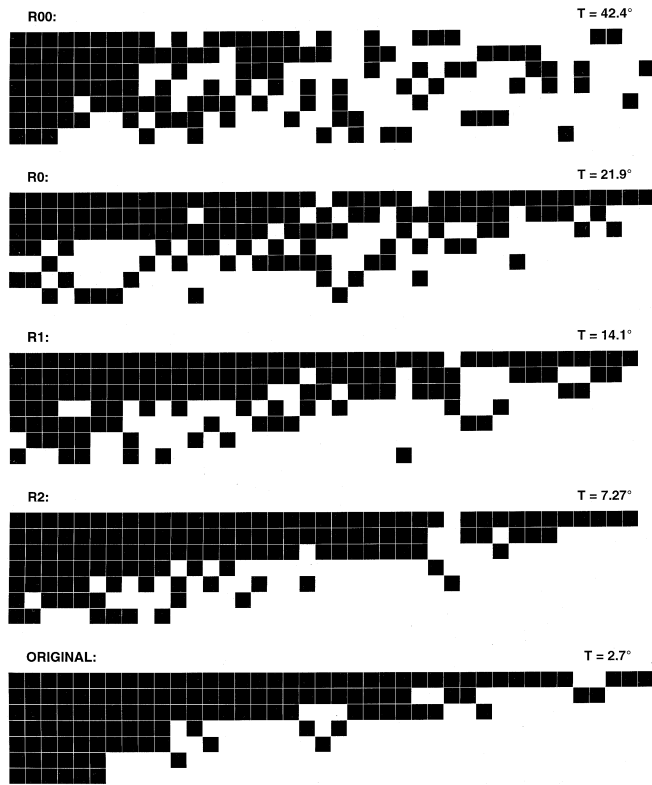


Fig. 1 A random matrix created under each null hypothesis – R00, R0, R1, and R2 – and the observed distribution of frogs in Amazonian forest fragments (“amazfrog” in Table 1). All matrices were sorted to minimize Atmar and Patterson’s (1993) temperature index of nestedness (T), which is shown at the *right* for each matrix. The tendency for simulations R00, R0, R1, and R2 to produce matrices packed successively more tightly into the upper-left corner, and hence which are differentially nested, is apparent

In order to assess the statistical likelihood of a particular nestedness measurement, we used normal probability (z scores). Wright and Reeves (1992) determined that the distributions of metrics N_0 , N_1 , and N_c were approximately normal, validating this means of testing significance. However, since their simulations produced distributions that were slightly skewed towards more strongly nested values, Wright and Reeves suggested conservative interpretations of statistical significance levels. We have therefore designated $P = 0.01$ as our nominal critical level in tests of the significance of nestedness z -scores.

Definition of terms

1. Archipelago – a geographically coherent cluster of islands. We also use the term loosely to include clusters of insular habitats or non-insular sites in our analysis.
2. Fill – the proportion of 1s (presences) in a presence-absence matrix.
3. Fragment – an island or site formerly connected with a much larger area of habitat but which has recently (within the last few hundred generations) become more or less isolated, often due to alteration of surrounding habitat by humans.
4. Hole – an absence of a species from a site that deviates from perfect nesting.
5. Landbridge – of islands or sites formerly connected with much larger areas of habitat and which have subsequently become isolated, e.g., by sea-level rise or climate change. Landbridge sites have a longer history of isolation than fragments.

6. Oceanic – of islands or sites colonized by dispersal across unsuitable habitat, having been isolated throughout the period during which the current local biotas were established.
7. Outlier – a presence of a species on a site that deviates from perfect nesting.
8. Rank – the total number of elements in a presence-absence matrix (rows \times columns = sites \times species).

Results

Characteristics of the data and the metrics

The data set

In total, we compiled 279 presence-absence matrices (Table 1). These matrices and a bibliography of sources are available at the Field Museum of Natural History’s World Wide Web site [<http://www.fmnh.org/>]. Once there, look in “science” and “gopher server” (<gopher://fmppr.fmnh.org>) for “Nestedness Temperature Calculator.” Additional information and links are available at www.aics-research.com/nested/. We restricted most of our analyses to 163 of these datasets – those that were “independent” in that they did not overlap in their coverage of both species and sites. Datasets with overlapping sets of sites were allowed so long as they sampled different species. For example, all but one of the repeated samples of Simberloff and Wilson (1969) of arthropods on experimental mangrove islands were excluded (see Patterson 1990 for an analysis of nestedness in this famous experiment), but four presence-absence matrices for landbridge islands in the Sea of Cortez (Gulf of California) were included, detailing distributions of plants, birds, mammals, and herpetofauna, respectively.

The data gathered cover a wide variety of taxa. Among the non-overlapping datasets, there are 27 on non-flying land mammals, 5 on bats, 32 on land and freshwater birds, 18 on reptiles and amphibians, 9 on fish, 27 on terrestrial arthropods, 6 on terrestrial mollusks, 21 on plants, and 12 on miscellaneous species – mostly colonizers of freshwater habitats (crustaceans, diatoms) or marine fouling communities. In addition, there are 3 matrices for seabirds, 2 for cave faunas, and one in which the “species” are habitat types.

The data are also geographically diverse. Of 163 datasets, 97 are centered in north temperate latitudes, 51 in the tropics, 14 in south temperate latitudes and 1 within the Arctic Circle. Of the datasets, 90 deal with real islands, 31 with island-like habitats (e.g., isolated mountaintops), 10 with artificial experimental islands, 25 are not insular but are samples from surrounding contiguous habitat, and 7 datasets do not fit these categories.

Isolation history is an important factor in determining species distributions and thus nestedness, so we classified each “archipelago” by the nature of isolation of its sites: 43 are oceanic, 26 are landbridge, 11 are mixtures of oceanic and landbridge islands, 15 are

Table 1 Summary of the datasets compiled in the survey. The second column, (I?) indicates whether the dataset is (y) or is not (n) treated as independent of the other datasets. Under *Taxon*, *mamm*, *nv* stands for non-flying mammals; under *Isolation type*, *mixed l & o* stands for archipelagos with a mix of landbridge and oceanic is-

lands, and *non & real mixed* means the data include both real islands and non-isolated sites. The original data, full references, and other information can be obtained at the Internet sites described in the Results section, or from the authors

Dataset name	I?	Isl	Spp	Location	Taxon	Isolation type	Source
1000islm	y	18	10	Thousand Islands, New York	mamm,nv	mixed l & o	Lomolino (1986)
afrlm	y	19	95	East Africa parks	mamm,nv	fragment	Williams (1968)
afrlmq	n	18	91	East Africa parks	mamm,nv	fragment	same as above
afrlmqm	n	17	88	East Africa parks	mamm,nv	fragment	same as above
afrm	n	19	135	East Africa parks	mammals	fragment	same as above
afrmq	n	18	129	East Africa parks	mammals	fragment	same as above
afrmqm	n	17	125	East Africa parks	mammals	fragment	same as above
afrmtbrd	n	7	222	Afrotropical mountains	birds	–	Dowsett (1986)
afroalpb	y	6	53	Afrotropical mountains	birds	–	Dorst & Vuilleumier (1986)
alandbrd	y	16	82	Aland Is., SW Finland	birds	non & real mixed	Haila et al. (1980)
amazfrog	y	7	40	Central Amazon	herps	fragment	Zimmerman & Bierregaard (1986)
antilbat	n	21	56	Antilles (West Indies)	bats	oceanic	Griffiths & Klingener (1988)
antilbrd	n	19	212	Antilles (West Indies)	birds	oceanic	Ricklefs & Cox (1972)
artiherb	y	43	84	Minnesota	plants	–	Scanlan, M., unpublished
artreeff	y	3	113	St. John, U.S. Virgin Is.	fish	immigr. expt.	Randall (1963)
ausismam	y	26	49	W and S Australia	mamm,nv	landbridge	Kitchener et al. (1980b)
auslizrd	y	23	70	W Australia	herps	fragment	Kitchener et al. (1980a)
ausmam	y	22	18	W Australia	mamm,nv	fragment	Kitchener et al. (1980b)
austante	n	8	6	Austral Is.	arthropods	oceanic	Wilson & Taylor (1967)
austantt	y	8	15	Austral Is.	arthropods	oceanic	same as above
bahabma	y	6	6	Bahamas	habitats	–	Maly & Doolittle (1977)
bahamasn	y	6	11	Bahamas	mollusks	oceanic	same as above
bajaball	n	26	37	Sea of Cortez	birds	mixed l & o	Cody (1983)
bajabl	y	9	37	Sea of Cortez	birds	landbridge	same as above
bajabn	n	11	32	N Sea of Cortez	birds	mixed l & o	same as above
bajabo	y	13	28	Sea of Cortez	birds	oceanic	same as above
bajabs	n	15	25	S Sea of Cortez	birds	mixed l & o	same as above
bajahall	n	48	84	Sea of Cortez	herps	mixed l & o	Murphy (1983)
bajahl	y	8	52	Sea of Cortez	herps	landbridge	same as above
bajahm	y	23	22	Sea of Cortez	herps	mixed l & o	same as above
bajaho	y	17	56	Sea of Cortez	herps	oceanic	same as above
bajamall	n	34	27	Sea of Cortez	mamm,nv	mixed l & o	Lawlor (1983)
bajaml	y	20	25	Sea of Cortez	mamm,nv	landbridge	same as above
bajamo	y	14	9	Sea of Cortez	mamm,nv	oceanic	same as above
bajapall	n	20	597	Sea of Cortez	plants	mixed l & o	Cody, Moran, & Thompson (1983)
bajapl	y	9	479	Sea of Cortez	plants	landbridge	same as above
bajapo	y	11	412	Sea of Cortez	plants	oceanic	same as above
bassanss	n	3	11	Bass Strait	herps	landbridge	Littlejohn & Martin (1974)
bassanu	y	3	10	Bass Strait	herps	landbridge	same as above
bassmhmp	n	18	10	Bass Strait	mamm,nv	landbridge	Hope (1973)
basshmp	n	10	10	Bass Strait	mamm,nv	landbridge	same as above
bassmam	n	9	15	Bass Strait	–	landbridge	same as above
bassmamm	y	19	10	Bass Strait	mamm,nv	landbridge	Hope (1974)
basspass	y	4	25	Bass Strait	birds	landbridge	Abbott (1973)
bassrept	y	10	17	Bass Strait	herps	landbridge	Rawlinson (1974)
behle78	n	15	81	Great Basin, W USA	birds	landbridge	Behle (1978)
bonnfish	y	7	19	L. Bonneville drainages, USA	fish	linear	Smith (1978)
brazbird	y	3	216	Brazil	birds	fragment	Willis (1979)
brazbmi	n	3	188	Brazil	birds	fragment	same as above
brazofb	y	29	71	Brazil	birds	non-isolated	Stotz, D., unpublished data
brazpfb	y	13	20	Brazil	birds	non-isolated	same as above
brazufb	y	30	71	Brazil	birds	non-isolated	same as above
britbird	y	25	8	Great Britain	birds	–	Reed (1980)
britchah	y	5	9	British Channel Is.	herps	landbridge	Frazer (1949)
britcham	y	5	9	British Channel Is.	mamm,nv	landbridge	Southern (1964)
brivirgh	y	43	23	British Virgin Is.	herps	mixed l & o	Lazell (1983)
butter1	n	17	285	Antilles (West Indies)	arthropods	non&real mixed	Scott (1970)
butter2	y	6	261	Antilles (West Indies)	arthropods	oceanic	same as above
cage342	n	3	10	NW Florida, week 42	arthropods	extinc. expt.	Rey (1981)

