



Nestedness, niche metrics and temporal dynamics of a metacommunity in a dynamic natural model system

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Prediction of extinction and colonization rates for whole species assemblages emerges as an urgent task for ecology. We hypothesized that nestedness of species assemblage reflects differential ability of species to occupy sites and of sites to support species. If correct, a nested ordering of species and sites should condense long-term dynamics of metacommunities. To test this we characterized the differential ability of species to use habitat (niche position and niche breadth) using eight surveys of invertebrate communities inhabiting 49 tropical rock pools. We examined temporal consistency of the nested rank of species and pools, and related them to species and pool characteristics to infer temporal dynamics of species composition. Invertebrate assemblages in the rock-pools were significantly nested and species ranks were generally preserved over time. By contrast, pool ranks were usually conserved between adjacent years only but their similarity declined with time separating surveys. The nested species-by-pool matrix of the first survey served as a benchmark to assess individual species and local community changed in subsequent years. As hypothesized, benchmark cells with high state occupancy probability had low extinction rates in subsequent years. Moreover, species high in the nested matrix (also with high regional occupancy probability) were better survivors and colonizers relative to species that ranked low. The year-to-year dynamics were similar. Species with non-marginal niche position retained high ranks in the matrix. Yet, niche position predicted only colonization rate of species. Niche breadth and species' nested ranking, extinction risk, or ability to colonize a pool showed no relationship. Counter to the expectation, pool ranks did not predict species extinction and colonization rates. Apparently, even in dynamic systems, regional nested pattern remains consistent and the underlying extinction and colonization dynamics appear to be largely determined by the hierarchical order among species and much less by that among sites.

Ecologists seek to elucidate the spatio-temporal dynamics of species and communities and the mechanisms involved. One answer to this challenge relies on analyzing temporal variation in the distribution of species in the context of the richness and composition of communities at the same locations (Leibold et al. 2004, Azeria et al. 2006, Werner et al. 2007). Specifically, several general models have been developed to explain spatio-temporal dynamics of species and communities in response to environmental conditions. Niche-based models elucidate how niche characteristics (niche breadth and marginality) of species affect their response to disturbance and regional rarity and commonness (Brown 1984, 1995, Hanski et al. 1993, Vázquez and Simberloff 2002). Metacommunity theory analyzes the interplay between species competitive and dispersal abilities and environmental conditions to infer the local and regional diversity dynamics (Shurin and Allen 2001, Leibold et al. 2004). On a different scale, the equilibrium theory of island biogeography (MacArthur and Wilson 1967) asks how the dynamic relationship between isolation-dependent immigration and area-dependent extinction rates determines community species richness. The analysis of nestedness

pattern, i.e. species compositions where species-poor biotas are predictable subsets of those of species-rich biotas (Patterson and Atmar 1986), may provide a more comprehensive framework in that it addresses patterns of both species richness and composition. As such, it has been widely applied to infer complex spatial and temporal dynamics of ecological communities (Hansson 1998, Wright et al. 1998, Whittaker 2000, Fleishman and Mac Nally 2002, Maron et al. 2004, Azeria et al. 2006, Srinivasan et al. 2007).

Commonly, nestedness has been examined in a single snapshot in time but its temporal stability (Hadly and Maurer 2001, Maron et al. 2004, Azeria et al. 2006) and, more importantly, its suitability for addressing temporal dynamics of assemblages has not been explored (but see Maron et al. 2004, Azeria et al. 2006). Does the ability of nestedness to predict extinction–colonization dynamics of species and communities vary systematically as the period between reference time and subsequent times increase? How do the nested ranks of species and sites vary?

We concur with others (Hadly and Maurer 1991, Atmar and Patterson 1993, Doak and Mills 1994, Worthen 1996,

Patterson and Atmar 2000, Zavaleta and Hulvey 2004, Azeria et al. 2006, Srinivasan et al. 2007; but see Maron et al. 2004) that nestedness of species assemblages at a given time has the potential to predict the probability and sequence of local and regional species extinctions and colonizations. This proposition relies on the premise that “Nestedness is fundamentally a type of hierarchical organization” (Patterson and Atmar 2000, p. 20) caused by a hierarchy (ranking) of ecological relationship among species, among sites, or both (Patterson and Brown 1991, Patterson and Atmar 2000). Species differ in their dispersal ability, range of resources they use (niche width and marginality), tolerance to stress, competitive ability, and others. Differences in these traits are likely to translate into a gradient of vulnerability of species to extinction or into ability to colonize a habitat, and hence, differences in their distribution across space (Cutler 1991, Hanski et al. 1993, Kodric-Brown and Brown 1993, Brown 1995, Kolasa et al. 1996, Patterson and Atmar 2000, Vázquez and Simberloff 2002, Bruno et al. 2003, Azeria et al. 2006). Similarly, differences in suitability among sites such as in resource availability, habitat diversity, stability, accessibility and other attributes affect the probability of extinction or colonization by a species and, consequently, determine the number and composition of species inhabiting the sites (Patterson and Brown 1991, Patterson and Atmar 2000).

In a nested species-by-site matrix, the nested rank of species should reflect these hierarchical relationships in species attributes, and, consequently their order of vulnerability to extinction and ability to colonize (Patterson and Brown 1991, Patterson and Atmar 2000, Zavaleta and Hulvey 2004, Srinivasan et al. 2007). Similarly, the nested ranks of sites should indicate hierarchy of suitability among site, e.g. the ecological attributes of low ranking sites are expected to be subsets of attributes of sites occupying higher position on the ordering axis (Hylander et al. 2005). If correct, extinction–colonization dynamics of communities and species (populations) should be predictably influenced by the ordering of sites, ordering of species and the species–site combinations (i.e. cell state occupancy probability) in the maximally nested matrix (Worthen 1996, Patterson and Atmar 2000). For example, extinction risk is expected to be lower for cells with high state occupancy probabilities in top-left of the nested matrix, i.e. most ubiquitous species in the most hospitable habitat, and vice versa (Fig. 1). Earlier studies offer partial (Azeria et al. 2006) or no (Maron et al. 2004) support to these predictions.

These expected relationships between the nested rank order of the species and sites and turnover dynamics, however, also assume that the ecological traits that underpin the respective nested ranks remain relatively stable over time. Species characteristics that determine relative vulnerability to extinction (and colonization) often appear to be conservative over ecological and evolutionary time scales (McKinney 1997, Russell et al. 1998, Peterson et al. 1999; but see Losos et al. 2003). Site characteristics that determine their suitability, however, may be less conservative, particularly in dynamic ecosystems (Scheffer et al. 2001, Maron et al. 2005). As the applicability of the nestedness analysis hinges on the assumption that the ecological traits that underpin the nested ranks of species and sites are stable in time, this assumption needs validation over short and long

time scales (Patterson 1990, Simberloff and Martin 1991, Patterson and Atmar 2000, Azeria et al. 2006). Furthermore, the relative role of differences among species may not be the same as that among sites. For example, in systems that lack hierarchical relationships among site-attributes (e.g. in areas of low habitat diversity or highly variable areas) nestedness could arise solely as a consequence of variation in ecological characteristics among species. This may be the case with nestedness over geological time scales (Hadly and Maurer 2001, also see Patterson 1990).

In this study we examine nestedness in repeated survey data of invertebrates in 49 rock pool microcosms collected over 12 years (Romanuk and Kolasa 2002). These data permit us to quantify compositional changes, to evaluate stability of the nested ranks, and to evaluate the ability of the nested ranks to predict the local and regional status of a species over short and long time scales. The study system also offers an opportunity to evaluate application of nestedness for biodiversity conservation because (a) data span tens to hundreds of generations for most of the constituent species (Kolasa and Romanuk 2005) – a comparably long time scale that conservation objectives espouse, and (b) variable physical environment induces dynamic responses in community structure at local and regional scales (Kolasa et al. 1996, Therriault and Kolasa 2000) – a characteristic of many ecological systems. Indeed, microcosms as general model systems make significant contribution to ecological and conservation studies (Srivastava et al. 2004).

