

## Nestedness of insular avifaunas: simple summary statistics masking complex species patterns

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Nestedness patterns have been recommended as a guide in designing refuges. The birds of three island archipelagoes and one set of mainland quadrats display strongly nested patterns, exactly as do most systems studied in this way. Nestedness may be expressed by several statistics, which are likely to be highly correlated, and may be viewed from either the community-wide or individual species vantagepoint. The latter is more informative. Individual species' nestedness scores can be similar even though the ecological forces generating them differ greatly. Nestedness scores based on island or site area are not directly comparable to those based on species richness. It is neither intuitively apparent nor empirically demonstrated that extinction would produce characteristically different nestedness scores than would colonization. Nestedness statistics are closely related to incidence functions in the ecological literature and to SLOSS comparisons in the conservation literature. None of these statistics is likely to provide much insight into refuge design.

### 1. Introduction

For a set of species distributed among a set of sites, a “nested” pattern exists if the species of every site consist of a subset of those species found on the next larger site. Most authors have followed Patterson and Atmar (1986) in construing “larger” to mean “containing more species,” although area of the site may also be an index of size. East and Williams (1984) argued that several studies of bird species distributed among a set of sites show a predictable sequence of species loss with area — in other words, nestedness with respect to area — but did not quantify the nestedness. Of course, number of species is often

highly correlated with area — this is the well-known species-area relationship, one of ecology's oldest “rules” (Connor and McCoy 1979). However, the species-area relationship often explains little of the variation in species richness among sites; Connor and McCoy (1979) found that log (area) explained only 44.8% of the variation in log (number of species), on average, for 100 published species-area relationships. Thus the degree of nestedness for a system need not be the same for sites ranked by species richness as for sites ranked by area.

Patterson and Atmar (1986), Patterson (1987, 1990), Blake (1991), Bolger et al. (1991), and Soulé (1991) suggest that strongly nested pat-

terns are important in designing refuges for species conservation. They argue that, to the degree that a system is nested, small sites will tend to have the same species as one another, and lack species found on larger sites. Thus, a single large site will likely contain more species than a collection of small sites with total summed area equal to that of the large site. In other words, nestedness patterns have resurrected the SLOSS (single-large-or-several-small) issue (Simberloff and Abele 1982) that Soulé and Simberloff (1986) believed should be buried as not useful in designing refuges.

Here we examine nestedness for land-birds of three island archipelagoes plus a set of mainland patches. We interpret the results in terms of the biology of the species. We discuss other nestedness studies, particularly of birds, and the relevance of nestedness to ecology in general and to conservation in particular. Finally, we relate nestedness to incidence functions and the SLOSS issue.

## 2. Statistics

Nestedness, where size of a site means its species richness, can be expressed in several ways. Patterson and Atmar (1986) used a simulation, later used also by Patterson (1987, 1990), Blake (1991), Bolger *et al.* (1991), and Patterson and Brown (1991). Consider a binary matrix with "1" representing presence of a species at a site and "0" representing its absence. First Patterson and Atmar (1986) arranged a matrix of  $r$  sites (rows) by  $s$  columns (species) in order of decreasing row sums (species richnesses of the sites). They then tabulated deviation from perfect nestedness by counting the numbers of 0's appearing above 1's in each column, and summing across columns. Each 0 appearing above a 1 represents a species missing from a larger site while being present on a smaller one. (In this paper we let rows represent species and columns represent sites, and make an analogous tabulation.) In order to assess how much more nested a system is than a "random system" of the same size, and to compare degrees of nestedness among different systems, Patterson and Atmar (1986) randomized the matrix in a particular way. They

placed ones and zeroes in the matrix randomly, subject to two constraints:

- 1) The number of species on each site (row sum) was fixed at the observed value.
- 2) The likelihood that a species would be chosen for each site was proportional to the number of sites it occupies in nature. Thus, total number of occurrences of each species was not constrained to equal the observed number.

Then, for each simulation run, they tallied the deviation from perfect nestedness just as for the observed data. The distribution of this statistic over many runs permitted estimates of mean and standard deviation, so the observed statistic could be transformed to number of standard deviations from the mean and its probability assessed from a normal distribution.

Ryti and Gilpin (1987) attempted to fit a logistic model for the entire matrix that predicts a set of probability values  $p_{ij}$  that the  $i^{\text{th}}$  species occurs on the  $j^{\text{th}}$  site. The model has three parameters, and also produces the statistic "explained variance". They suggested that one of the parameters and the explained variance are both suitable statistics for expressing nestedness. Perhaps because the parameters do not have intuitively obvious interpretations and the model is highly abstract, this method seems not to have been used subsequently.

Schoener and Schoener (1983) and Simberloff and Levin (1985) suggested using the Wilcoxon 2-sample rank-sum statistic (also known as the MannWhitney U-test) on the individual species of a set to assess nestedness. (Patterson [1984] took a similar approach but used area of a site to express its size.) The underlying reasoning for using this test is simple. For a matrix with rows representing species and columns representing sites, if sites are rank-ordered in terms of increasing number of species, and species rank-ordered in terms of increasing number of sites occupied, then a perfectly nested system would have each species represented by a row of "0's" followed by a row of "1's". The Wilcoxon statistic gives the null probability for deviation of the actual sequence for any species from a sequence in which the same numbers of "0's" and "1's" are randomly arranged. This approach allows one to observe which species conform (or do not

conform) to a nested pattern and to what degree (Simberloff and Levin 1985).

Many other statistics can be concocted to express nestedness. There is a fundamental difference in how they have been used between the Patterson-Atmar simulation statistic and Rytigilpin logistic statistic, which give a single value for the entire system, and the Wilcoxon statistic, which yields a value for each species. However, this difference is not inherent in the statistics. For example, for the simulation statistic, one can easily calculate the deviation statistic and expected deviation statistic for each species ("partial nestedness scores" of Blake [1991]) to see which species contribute strongly to a pattern. We perform this procedure below. Similarly, one can generate a single system-wide nestedness statistic from the Wilcoxon analysis, by assuming the species are independent (just as the simulation does), then combining the tail probabilities for the individual species (say, by Fisher's method of combining probabilities). Because these statistics, and others that might be suggested, would all vary approximately the same way with the above commonsensical definition of "nestedness" (or else they would not have been suggested), one would expect the species statistics to be highly correlated between different methods. We test this supposition for the simulation and Wilcoxon statistics on two data sets (1 and 3 below).