Table 1 (Continued)

Dataset name	I?	Isl	Spp	Location	Taxon	Isolation type	Source
cage36	n	3	14	NW Florida, week 6	arthropods	extinc. expt.	Rey (1981)
cage41	y	4	36	NW Florida, week 1	arthropods	extinc. expt.	same as above
cage45	n	4	15	NW Florida, week 5	arthropods	extinc. expt.	same as above
calirept	n	15	27	California islands	herps	oceanic	Wilcox (1980)
canabo	y	7	61	Canary Is.	birds	oceanic	Bacallado (1976)
canaboss	n	7	78	Canary Is.	birds	oceanic	same as above
canaho	y	7	10	Canary Is.	herps	oceanic	Klemmer (1976)
canahoss	n	7	14	Canary Is.	herps	oceanic	same as above
canlauio	y	7	120	Canary Is.	arthropods	oceanic	Machado (1976)
canlauss	n	7	130	Canary Is.	arthropods	oceanic	same as above
caveio	n	6	28	West Virginia caves	invertebrates	–	Culver, Holsinger & Baroody (1973)
caveio22	y	6	12	West Virginia caves	invertebrates	–	same as above
caveio23	y	7	16	West Virginia caves	invertebrates	–	same as above
chanb	n	16	45	California Channel Is.	birds	oceanic	Power (1972)
chanbpr	y	8	38	California Channel Is.	birds	oceanic	Diamond & Jones (1980)
chanherp	y	15	28	California Channel Is.	herps	oceanic	Savage (1967)
chanlbat	y	6	10	California Channel Is.	bats	oceanic	Brown (1980)
chanmamm	y	8	6	California Channel Is.	mamm,nv	oceanic	von Bloeker (1967)
chanrept	n	8	12	California Channel Is.	herps	oceanic	Wilcox (1980)
chfbird	y	30	5	S California	birds	fragment	Bolger, Alberts & Soule (1991)
chihdgro	y	24	14	Chihahuan Desert, SW USA	mamm,nv	non-isolated	Brown & Kurzius (1987)
chihdsro	y	21	14	Chihahuan Desert, SW USA	mamm,nv	non-isolated	same as above
chihrod	n	45	17	Chihahuan Desert, SW USA	mamm,nv	non-isolated	same as above
chilemam	y	9	8	N Chile	mamm,nv	non-isolated	Meserve & Glanz (1978)
chiweed	n	26	128	Illinois	plants	immigr. expt.	Crowe (1979)
chiweedo	y	13	123	Illinois	plants	immigr. expt.	same as above
chiweedy	y	13	75	Illinois	plants	immigr. expt.	same as above
chufbird	y	9	5	S California	birds	non-isolated	Bolger, Alberts & Soule (1991)
clinbell	y	15	152	Illinois	plants	fragment	Clinebell, R., unpublished
colofish	y	6	26	Colorado R. drainages, USA	fish	linear	Smith (1978)
deadfish	y	5	8	Death Valley drainages, USA	fish	linear	same as above
defau610	n	6	25	NW Florida, week 10	arthropods	immigr. expt.	Rey (1981)
defau611	n	6	26	NW Florida, week 11	arthropods	immigr. expt.	same as above
defau612	n	6	26	NW Florida, week 12	arthropods	immigr. expt.	same as above
defau613	n	6	27	NW Florida, week 13	arthropods	immigr. expt.	same as above
defau614	n	6	28	NW Florida, week 14	arthropods	immigr. expt.	same as above
defau615	n	6	29	NW Florida, week 15	arthropods	immigr. expt.	same as above
defau616	n	6	30	NW Florida, week 16	arthropods	immigr. expt.	same as above
defau617	n	6	27	NW Florida, week 17	arthropods	immigr. expt.	same as above
defau618	n	6	30	NW Florida, week 18	arthropods	immigr. expt.	same as above
defau619	n	6	31	NW Florida, week 19	arthropods	immigr. expt.	same as above
defau620	n	6	33	NW Florida, week 20	arthropods	immigr. expt.	same as above
defau621	n	6	34	NW Florida, week 21	arthropods	immigr. expt.	same as above
defau622	n	6	35	NW Florida, week 22	arthropods	immigr. expt.	same as above
defau623	n	6	37	NW Florida, week 23	arthropods	immigr. expt.	same as above
defau624	n	6	39	NW Florida, week 24	arthropods	immigr. expt.	same as above
defau625	n	6	41	NW Florida, week 25	arthropods	immigr. expt.	same as above
defau626	n	6	41	NW Florida, week 26	arthropods	immigr. expt.	same as above
defau631	n	6	35	NW Florida, week 31	arthropods	immigr. expt.	same as above
defau653	y	6	33	NW Florida, week 53	arthropods	immigr. expt.	same as above
defau69	n	6	23	NW Florida, week 9	arthropods	immigr. expt.	same as above
defauni0	y	6	250	S Florida, mangrove islets	arthropods	–	Simberloff & Wilson (1969)
defauni1	n	6	39	S Florida, mangrove islets	arthropods	immigr. expt.	same as above
defauni2	n	6	62	S Florida, mangrove islets	arthropods	immigr. expt.	same as above
defauni3	n	6	76	S Florida, mangrove islets	arthropods	immigr. expt.	same as above
defauni4	n	6	112	S Florida, mangrove islets	arthropods	immigr. expt.	same as above
defauni5	n	6	134	S Florida, mangrove islets	arthropods	immigr. expt.	same as above
defauni6	n	6	154	S Florida, mangrove islets	arthropods	immigr. expt.	same as above
defauni7	n	6	190	S Florida, mangrove islets	arthropods	immigr. expt.	same as above

Table 1 (Continued)

Dataset name	I?	Isl	Spp	Location	Taxon	Isolation type	Source
defauni8	n	6	217	S Florida, mangrove islets	arthropods	immigr. expt.	Simberloff & Wilson (1969)
defauni9	n	6	232	S Florida, mangrove islets	arthropods	immigr. expt.	same as above
eiremoth	y	5	119	N Ireland	arthropods	non-isolated	Magurran (1985)
ereptile	y	9	17	W Lake Erie, E N. America	herps	landbridge	King (1988)
erisopod	y	22	12	W Lake Erie, E N. America	arthropods	landbridge	Dexter, Hahnert & Beatty (1988)
faerbird	y	22	40	Faeroe Is.	birds	oceanic	Bengtson & Bloch (1983)
faerio	y	17	26	Faeroe Is.	arthropods	oceanic	Bengtson (1982)
finbird	y	6	23	Finland	birds	non-isolated	Jarvinen & Vaisanen (1980)
finlaks1	y	16	5	Finland	mamm,nv	mixed l & o	Hanski (1986)
finlaks2	n	17	5	Finland	mamm,nv	mixed l & o	same as above
frigbo	y	9	18	French Frigate Shoals, Hawaii	birds,sea	oceanic	Amerson (1971)
frigpo	y	8	40	French Frigate Shoals, Hawaii	plants	oceanic	same as above
fullglas	n	102	39	Iowa and Minnesota	plants	fragment	Glass, W.D., unpublished
gabab	y	4	38	Greater Antilles (W. Indies)	bats	oceanic	Griffiths & Klingener (1988)
gababpgc	n	5	38	above plus Grand Cayman I.	bats	oceanic	same as above
galabo	y	15	23	Galapagos Is.	birds	oceanic	Harris (1973)
gambantt	y	7	9	Gambier Is., Polynesia	arthropods	oceanic	Wilson & Taylor (1967)
gatbird	y	6	102	Gatun Lake, Panama	birds	fragment	Wright (1985)
gbdgrod	y	5	3	Great Basin, W USA	mamm,nv	non-isolated	Brown & Kurzius (1987)
gbdsrod	y	25	13	Great Basin, W USA	mamm,nv	non-isolated	same as above
gbfish	n	48	78	W USA drainages	fish	linear	Smith (1978)
gbmtbird	y	13	11	Great Basin, W USA	birds	landbridge	Brown (1978)
gbmtmam	y	19	16	Great Basin, W USA	mamm,nv	landbridge	same as above
gbrod	n	57	14	Great Basin, W USA	mamm,nv	non-isolated	Brown & Kurzius (1987)
gbsdrod	y	15	13	Great Basin, W USA	mamm,nv	non-isolated	same as above
gbsrod	y	12	6	Great Basin, W USA	mamm,nv	non-isolated	same as above
grbrfish	y	30	35	West Virginia	fish	non-isolated	Hocutt, Denoncourt & Stauffer (1978)
guineap	y	4	683	Gulf of Guinea is., W Africa	plants	mixed l&o	Exell (1944)
halfglas	y	56	39	Iowa and Minnesota	plants	fragment	Glass, W.D., unpublished
hawaante	n	9	6	Hawaii	arthropods	oceanic	Wilson & Taylor (1967)
hawaantt	y	14	32	Hawaii	arthropods	oceanic	same as above
hawabend	n	6	35	Hawaii	birds	oceanic	Scott et al. (1986)
hawabug1	y	6	263	Hawaii	arthropods	oceanic	Hardy & Kohn (1964)
hawabug2	y	6	400	Hawaii	arthropods	oceanic	Hardy (1965)
hawanb19	y	8	36	Hawaii	birds	oceanic	Juvik & Austring (1979)
hawapele	y	6	66	Hawaii	plants	oceanic	Stone (1969)
hawapepr	y	7	38	Hawaii	plants	oceanic	Yuncker (1933)
hawapess	n	7	63	Hawaii	plants	oceanic	same as above
hebirds	y	19	22	NW Scotland	birds, sea	-	Bourne & Harris (1979)
hebwoffb	y	14	18	W Scotland	birds, sea	-	same as above
illwdb79	y	12	46	Illinois	birds	fragment	Blake (1991)
illwdb80	n	12	49	Illinois	birds	fragment	same as above
italiant	y	21	48	Tuscan Archipelago, Italy	arthropods	landbridge	Baroni-Urbani (1971)
jamaanol	y	9	6	Jamaica	herps	non-isolated	Haefner (1988)
kirim	y	7	55	Venezuela	bats	mixed l & o	Koopman (1958)
labatpgc	y	17	24	Lesser Antilles + Grand Cayman	bats	oceanic	Griffiths & Klingener (1988)
lahofish	y	9	12	L. Lahontan drainages, W USA	fish	linear	Smith (1978)
lakmichm	n	9	8	Lake Michigan, N. America	mamm,nv	mixed l & o	Lomolino (1986)
lineantt	y	6	13	Line Is., central Pacific	arthropods	oceanic	Wilson & Taylor (1967)
lmamphib	y	9	10	Lake Michigan, N. America	herps	mixed l & o	Hatt et al. (1948)
lmaves	y	15	152	Lake Michigan, N. America	birds	mixed l & o	Hatt et al. (1948)
lmlbamph	n	5	9	Lake Michigan, N. America	herps	landbridge	Hatt et al. (1948)