This study has three major objectives. First, it examines whether the regional invertebrate assemblage is nested and stable over many (50–500) generations of the constituent species. Second it aims to examine whether pool characteristics (morphometric and physical measures) and species characteristics (niche position and breadth on a habitat attributes gradient) are related to nestedness and how consistent these relationships are over time. Third, it examines whether the short and long term extinction–colonization dynamics in these communities can be predicted by patterns of nestedness (state occupancy probabilities, nested rank of pools and species) and species niche attributes (niche breadth and marginality). Evaluation of these aspects using long-term data set in multiple snapshots will provide a better understanding about spatio-temporal dynamics of species and communities than that derived from a single snapshot.

Material and methods

Study system

This study was based on extensive data of aquatic meio- and micro-invertebrates inhabiting a system of 49 rock pool microcosms located within a radius of 30 m and monitored every winter from 1989/90 to 2002, at the Discovery Bay Marine Laboratory, on the north coast of Jamaica (Therriault and Kolasa 2000, Kolasa and Romanuk 2005). The rock pools are small (20–60 cm along longer axis), situated 1–235 cm (mean ~76 cm) above the high tide level, with the tide rarely exceeding 30 cm range. Therefore, most pools are filled by rainfall but seven pools receive also

seawater by direct inflows or occasional wave splash. The invertebrate communities are composed of fresh, marine, and brackish water invertebrates, with a particular species mix dependent on the salinity regime of a pool. Pools are 5–55 cm (mean ~28 cm) deep, and some of the pools, especially the shallow ones and during summer, experience frequent desiccation (Therriault and Kolasa 2001). The invertebrate communities are thus subject to frequent changes of physio-chemical conditions, and consequently are characterized by significant turnover dynamics (Romanuk and Kolasa 2002).

Invertebrates were collected by filtering 500 ml samples of pool water through 63 μ m net, and by preserving them in 50–70% ethanol. Before collecting the samples, pools were thoroughly stirred to dislodge invertebrates from the pool sides and to homogenize their distribution. Over 70 species have been identified and counted over the sampling years. Many species are rare and occur only occasionally. To reduce sampling error and biases due to these rare species, we restricted our study to 41 species that occurred at least in 1% of the samples. Details of the study: the map, sampling protocol, physio-chemical conditions of the pools, and biotic composition are described elsewhere (Kolasa and Romanuk 2005).

Analysis

Testing for nestedness

We used the Nestedness temperature calculator, NTC, (Atmar and Patterson 1995) and the Binary matrix nestedness temperature calculator, BINMATNEST, (Rodríguez-Gironés and Santamaría 2006) to examine nestedness of invertebrates in the rock pools for each sample year individually. Both methods pack the matrix elements, by reorganizing entire rows (sites) and columns (species), until nestedness is maximized and unexpectedness is minimized. Both NTC and BINMATNEST are similar in principle, however, the BINMATNEST uses a genetic algorithm and appears to be more efficient than NTC in reordering rows and columns so as to maximize nestedness, i.e. to give minimum matrix temperature (Rodríguez-Gironés and Santamaría 2006). For primary analyses we used NTC but we used the BINMATNEST to check if any differences in the nested rank order of species and sites led to different interpretations of observed patterns.

The degree of nestedness of species or sites is represented by ‘temperature’ (T) – a measure of deviation of the observation distribution data from a perfect nestedness (Atmar and Patterson 1993, Patterson and Atmar 2000). In a perfectly nested matrix, all presences will be in the upper-left corner of a theoretical isocline, that is also called extinction curve, and the value of the metric will be zero degrees. The isocline is a curvature of maximum packing given the species-by-site matrix size and fills and does not depend on the structure of the data (Atmar and Patterson 1993). The matrix temperature is higher for systems that are stochastic and less predictable, which is represented by a matrix with many unexpected absences above the isocline (holes) and unexpected presences (outliers) below the line. The statistical significance of the nestedness of a given matrix is examined by comparing the observed matrix temperature with that of null communities generated by randomizing the original matrix in Monte-Carlo simula-

tions. According to the default null model of NTC, each cell in the presence/absence matrix has equal probability of being occupied, i.e. there is no row and column constraint (herein referred to as NM1). Only the total number of presences from the original matrix is maintained in the randomized matrices. The significance of the nestedness for each of the distribution year was compared against the temperature of 1000 null communities generated under NM1. However, the default null model may not be always appropriate as it may detect nestedness as an artifact of passive sampling (Jonsson 2001, see also Wright et al. 1998, Fischer and Lindenmayer 2002, Azeria 2004, Rodríguez-Gironés and Santamaría 2006, Ulrich and Gotelli 2007). Therefore, following the suggestion by Jonsson (2001), see also Fischer and Lindenmayer 2002, we have considered an additional null model – the RANDNEST null model (NM2) in which null communities are generated such that the probability of selecting a certain species is proportional to its actual frequency (incidence-constrained) and all sites are randomly filled. We generated 100 random matrices by independent swapping in EcoSim 7 (Gotelli and Entsminger 2006) and, then, manually loaded the matrices into the Nestedness temperature calculator. The BINMATNEST provides three alternative null models. Following recommendation of Rodríguez-Gironés and Santamaría (2006), we employed a randomization algorithm (‘third’ null model, NM3) where the probability of each cell in the species-by-site matrix being occupied is the average of its row and column occupancy probabilities. The significance of nestedness for each observed distribution was determined by comparing its temperature against that of 1000 null communities generated by randomizing the actual data under NM1, NM2 and NM3.

The NTC also calculates state occupancy probability, SOP, of each cell, i.e. the species-site combination as a function of its position in the maximally nested species-by-site matrix (Fig. 1). The state probability is highest (97–100%) for cells at the upper-left corner of the matrix, i.e. the most common species in the most species-rich site, and decreases gradually (0–5%) for the cells at the bottom-right most corner, i.e. the most rare species in the most species-poor site. The isocline separates cells in the range 0–50% from those in the range 50–100%. Thus, the temperature metric treats state occupancy probability of cells (species and site combinations) and their unexpectedness differently, such that the ‘unexpectedness’ (presence below the isocline and absence above isocline) of cells distant from the isocline is weighted more than that of cells near the isocline. The logic underlying the temperature metric (unequal extinction and colonization probabilities within a matrix) has never been tested rigorously prior to our study. This logic also represents fundamental core difference between the temperature method and other nestedness metrics (reviewed by Wright et al. 1998, Ulrich and Gotelli 2007) which treat species (unexpectedness) presences and presences across sites as equal.

Recently, Ulrich and Gotelli (2007) criticized the temperature method because the metric value depends on matrix size (see also Wright et al. 1998, Greve and Chown 2006, Rodríguez-Gironés and Santamaría 2006). However, such size-dependence, if any, only limits the use of the metric value to compare degree of nestedness across

different assemblages (for suggestions on how to adjust tests for matrix size see Greve and Chown 2006), and does not affect the test itself as the comparison is made against random matrices of same size and fill (Greve and Chown 2006, Rodríguez-Gironés and Santamaría 2006). In addition, the algorithm implemented in BINMATNEST is designed to alleviate such size-dependence (Rodríguez-Gironés and Santamaría 2006). In our study, although comparison of nestedness metric value across years was not the focus, doing so will have little effect as the comparison was done on data matrices with similar size (same number of pools and similar number of species).