For the simulation, we wrote a Fortran program analogous to the BASIC program published by Patterson and Atmar (1986). To assess the significance of the Wilcoxon statistics, we used one-tailed tests because we had a prior hypothesis (see Discussion) and followed the procedures of Zar (1984). Scores were transformed to standard deviations from mean to use the normal approximation (Zar 1984). To compare how the two methods rank the different species in terms of conformation to the nestedness hypothesis, we used Spearman's rank correlation tests.

### 3. Data

Our data consisted of the following four sets: 1) 30 species on 41 islands covered by Pacific Northwest coastal forest (Appendix 1) in the Queen Charlotte Islands, British Columbia (original data; for de-

scription of islands, see Martin and Gaston, unpubl. manuscript); 2) 45 species on 35 isolated fragments (Appendix 2) of old coniferous taiga in southern Finland (Haila et al. 1987); 3) 62 species on 18 islands plus a mainland fragment covered by coniferous forest (Appendix 3) in the Sipoo archipelago, southern Finland (Martin 1983); 4) 62 species on 16 islands mainly covered by Mediterranean shrublands (Appendix 4) in the Maddalena archipelago off Corsica and Sardinia (Thibault et al. 1990). In all examples, the island area ranged from one to a few hundred hectares. The cited references provide details of the censusing procedures.

### 4. Results

For the Queen Charlotte Islands, the Wilcoxon statistics of the different species are given in Appendix 1. The more the data conform to the nestedness hypothesis, the more negative the score. In order for a species *not* to conform to the nestedness hypothesis, with  $P < 0.05$ , the score would have to be greater than 1.96. No species comes close. Only two have positive scores — Song Sparrow *Melospiza melodia* and Pacific Crow *Corvus caurinus* — but for neither would one reject the hypothesis of nestedness. The simulation shows virtually the same result. The entire matrix is more nested than the expectation for a random one ("random" defined as above) by 6.767 standard deviations. The species contributing most to the nested pattern in the simulation are those whose Wilcoxon statistics are most in accord with the nestedness hypothesis: the rank correlation was  $r_s = 0.907$ ,  $P_{2\text{-tailed}} \ll 0.001$ .

For the islands in the Sipoo archipelago, the result (Appendix 3) is very similar. By the Wilcoxon test, no species comes close to falsifying the nestedness hypothesis. Only two — Hobby *Falco subbuteo* and Golden Oriole *Oriolus oriolus* — have positive scores; both are found on only one island. By the simulation, the entire matrix is more nested than the random expectation by 8.525 standard deviations. Again the species contributing most to the nested pattern in the simulation are exactly those with the most extreme Wilcoxon statistics: a 2-tailed rank correlation was 0.870,  $P_{2\text{-tailed}} \ll 0.001$ .

We found similar results for the Finnish mainland site (Appendix 2) and the Maddalena

archipelago (Appendix 4). In neither data set do species have positive Wilcoxon scores. No species approach falsification of the nestedness hypothesis.

## 5. Discussion

### 5.1. The four data sets

The mainland and all three of our island systems show a strongly nested pattern, with no species falsifying the hypothesis. However, some individual species in each archipelago were distinctly less nested than others.

Martin and Gaston (unpubl. manuscript) used point counts to estimate intraspecific variation in densities of the Queen Charlotte Islands avifauna. They found that these birds can be roughly divided into three groups: a set of highly area-sensitive species, a set of species that specialize in edge habitat, and a set of species whose presence depends on specific habitat features (such as large or dead trees). Of course, because the presence of specific habitat features may be correlated with area, species in this latter group may appear to be area-sensitive, but the key is the habitat and not the area *per se*. The four species whose densities show a significantly negative Spearman rank correlation with area are among the species with the highest Wilcoxon scores; i. e. are least nested. These are Orange Crowned Warbler *Vermivora celata*, Song Sparrow, Fox Sparrow *Passerella iliaca*, and Rufous Hummingbird *Selasphorus rufus*. All four species have higher densities on the smaller islands because the habitat feature they use for foraging, reproducing, or shelter becomes proportionally more abundant as island area decreases. Features such as shrub cover, flowering shrubs, and open canopy are relatively more abundant on smaller islands partly because there is proportionally more edge (perimeter-to-area ratio increases), and edge promotes these features, and partly because browsing of the brushy undercover by black-tailed deer *Odocoileus hemionus* is less severe on smaller islands, which lack permanent deer populations. The Pacific Crow, which forages largely on the shoreline, also has higher densities on small islands. For such species more pairs per unit area occur in fragmented habitat.

Martin (1983) used identical methods in the Sipoo archipelago, and, although he viewed the overall pattern for the bird community as consisting of nested subsets of species, he also underscored the variation in response of individual species to changes in island area. Four species, Goldcrest *Regulus regulus*, Hooded Crow *Corvus corone*, Lesser Whitethroat *Sylvia curruca* and Greenish Warbler *Phylloscopus trochiloides*, all had higher densities on the islands than on the mainland. All of these species have Wilcoxon scores tending toward nestedness (Appendix 3), three of them strongly so. For the Hooded Crow and the Lesser Whitethroat, proportionally larger amount of shoreline for foraging or increased proportion of edge habitat were again the apparent reason. For the Greenish Warbler, a locally uncommon species, both habitat and geography may play a role. The species reaches the limits of its distributional range in southeastern Finland and the fact that it has higher densities on these Baltic islands than on the nearby mainland has already been noted by Tiainen (1980). No clear explanation was found for the increased density of the Goldcrest on islands. A fifth species, the Chaffinch *Fringilla coelebs*, present in all samples, is seen as nested by the simulations (see below). In fact, Martin (1983) has shown that this species has higher densities on the islands (cf. Nilsson 1977, Nilsson and Ebenman 1981, Ebenman and Nilsson 1982), a pattern that Martin and Lepart (1989) related to the positive effect the increase in proportion of edge habitat can have on passerine bird densities (cf. Haila et al. 1983). Finally, Martin and Lepart (1989) used the same methods and found, in a study of a larger sample of the Sipoo islands, a group of three species that had highest densities on small nearshore islands. They explained these densities by the presence on these islands of summer cottages or permanent human settlements providing rare habitat features such as nesting cavities in the form of nest boxes or foraging sites such as small clearings.