Table 1 (Continued)

Dataset name	I?	Isl	Spp	Location	Taxon	Isolation type	Source
lmlbaves	n	5	151	Lake Michigan, N. America	birds	landbridge	Hatt et al. (1948)
lmlbmamm	n	5	23	Lake Michigan, N. America	mammals	landbridge	same as above
lmlbrept	n	5	7	Lake Michigan, N. America	herps	landbridge	same as above
lmlbvert	n	5	190	Lake Michigan, N. America	vertebrates	landbridge	same as above
lmmammal	y	12	28	Lake Michigan, N. America	mammals	mixed l & o	same as above
lmocamph	n	3	5	Lake Michigan, N. America	herps	oceanic	same as above
lmocaves	n	3	66	Lake Michigan, N. America	birds	oceanic	same as above
lmocmamm	n	3	4	Lake Michigan, N. America	mammals	oceanic	same as above
lmocvert	n	3	78	Lake Michigan, N. America	vertebrates	oceanic	same as above
lmreptil	y	8	8	Lake Michigan, N. America	herps	mixed l & o	same as above
lmvertbt	n	15	198	Lake Michigan, N. America	vertebrates	mixed l & o	same as above
madbird	y	12	78	Madagascar	birds	fragment	Schulenberg, T., personal communication
maddabrd	y	16	61	Maddalena Archipelago, France	birds	landbridge	Simberloff & Martin (1991)
mahop	y	18	70	Barbados, West Indies	plants	–	Watts (1978)
marqante	n	10	8	Marquesas Is., Polynesia	arthropods	oceanic	Wilson & Taylor (1967)
marqantt	y	13	16	Marquesas Is., Polynesia	arthropods	oceanic	same as above
microhi	y	9	11	beakers	miscellaneous	immigr. expt.	Dickerson & Robinson (1984)
microli	y	5	9	beakers	miscellaneous	immigr. expt.	same as above
mindanam	y	9	35	Mindanao region, Phillippines	mamm,nv	landbridge	Heaney (1986)
mojadsro	y	49	14	Mojave Desert, SW USA	mamm,nv	non-isolated	Brown & Kurzius (1987)
mojarod	n	52	14	Mojave Desert, SW USA	mamm,nv	non-isolated	same as above
mojasdro	y	3	5	Mojave Desert, SW USA	mamm,nv	non-isolated	same as above
namlage	y	14	37	W N. America	mamm,nv	fragment	Newmark (1986)
namlago	n	14	39	W N. America	mamm,nv	fragment	same as above
namlagpp	n	14	37	W N. America	mamm,nv	fragment	same as above
natuherb	y	22	116	Minnesota	plants	–	Scanlan, M., unpublished
ncall	n	150	21	NW Australia	mollusks	non&real mixed	Solem, A., personal communication
nccoast	y	36	18	NW Australia	mollusks	non-isolated	same as above
ncinland	y	31	19	NW Australia	mollusks	non-isolated	same as above
ncisland	y	83	19	NW Australia	mollusks	–	same as above
newzbird	n	31	57	New Zealand region	birds	mixed l&o	Patterson (1987)
newzbl	y	22	53	New Zealand region	birds	landbridge	same as above
newzbo	y	9	31	New Zealand region	birds	oceanic	same as above
ohebcoll	y	6	155	Outer Hebrides, Scotland	arthropods	landbridge	Welch (1979)
ohebspid	y	6	38	Outer Hebrides, Scotland	arthropods	landbridge	same as above
ontarioc	y	34	25	NW Ontario, Canada	arthropods	linear	Patalas (1971)
orealbut	y	13	87	Andes mountains, S. America	arthropods	–	Descimon (1986)
oregfish	y	11	15	Oregon Lakes drainages, W USA	fish	linear	Smith (1978)
pacifish	y	16	179	Pacific Ocean	fish	non-isolated	Springer (1982)
palawam	y	4	29	Palawan region, Phillippines	mamm,nv	landbridge	Heaney (1986)
papahall	y	17	24	E Papua-New Guinea	herps	–	Heatwole (1975)
penobm20	n	7	29	Penobscot Bay, Maine	mamm,nv	landbridge	Crowell (1986)
penobm85	y	7	32	Penobscot Bay, Maine	mamm,nv	landbridge	same as above
perthp	y	49	147	W Australia	plants	oceanic	Abbot & Black (1980)
polyante	n	62	43	Polynesia	arthropods	oceanic	Wilson & Taylor (1967)
polyantt	n	93	40	Polynesia	arthropods	oceanic	same as above
pueranol	y	11	8	Puerto Rico	herps	non-isolated	Haefner (1988)

Table 1 (Continued)

Dataset name	I?	Isl	Spp	Location	Taxon	Isolation type	Source
queenbrd	y	41	30	Queen Charlotte Is., W Canada	birds	landbridge	Simberloff & Martin (1991)
reefmang	y	22	16	Great Barrier Reef, Australia	plants	–	Stoddart (1980)
reefmass	n	22	17	Great Barrier Reef, Australia	plants	–	same as above
relax1	y	8	205	S. Florida, mangrove islands	arthropods	extinc. expt.	Simberloff (1976)
relax2	n	8	174	S. Florida, mangrove islands	arthropods	extinc. expt.	same as above
relax2ex	n	8	125	S. Florida, mangrove islands	arthropods	extinc. expt.	same as above
relax2in	n	8	148	S. Florida, mangrove islands	arthropods	extinc. expt.	same as above
relax3	n	5	133	S. Florida, mangrove islands	arthropods	extinc. expt.	same as above
relax3ex	n	5	85	S. Florida, mangrove islands	arthropods	extinc. expt.	same as above
relax3in	n	5	109	S. Florida, mangrove islands	arthropods	extinc. expt.	same as above
rockymam	y	28	26	S Rocky Mountains, USA	mamm,nv	landbridge	Patterson & Atmar (1986)
samoante	n	5	38	Samoa	arthropods	oceanic	Wilson & Taylor (1967)
samoantt	y	7	24	Samoa	arthropods	oceanic	same as above
scum1	y	4	54	Pennsylvania	miscellaneous	immigr. expt.	Patrick, in MacArthur & Wilson (1967)
scum2	y	4	31	Pennsylvania	miscellaneous	immigr. expt.	same as above
scum65	y	8	182	Pennsylvania	miscellaneous	immigr. expt.	Patrick (1968)
scum66	y	4	180	Pennsylvania	miscellaneous	immigr. expt.	same as above
sipoo brd	y	18	50	Sipoo archipelago, S Finland	birds	oceanic	Simberloff & Martin (1991)
snakfish	y	4	29	Snake River drainages, W USA	fish	linear	Smith (1978)
sociante	n	7	11	Society Is., Polynesia	arthropods	oceanic	Wilson & Taylor (1967)
sociantt	y	10	21	Society Is., Polynesia	arthropods	oceanic	same as above
sofinbrd	y	34	45	S Finland	birds	fragment	Simberloff & Martin (1991)
solid1	y	11	11	E Canada	arthropods	–	Pielou (1974)
solid2	y	13	12	SE Ontario, Canada	arthropods	–	same as above
sonodsro	y	45	14	Sonoran Desert, SW USA	mamm,nv	non-isolated	Brown & Kurzius (1987)
sonorod	n	48	14	Sonoran Desert, SW USA	mamm,nv	non-isolated	same as above
sotaherb	y	12	102	Minnesota River Tract	plants	–	Scanlan, M., unpublished
sulawbat	y	13	59	Sulawesi, Indonesia	bats	oceanic	Musser (1987)
swusdgro	n	29	15	SW USA desert grassland	mamm,nv	non-isolated	Brown & Kurzius (1987)
swusdsro	n	140	27	SW USA desert scrub	mamm,nv	non-isolated	same as above
swusrod	n	202	29	SW USA	mamm,nv	non-isolated	same as above
swussdro	n	21	14	SW USA sand dunes	mamm,nv	non-isolated	same as above
tanganyo	y	38	104	Lake Tanganyika, E Africa	arthropods	non-isolated	Cohen, A., personal communication
tiles272	y	16	21	North Carolina	miscellaneous	immigr. expt.	Sutherland & Karlson (1977)
tiles273	y	18	37	North Carolina	miscellaneous	immigr. expt.	same as above
tiles274	y	18	41	North Carolina	miscellaneous	immigr. expt.	same as above
tilesc1	y	12	41	North Carolina	miscellaneous	immigr. expt.	same as above
tongante	n	6	12	Tonga	arthropods	oceanic	Wilson & Taylor (1967)
tongantt	y	3	11	Tonga	arthropods	oceanic	same as above
tresmarb	y	4	61	Tres Marias Is.	birds	oceanic	Grant & Cowan (1964)
tresmarh	y	4	20	Tres Marias Is.	herps	oceanic	Zweifel (1960)
tristwe1	n	4	9	Tristan archipelago, S Atlantic	arthropods	oceanic	Williamson (1981)
tristwe2	y	4	16	Tristan archipelago, S Atlantic	arthropods	oceanic	same as above
usambird	y	10	31	Tanzania, montane	birds	fragment	Newmark (1991)
wauother	n	55	15	W Australia	mollusks	non-isolated	Cameron (1992)
wauotlmp	y	7	15	W Australia	mollusks	–	same as above
wauscama	n	55	20	W Australia	mollusks	non-isolated	same as above