Ulrich and Gotelli (2007) also recommended the use of fixed-fixed (FF) null model (i.e. a null model that holds both row and column total fixed) to test nestedness because it is less vulnerable to type I errors. The debate of null model choice has yet to arrive at a resolution (for discussions of null model choices see Jackson et al. 1992, Wright et al. 1998, Jonsson 2001, Sfenthourakis et al. 2005, Rodríguez-Gironé and Santamaría 2006, Moore and Swihart 2007). However, the FF null model has its own significant drawbacks. Using FF null model has a high risk of committing type II error, i.e. of falsely accepting a null hypothesis that assemblages are not nested (risk as high as 98%; Table 2 in Ulrich and Gotelli 2007). Also, in the FF model the properties of sites and species might be implicitly incorporated into the null communities (Jackson et al. 1992, Jonsson 2001, Sfenthourakis et al. 2005, Moore and Swihart 2007).

Testing for temporal consistency and causal factors of nestedness

In a nested matrix, the order of sites suggests a predictable order of species 'absence' (or expectation of absence) from species-rich to species-poor sites, due to extinction or failure of colonization. Similarly, species are ordered from common to rare reflecting large to small ecological range of species, respectively. The order of sites and species, however, is not strictly based on richness (of sites) and incidence (of species) and it is not uncommon for reversal of ranks to occur over time, for example a given site may be ranked higher than another site with more species. To examine the temporal consistency of the orderings, we performed Spearman's rank correlation of the nested rank orders among species and among pools for each pair of years, and calculated the respective mean values of correlation coefficients (including 95% CI) across years.

The NTC and BINMATNEST do not make any assumptions as to causal factors re-organizing sites and species. Such factors however can be inferred by relating the nested rank of sites and species to attributes of sites or species (Patterson and Atmar 2000, Azeria 2004). To test the hypothesis that assemblages are nested as a result of hierarchical ordering among pool-characteristics, we ran Spearman's rank correlation between the pool ranks in each year against ranked physical attributes of pools (depth from lip, surface area, volume, elevation, temperature, salinity, pH, and oxygen concentration) for respective years. Because collinearities exist among these variables (Therriault and Kolasa 2000), we computed partial correlations to separate out the independent effect of these variables on nestedness.

Similarly, to examine if variation in species-traits explains nestedness, we correlated (Spearman's rank correlation) species ecological range against species nested rank. Estimation of species ecological range is difficult because it is a product of a complex interaction among local biological and physical factors as well as regional dynamics, such as dispersal (Pulliam 2000). First, we used the species incidence as surrogate for species' ecological range (sensu Kolasa et al. 1996). However, the nested rank order of species is not independent of species incidence and, therefore, the correlation coefficient between the two would be inflated. To overcome this problem, we computed two niche parameters: the niche position and breadth of species to represent 'ecological range', using a multivariate technique called the outlying mean index (OMI) analysis (Dolédec et al. 2000) in the 'niche' analysis module as implemented in the software ADE-4 (Thioulouse et al. 1997). Niche position is represented by OMI index, which is a measure of the deviations of the mean habitat conditions used by a species from the mean habitat conditions of a 'hypothetical' species that is uniformly distributed across all habitat conditions over the sampling area. Accordingly, species that have low OMI values have non-marginal niche, i.e. occur in typical habitats in a region and are expected to be regionally common while species that have high OMI values should be rare. Thus, species' rarity and commonness is contingent on the extent to which their habitat is regionally widespread (habitat availability hypothesis, Hanski et al. 1993). Similarly, niche breadth is represented by 'species tolerance', which is a measure of the dispersion from the mean of the environmental variables used by a species. Species that have a wide niche breadth tolerate wider range of environmental conditions, and thus will be regionally common as opposed to species with narrow niches (Dolédec et al. 2000). Niche breadth (also position) is not necessarily correlated with species incidence (Gregory and Gaston 2000). This is because niche metrics depend not only species' presence-absence patterns (the extent to which they are widespread), but also on species' abundance pattern and in relation to environmental gradient. For example, a species might be widespread, yet have a small value of niche breadth if those sites where it occurred have a low site to site environmental variability or if it is abundant in one site and occurs rare on the other sites. Conversely, a moderately common species may have a wider niche breadth because the sites it occurred have a higher site-to-site variation and because it has a more even distribution across sites.

OMI analysis has several merits compared to other ordinations because it can describe both linear and unimodal response curves of species along environmental gradients simultaneously. Other traditional ordination methods assume either unimodal (as in canonical correspondence analysis CCA) or linear (as in redundancy analysis RDA) response of species to environmental gradients (Dolédec et al. 2000). We based OMI analysis on species abundance data, on four morphometric variables, and on four physical variables that were measured in eight sampling years along with the faunal collections. We transformed the species abundance into $\log_{10}(x+1)$ to reduce the effect of dominant species and reduce skewness in species distributions. The long term data series enabled

us to calculate species niche position and breadth across the 'full' environmental gradients a species may be exposed to. This alleviated the problems of apparent niche constraints that may have arisen due to species dispersal limitations and/or local extinctions, i.e. species may be absent from an otherwise suitable habitat (Kadmon and Pulliam 1993, Pulliam 2000), and from constraints of low variation of environmental variables in some years (Kolasa and Romanuk 2005). On the other hand, in such long term observation series, species may also occur more often in pools outside the environmental range where they can actually persist indefinitely, including sink habitats where their presence depend on dispersal of individuals from source habitats (Pulliam 1988). Although our approach to niche position and breadth does not account for idiosyncrasies and constraints due to biotic interactions and species' dispersal abilities, it represents an improvement over earlier practices.

Testing predictability of extinction-colonization patterns

To evaluate the ability of nested ranks to predict dynamics of extinctions and colonizations over short and long time scales, we compared the community and occupancy changes in each of the following sampling years in relation to distribution data collected in December 1989 and January 1990 (hereinafter benchmark). We define extinction as the absence of a species (from a given pool) that was present in the benchmark census, and colonization as the presence of a species originally missing from that census. We assessed extinction and colonization rates by comparing multiple snapshots (seven sampling years, 1991–2002). We also determined whether the rates varied systematically with time elapsed since the benchmark year (1989/90). This approach enabled us to mimic how the community structure might vary in 10, 100 or 1000 generations. Admittedly, this definition of extinction and colonization rate does not consider all the extinction and (re)colonization events that occurred between the year of interest and the benchmark year. A species that appears extinct in 2002 could have recolonized and gone extinct several times in between the consecutive census dates. To make sure that the temporal window of sampling does not introduce major bias, we also examined the year-to-year turnover dynamics in relation to nested pattern (nested rank of species and pools) in the preceding year, e.g. turnover in 1991 vs nestedness in 1989/90, turnover in 1992 vs nestedness in year 1991 and so on.

We calculated the extinction and colonization rates on per pool and per species basis. Because the measures of extinction and colonization rates we chose depend on the number of species that were present and absent (for pools) and number of pools a species was present in or absent from (for species), we used proportions (Crooks et al. 2001, Azeria et al. 2006). To normalize the results for different numbers of species in each pool, we calculated relative extinctions as: $E_{\text{pool}} = S_{\text{ext}}/S_{\text{BM}}$ (for each pool) and $E_{\text{spp}} = P_{\text{ext}}/P_{\text{BM}}$ (for each species) and relative colonizations as $C_{\text{pool}} = S_{\text{col}}/(S_{\text{total}} - S_{\text{BM}})$ (for each pool) and $C_{\text{spp}} = P_{\text{col}}/(P_{\text{total}} - P_{\text{BM}})$ (for each species). S_{BM} and P_{BM} denote the species richness of a pool and incidence of a species, respectively, in the benchmark census period (or preceding

year in the year-to-year turnover dynamics analysis). S_{ext} and S_{col} , denote the number of species that went locally extinct and colonized a pool, respectively, from the benchmark year to a particular sampling year. P_{ext} and P_{col} are the number of pools from which a given species went locally extinct or colonized, respectively, from the benchmark year to another sampling year. S_{total} is the total species pool and P_{total} is the total number of pools examined (49). The total number of species that met the analysis criteria (see above) across years was 41 species, of which 35 species were recorded in the benchmark year. This limited our tests to those 35 species. Relative colonization of a pool (C_{pool}) was estimated by using 35 and 41 species as potential number of colonizer species. The differences between results based on these two estimates were insignificant; probably because six species were rarely recorded and, when they were, they did colonize or went extinct from a pool in isolation from the other five species of this group. Therefore, we present only the calculations that were based on the 35 species present in the benchmark year. For the species-based extinction and colonization estimates, the number of pools is adjusted, as necessary, to reflect the number of samples collected for a given annual survey as some pools were not sampled due to dry conditions or a sample was damaged.