On the Finnish mainland, Haila et al. (1987) examined preferences of 20 species. They found that only two species prefer large patches, while six species prefer smaller patches. For four of the latter group, this preference seemed clearly linked to edge effect. The remaining species did not

show clear preferences with respect to patch size. So again a generally nested pattern masks a complex reaction of species in patch size.

The comparison of the Sipoo archipelago data with those of the Finnish mainland reveals another shortcoming of nestedness statistics. The Great Tit *Parus major* and the Tree Creeper *Certhia familiaris*, which appear in both study areas, show a marked shift toward greater nestedness (more negative Wilcoxon scores) in the island data set (−1.60 to −4.91 and −1.74 to −4.35, respectively). But the original data (Appendices 2 and 3) reveal contrasting underlying causes. For the Great Tit the range of patch or island area in which the species is observed is the same but the distribution sequence of 1's includes more 0's on the islands than on the mainland. The Tree Creeper is observed in the island data set only on the mainland reference area and on two of the three largest islands (and has a pattern conforming to the nested hypothesis). On the mainland (Appendix 2) it is observed in patches as small as 2 ha and with few 0's relative to 1's to the right of the first occurrence. The comparison of the distribution of other species common to the two data sets yields further biological insights. Six species — Chiffchaff *Phylloscopus collybita*, Spotted Flycatcher *Muscicapa striata*, Pied Flycatcher *Ficedula hypoleuca*, Crested Tit *Parus cristatus*, Willow Tit *P. montanus*, and Bullfinch *Pyrrhula pyrrhula* — are restricted to the mainland or the larger islands in the Sipoo archipelago, whereas they all occupy a large range of forest patch sizes on the mainland. All occur in patches of 2 ha or less. Such variation between island and mainland situations is independent of the nestedness scores. The latter take into account primarily the continuity of 1's in a sequence and not the range of the sequence. Comparisons like these can reveal the importance that contiguity of patches or dispersion of patches within a hostile habitat can have in determining the distribution of individual species.

Additional implications of the Maddalena archipelago data for nestedness relate to the fact that presence/absence data, though often the only data available, contain but a small fraction of the potentially important information. Here bird communities have been monitored for 3 to 10 years (Thibault et al. 1990), allowing an assess-

ment of the persistence of a given species on each island (Appendix 4). Thibault et al. (1990) discuss possible consequences of irregular breeding for conservation. What must be stressed here is that the analysis of occurrence sequences including such information provides insights on minimum areas required for persistent populations of particular species. The clearest example is that of Marmora's Warbler *Sylvia sarda*, which breeds regularly on islands down to about 100 ha. The species becomes irregular on smaller islands and is absent from islands of less than 10 ha. The nestedness statistics provide poor descriptions for other species in this archipelago. For example, the two species that score zero — Rock Dove *Columbia livia* and Little Ringed Plover *Charadrius dubius* — are extremely different distributionally. The Rock Dove is found across the entire range of island sizes. It is absent from only two of 16 islands and breeds constantly on 13 of the 14 islands on which it is found. The Little Ringed Plover, on the contrary, has been observed only once in the archipelago and bred only one year. Yet these two birds have the same nestedness score!

## 5.2. The appropriate null hypothesis

The three general explanations proposed for the species-area relationship (Connor and McCoy 1979) all predict that most species would be increasingly likely to be found on increasingly large sites. First, to the extent that species are tied to particular macro- or microhabitats, for most habitats, the probability that the habitat is present at a site would increase with size of the site. Second, to the extent that immigration-extinction dynamics determine whether a species persists on a site, a large site would contain, on average, a larger population of most species, thus a lower probability of (local) extinction at the site. So, on average, most species would be present a greater fraction of the time on the larger site. Third, if the species-area relationship is largely one of different sizes of collection apparatus collecting different numbers of individuals from a regional species pool, a large site might sample more species than a small site in much the same way that a large plankton net samples more spe-

cies than a small one does. Thus, we viewed the appropriate null hypothesis for each species to be distribution in accord with the nestedness hypothesis, and performed one-tailed tests.

### 5.3. Incidence and nestedness as functions of area and species richness

The degree to which a species conforms to the nestedness hypothesis is closely linked to the notion of incidence functions (Diamond 1975), which describe frequency of presence of species on islands in different size classes. Diamond (1975) took "size" to mean "number of species". Diamond (1978a,b, 1984) and most other workers (e.g. Samson 1980, Robbins et al. 1989, Hanski 1991, Taylor 1991) on incidence functions took "size" to mean "area". Diamond (1975) observed that, for most species, this frequency increased monotonically (though not linearly) with size, and sought explanations in minimum territory or area requirements, differing isolation of islands, and competitive exclusion among species. A small minority of species, termed "supertramps," showed the opposite pattern: increased frequency on islands with few species.