Table 1 Contd.

Dataset name	I?	Isl	Spp	Location	Taxon	Isolation type	Source
wausclmp	y	7	20	W Australia	mollusks	–	Cameron (1992)
wausnail	n	55	35	W Australia	mollusks	non-isolated	same as above
wausnmp	n	7	35	W Australia	mollusks	–	same as above
willis98	n	3	72	Brazil	birds	fragment	Willis (1979)
willis99	n	3	74	Brazil	birds	fragment	same as above
windbird	y	19	211	Antilles (West Indies)	birds	oceanic	Gotelli & Abele (1982)
windiall	y	18	51	Antilles (West Indies)	arthropods	mixed l & o	Nichols (1988)
winleed1	y	14	112	Lesser Antilles (West Indies)	plants	oceanic	Beard (1948)
winleed2	n	11	61	Lesser Antilles (West Indies)	plants	mixed l & o	same as above
winleem1	y	9	23	Lesser Antilles (West Indies)	plants	oceanic	same as above
winleem2	n	10	23	Lesser Antilles (West Indies)	plants	mixed l & o	same as above
winleer1	y	12	102	Lesser Antilles (West Indies)	plants	oceanic	same as above
winleer2	n	10	84	Lesser Antilles (West Indies)	plants	mixed l & o	same as above
winlees	y	10	6	Lesser Antilles (West Indies)	plants	oceanic	same as above
woodtree	y	10	30	S Ontario, Canada	plants	fragment	Weaver & Kellman (1981)

relatively recently isolated (and sometimes partially isolated) fragments of once-larger habitats, 7 are streams or rivers, and 14 were immigration experiments. Non-isolated sites make up 23 of the datasets, and 24 cases could not be classified.

Prevalence of nestedness

Some degree of nestedness appears to be the rule in nature. Significant nestedness relative to the simple $R0$ null hypotheses was commonplace in our survey (Fig. 2). Measured by T , under $R0$, 176 of 279 cases (63%) were significantly nested. Relative to the more sophisticated $R1$ null hypothesis, most metrics rated roughly half of all 279 cases to be significantly nested (Fig. 2). Cook and Quinn (1995) also found that nestedness is common.

A few archipelagos were found to be significantly non-nested or anti-nested, i.e., to have species communities that were more heterogeneous than expected by chance. In most cases these data were from experiments on the effects of immigration or extinction on coastal arthropod communities (“cage”, “defau” and “defauni” series in Table 1). For example, under $R0$ and as measured by three metrics ($N0$, Ut , and Nc), arthropod communities on *Spartina alterniflora* caged to prevent immigration (Rey 1981) were significantly anti-nested at weeks 1 and 6. Under $R1$, nine of ten archipelagos consistently rated as anti-nested by $N0$, Ut and Nc were from arthropod experiments [Simberloff and Wilson 1969 (1), Rey 1981 (8)]. The tenth was plants on the four main islands of the Gulf of Guinea (“guineap”). Such community heterogeneity could result from underlying environmental heterogeneity, endemic speciation, checker-

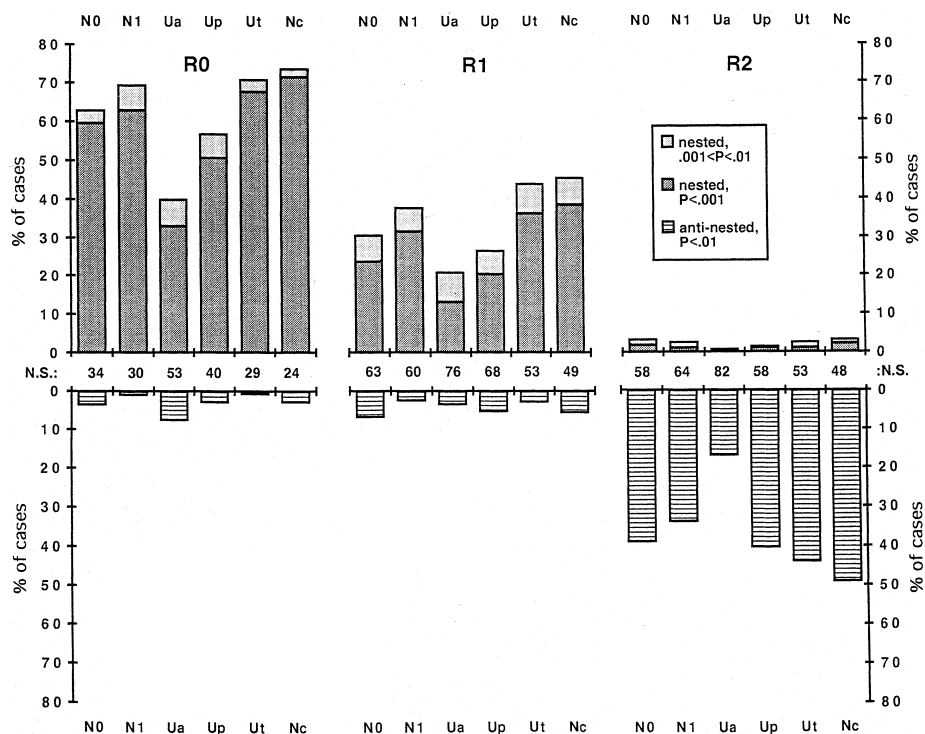
board patterns of competitive exclusion, or other factors.

In contrast, under $R2$, roughly half of all 279 datasets were significantly anti-nested, and few were significantly nested (Fig. 2). Most real matrices are less structured than matrices created under $R2$, and we devote limited attention to this null model hereafter. However, the 11 archipelagos that did prove nested even under $R2$ may deserve mention: frogs in Amazonian forest fragments (“amazfrog” in Table 1 and Fig. 1), birds on islands in the northern Sea of Cortez (“bajabn”), chaparral-requiring birds in chaparral remnants in southern California (“chfbird”), both birds and carabid beetles in the Faeroe Islands (“faerbird”, “faerio”), plants on the French Frigate Shoals (part of the Hawaiian chain: “frigpo”), birds on landbridge islands of New Zealand (“newzbl”), families of warm-water shorefishes in the Pacific (“pacifish”), non-flying mammals on islands off Maine before 1920 (“penobm20”), montane non-flying mammals on mountaintops in the southwestern United States (“rockymam”), and non-gap-crossing birds in forest fragments in Brazil (“willis98”). Landbridge archipelagos and habitat fragments, which are presumably relaxing toward lower species richnesses via extinction, are well represented in this list.

Differences between metrics

Different metrics occasionally yielded markedly different percent nested (PN) values. In the case of Ua and Up or $N0$ and $N1$ this is not entirely unexpected, because these metrics measure different characteristics of the presence-absence matrix – and, in the case of Ua and Up , are intended to. However, we expected PNc and $PNUt$ to be

Fig. 2 Percent of all 279 presence-absence matrices that were significantly nested (*top*), not significant (numbers between horizontal axes), or significantly anti-nested (*bottom*). Significant nestedness was common under null hypotheses *R0* and *R1*. Percentages for six different raw metrics under three null hypotheses are shown. To simplify presentation, anti-nested bars are not subdivided. Significance was based on z -scores (see Methods). [The percentage of *Nc* values rated significant is slightly exaggerated by the use of z -scores, since the distribution of *Nc* is not precisely normal (Wright and Reeves 1992). For example, using a conservative chi-square to assess significance, the number of *Nc* values nested at $P < 0.01$ under *R0* is reduced from 73% to 69%.] For discussion of *T* see text



similar, yet PNC values were low for some matrices that were rated as highly or even perfectly nested by PNUt and other standardized metrics. This is because *Nc* checks for differences in species composition between sites that are tied in species richness, but the other metrics do not. Examples in Table 1 include “gbdgrod” (3 granivorous rodent species at 5 Great Basin desert grassland sites) and “lahofish” (12 fish species in 9 drainage units in the Lahontan drainage system). On the other hand, a matrix of communities of small mammals in Chile (“chilemam”), which does not show the ambiguity of tied sites, was rated as perfectly nested by all metrics.

The *Nc* and *T* metrics allow tests of significance in some cases of perfect nesting that cannot be assessed using other metrics. Among the 163 non-overlapping datasets, we observed two cases, each with only three sites, where the variances of all metrics except *Nc* and *T* were zero. With zero variance, z -scores are undefined and so are the corresponding percent nested metrics. PNC and *T* could be calculated because they do not ignore differences between tied sites.