To test whether species nestedness scores predict extinction and colonization probabilities, we counted first the number of cells in each state probability range in the nested matrix of the benchmark data and then examined if they persisted or went extinct in each of the following years (1991 to 2002). Similarly, we examined whether empty cells in the nested matrix of the benchmark remained vacant or became occupied in each of the following years. We expected low extinction rates in cells with high state probabilities (cells in the above-left of the matrix-common species in the most hospitable pools), and high extinction rates in the lower-right part (rare species in most inhospitable pools). By analogy, colonization should be higher for cells in the upper-left of the nested matrix than for cells in the lower-right part. We used regression analysis to test the relationship between state occupancy probabilities (SOP) of the occupied cells and proportion of extinctions in each probability range (0–10, 10–20 ... 95–100) (Maron et al. 2004, Azeria et al. 2006). However, the NTC does not provide the SOP of the vacant cells, and it was difficult to extrapolate it from neighboring occupied cells, especially in the lower-right part of the matrix. Therefore, we simply compared the total colonization instances observed in cells above to that below the extinction curve using chi-square test. For the sake of completeness, we carried out a similar comparison for the sum of extinctions in cells above (with 50–100% SOP) and below (0–50%) the isocline (Fig. 1).

Because SOP depends on both species and site characteristics, a rare species in a species-rich site may have as low a SOP as a common species in a species-poor site. Therefore, to separate relative effects of species and pools on turnover dynamics, we calculated Spearman's rank correlation coefficient between the nested ranks of species and sites in the benchmark year and estimated extinction and colonization rates at species- and pool-level, respectively, across years. To reiterate, the SOP of a cell in a maximally nested matrix represents occurrence probability of a species

at a given site (Fig. 1). We averaged these values across sites (rows) to represent the regional occupancy probability of a species (ROP_{Spp}). Following this logic, we computed regional occupancy probability of a species (ROP_{Spp}) in the benchmark distribution, and examined its correlation with the species-based extinction and colonization rates in the following years. Finally, we examined the relationship between species niche metrics (breadth and position) with species-based extinction and colonization rates. The statistical analyses were performed using STATSTICA (StatSoft 2003) and MINITAB (Minitab 2005) software packages.

Results

Regional nestedness

Whether we used NTC and BINMATNEST the aquatic invertebrate assemblages in the rock-pools were significantly nested in all years, even when compared against the constrained null model (Fig. 1, Table 1). Although both methods show relatively high matrix temperature in 1991

and 2002, there was no systematic increase or decrease in nestedness with time. Such fluctuations may arise because of minor sensitivity of the temperature metric to differences in matrix size and fill (Rodríguez-Gironés and Santamaría 2006). Overall, the matrix temperatures obtained by both methods were highly correlated across years ($r=0.944$), albeit the temperatures obtained by NTC were slightly higher (slope 1.02) than those of BINMATNEST. Moreover, nested rank orders of species and pools obtained by both methods were very similar across years and thus indicated equivalence of the two algorithms.

The nested ranks of species were strongly correlated among years (Fig. 2; mean \pm SD = 0.746 ± 0.085 [NTC]; 0.749 ± 0.078 [BINMATNEST]) and did not appear to change with the length of time interval among years (NTC: $r = -0.0331$; BINMATNEST: $r = -0.101$, $p > 0.5$). Thus, the species retained consistently similar nested ranks over short and long time scales. Although ordering of pools in the nested matrix was usually conserved between adjacent years, the correlation values of the nested ranks among years were generally low (Fig. 2; mean \pm SD = 0.408 ± 0.145 [NTC]; mean \pm SD = 0.437 ± 0.138 [BINMATNEST]),

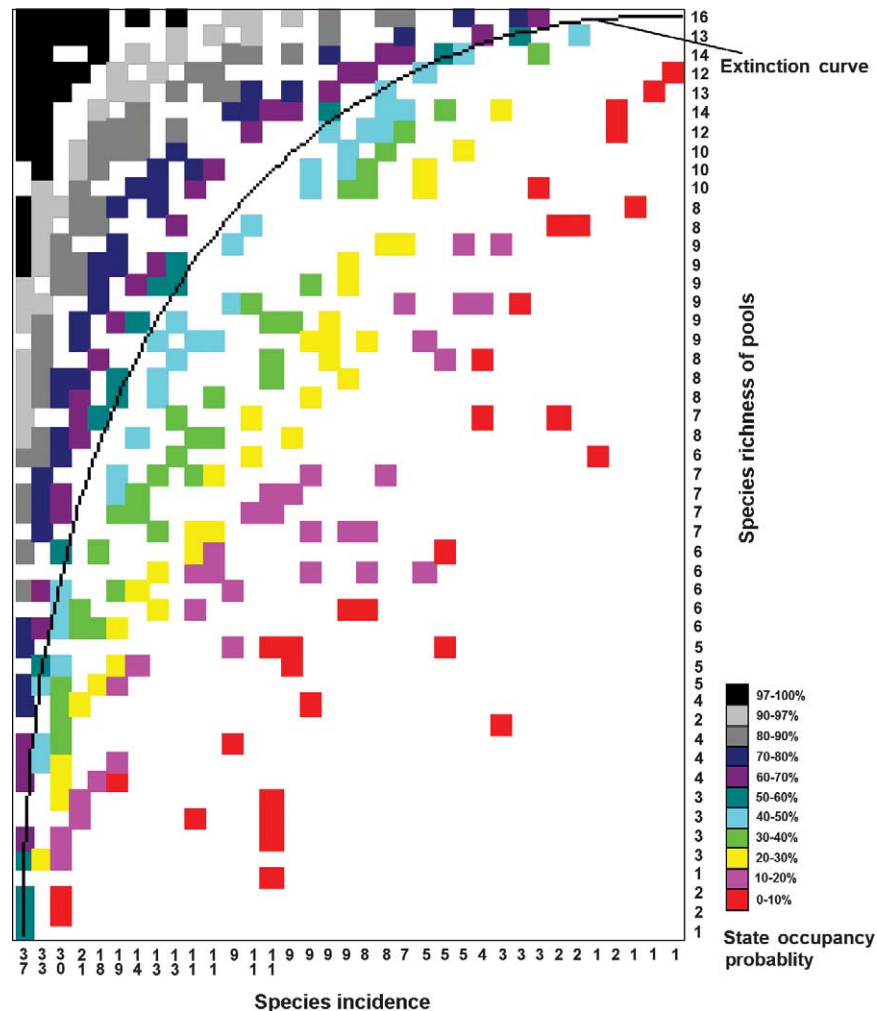


Figure 1. Maximally nested matrix and state occupancy probability of aquatic invertebrates (columns) in rock pools (rows) generated by Nestedness temperature calculator for the benchmark census (1989/90). The curve is the isocline, also called extinction curve. Extinction is expected to be lower for cells with high state occupancy probabilities (cells in the above-left part of the matrix) than for cells in the lower-right part and vice versa. The opposite is expected for colonization.