Gilpin and Diamond (1981), studying birds of the Bismarck archipelago, argued that similar incidence curves arise whether area or number of species is the abscissa. They even produced an equation for each species' incidence function based solely on areas of islands and assuming that extinction probability on any island is independent of which other species and how many other species are present (as did Diamond [1978b]). However, it is difficult to compare nestedness or incidence functions constructed on the basis of number of species with nestedness or incidence functions constructed on the basis of area because variance about species-area curves is often great, as noted above. The fact that the species-area relationship is usually significant and positive suggests that a nested system or a monotonic incidence function where area represents size should also be nested or monotonic where species richness represents size, and *vice-versa*. However, ranking sites by number of species rather than by area is likely to produce a more nested system-wide pattern. Consider a

matrix where rows represent sites and columns represent species. Because of the frequently large variance of species-area curves, if sites are ranked by decreasing area there will often be many situations where one row in a matrix will have substantially more 0's than a row below it. This pattern will tend to increase the number of 1's below 0's in any column, thus decreasing the nestedness statistic in the simulation.

### 5.4. Individual species or entire biotae?

To us, the informative outcome of a nestedness analysis is not likely to be whether or not a system as a whole is nested. Most are (Simberloff and Levin 1985, Patterson and Atmar 1986, Patterson 1987, 1990, Blake 1991, Bolger et al. 1991). Rather, it is which species do *not* conform to the expected pattern, and why they do not. This question is equivalent to one that has dominated the conservation literature but has yet to be answered satisfactorily for almost all species: What factors, exactly, cause extinction on small sites or allow persistence (Simberloff 1988)? An answer to this question would explain any aspect of a nestedness pattern, including deviations. Our results suggest there are different reasons why species violate the expectation, and different reasons why species conform to the expectation. These different reasons, in turn, have different conservation implications. Part of our ability to suggest reasons for a particular species' pattern comes from the fact that we have data not only on presence or absence of a species at a site, but information on species' abundances, habitats at different sites, habitat usage, and temporal regularity in occupying an island or mainland patch. Such information is critical in thoughtful refuge design. Whether nestedness statistics are useful seems doubtful to us, particularly in matters of refuge design (see below). However, because the system-wide statistic seems to us to provide even less insight than the individual species scores, if nestedness is to be used at all, we prefer to use the latter, and to use the Wilcoxon statistic to produce these because it is easily tabulated, aspects of its statistical properties are known, and significance levels can be assessed from readily accessible tables and do not require a simulation.

### 5.5. Constraints and an artifact of the nestedness simulation

The Patterson-Atmar simulation, as noted above, constrains sites to have the actual number of species they have in nature, but does not force species to occur on their observed numbers of sites. Patterson and Atmar (1986) did not discuss this convention, although Patterson and Brown (1991) suggested that the reason is that “simulations that employ both ‘row’ and ‘column’ constraints generate model assemblages that scarcely differ from their parent”. They did not define what they meant by “scarcely differ,” or what statistic would express how much two assemblages differ, so it is difficult to assess whether this contention is tautological and refers simply to the fact that all row and column sums are fixed, or to absence of some other kind of difference. They cite Gilpin and Diamond (1984) in connection with this assertion, but Gilpin and Diamond (1984), who used a convention similar to that of Patterson and Atmar (1986) to fill their random matrices, also did not define what constitutes matrix difference or lack thereof, or prove that matrices with identical row and column sums scarcely differ. In fact, for most sets of row and column sums, very many matrices are possible. These can be randomly sampled (Zaman and Simberloff, unpubl.) and the randomly drawn matrices do not appear, to our eyes, less different from one another than those produced by the unconstrained simulation.

Because species occurrences are not fixed, the simulation leads to a peculiar situation with respect to species found on all sites, such as the Chaffinch in the Sipoo archipelago. In fact, such an omnipresent species neither conforms to nor contradicts the nestedness hypothesis. In the simulation, it is among the species appearing to conform most strongly to the hypothesis. This artifact is doubtless because the species was not selected for some sites in some runs of the simulation, and these sites were predominantly those with few species. The data of Blake (1991) on birds in Illinois woodlots showed precisely the same effect. The partial nestedness scores for omnipresent species were among the largest contributors to the appearance of nestedness yielded by the system-wide statistic. As Patterson

(1990) notes, limitation on computer memory alone can preclude a simulation analysis of some systems. However if the simulation is used and a system-wide statistic is calculated it should omit the omnipresent species.

### 5.6. Extinction, colonization and conservation implications

Patterson and Atmar (1986) suggested that sets of sites whose biotae were shaped primarily by selective extinction — for example continental islands once part of a larger landmass but now isolated by rising sea levels — are typified by a highly nested pattern. On the other hand, sets of sites whose biotae are formed largely by occasional colonization — for example, distant oceanic islands that arose volcanically and were colonized by sporadic long-distance dispersal — should be far less nested. They argued that this pattern would arise because colonization is inherently less predictable than extinction. This prediction is not intuitively obvious, as witness the fact that Darlington (1957 p. 485) made exactly the opposite prediction: that colonization of empty islands should lead to a strongly nested pattern while extinction on a set of islands that all originally contained the same set of species would lead to an irregular less nested pattern.

The Patterson-Atmar interpretation has been adopted by Patterson (1987) for birds of land-bridge and oceanic islands of New Zealand and partially by Bolger et al. (1991) and Soulé (1991) who studied birds of isolated chapparral fragments as well as quadrats within continuous chapparral. Although it is quite likely that recently isolated fragments of formerly continuous habitat will suffer species loss, the conclusions of these particular studies may be questioned. Patterson (1987) found, by the Patterson-Atmar simulation, that 22 land-bridge islands had highly nested avifaunas while nine oceanic islands did not. However, extinctions have not actually been observed on these islands, and the hypothesized “relaxation” to a lower equilibrium on the land-bridge islands is exactly that — hypothesized. Nor is the assumption that all the land-bridge islands originally had the same species set necessarily valid. It is not inconceivable that many of

the absences of particular species from particular islands are due to habitat insufficiency, and that ongoing populations of these species never existed. Aside from habitat differences, the other common explanations for the species-area relationship also predict that species sets would differ somewhat for area reasons alone. Bolger et al. (1991) found a strongly nested pattern for five bird species in 36 patches, and a much less nested (not statistically significant) pattern for the same species in nine quadrats within continuous chaparral. They attributed the patch pattern to differential extinction and the mainland pattern mostly to differential extinction. Again there is no direct evidence for this extinction. Soulé et al. (1988) inferred extinction from the fact that, on average, the most recently fragmented patches have more species, all other things being equal, while Bolger et al. (1991) inferred it from the fact that patches less than about six ha had fewer species than similar sized quadrats. Both patterns are certainly consistent with a relaxation hypothesis but do not clinch it.