Effects of matrix size

All of the raw nestedness metrics *N0*, *N1*, *Ua*, *Up*, *Ut*, and *Nc* are correlated with matrix size, because they simply count the number of relationships of particular kinds between presences and absences in a matrix. The bigger the matrix, the larger the count can be. The standardized metrics, on the other hand, are intended to eliminate bias with respect to size and allow compar-

isons of nestedness between different matrices. How well did they perform?

For the most part the standardized nestedness metrics succeeded in eliminating correlation with matrix size (Table 2). Significant negative correlations of PNUa and PN1 with matrix size were probably due to the positive dependence of these variables on matrix fill, which was negatively related to matrix size. We also found a suggestive positive correlation of *T* with matrix size (Spearman rank correlation $r_s = 0.143$, $n = 163$, $P = 0.069$). Given that smaller random matrices have lower temperatures (“characteristic temperature”, Atmar and Patterson 1993), we consider this weak effect of matrix rank on *T* to be significant. Characteristic temperatures of matrices in our dataset were highly correlated with matrix rank ($r_s = 0.67$, $P < 0.0001$).

We noted a tendency for nestedness to be more variable for small matrices. While we have not quantified this tendency, inspection of the data suggests that nestedness measurements from datasets with matrix rank less than 16 or with fewer than 4 species or sites are more variable than values for larger matrices.

Effects of matrix fill, and holes versus outliers

The presence-absence matrices covered by this survey had a mean fill of 0.39 (SD = 0.161, $n = 163$). More than three-quarters of all matrices were less than half filled.

Fill was negatively correlated with matrix size in our compilation: larger matrices tended to be emptier ($r_s = -0.381$, $n = 163$, $P < 0.0001$). Not surprisingly,

Table 2 Spearman rank correlations of matrix size with percent nested (PN) metrics, under $R0$ and $R1$ assumptions ($n = 162$, one matrix eliminated with missing values). Only PN1 and PNUa were significantly correlated with matrix size. See text for results for T

Metric	Correlation with matrix rank:	
	Under $R0$	Under $R1$
PN0	0.009	-0.019
PN1	-0.174*	-0.137
PNUa	-0.309***	-0.242**
PNU _p	0.121	0.038
PNU _t	-0.024	-0.078
PNc	0.064	-0.001

* $P < 0.05$, ** $P < 0.005$, *** $P < 0.0001$ (two-tailed)

we found that the raw metrics, which are all strongly affected by matrix size, were correlated with fill.

A less anticipated result was that many of the standardized nestedness metrics were also correlated with matrix fill. Under $R0$ (or $R00$, for T), PN1 and PNUa showed strong positive correlations, PNU_t and PNc weaker ones ($r_s = 0.543, 0.657, 0.307$, and 0.257 , respectively; $n = 162$; $P < 0.0001$ except for PNc: $P = 0.0011$). PN0, PNU_p, and T were uncorrelated with fill ($r_s = 0.034, -0.020$, and 0.060 , respectively, all $P > 0.4$). Similar responses to fill were seen for the standardized metrics computed under $R1$, though r_s decreased slightly for PN1 and PNUa and increased slightly for all the others. These correlations of nestedness with fill may be due to a bias of the metrics, or may reflect a real tendency for “fuller” communities to be more nested.

Cutler (1991) noted that higher fill might favor higher values of U_a relative to U_p . We found such an effect of fill in our survey, not only on U_a compared with U_p but also on the relative magnitudes of $N1$ and $N0$. In our compilation of mostly sparsely filled matrices, $N0$ was usually greater than $N1$ (124 of 162 cases, 15 ties). We found that the mean fill of the 124 matrices where $N0$ was greater than $N1$ was significantly lower than the mean fill of the 23 where $N1$ was greater than $N0$ (0.363 versus 0.475 , $P = 0.0025$, Mann-Whitney U -test). Similarly, U_p was usually greater than U_a (121 of 162 cases, 16 ties), and matrix fill was significantly lower when $U_p > U_a$ than when $U_a > U_p$, (mean fill 0.356 versus 0.494 , $P < 0.0001$). Standardization did not affect these trends: PN0 and PN1, and PNUa and PNU_p showed the same patterns.

We believe that this effect of fill on the relative values of $N0$ and $N1$, and U_p and U_a , exists because of the reciprocal nature of holes and outliers in presence-absence matrices. Holes are determined by the presence of at least one outlier on a less species-rich site; and outliers are determined by the existence of at least one hole on a more species-rich site. In sparsely filled matrices, a few outliers can “create” many holes. On the other hand, in full matrices, a few strategically located holes can result in large numbers of outliers. This frequently uneven tradeoff between holes and outliers explains one puzzle:

Cutler’s metric U_a , named for “unexpected absences”, behaves like $N1$, which counts unexpected presences; and U_p (“unexpected presences”) behaves like $N0$, which counts unexpected absences. This is so because Cutler’s metrics parsimoniously identify the minimum number of changes needed to produce the observed matrix from a perfectly nested state. Because a few outliers can “create” many holes, a matrix that is “outlier-dominated” in Cutler’s sense ($U_p > U_a$) typically has more holes than outliers in absolute terms ($N0 > N1$). To avoid confusion, we focus on the relative values of U_p and U_a or $N0$ and $N1$, but it is worth remembering that matrices with many unexpected holes ($N0 > N1$) may in fact be produced by processes that create unexpected presences ($U_p > U_a$).

Our results on the effects of fill reinforce the caution of Cutler (1991) that “archipelagos differing in their proportions of species-poor and species-rich islands could conceivably differ in their number of holes and outliers simply on this basis.” However, we found that holes outnumber outliers even when we expect outliers to be more numerous: among matrices that are more than half full, U_p still exceeded U_a in 16 of 28 cases, and $N0$ exceeded $N1$ in 19 of 28 cases. In one possible explanation, Cutler (1994) found that sampling from a pool of species with widely differing abundances nearly always resulted in presence-absence matrices with greater U_p than U_a . Still, like nestedness analysis in general, hole versus outlier analysis cannot prove the existence of causal processes.

Because of the potential for bias, comparative studies of nestedness using existing metrics should pay close attention to possible effects of fill. PNc and T may be useful because their correlation with fill is weak. Even though fill clearly affects $N0$ and the relative magnitude of PN0 and PN1, we observed almost no correlation of PN0 with fill – perhaps because fill was usually too low to constrain unexpected absences. Thus we also chose PN0 as a candidate for further analysis. In all tests discussed below, we have looked for effects of fill and, unless otherwise noted, rejected the possibility that the result is an artifact of underlying differences in fill. Fill rarely affected the patterns we studied.

Correlations between metrics

We looked for similarities and differences in the behavior of the standardized metrics by examining rank correlations (Table 3). (Because of their strong dependence on matrix size, the raw metrics are all spuriously intercorrelated.) Under $R0$, the metrics PNc and PNU_t were so highly correlated ($r_s = 0.931$) that for practical purposes they are nearly interchangeable. PNUa and PNU_p had a low correlation (0.284), not unexpected since Cutler (1991) invented the raw forms of these metrics to measure contrasting patterns in presence-absence matrices. Also of interest were strong correlations between PN0 and PNU_p and between PN1 and PNUa,

which we interpret as evidence that the metrics in each pair measure nestedness in similar ways. We found little change in the rank correlations under *R1*. This was because, although percent nested values were lower under *R1*, they were rather consistently lower, and the ranking of datasets remained similar.

In the remainder of the Results section we examine geographic and taxonomic patterns of nestedness. Because this requires comparisons between different matrices, we use only standardized metrics. In order to simplify analysis, we reduce our focus to three metrics: PNC, PN0, and *T*. We chose PN0 partly for reasons of continuity: it is the standardized version of the oldest and most widely used metric (Patterson and Atmar's "N"). It was also sensitive to the null hypotheses examined (Fig. 2) and was uncorrelated with fill. PNC had similar desirable characteristics. Results for the "temperature" metric of Atmar and Patterson (1993), *T*, are presented where they illuminate or differ from the results for PN0 and PNC. Other metrics were either more strongly correlated with fill or were highly correlated with PN0 or PNC.

For most analyses below, only results under the *R0* null hypothesis (or *R00*, for *T*) are presented. In comparative analyses of percent nestedness, we found that the patterns observed under *R1* paralleled those found under *R0*, for the same reason mentioned above. Significance tests under *R1* usually showed the patterns to be slightly less strong, because lowered nestedness under *R1* reduced the range of variation subject to statistical explanation.

In any search for ecological pattern, the quality of the supporting data should be examined. The data represented by the matrices in our compilation are uneven in quality. Furthermore, nestedness metrics are sensitive to defects in the distributional data they summarize. At present we are unable say just how serious the defects are or how large the changes that improved data might yield. These are crucial areas for further investigation. In

Table 3 Spearman rank correlations between standardized nestedness metrics. Correlations under *R0* (except *T*) are in the lower left, correlations under *R1* in the upper right. Correlations with *T* are negative because, unlike the PN metrics, lower values of *T* indicate stronger nesting. All values are significant at $P = 0.0004$ or less ($n = 162$ non-overlapping datasets)

	PN0	PN1	PNUa	PNUp	PNUt	PNC
PN0	–	0.578	0.338	0.891	0.798	0.866
PN1	0.600	–	0.829	0.515	0.803	0.802
PNUa	0.338	0.850	–	0.301	0.721	0.624
PNUp	0.900	0.513	0.284	–	0.844	0.839
PNUt	0.825	0.801	0.684	0.866	–	0.930
PNC	0.864	0.799	0.586	0.849	0.931	–
<i>T</i> ^a	–0.755	–0.467	–0.280	–0.637	–0.611	–0.656

^a *T* values are based on *R00* but are correlated here with *R0*-based values of other metrics. Correlations under matching null hypotheses would differ somewhat

the comparative analyses that we present below, however, random errors only make the detection of pattern more difficult. Only errors that are systematically biased cause faulty conclusions (for example, if something about sampling tropical areas tended to inflate nestedness estimates, we would incorrectly assert that tropical communities are more nested). Just as with "clean" data, any patterns that do emerge from the analysis of noisy but unbiased data are as valid as their statistical confidence level.