Table 1. Nestedness analysis of aquatic invertebrate communities in rock pools for each year by Nested temperature calculator (NTC) and Binary matrix nestedness temperature calculator (BINMATNEST). T_{OBS} is the observed temperature and T_{NM1} , T_{NM2} and $T_{NM3} \pm SD$ is the mean ± 1 SD temperature of the null communities generated under null model 1, 2 and 3, respectively.

Year	NTC			BINMATNEST		
	T_{OBS}	$T_{NM1} \pm SD$	$T_{NM2} \pm SD$	T_{OBS}	$T_{NM1} \pm SD$	$T_{NM3} \pm SD$
1989/90	17.81	56.38 \pm 3.16***	34.01 \pm 2.71**	14.34	48.35 \pm 3.15***	35.68 \pm 2.99***
1991	19.11	53.88 \pm 4***	31.98 \pm 2.83**	16.02	45.91 \pm 3.63***	34.35 \pm 3.56***
1992	25.29	54.14 \pm 3.34***	32.71 \pm 2.83**	20.13	46.37 \pm 3.21***	34.60 \pm 3.10***
1993	17.67	51.48 \pm 3.89***	28.76 \pm 2.91**	12.90	41.90 \pm 3.46***	29.02 \pm 3.11***
1997	17.08	52.19 \pm 3.66***	31.66 \pm 2.71**	13.69	43.27 \pm 3.37***	32.35 \pm 3.19***
1998	21.89	48.77 \pm 3.25***	30.71 \pm 2.58**	16.14	40.80 \pm 3.17***	31.32 \pm 3.00***
2001	21.86	52.48 \pm 3.67***	33.52 \pm 2.67**	18.09	43.74 \pm 3.47***	34.04 \pm 3.26***
2002	23.44	57.44 \pm 3.34***	33.84 \pm 2.42**	20.17	48.96 \pm 3.09**	37.26 \pm 3.16***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

and pools tended to diverge with time between censuses ($r = -0.393$ [NTC]; $r = -0.417$; $p < 0.05$ [BINMATNEST]). Thus, in contrast to species, the variation in the way pools are ranked in the nested matrix increased with time.

Determinants of nestedness

As expected, the nested rank order of species was negatively correlated with species incidence across all years (mean $r \pm SD = -0.979 \pm 0.024$ [NTC]; mean $r \pm SD = -0.951 \pm 0.027$ [BINMATNEST]) meaning that consistency of species occurrence in a site and broad distribution are strongly linked. Because the nested rank order of species is

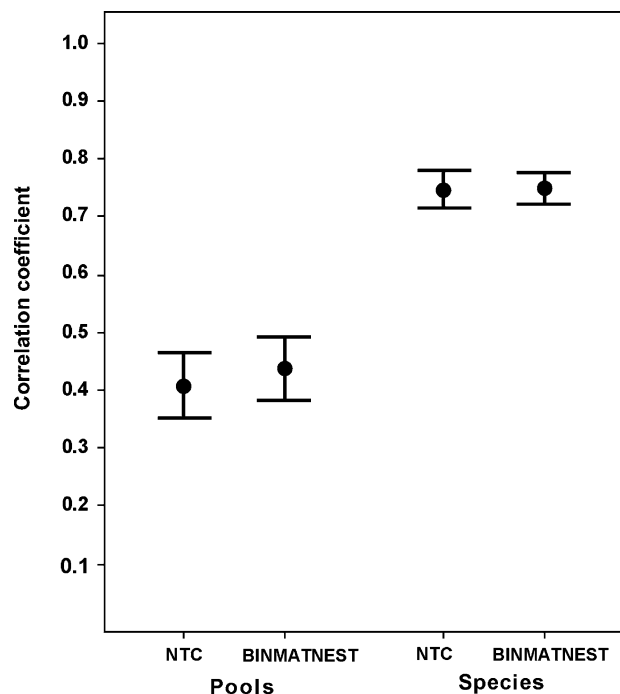


Figure 2. Stability of nested rank orderings of pools and species across years: the correlation values (mean $\pm 2SD$) among nested rank order pools and among nested rank of species across sampling years. The nested rank orderings of species were highly stable whereas that of pools was more variable, although still significantly correlated. The yearly species by pools matrices were maximally packed by NTC and BINMATNEST.

highly dependent on species incidence, we also used ecological attributes of species that are, in principle, independent of their incidence: the niche position and niche breadth (Supplementary material Appendix 1). Across all years, niche position was positively correlated with nested rank of species as packed by NTC (Fig. 3), i.e. species that utilize typical environmental condition (low OMI value or less marginal) ranked high in the nested matrix and vice versa. In contrast, niche breadth was unrelated to nested rank of species, except in 2001 and marginally in 1997, in which, as expected, there was negative correlation (Fig. 3). Species with wide niches occupy a wider environmental range and, consequently, were expected to be more common and rank higher in the nested matrix. Similarly, species incidence in each of the years was significantly correlated with niche position (mean $r \pm SD$: $r = -0.55 \pm 0.08$; $p < 0.05$, and marginally in 1991), but not with niche breadth (mean $\pm SD$: $r = 0.155 \pm 0.11$; $p > 0.10$) of species. Likewise, nested ranks of species produced by BINMATNEST showed the same relationships – they were positively correlated with supplementary material niche position, but unrelated to niche breadth (Supplementary material Appendix 2). Intriguingly, there was a negative correlation between species' nested rank and the residual tolerance index, which is the amount of variation in niche-characteristics of species that was not explained by the measured environmental conditions (Supplementary material Appendix 2). It is thus possible that niche parameters we computed were inadequate to explain regional distribution of species, particularly that of high ranking (common) species (residual tolerance: mean $\pm SD = 60\% \pm 17.8$; Supplementary material Appendix 1).

The relationship between nested rank of pools and morphometric and physical measures over time was inconsistent (Table 2). However, when marginally significant, the pattern of relationships was as anticipated. Ordering of pools in the nested matrix was negatively correlated with pool cavity depth and/or surface area: pools that ranked high in the nested matrix were characteristically deeper and/or had larger surface area than those ranking low (Table 2). Some interesting patterns also emerged: pools at low elevation above the sea ranked high in the nested matrix. Significant or nearly significant relationships between nested rank of pools and physical variables were infrequent. Pools generally ranked low in the matrix if their mean