Nor does the nestedness *per se* observed in the two studies just mentioned strongly implicate extinction. Patterson (1987) conceded that differences in colonization ability could lead to a nested pattern, exactly as Darlington (1957) had suggested, so long as the ranges of isolation of the sites and of colonization abilities of the species were appropriate; he felt that this was not the case for birds of New Zealand islands. However Patterson (1990) found several examples of nestedness he felt were produced by colonization rather than selective extinction. Among these were landbirds of the islands off Baja California for which both land-bridge and oceanic islands show nested patterns, and birds of boreal mountaintop "islands" in the Great Basin. Again, the evidence for repeated differential colonization among the islands is indirect, Patterson (1990) citing Brown (1978) to the effect that "recurrent dispersal is demonstrably important in maintaining the distributions of non-resident species". Brown (1978) did not directly demonstrate recurrent dispersal; he inferred it from the facts that isolation does not contribute significantly to a stepwise regression of species number on area, elevation, and isolation and that species number is highly correlated with an index of habitat diversity.

The scenario of inevitable extinction of species in sites with decreased area is an old one (*e.g.* Diamond 1972, Terborgh 1974, Soulé et al. 1979). Probably there is often species loss in such situations, at least if area is greatly reduced. If reduction is sufficiently severe, extinction is inevitable. The key factor for each species is the minimum area required to maintain a viable population (Simberloff 1991). However, a distressingly large fraction of the published examples are based not on direct evidence of extinction but on statistical extrapolation underlain by procedural errors and questionable assumptions (Abele and Connor 1979, Faeth and Connor 1979, Boecklen and Gotelli 1984, Boecklen and Simberloff 1986). The ongoing experiment on forest patches of different size in Amazonia (Lovejoy et al. 1983) will have to be repeated in many systems and with many size ranges to yield a better sense of the amount and speed of extinction that might be expected for specific degrees of area reduction. Certainly the statistics of the species-area relationship will not capture all the biological mechanisms that might lead to increased extinction following fragmentation; for example, several empirical studies show increased predation on birds in a fragmented landscape (Simberloff 1991).

The fact that some small populations persist for very long times suggests that a useful focus for conservation is on the precise reasons why individual species persist or go extinct on individual sites (Simberloff 1988). Whether an entire system tends to be nested or not, or whether a group of small sites, on average, contains more species than a single large one, is far less important than the distributions of the individual species. As the above examples suggest, a careful consideration of the habitat requirements and minimum area and/or territory requirements of species of concern would be the surest way to make the most efficacious refuge acquisitions.

Neither the SLOSS literature nor that on nestedness (at least as a system-wide feature) is likely to be very useful in conservation. Both use single summary statistics to characterize an entire community and generate refuge design recommendations on the basis of that statistic, with the goal of maximizing the number of species in the refuge community. This is a naive view of



the goal of refuge design. Usually the goal is to save a particular species or group of them that would not otherwise be conserved (Simberloff 1988). To design refuges effectively to achieve such a goal, one must understand the ecology and distribution of individual species. A summary statistic for an entire community fails to provide such understanding. As we have shown above, even the nestedness scores of individual species are often ambiguous, because similar scores can reflect different ecological traits and very different scores can characterize species that have the same habitat relationships. Further, it is difficult to believe that an individual nestedness score would reveal a pattern of site or island occupancy (such as a preference for small islands) that would not already have been revealed by the data necessary to assess nestedness.

Aside from the relevance or irrelevance of nestedness for conservation, it is interesting that, in a general way, published studies of nestedness and SLOSS present a mixed message. As noted above, almost all systems are nested; most are highly nested. As observed at the outset by Patterson and Atmar (1986) nestedness suggests that single large sites will have more species than groups of small sites with equal total area. However, in virtually all the empirical studies of this matter, for both naturally and anthropogenically fragmented systems, groups of small sites have the larger number of species (Järvinen 1982, Simberloff and Abele 1982, Simberloff 1988, Quinn and Harrison 1988). But SLOSS and nestedness are simply two sides of the same coin. Of course, the empirical studies of the SLOSS issue did not focus on the same systems of sites and species as the nestedness studies have. However, the two literatures encompass the same taxa and a wide variety of geographic settings. If either topic is worth pursuing from a purely academic standpoint, it would be interesting to study the same system formally from both perspectives. It may also be of academic interest that, to the extent a system is nested, it is unlikely to be dominated by competitive exclusion (cf. Patterson and Brown 1991). Pairs of species that exclude one another would be found on alternate sites. Thus small sites would not all have the same species and it would be exceedingly unlikely that each site would have all the species of all sites

with fewer species. By the same token, to the extent that competitive exclusion operates, one might expect groups of small sites to contain more species than single large ones (though alternative hypotheses for the same observation are possible; cf. Simberloff and Abele [1982]). However, it is doubtful that either nestedness or SLOSS statistics would help to parse a set of biogeographic distributional data into fractions caused by interspecific competition, by habitat differences among sites, by non-competitive actions, and by other forces.

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Appendix 1. List of land-birds observed on each of the 41 islands sampled in the Queen Charlotte Islands. PA refers to the Patterson-Atmar score, z refers to Wilcoxon score.