Geographic and taxonomic patterns

Latitude and latitudinal range

Existing studies suggest that tropical and temperate areas are populated by species with different range sizes. Rapoport (1982) showed that, in North America, microendemic species of mammals are most numerous at lower latitudes. Terborgh and Winter (1983) reported that microendemic birds constitute about 1% of the avifauna of mainly temperate North America, versus 12% in mainly tropical South America. Tiny geographic ranges would tend to decrease nestedness, or reduce the spatial scale at which it is observed, because fewer species would be distributed throughout the sites or islands comprising an archipelago – instead, species would replace each other from site to site.

In our compilation, however, we observed no effect of the latitudinal midpoint of the archipelago on nestedness as measured by PN0 or PNC (north and south latitudes combined; $r_s < 0.11$, $n = 160$, $P > 0.15$, two-tailed). This remained true when major taxonomic groups were examined separately for effects of latitude on nestedness. Nor did exclusion of insular datasets from the analysis affect the result.

Similarly, we hypothesized that archipelagos comprising more widely dispersed sites would be more heterogeneous in species composition and thus show lower nestedness, but the data do not bear this out. We found no correlation of the range of latitude covered by sites in an archipelago (a measure of spatial dispersion) with PN0 or PNC, either over the entire compilation or within major taxonomic groups ($P > 0.10$). This may simply show that ecologists adjust the spatial scale of their studies to maintain relatively uniform species assemblages.

Effects of range in area

Because habitable area strongly affects insular species richness and probably species composition as well (Schoener and Schoener 1983; Patterson 1984; Simberloff and Levin 1985), we examined the effects of differences in area among islands on the percent nested metrics for 51 archipelagos with suitable area data. We expected some correlation, since if some species require minimum areas that are larger than the smallest island, a

nested pattern can result. The greater the range of island areas, the greater the chance that different species' area requirements would be expressed in nested distributions.

We found PN0 and PNC to be weakly positively correlated with the ratio of the areas of the largest and smallest sites (for PN0: $r_s = 0.295$, $n = 51$, $P < 0.02$, one-tailed). These correlations were almost unchanged under R1. T was more strongly correlated with the area ratio ($r_s = -0.425$, $P < 0.003$; r_s is negative because smaller values of T are more nested). The correlation with T is stronger because, under R00, differences in species richness – common among islands differing in size – are ignored in the null simulations. Thus archipelagos with wider area ratios tend to rate as more strongly nested under R00.

The area ratio was also correlated, but negatively, with fill ($r_s = -0.415$; $P = 0.0033$, two-tailed). This probably reflects a tendency of ecologists to include more small islands than large in their surveys: with many small islands each supporting few species compared to the few large islands, relatively empty presence-absence matrices result. When the effect of fill was removed, the correlation of PNC with the area ratio became highly significant ($P = .004$), supporting our expectation that archipelagos with a wide range of island sizes would exhibit stronger nestedness.

Effects of isolation

Essentially all authors have agreed that either extinction or colonization may shape nested patterns. Some disagree, however, on whether nestedness is empirically more common among communities dominated by extinction or those dominated by colonization (Patterson and Atmar 1986; Patterson 1987, 1990; Simberloff and Martin 1991; Wright and Reeves 1992; Cook and Quinn 1995; Kadmon 1995).

Landbridge islands provide natural experiments relevant to this question, remnant habitat fragments not-so-natural ones. In both situations extinction is expected to dominate as the species community relaxes toward a lower richness appropriate to the reduced area (especially if, in the case of fragments, edge species are omitted). Patterson and Atmar (1986) and Lawlor (1986) hypothesized that community structure in isolated systems like oceanic archipelagos is more likely to be dominated by rare colonization events.

Our results support the contention that nestedness is more clearly observed in extinction-dominated systems. We found significant variation in percent nestedness among archipelagos of differing isolation ($P < 0.002$; Fig. 3). Landbridge archipelagos were most nested, and immigration experiments showed the least nesting, as measured by PN0, PNC, or T . Nestedness of oceanic archipelagos averaged significantly lower than landbridge archipelagos, and significantly higher than immigration experiments ($P < 0.05$ in all tests, Fisher's protected least significant difference, PLSD). PN0 and

PNC, but not T , rated fragments significantly more nested than oceanic archipelagos.

A possible concern about Fig. 3 and our associated analysis is that the "immigration experiment" category contains mostly artificial habitats and is dominated by aquatic fouling communities (10 of 14 cases). If we omit this category, the probability that the observed variation in nestedness among the remaining five categories could have occurred by chance rises to about $P = 0.05$ (in Kruskal-Wallis tests on PN0, PNC, and T : $P = 0.043$, 0.054 , and 0.030 , respectively). If these probabilities are considered significant, the differences between oceanic and landbridge islands or fragments remain significant ($P < 0.05$, Fisher's PLSD).

Isolation as measured by *distance* to a source of potentially colonizing species, without reference to the islands' isolation history, explained little variation in percent nestedness. We obtained three distance variables

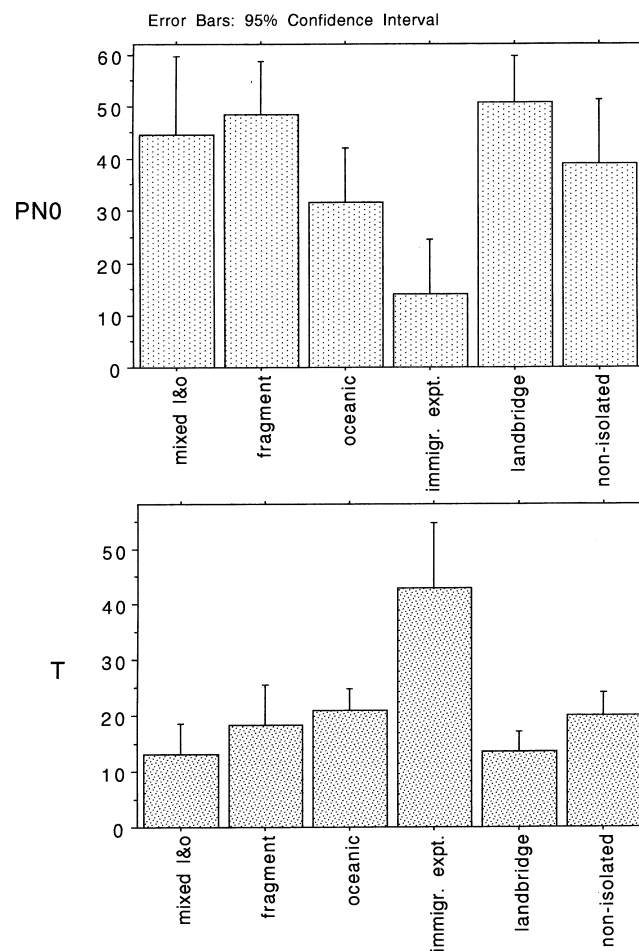


Fig. 3 Effects of different isolation types on two standardized measures of nestedness, PN0 and T (*mixed l & o* stands for archipelagos containing both landbridge and oceanic islands.). Lower values of T indicate stronger nesting. Both non-parametric Kruskal-Wallis tests and analyses of variance showed significant differences among the isolation types for both metrics (all $P < 0.002$). Landbridge archipelagos were significantly more nested than either oceanic archipelagos or immigration experiments (all $P < 0.05$, Fisher's PLSD)

for 61 archipelagos isolated by water: distance of a source area to the nearest island, distance to the farthest island, and the ratio of the difference between these distances to the distance to the nearest island (this ratio scales the spatial span of the archipelago relative to the trip required of an immigrant reaching the nearest island – a measure of the range of immigration abilities the archipelago demands of its colonists). Nestedness was not correlated with any of these distance variables ($P > 0.20$ for all three metrics).

Taxonomic comparisons

Tremendous variation exists among organisms in vagility, population density, reproductive rate, generation time, and vulnerability to environmental extremes. These and other variables affect processes that determine nestedness, such as immigration and extinction, and the spatial scale at which nestedness is manifested. If there are consistent differences among higher taxa in these variables, we expect to find taxonomic differences in nestedness. For example, if frequent colonization tends to dilute the effects of extinction in producing nested structure (as our findings on the effects of isolation imply), then one might expect more vagile taxa to show lower percent nestedness than other groups. On the other hand, other factors may act in exactly the opposite direction: over time, the differentiation of species into endemics at different sites can disrupt nested structure; and since frequent immigration can swamp local genetic differentiation, vagile taxa might also show higher nestedness.

We found rather weak differences in nestedness among taxa in our survey ($P < 0.05$; Fig. 4). Birds, in many cases quite vagile, and non-flying mammals, presumably less vagile, both showed high levels of percent nestedness. Arthropod and “miscellaneous” communities (small aquatic organisms, planktonic or sessile, 10 of 12 cases in experimental settings) had significantly lower percent nested values ($P < 0.05$, Fisher’s PLSD). If experimental studies are excluded, there were no significant differences in nestedness among taxa ($P > 0.15$ for all metrics). Taxonomic differences in nestedness, if they exist, may be so confounded by other differences in these datasets as to obscure patterns in this simple analysis.