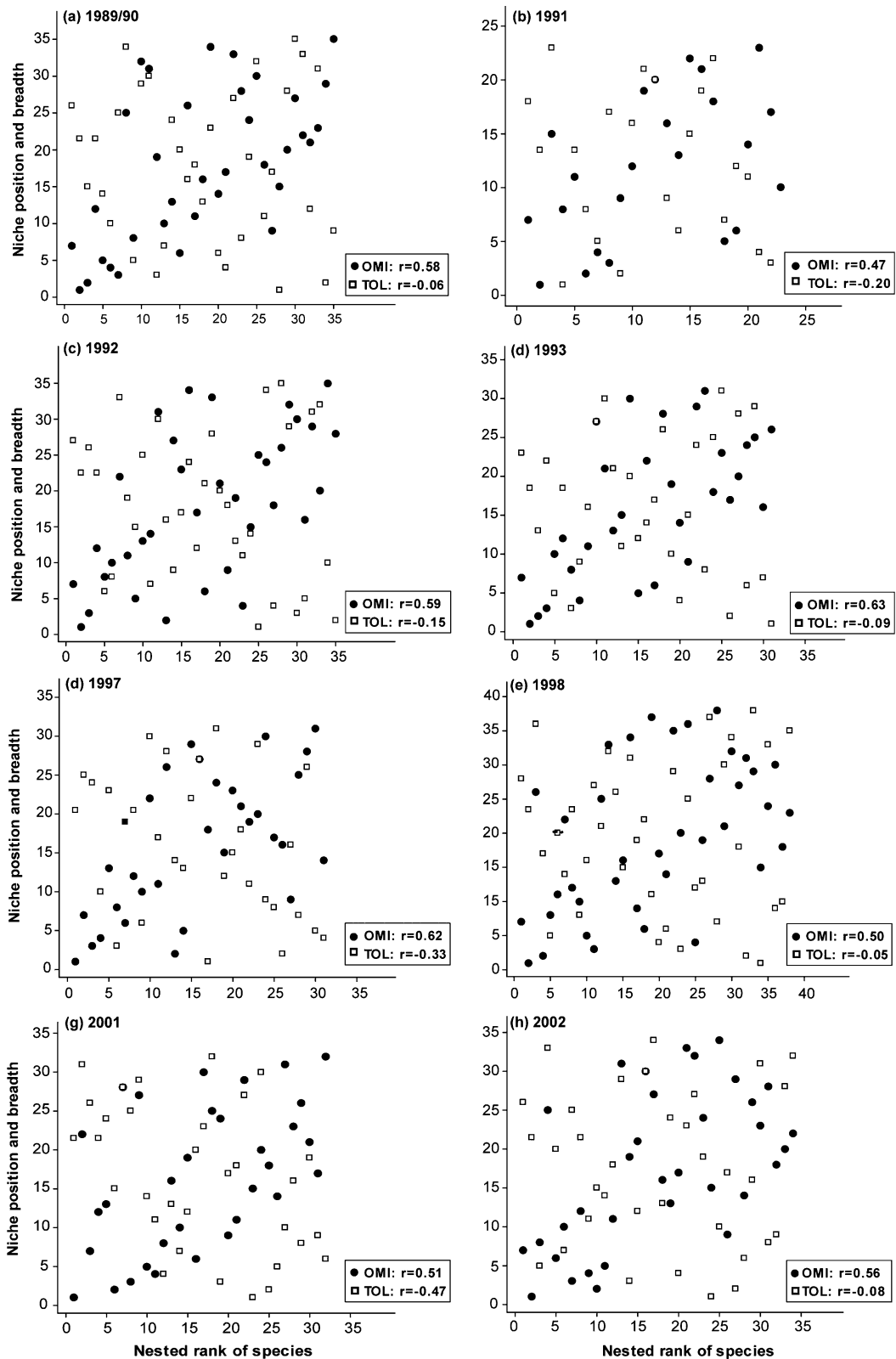


Figure 3. Correlation between nested ranks of species as maximally packed by Nested temperature calculator (NTC) for each year and species' niche position (OMI: filled circles) and niche breadth (Tol: open squares). Values are Spearman's rank correlation coefficient.

temperature, salinity, and pH were higher, possibly an indication of harsher conditions (Table 2). However, in 1993, pools with high pH tended to rank high in the nested

matrix. Finally, in year 1991, pools that ranked high in the nested matrix had a higher concentration of oxygen, possibly an indication of higher productivity.

Table 2. The relationship between nested rank of pools and measures of morphometric and physical attributes of pools. Values are partial Spearman's rank correlation. Bold-face indicate significant results.

Year	Explanatory variables							
	Morphometric variables				Physical variables			
	Depth	Vol	S-area	Elvt	Temp	Sal	Oxy	pH
1989/90	-0.321 ^{*§}	0.019 [§]	-0.281 ^a	0.325 ^{**}	0.383 ^{**§}	0.056	–	–
1991	0.119 [§]	0.109	-0.383 ^{*§}	0.278 ^a	0.172	0.371 [*]	-0.382 [*]	0.406 ^{**§}
1992	-0.015 [§]	-0.225 [§]	-0.364 ^{*§}	0.599 ^{***§}	0.114	0.476 ^{**}	-0.003	–
1993	-0.381 ^{*§}	0.014 [§]	-0.271	0.280	0.308 ^{a§}	0.302 ^a	0.218 [§]	-0.297 ^a
1997	-0.274 ^{a§}	0.188 [§]	-0.494 ^{***§}	0.171	0.047 [§]	0.039	0.198 [§]	0.221
1998	-0.187 [§]	-0.001	-0.270 ^a	0.357 [*]	0.073 [§]	0.112	-0.023 [§]	0.305 ^{a§}
2001	-0.240 [§]	-0.252 [§]	-0.367 ^{a§}	0.114	-0.266	0.081	0.312	-0.167
2002	-0.422 ^{**§}	0.239	-0.075	0.032	-0.005	-0.097	0.156	0.100

^ap < 0.10; *p < 0.05; **p < 0.01; ***p < 0.001.

[§]indicate variables that are also significant in a simple correlation (at least p < 0.10).

Nestedness and temporal dynamics of species composition

A nested matrix congregates presences in the upper-left corner above the isocline (extinction curve; Fig. 1). Absences (holes) above the isocline and presences (outliers) below the line are less likely. Therefore, the unexpected presences below the curve are more likely to go extinct (in time) than those above the curve. Conversely, absences above the isocline are more likely to be replaced with presences (colonized) than absences below the curve. Overall, the number of extinctions and colonization of invertebrates observed across years (1991–2002) in relation to the benchmark (1989–1990) concurred with these expectations (Table 3), except in 2001.

Moreover, extinction rate declined significantly with increasing cell state occupancy probabilities (Fig. 4). Cells SOPs reflect a joint effect of species and pools rankings in the nested matrix. When we examined the relative contribution species and pools to turnover dynamics, we found that the relative extinctions and colonizations were predominantly related to the nested rank of species (Table 4; Spearman's rank correlation), but not the nested rank of pools (Supplementary material Appendix 3). Thus, species that rank high in the nested matrix experienced low extinctions and high colonization rates and vice versa (Table 4). This was also corroborated using a related species attribute: the regional occupancy probabilities (ROP_{spp}) of species in the benchmark year (from NTC). Species with high ROP_{spp} were less likely to go extinct and more likely to colonize pools than those species with low ROP_{spp} (Table 4, simple correlation). In the analysis of nested rank of species in the preceding year results were very similar (year-to-year analysis; Supplementary material Appendix 4). The nested ranks of species obtained by BINMATNEST gave very

similar relationships to those of NTC (Supplementary material Appendix 3).

When we examined the relationship between species niche characteristics and turnover dynamics, species with low OMI value, i.e. those utilizing more typical 'habitat condition', were consistently more successful in colonizing pools which they were absent from (Table 4). In contrast to colonizations, niche position was not related to extinctions. Furthermore, species niche breadth was not related to either colonization or extinction rates (Table 4). Interestingly, species with higher residual tolerance index were again more likely to colonize pools they were absent from (Appendix 5).

Contrary to our expectations, nested ranks of pools and extinction and colonization rates were not related (Supplementary material Appendix 3, 4).

Discussion

Our study highlights previously undocumented relationship between pattern of nestedness, niche parameters, and temporal dynamics over multiple snapshots in time that span many generations of constituent species. Overall, the study leads to two important findings. One is that the nested pattern of species persists over longer time scales, even in dynamic systems, and that the hierarchical order of species in the nested matrix (species nested rank) was highly conservative. The second is that colonization and extinction probabilities for individual species can be inferred from nested rank order of species. Variation in species' niche position partly accounted for the nested rank of species. These findings are best evaluated in a broader context (Supplementary material Appendix 6). The nested ranks of pools across years, notwithstanding correlated, tended to be more variable and did not show consistent relation with

Table 3. Differences in extinctions and colonizations between cells above and below the isocline in the maximally packed matrix of the benchmark census (1989/90) for each year. Values are χ^2 -values, DF = 1. Bold-face indicate significant results.

	1991	1992	1993	1997	1998	2001	2002
Extinction	3.44 ^a	9.47 ^{**}	11.31 ^{***}	2.63	6.36 [*]	1.70	13.08 ^{***}
Colonization	11.16 ^{***}	10.71 ^{***}	12.17 ^{***}	17.87 ^{***}	5.63 [*]	0.18	6.63 ^{**}

^ap < 0.10, *p < 0.05, **p < 0.01, ***p < 0.001.