Islands	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	z	PA													
<i>Haliaetus leucocephalus</i>				1			1				1	1	1				1		1	1			1				1	1		1	1		1	1		1	1	1	1	1	1	1	1	-2.32	0.58											
<i>Accipiter striatus</i>																																															-1.74	-0.92								
<i>Falco peregrinus</i>																			1																					1		1					-2.18	-0.91								
<i>Buteo jamaicensis</i>																																																-1.31	-0.54							
<i>Dendragapus obscurus</i>																																																	-2.71	-1.44						
<i>Sphyrapicus ruber</i>						1																																											-2.08	-0.43						
<i>Picoides villosus</i>																	1																																	-4.09	-1.85					
<i>Colaptes auratus</i>	1																																																-0.62	0.26						
<i>Selasphorus rufus</i>		1					1		1		1	1			1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-0.96	2.48						
<i>Empidonax diffilis</i>											1						1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-4.71	-2.41					
<i>Tachycineta bicolor</i>																																																				-1.70	-0.87			
<i>Corvus caurinus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.29	0.14					
<i>Corvus corax</i>																																																					-4.01	-1.98		
<i>Parus rufescens</i>	1		1	1	1	1					1						1			1		1				1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-3.07	-0.52					
<i>Sitta canadensis</i>																																																					-3.70	-1.93		
<i>Certhia familiaris</i>																																																					-4.78	-2.46		
<i>Troglodytes troglodytes</i>	1						1	1		1	1				1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-3.61	-2.06				
<i>Turdus migratorius</i>																																																						-2.40	-1.27	
<i>Ixoreus naevius</i>																																																					-4.16	-1.81		
<i>Catharus guttatus</i>	1						1			1		1					1			1	1	1					1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-3.91	-1.37				
<i>Catharus ustulatus</i>																																																						-2.27	-0.83	
<i>Regulus satrapa</i>																																																					-3.80	-1.71		
<i>Vermivora celata</i>		1		1	1						1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-1.46	0.84			
<i>Dendroica townsendii</i>	1			1	1						1	1					1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-4.52	-3.07		
<i>Wilsonia pusilla</i>																																																						-2.23	-1.20	
<i>Carduelis pinus</i>																																																						-4.84	-2.61	
<i>Loxia curvirostra</i>		1	1										1							1		1		1					1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-3.50	-0.98			
<i>Junco hyemalis</i>																																																							-3.08	-1.66
<i>Passerella iliaca</i>																																																							-0.89	2.21
<i>Melospiza melodia</i>		1	1	1	1																																																	0.96	4.11	

Island area (in ha): 1: 1.0; 2: 1.0; 3: 1.0; 4: 1.0; 5: 1.5; 6: 1.5; 7: 1.7; 8: 2.0; 9: 2.0; 10: 2.0; 11: 2.0; 12: 2.9; 13: 3.5; 14: 3.8; 15: 4.5; 16: 5.0; 17: 5.3; 18: 5.6; 19: 5.6; 20: 5.6; 21: 6.0; 22: 6.0; 23: 8.2; 24: 9.6; 25: 10.0; 26: 10.0; 27: 10.4; 28: 12.0; 29: 13.3; 30: 16.0; 31: 20.0; 32: 20.5; 33: 21.0; 34: 40.0; 35: 40.0; 36: 44.0; 37: 48.0; 38: 249.0; 39: 400.0; 40: 1500.0; 41: 35000.0.

Appendix 2. List of land-bird species observed in 35 forest patches in Southern Finland (after Haila et al. 1987); z refers to Wilcoxon score.

Mainland patches	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	z					
<i>Accipiter gentilis</i>																																					1	-1.74			
<i>Accipiter nisus</i>																																							1	-1.44	
<i>Bonasa bonasia</i>															1				1																				1	-2.85	
<i>Tetrao tetrix</i>															1																								1	-2.05	
<i>Tetrao urogallus</i>																1																							1	-2.47	
<i>Scolopax rusticola</i>																																							1	-1.82	
<i>Tringa ochropus</i>																																							1	-2.60	
<i>Columba palumbus</i>																																							1	-2.55	
<i>Cuculus canorus</i>																																							1	-3.38	
<i>Aegolius funereus</i>																																							1	-1.74	
<i>Strix uralensis</i>																																							1	-1.29	
<i>Apus apus</i>																																							1	-2.72	
<i>Jynx torquilla</i>																																							1	-1.89	
<i>Picooides tridactylus</i>																																								1	-2.51
<i>Dendrocopos major</i>																																								1	-4.03
<i>Dryocopus martius</i>																																								1	-3.06
<i>Anthus trivialis</i>				1				1							1																									1	-3.73
<i>Motacilla alba</i>																																								1	-1.54
<i>Prunella modularis</i>																																								1	-3.07
<i>Erithacus rubecula</i>																																								1	-4.70
<i>Phoenicurus phoenicurus</i>																																								1	-3.03
<i>Turdus philomelos</i>																																								1	-4.38
<i>Turdus iliacus</i>																																								1	-3.45
<i>Turdus viscivorus</i>																																								1	-2.62
<i>Sylvia curruca</i>																																								1	-0.84
<i>Sylvia borin</i>																																								1	-2.83
<i>Phylloscopus sibilatrix</i>																																								1	-1.90
<i>Phylloscopus collybita</i>																																								1	-3.73
<i>Phylloscopus trochilus</i>																																								1	-3.13
<i>Regulus regulus</i>																																								1	-3.27
<i>Muscicapa striata</i>																																								1	-3.29
<i>Ficedula hypoleuca</i>																																								1	-3.62
<i>Parus montanus</i>																																								1	-4.22
<i>Parus cristatus</i>																																								1	-3.83
<i>Parus major</i>																																								1	-4.91
<i>Certhia familiaris</i>																																								1	-4.35
<i>Garrulus glandarius</i>																																								1	-2.32
<i>Corvus corax</i>																																								1	-1.74
<i>Fringilla coelebs</i>																																								1	-2.35
<i>Fringilla montifringilla</i>																																								1	-3.02
<i>Carduelis spinus</i>																																								1	-1.74
<i>Loxia curvirostra</i>																																								1	-3.05
<i>Pyrrhula pyrrhula</i>																																								1	-4.76
<i>Emberiza citrinella</i>																																								1	-1.44
<i>Emberiza rustica</i>																																								1	-2.54

Patch area (in ha): 1: 0.4; 2: 0.5; 3: 0.7; 4: 0.8; 5: 0.8; 6: 0.9; 7: 1.2; 8: 1.5; 9: 1.6; 10: 1.6; 11: 2.0; 12: 2.0; 13: 2.1; 14: 2.1; 15: 2.2; 16: 2.3; 17: 2.8; 18: 3.0; 19: 3.1; 20: 3.2; 21: 3.4; 22: 3.6; 23: 4.4; 24: 4.4; 25: 5.4; 26: 8.4; 27: 11.5; 28: 11.7; 29: 12.8; 30: 14.5; 31: 15.2; 32: 15.8; 33: 49.2; 34: 55.8; 35: 101.0.