Comparisons within archipelagos

A powerful way to control confounding variation and test for differences in nestedness among taxa is to simultaneously examine different taxa on the same set of islands. Studies on species-area slopes (e.g., Wright 1981; Lawlor 1986) as well as nested subsets (Cook and Quinn 1995) have uncovered significant differences between groups of organisms when geographic variation is controlled. In our compilation there are 14 archipelagos

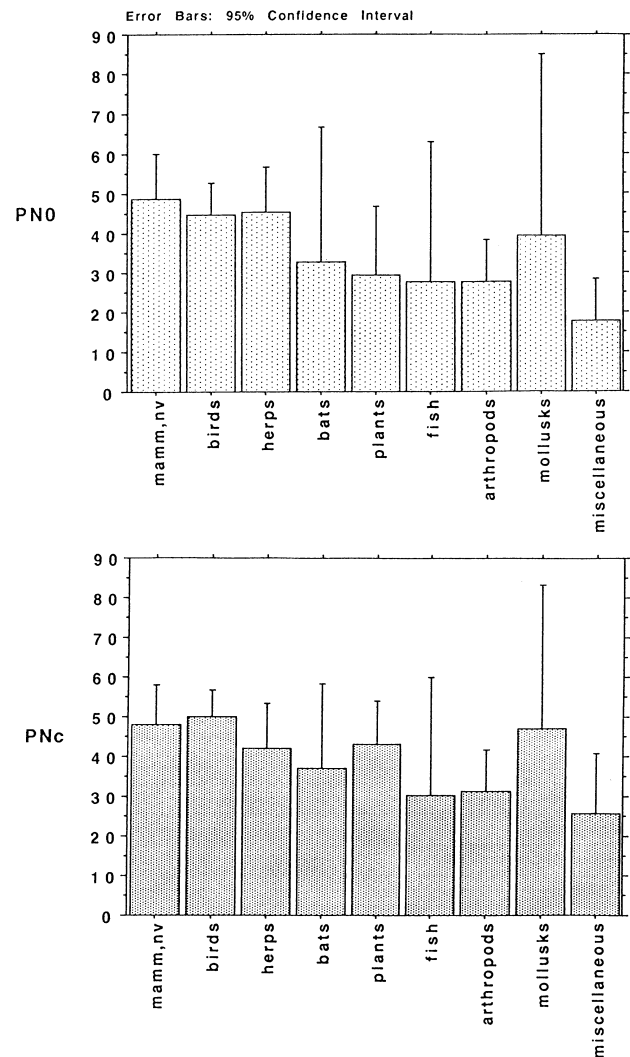


Fig. 4 Differences among major taxonomic groups of two measures of percent nestedness, PN0 and PNc (*mamm, nv* stands for non-flying land mammals). Both non-parametric Kruskal-Wallis tests and analyses of variance showed significant heterogeneity in nestedness among taxa for both metrics (all $P < 0.05$), but differences were weak. If experimental habitats are excluded from the analyses, there are no significant differences

for which data on more than one major taxonomic group is available. For this analysis, we restricted the islands included to those on which all groups were surveyed. Only PN0 and PNc were calculated. Comparisons of percent nestedness among taxa within these archipelagos yielded mixed results (Table 4).

Rankings of taxa were not consistent across archipelagos. For example, using PNc, birds ranked as more nested than non-flying mammals on three archipelagos and more nested than herpetofauna on six, while mammals ranked above birds twice and herpetofauna above birds twice. Ranking PN0 or PNc scores within archipelagos, mean ranks by taxon revealed no significant differences among taxa ($P > 0.05$). Restricting this analysis to sets of distributions on either landbridge or oceanic islands again uncovered no significant differences.

Table 4 Orderings of taxa by nestedness on archipelagos where two or more major taxa were sampled. When the difference in percent nested values is less than 10, \geq is used; when it is more than 30, \gg is shown. These symbols do not imply statistical significance. In parentheses following the archipelago name is the number of islands included. (Abbreviations: *M* non-flying mammals, *Ch* bats, *B* land and freshwater birds, *B1* sea birds, *H* amphibians and reptiles, *H1* amphibians, *H2* reptiles, *A1* ground beetles – Carabidae, *A2* butterflies, *A3* terrestrial isopods). No consistent order among taxa is apparent

Archipelago	Ranking by PNO	Ranking by PNc
<i>Oceanic islands</i>		
California Channel Is. (8)	$M \gg H \geq B \gg Ch$	$M \gg B > Ch \geq H$
Canary Is. (7)	$H \geq B$	$B > H$
Sea of Cortez (8)	$B > P > M \geq H$	$B \gg P > H \geq M$
Faeroe Is. (17)	$A1 > B$	$A1 \geq B$
French Frigate Shoals (8)	$P > B1$	$P > B1$
Tres Marias Is. (4)	$H \gg B$	$H \gg B$
<i>Landbridge islands and fragments</i>		
Australia wheat belt (23)	$M > H$	$M > H$
Bass Strait Is. (3)	undefined	$M \gg B \gg H$
British Channel Is. (5)	$H \gg M$	$H > M$
Sea of Cortez (8)	$B \geq M > H \geq P$	$B \gg M > H \geq P$
Great Basin mts. (13)	$M \geq B$	$B \geq M$
<i>Isolation status uncertain</i>		
Greater Antilles (4)	$Ch \geq A2 \gg B > A1$	$A2 \geq Ch > B > A1$
Lake Erie Is. (8)	$H2 > A3$	$H2 > A3$
Lake Michigan Is. (5)	$H2 > H1 > B \gg M$	$H1 \geq B > H2 \geq M$

Effect of “taxonomic scale”

Because species are more widely distributed than their subspecies, genera more widely than their species, and families more widely than their genera, higher taxa have lower levels of endemism and less idiosyncratic distributions than lower level taxa. Higher taxonomic categories are also less likely to exhibit distributional “checkerboards.” Because endemism, idiosyncratic distributions, and checkerboards all reduce nestedness, we expected that higher taxonomic levels would show higher nestedness than their constituent lower taxa.

We found that higher taxa do tend to be more nested. For six archipelagos we obtained data on both species and subspecies, and for another data on species and superspecies. For PNO, nestedness of the higher taxa was greater in five of six cases and undefined in one case ($P = 0.058$, one-tailed, Wilcoxon signed-rank test). Nestedness of the higher taxa was greater in six of seven cases when measured by PNc, and in all seven cases when measured by *T* (one-tailed $P = 0.014$ and 0.0078 , respectively). Results under *R1* were similar.

A further, anecdotal example is the presence-absence matrix for reef fish in different regions of the Pacific Ocean, in which the taxa studied were families (“pacific fish” in Table 1). This was one of the most strongly nested matrices in our analysis, with PNO = 62.5, PNc = 74.1, and *T* = 10.3, all more than 30 standard deviations away from their *R0* expected values.

Multi-factorial analyses

Many factors are acting on archipelagos that may affect nestedness in different ways, so we attempted to simultaneously account for up to three factors using multiple regression, ANOVA, or ANCOVA. Because of imbalances in the compilation, these analyses used various subsets of the entire dataset. None of our many multi-

factorial analyses shed additional light beyond the analyses already presented.

Discussion

Our survey of 279 empirical datasets has confirmed, as was suggested by Patterson (1990), Wright and Reeves (1992), and Cook and Quinn (1995), that nestedness is common in ecological communities of almost every kind examined. What are the physical, statistical, ecological, or evolutionary factors that produce nestedness?

Causes of nestedness

Nestedness is fundamentally *ordered composition* (Patterson 1984; Patterson and Atmar 1986). Any factor that favors the “assembly,” or disassembly (Mikkelsen 1993), of species communities from a *common pool* in a *consistent order* will produce nested structure. We believe there are several such mechanisms. Clarifying their relative importance is a major task facing future studies of nestedness. We see four causes of nestedness as potentially important: “passive sampling”, habitat nestedness, distance, and area.

Passive sampling

Nestedness can result if islands or sites are more likely to be occupied by species that are more abundant. Cutler (1994) has demonstrated this possibility by simulation, drawing individuals from lognormal species-abundance distributions to fill an archipelago of empty sites. If islands are considered “full” before acquiring all the species in the pool, nestedness results. The “random placement” model of Coleman (1981) is similar, but distributes individuals from a finite pool without re-

placement. The shared species pool is assumed in this example, and the consistency in ordering comes from the fact that the most abundant species is the most likely to be drawn, followed by the second most abundant, and so on.

In our study we did not collect data to test whether random sampling from abundance distributions could account for patterns of nestedness in nature. Of course, passive sampling is a process, not a pattern, and finding nested distributions consistent with passive sampling does not prove that the process created the pattern. Nevertheless, some investigation along these lines is needed. We suspect studies will show that random sampling from species-abundance distributions usually produces matrices that are more nested than real communities, because species are not passive but interact with their environments. Rare species may persist on islands or sites where their niche requirements are met, even if their statistical chance of being selected from an abundance distribution is low. Similarly, an abundant species may have a high probability of being drawn in passive sampling, but still faces the problem of making a living on-site. Therefore, sampling from species-abundance distributions should generally underestimate the incidence of rare species and overestimate that of abundant species, exaggerating nestedness.

Any real communities that are assembled in a way that resembles passive sampling from a common species pool we expect to be highly nested. For example, the bird assemblages on islands in Lake Pymatuning, western Pennsylvania, which Coleman et al. (1982) found to conform to their passive sampling model, are strongly nested (1978 data: $P_{Nc} = 72$, 1979 data: $P_{Nc} = 64$; both $P \ll 0.001$) (only P_{Nc} under R_0 can be calculated from the published data). Andrén (1994) found that one bird community that appeared to be a random sample of surrounding populations (southern Finland) was 6.5 SDs more nested than R_1 simulations, whereas another that did not reflect passive sampling (birds in Swedish bogs) was not significantly different from R_1 .

Cutler (1994) suggested that communities assembled by random sampling from abundance distributions would tend to have $U_p > U_a$, and since U_p is highly correlated with N_0 and U_a with N_1 , we also expect $N_0 > N_1$ for such matrices. Cutler observed that extinction-dominated systems, on the other hand, sometimes exhibit $U_a > U_p$. If general, such patterns would offer valuable clues to the mechanisms producing nested patterns. We found no evidence in our survey, however, for an effect of isolation history (oceanic, landbridge, fragment, non-isolated, immigration experiment) on the ratios U_a/U_p or N_1/N_0 , even when the effects of fill were accounted for (ANCOVAs of log-transformed ratios, both $P > 0.35$).

Although we and other authors have used a colonization scenario when discussing passive sampling, passive sampling does not specify a particular mechanism of community assembly, and other scenarios are conceiv-

able. The R_1 “null” model could be thought of as a passive sampling model – one that adjusts probabilities by incidence (number of sites occupied) rather than by size of the species’ population (number or density of individuals).

What will remain unanswered even after a nested pattern has been convincingly ascribed to passive sampling is, why are some species more abundant than others? This simple question is still a central issue in ecology.