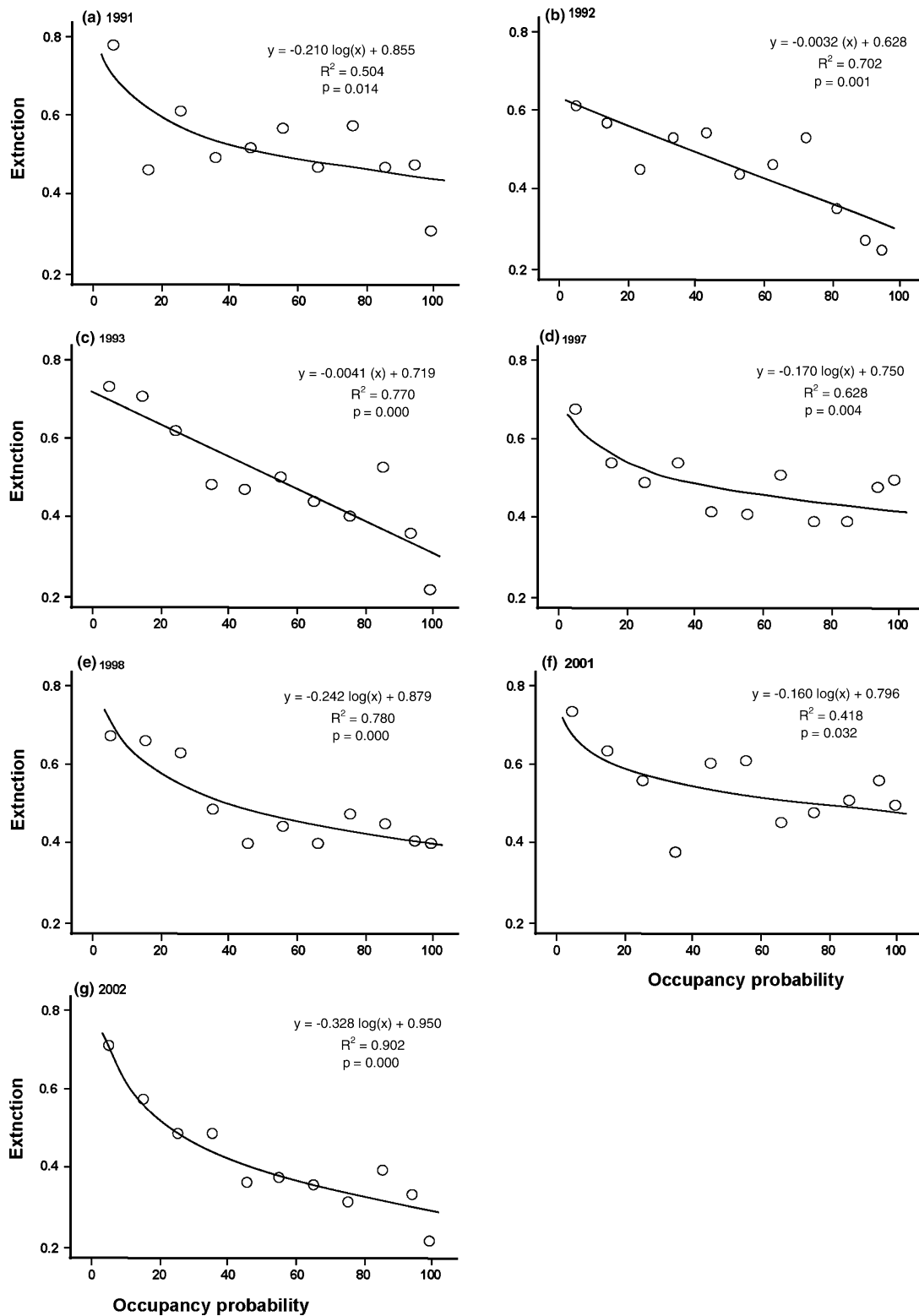


Figure 4. The relationship between the state occupancy probabilities (SOP) of occupied cells (i.e. species-pool combination) in the 1989/1990 census and the proportions of extinctions that occurred in subsequent years. The proportion of extinctions was high for cells with lower occupancy probability and low for cells with higher occupancy probability. Best fit regression models, p-value and r^2 are given for each year.

physical attributes of pools. This indicates slight variation in pool suitability due to environmental variability, which is well documented in our study system (Therriault and

Kolasa 2000). The latter result concurs with that of Azaria et al. (2006) who reported a fairly consistent ranking of islands (bird communities) in two surveys separated by over

Table 4. Correlation between species-specific attributes and the proportion of pools on which a given species went locally extinct (E_{Spp}) or colonized (C_{Spp}) in successive years in relation to the benchmark year. SNR_{Spp} and ROP_{Spp} are nested ranks and regional occupancy probability (ROP_{Spp}) of species, respectively, in the benchmark year (calculated by NTC). All values, except in column SNR_{Spp} that are Spearman's rank correlation, are simple correlation. OMI = outlying mean index, i.e. niche position or marginality; Tol = species tolerance or niche breadth. Bold-face indicate significant results.

	Year	Proxies for species' ecological range			
		Nestedness analysis		Niche analysis	
		\S SNR_{Spp}	ROP_{Spp}	\S OMI	Tol
Extinctions (E_{Spp})	1991	0.709***	-0.526**	-0.013	-0.259
	1992	0.239	-0.332*	0.034	0.156
	1993	0.571***	-0.411*	0.007	0.059
	1997	0.606***	-0.486**	0.069	0.147
	1998	0.351*	-0.321^a	-0.117	0.011
	2001	0.518**	-0.336*	-0.16	0.022
	2002	0.413*	-0.535**	0.033	0.255
Colonizations (C_{Spp})	1991	-0.734***	0.630***	-0.399*	0.024
	1992	-0.532**	0.719***	-0.518***	-0.043
	1993	-0.690***	0.692***	-0.603***	-0.015
	1997	-0.571***	0.513**	-0.550**	-0.053
	1998	-0.416*	0.461**	-0.503**	-0.097
	2001	-0.574***	0.425*	-0.469**	-0.014
	2002	-0.747***	0.695***	-0.488**	0.035

^a $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

[§]Species that rank high in the nested matrix and species whose niche position (OMI) is closer to average habitat condition received smaller values; hence the sign of relation becomes positive with extinction and negative with colonization.

30 years. In contrast, Maron et al. (2004) reported a lack of correlation between the nested ranks of sites in two surveys separated by seven years. Their study involved habitat fragments whose bird assemblages did not form independent communities.

Our study suggests that most of the temporal compositional dynamics in this system can be accounted for by nested pattern of the assemblages. As expected, in the nested matrix, cells with high state occupancy probability (SOP; typically common species in species-rich pools) had lower extinction risk than cells with low SOP. Cells with low SOP typically identify populations of rare species in relatively depauperate pools (and relatively common species in ephemeral pools, or rare species in relatively species-rich pools) – traits that would increase the vulnerability of a given species to extinction in a corresponding pool. Our result differs from that of Azeria et al. (2006) who found a unimodal relationship between SOP and extinction rates, i.e. extinction rates were rare among cells with high and low SOP. The unexpected low extinctions among cells with low SOP was attributed to persistence of rare 'idiosyncratic' species that occupy restricted but stable habitats (Azeria et al. 2006).