Appendix 3. Land-bird species composition of 18 islands and one mainland reference area in the Sipoo archipelago of Southern Finland (after Martin 1983), PA refers to the Patterson-Atmar score; z refers to the Wilcoxon score; in. refers to an introduced species.

Islands	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	z	PA		
<i>Pandion haliaetus</i>																		1	1	-2.33	-1.09		
<i>Pernis apivorus</i>																			1	-1.74	-0.78		
<i>Falco subbuteo</i>	1																			1.19	2.10		
<i>Bonasa bonasia</i>																			1	-1.74	-0.89		
<i>Tetrao tetrix</i>																		1	1	1	-2.75	-1.24	
<i>Tetrao urogallus</i>																			1	-1.74	-0.77		
<i>Phasianus colchicus</i> in.																			1	-1.74	-0.75		
<i>Scolopax rusticola</i>							1												1	1	-1.18	-0.49	
<i>Columba palumbus</i>																			1	1	-2.33	-0.97	
<i>Cuculus canorus</i>																			1	1	-2.19	-0.84	
<i>Caprimulgus europaeus</i>																				1	-1.74	-0.86	
<i>Apus apus</i>														1						1	-1.80	-0.92	
<i>Picus canus</i>																			1	1	-2.33	-1.13	
<i>Dendrocopos major</i>																				1	-1.74	-0.79	
<i>Dryocopus martius</i>															1					1	-1.93	-0.62	
<i>Jynx torquilla</i>														1						1	-1.80	-0.43	
<i>Delichon urbica</i>																			1	1	-2.06	-0.71	
<i>Hirundo rustica</i>							1					1		1					1	1	-2.00	0.29	
<i>Motacilla alba</i>	1	1	1		1			1				1	1	1					1	1	-0.74	2.42	
<i>Anthus trivialis</i>													1		1	1				1	1	-2.83	-0.90
<i>Lanius collurio</i>																				1	-1.74	-0.75	
<i>Troglodytes troglodytes</i>												1							1	1	-2.51	-0.76	
<i>Prunella modularis</i>																		1	1	1	-3.06	-1.30	
<i>Turdus pilaris</i>																			1	1	-2.75	-1.26	
<i>Turdus philomelos</i>											1			1				1	1	1	-3.30	-1.28	
<i>Turdus merula</i>								1	1	1	1	1	1	1	1	1	1	1	1	1	-3.60	-2.11	
<i>Turdus iliacus</i>												1	1	1	1	1	1	1	1	1	-3.52	-1.77	
<i>Erithacus rubecula</i>								1				1	1	1	1	1	1	1	1	1	-2.98	-0.85	
<i>Oenanthe oenanthe</i>			1					1							1				1	1	-1.48	0.70	
<i>Phoenicurus phoenicurus</i>												1								1	-1.66	-0.33	
<i>Acrocephalus arundinaceus</i>																			1		-1.56	-0.55	
<i>Acrocephalus scirpaceus</i>											1								1		-1.40	-0.11	
<i>Hippolais icterina</i>																			1	1	-2.33	-0.99	
<i>Sylvia atricapilla</i>																				1	-2.33	-0.94	
<i>Sylvia borin</i>													1				1	1	1	1	-3.01	-1.07	
<i>Sylvia curruca</i>						1		1	1		1		1		1	1	1	1	1	1	-2.91	-0.84	
<i>Sylvia communis</i>														1	1					1	-1.96	-0.30	
<i>Phylloscopus sibilatrix</i>															1	1	1	1	1	1	-3.29	-1.52	
<i>Phylloscopus collybita</i>																					-1.74	-0.80	
<i>Phylloscopus trochilus</i>					1	1	1			1	1	1	1	1	1	1	1	1	1	1	-2.64	-0.92	
<i>Phylloscopus trochiloides</i>																			1	1	-2.30	-0.76	
<i>Regulus regulus</i>		1	1		1	1					1	1	1	1	1	1	1	1	1	1	-2.29	-0.44	
<i>Muscicapa striata</i>															1				1	1	-2.96	-1.22	
<i>Ficedula hypoleuca</i>																1	1	1	1	1	-2.52	-1.02	
<i>Parus major</i>		1				1		1	1	1	1	1			1			1	1	1	-1.60	-0.99	
<i>Parus caeruleus</i>								1			1									1	-1.46	-0.26	
<i>Parus ater</i>																					-1.74	-0.79	
<i>Parus cristatus</i>																				1	1	-2.33	-1.15
<i>Parus montanus</i>																	1			1	-2.63	-1.06	
<i>Certhia familiaris</i>																				1	-1.74	-0.73	
<i>Emberiza citrinella</i>																					-1.74	-0.74	
<i>Carduelis chloris</i>																			1	1	-1.80	-0.50	
<i>Carduelis spinus</i>		1		1				1			1	1	1	1	1	1	1	1	1	1	-2.60	-1.18	
<i>Pyrrhula pyrrhula</i>																				1	-2.20	-0.84	
<i>Loxia curvirostra</i>											1	1									-0.33	1.11	
<i>Fringilla coelebs</i>		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-1.72		
<i>Sturnus vulgaris</i>											1			1						1	-1.95	-0.11	
<i>Oriolus oriolus</i>											1										0.92	0.88	
<i>Corvus corone</i>				1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	-1.55	-0.14	
<i>Corvus corax</i>																				1	-1.56	-0.61	
<i>Pica pica</i>																				1	-1.74	-0.77	
<i>Garrulus glandarius</i>																				1	1	-2.33	-1.05

Island area (in ha): 1: 1.1; 2: 2.1; 3: 2.2; 4: 3.1; 5: 3.5; 6: 5.8; 7: 6.0; 8: 6.1; 9: 6.5; 10: 11.4; 11: 13.0; 12: 14.5; 13: 16.1; 14: 17.5; 15: 28.7; 16: 40.5; 17: 104.5; 18: 233.0; 19 (mainland reference area): 670.