Habitat nestedness

In contrast to the stochastic approach of the passive sampling hypothesis is the view that species occupy particular habitats and that the habitats themselves have nested distributions (Simberloff and Martin 1991; Cook and Quinn 1995). This is similar to D. Lack’s deterministic vision of island bird faunas (Lack 1976). Any species that uses the most common habitat is likely to be widespread, whereas species that are restricted to uncommon habitats will only occur at a few sites. If the habitats are nested, so will be the species.

One dataset in our compilation describes the presence or absence of six habitat types on six islands in the Bahamas (“bahabma” in Table 1). This matrix was not significantly nested under any null model ($P \geq 0.09$), but this a weak test of the idea that habitats may be nested. One of us has found that soil types can have significantly nested distributions (D.H. Wright, unpublished).

If habitat types are defined by vegetation, as they were in the “bahabma” dataset, this raises the question, why are vegetation types nested? Soil types also suffer somewhat from this circularity, since they are strongly influenced by vegetation. Ultimately, any mechanism relying on habitat nestedness must demonstrate nestedness of the underlying abiotic environment.

Distance

Darlington (1957) discussed how islands at different distances from a source of colonists could produce nested sets of species (see also Patterson and Atmar 1986, Fig. 4; Lomolino 1996). Good dispersers would be found in all communities, even the most isolated and depauperate, while the least dispersive species would be found only on the closest (and presumably most diverse) islands. The “rescue effect” (Brown and Kodric-Brown 1977) could augment a colonization-mediated distance effect by also lowering the extinction rates of dispersive species. Distance effects on nestedness should be strongest in archipelagos with wide variation in isolation distances, colonized by species with a range of dispersal abilities comparable to the range of distances provided by the archipelago.

Island area potentially complicates this picture. Most archipelagos have different sizes of islands, and even the

more dispersive species will be absent from nearby islands if they are sufficiently small, while less dispersive species may persist almost indefinitely on large far islands that they happen to reach, breaking the distance-nested pattern. Distance and area may also enhance one another in their effects on nestedness if islands closer to the source tend to be bigger. We expect the latter to be true of landbridge archipelagos more often than oceanic, which could confound our conclusions about differences in nestedness between landbridge and oceanic archipelagos. However, we saw little evidence of distance effects in our analyses. Studies more detailed than ours, assessing the relative magnitude of area and distance effects, will be needed to definitively answer such questions. Some preliminary studies along these lines are mentioned below.

Area

Nestedness can result from different needs for area by different species. Species with large area requirements will only be found on large (and presumably diverse) islands, while species that can survive even on the smallest islands are likely to be found everywhere. Consistent with this mechanism, we found that nestedness is positively correlated with the disparity in size between the largest and smallest islands sampled. We also found nestedness to be higher on average among landbridge islands and habitat fragments, where area effects mediated by extinction are presumed to be strong. Area effects on nestedness should be strongest in archipelagos with wide variation in island area, colonized by species with wide variation in area requirements.

Distance effects can muddle the nested patterns that would be created by consistent extinction ordering among species. Kadmon (1995) and Lomolino (1996) have recently explored assessing the relative importance of area and distance effects by comparing the nestedness of matrices with islands ranked by area versus ranked by distance. In 0 of 1 cases analyzed by Kadmon (1995) and 4 of 5 cases analyzed by Lomolino (1996) (plus one ambiguous case, depending on the distance measure used), area had the stronger effect. Distance effects should be minimal in archipelagos of sites that vary little in their distances from a source of colonists, and in communities of vagile species that can all easily overcome the distances involved.

We find it useful to think of the nestedness-causing factors listed above as *filters*: they screen species with particular characteristics from occurring on islands with particular characteristics. Passive sampling is an abundance filter; habitat nestedness is a habitat filter; and the distance and area filters act on differences among species in immigration and extinction tendencies (see Lomolino 1994 for a discussion of distance as a species filter). These filters are usually probabilistic rather than absolute in action. Under the right conditions, one or more filters produce a consistent ordering of probability of

occurrence among species that results in nested communities.

This “filter” perspective implies that nestedness is likely to depend significantly on the particular mix of species and sites that is examined (Patterson and Brown 1991). In our geographic and taxonomic analyses, patterns in nestedness were often overshadowed by variation from matrix to matrix. We believe that predictable sources of this variation in nestedness will be found, and, given that we found few strong predictors in gross spatial or taxonomic variables, we suggest characteristics of individual species and sites as a likely place to look. However, we do not agree with the contention of Simberloff and Martin (1991) that synthetic studies should be abandoned and each species understood one by one. Rather, we suggest that the variables that will prove useful in clarifying general patterns in nestedness will include ones that capture the diversity of species and sites, such as the variance of population density among species, or the range of habitat diversity among sites. A detailed analysis might use vectors as variables, composed of individual values for each of the species or each of the sites in the archipelago. This approach incorporates important information about differences among species and sites, while retaining a framework for understanding and analyzing the data.

Constraints

In addition to factors that cause nestedness, we emphasize that there are constraints that limit nestedness. These constraints have a common theme: homogeneity. Since nestedness reflects homogeneity of species communities, anything that injects heterogeneity reduces the potential for nestedness to form. Patterson and Brown (1991) listed three conditions they believed necessary for the development of nestedness: islands or sites must be ecologically comparable, species inhabiting these sites must have shared similar biogeographic histories, and species must be hierarchically ordered in terms of their niches. Their third condition serves to summarize factors that order the incidence of species (filters). The first two conditions correspond to homogeneity constraints – unless areas are inherently similar and have been exposed to a common pool of species, nestedness is not expected.

For example, differences in the homogeneity of the study areas may explain the differing results of two analyses of nestedness of mammals in North American parks. In a survey of Canadian parks, Glenn (1990) found that species compositions of mammals were not nested. Yet, in an analysis of mammals in Western North American parks, including some of the same parks studied by Glenn, Patterson (1990) showed significant nested structure. The two studies covered similar geographic scales, eliminating geographic scope as an explanation for the discrepancy. However, the parks studied by Patterson experienced a more homogeneous biogeographic history (predominantly cordilleran and

boreo-cordilleran fauna), whereas Glenn's survey included these as well as distinctive Laurentian and Hudsonian elements.

In general, heterogeneity in species distributions among sites can result from:

1. Evolution. Speciation, local adaptation, and changes in species ranges over evolutionary time give rise to insular endemics and biogeographic variation in species pools.

2. History. Evolution and community assembly are ongoing and partly stochastic processes, so that the community found at a given site is often influenced by past events. If sites or sources of colonists have different biogeographic histories or have undergone divergent processes of community development, heterogeneous species communities are likely to result.

3. Spatial heterogeneity in the environment, including patchiness. Differences in the environment from place to place can cause geographic variation in species pools, and variation in the kinds or mix of habitats found at different sites.

It might be possible to examine the effect of various kinds and degrees of heterogeneity on nestedness, though this is beyond the scope of our present study. Future studies that focus on causal factors rather than constraints may wish to control for variables related to heterogeneity: by design in experimental studies; or statistically in survey data, by entering these variables as covariates into the nestedness analysis so that their effects can be removed as much as possible before looking for patterns.

Effects of scale

The scale of examination can affect the degree of nestedness observed, either through effects on homogeneity, or by controlling the range of raw material upon which filtering mechanisms can act. For example, if islands vary little in their distance from a source of colonists, or if species vary little in vagility, then there is little opportunity for a distance filter to work. Environmental homogeneity may be greatest at some intermediate spatial scale. Expanding the spatial scale examined can introduce heterogeneity by including new habitats and species not found in a smaller area. Less obvious is that reducing the size of samples can make them more heterogeneous. Imagine a region where distinct habitats occur in patches with a typical size of 1 ha. Samples 1 km² in size will contain about 100 such patches, and due to the law of averages will be relatively similar in the habitats they contain. Samples 1 ha in size, however, will typically contain only one or two habitats. Consequently, the habitats contained, as well as any species specific to them, would vary greatly among the smaller samples.

Species also sample their environment at different scales. What appears patchy to a grasshopper may appear uniform to a gnu. Levins (1968) referred to this

concept as "grain." Because of their larger size, higher trophic position, and homeothermy, birds and mammals range over and perhaps do not sense a great deal of variation in the environment that is treated as grainy by a beetle that eats only one plant species, or a plant that experiences only the soil and microclimatic conditions within a radius of 2 m. Warm-blooded vertebrates may thus be prime candidates for nestedness because they are more likely to pass the constraint of perceiving their environment as homogeneous. Similarly, high vagility may promote nestedness, by homogenizing patches that are effectively "worlds apart" for sedentary taxa or endemics. High nestedness of large, relatively vagile taxa is also consistent with operation of a habitat filter, since such species would be better able to seek out isolated patches of their preferred habitat.

On the other hand, perhaps homogeneous species pools and ecologically similar sets of islands have been easier and more natural for ornithologists than for entomologists to circumscribe. Vertebrates in general are closer to our own size and habitat-distinguishing capabilities. Could it be that arthropods are often sampled either at too small a scale (resulting in high variance from site to site) or too large a scale (resulting in gradients in habitats, history, or source pools across sites) to exhibit strong nestedness?

The "economy" of species lists

As noted in the Introduction, species lists at a number of sites are produced in the course of many biological field studies. Species lists are inexpensive to produce relative to more focused, longer-term studies. They permit rapid assessments of species richness, endemism, and species associations, all of which are critical components of biological theory and conservation practice (Patterson 1991; Doak and Mills 1994). Although species lists typified ecological research during its descriptive phase, they have fallen out of favor. It may be surprising to learn that a minority of the works cited by Connor and McCoy (1979) in their survey of species-area relationships published species lists. We hope our survey demonstrates the importance of these associations.

Far more and better field work will be required to expand our analyses to other spatial scales and biological groups. Initiatives for biological surveys in the United States and other countries promise a wealth of new data. Yet a vast source of co-occurring species data is already collected, harbored in the world's natural history museums. Unlike scientific papers, scientific collections and their catalogues are continually updated nomenclaturally and geographically. Evolving systematic techniques allow ever more precise determinations of taxonomic and phylogenetic relationships. To make good use of existing and future biological survey data, computerized databases and well curated and maintained collections will be essential.

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