Examining the relative roles of species and pools suggests that the relationship between the nestedness and turnover dynamics observed in the system studied are driven primarily by nested rank of species rather than ordering of pools (Supplementary material Appendix 6). Nested rank of species translates into gradient of species vulnerability to extinction or of ability to colonize (Patterson and Atmar 2000). The finding that colonizations were common and extinctions were rare among species that rank high, which have also high regional occupancy probabilities (ROP_{Spp}) in the nested matrix, and vice versa, has a plausible ecological explanation (Appendix 6). It implies that variation of attributes among species (such as dispersal, niche characteristics

or biotic interactions) thought to underpin nestedness as well as the species vulnerability to extinction or of ability to colonize (Patterson and Brown 1991) was conservative over ecological time scales. This concurs with McKinney (1997) that species-traits affecting relative vulnerability to extinction are conservative at least over ecological time scales (for different findings regarding evolutionary time scales see Losos et al. 2003). Across all years, we found that highly ranked species (widespread) were those that had a non-marginal niche position (low OMI), which is also consistent with the resource availability hypothesis (Hanski et al. 1993).

However, niche position of a species predicted only a portion of pools it would colonize; whilst niche breadth of a species was not related to either its extinction or colonization rates across pools, thus lending no support to the idea that niche-breadth or position affect local extinction risk (Manne et al. 1999). Indeed, niche breadth was not related to regional occupancy, nested rank (except in year 2001), or niche position of species. Thus, species that rank high (widespread) in the nested matrix do not necessarily occupy a wider environmental range (in space and time) than those ranking low (rare) species. Thus, our study system offers little support for the importance of niche breadth in generating nestedness (Brown 1984, 1995, Kodric-Brown and Brown 1993, Vázquez and Simberloff 2002). Our findings further corroborate also previous studies that failed to support niche breadth hypothesis (Gregory and Gaston 2000).

The difficulty of defining and measuring the multitude of factors that may affect species distribution hinders adequate estimation of niche axes and may negatively affect the use of niche width in predicting extinction risks (Vázquez and Simberloff 2002). In our niche analysis, the variation in species distribution unexplained (RTol) was generally high (approx. 60%; see species residual niche tolerance in supplementary material Appendix 1). Thus,

our computation of species-specific niche parameters only yield the range of potential abiotic 'environmental envelope' of a species, and leaves out other important factors, notably interactions among species (e.g. facilitation, competition) that may co-determine the ecological niche and thus distribution of a species (Bruno et al. 2003). In our study system, several species display significant and temporally consistent positive or negative species pairwise associations (Azeria and Kolasa unpubl.). In addition, difference in species dispersal ability determines species distributions; with most dispersive species being regionally common (Hanski et al. 1993, Pulliam 2000) because they colonize suitable sites more effectively and rescue small populations from extinction. Although we have not tested for this explicitly, the variation in species distribution unexplained by the niche-parameters (RTol) was positively related to species success to (re)colonize pools (Supplementary material Appendix 5). Furthermore, this unexplained variation was higher for regionally common species. Thus, it is possible that dispersal ability may partially explain the colonization success, regional distribution of species, and consequently, nestedness pattern.

However, it is not clear how dispersal ability affects extinction risk. Thus, while high dispersal ability might decrease species extinction risk through rescue effect (Brown and Kodric-Brown 1977), it might also increase observed extinction rate because in many instances species may occur in less suitable pools (source-sink dynamics; Pulliam 1988, 2000). To calculate species niche characteristics across 'full' environmental gradients (and alleviate apparent niche constraints that may have arisen due to species dispersal limitations) (Pulliam 2000), we used data aggregated across all annual surveys. Our computed niche-axis is thus likely to include values of environmental variables outside species' normal tolerance range, e.g. values observed in sink habitats (Pulliam 1988). Such exaggerated niche-breadth may have obscured its importance for assessing regional species distribution and extinction risk. By and large, our study suggests that nested ranks and regional occupancy probabilities of species provide a comprehensive representation of the hierarchical relationship among species and consequently their ability to establish and survive in a variable environment. This offers an advantage over the assessment of distribution and extinction risk based on data intensive niche parameters.

We expected that nested rank of pools reflects a suitability gradient among pools, such that increasing suitability may reduce extinction rates or promote colonizations and thus counter or complement, respectively, the expectations of extinction and colonization, due to rarity and commonness of species alone (Patterson and Atmar 2000). However, we found no relationship between nested rank pools and species extinction or colonization rates. This was counterintuitive given that the high ranking pools tended to be deeper, hence more likely to withstand desiccation (and reduce salinity and temperature variation) – a feature conducive to species persistence (Therriault and Kolasa 2001). In addition high ranking pools have larger surface area and lower elevation, which might increase the capture of individuals that disperse aerially or with water flowing from pools upstream – traits conducive to

(re)colonization and rescue effects (Brown and Kodric-Brown 1977).

The lack of relationship between nested ranks of sites (suitability gradient) and species extinction and colonization rates has been reported for bird communities (Maron et al. 2004, Azeria et al. 2006). This observation calls for explanation. In our study system, the occurrence of extreme environmental conditions such as desiccation or flooding may drive the extinction-colonization dynamics of the communities. More interestingly, we find an increasing divergence of nested ranks of pools with time elapsed between censuses. Thus, it is plausible that the influence of species that survive (ecological memory, Bengtsson et al. 2003) on local community assembly decays over time (Romanuk and Kolasa 2002). Another plausible cause may be related to the complex functional role and influence of surviving species have on the subsequent trajectory of local and regional community (re)assembly (Shurin and Allen 2001, Zavaleta and Hulvey 2004). Previous studies in our study system suggest biotic factors such as density of generalists species might have strong effect on dynamics of local communities (Therriault and Kolasa 2000) and, by doing so, might modulate the suitability (nested rank) of pools differently. Important questions arise of whether the decay of the correlation among nested rank (suitability) of pools observed in our system is general and applies to other systems and what the role of the biotic component is in stabilizing or shifting species composition over time (Zavaleta and Hulvey 2004).

To conclude, ranking of pools and rankings of species had different predictive values. Determining how they are related to nestedness and, indirectly, how the underlying factors are related, will enhance their ability to predict colonization and extinction probabilities of species. Our study suggests that compound species traits (including niche position) have important influence on the assembly, turnover, and maintenance of ecological communities in space and time. Thus, in our study system, the persistence of the regional nested pattern and the extinction and colonization dynamics associated with it appear to be largely determined by differences among species to occupy habitats and much less by differences among properties of the pools. Yet niche position of species, although related to nested rank of species, predicted only colonization rate of species; whereas niche breadth was not related either to nested rank of species or to the turnover dynamics of species. Consequently, studies that test for the importance of habitats and other environmental variables for the development of nestedness (Wright et al. 1998, Hylander et al. 2005) should examine the species 'ecological specializations' explicitly (Simberloff and Martin 1991, Kodric-Brown and Brown 1993, Gregory and Gaston 2000, Azeria et al. 2006), and tease apart how niche position and niche breadth relate to nested rank of species and to the spatio-temporal dynamics of species distribution (for niche models see Hanski et al. 1993, Vázquez and Simberloff 2002).

Our results have implications to the applicability of nestedness for conservation biology. Notably it highlights the importance of distinguishing the relative role of ecological difference among species and among sites (as proxies for the underlying mechanisms) to cause nestedness and its stability in time. For example, site-based

conservation planning assumes a strong hierarchical ordering among sites behind the nested structure and, if assemblages are nested, preserving the most species-rich locality (often a large area) would be a good strategy (Doak and Mills 1994, Wright et al. 1998, Azeria et al. 2006). Although this assumption may be valid on its own, in systems where the quality of sites changes substantially (Scheffer et al. 2001), the ranking may fail to reflect their potential for maintenance of species (combinations) in the long term. Also, nestedness could arise predominantly by ecological differences among species. If so, conservation designs thus should aim to create a network of reserves that is capable of buffering environmental variability (Scheffer et al. 2001, Bengtsson et al. 2003, Maron et al. 2004, Azeria et al. 2006) and/or ensure the environmental envelope (in this study niche position) required by target species is available and accessible in the 'changed' landscape.

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Supplementary material (available online as Appendix O16529 at www.oikos.ekol.lu.se/appendix). Appendix 1–6.