Appendix 4. Breeding bird species of the small islands of the Maddalena archipelago. 1 = proved breeder, p = possible breeder, i = irregular breeder, e = extinct, in = introduced, \* refers to irregular breeder everywhere (after Thibault et al. 1990); z refers to the Wilcoxon score.

Islands	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	z		
<i>Tachybaptus ruficollis</i>									e			1			1	1	-2.62		
<i>Anas platyrhynchos</i>									e			i				1	-1.96		
<i>Accipiter nisus</i> *													p		1		-1.83		
<i>Buteo buteo</i>										1			1	1	1		-2.85		
<i>Falco tinnunculus</i> *												p	p	1	1	1	-3.20		
<i>Falco peregrinus</i>														1	p	1	-2.50		
<i>Alectoris barbara</i>																1	-1.63		
<i>Coturnix coturnix</i>																p	-1.63		
<i>Phasianus colchicus</i> in.									e			1					-1.20		
<i>Rallus aquaticus</i>																p	-1.63		
<i>Gallinula chloropus</i>									i			1			1	1	-2.62		
<i>Fulica atra</i> *									e			p			p		-1.96		
<i>Charadrius dubius</i> *									i								0.00		
<i>Columba livia</i>	1	1	1		1	1	1	1	1	1	p	1	1		1	1	0.00		
<i>Streptopelia turtur</i>														1			-0.98		
<i>Cuculus canorus</i>														1			-0.98		
<i>Tyto alba</i>														1	1	1	-2.50		
<i>Athene noctua</i> *												p			1	1	-2.70		
<i>Caprimulgus europaeus</i>												1	1	1	1	1	-3.20		
<i>Apus apus</i>														1	p		-1.83		
<i>Apus pallidus</i>	1	1			1	1	1	1	1	1	p		p	1	1	1	-0.81		
<i>Apus melba</i>										p	p		p	1	1		-2.11		
<i>Upupa epops</i>																p	-1.63		
<i>Lullula arborea</i> *										p		p			1	1	-2.74		
<i>Ptyonoprogne rupestris</i>															p	1	-2.31		
<i>Anthus campestris</i> *								p	p	p		p			1	1	-2.56		
<i>Motacilla alba</i>														p			-0.98		
<i>Troglodytes troglodytes</i>						i				1	p	1	1	1	1	1	-3.11		
<i>Eriothacus rubecula</i>													1		1		-1.83		
<i>Saxicola torquata</i>						i		i	i	i	p	1	1		1	1	-2.82		
<i>Monticola solitarius</i>		p				1		1	1	1	p	1	1	1	1	1	-3.07		
<i>Luscinia megarhynchos</i>														p			-0.98		
<i>Turdus merula</i>										1	p	1	1		1	1	-2.94		
<i>Cettia cetti</i> *												p				1	-2.07		
<i>Cisticola juncidis</i>															p	1	-2.31		
<i>Sylvia atricapilla</i>																1	-1.63		
<i>Sylvia sarda</i>								i	i	1	p	1	1	1	1	1	-3.40		
<i>Sylvia undata</i>				p						p	1	p	1	1	1	1	-3.09		
<i>Sylvia conspicillata</i>															1		-0.98		
<i>Sylvia cantillans</i>														1	1	1	-2.10		
<i>Sylvia melanocephala</i>				p			p	1	1	1	p	1	1	1	1	1	-2.85		
<i>Regulus ignicapillus</i>														1			-0.98		
<i>Muscicapa striata</i>						p		1	1	1	p	1	1	1	1	1	-3.32		
<i>Parus major</i>											i	p	1	1		1	-2.94		
<i>Parus caeruleus</i>																1	-1.63		
<i>Lanius collurio</i>														1			-0.98		
<i>Lanius senator</i>															1	1	-2.31		
<i>Pica pica</i> in.																1	-1.63		
<i>Corvus monedula</i>																1	-1.63		
<i>Corvus corone</i> *													p			1	p	-2.38	
<i>Corvus corax</i>														1	1	1	-2.66		
<i>Passer domesticus</i>														1	i	1	1	-3.32	
<i>Passer montanus</i>																1	-1.63		
<i>Petronia petronia</i> *											p			1		1	-1.89		
<i>Fringilla coelebs</i>													p			1	-2.07		
<i>Serinus serinus</i>																1	-1.63		
<i>Serinus corsicana</i>															1		-0.98		
<i>Carduelis chloris</i>				p						i	i	p	p	1	1	1	p	-3.11	
<i>Carduelis carduelis</i>														i	p	1	1	1	-3.22
<i>Carduelis cannabina</i>														i	p	i	1	1	-3.40
<i>Emberiza cirius</i>														1	1	1	1	-2.93	
<i>Miliaria calandrat</i>															p	1	1	-2.50	

Island area (in ha): 1: 1.4; 2: 2.3; 3: 4.7; 4: 6.2; 5: 9.7; 6: 11; 7: 11.6; 8: 66; 9: 112; 10: 154; 11: 164; 12: 205; 13: 420; 14: 1950; 15: 1960; 16: 5100; (one island of 4.9 ha had no breeding land bird species and has been excluded from the matrix).