HABITAT COMPLEXITY

Species–area relationships arise from interaction of habitat heterogeneity and species pool

J. Kolasa · L. L. Manne · S. N. Pandit

Abstract Species–area relationships (SARs) represent a ubiquitous and useful empirical regularity characterizing biodiversity. The rate of species accumulation, captured by the value of the exponent, z, varies substantially and for many reasons. We hypothesized that one of the major contributors to this variation is heterogeneity and its change with scale. To test this hypothesis, we used an array of natural microcosms for which we had invertebrate species composition and physical properties of habitat. Using GIS and cluster analysis, we organized the species data into four sets: communities grouped by spatial proximity in the field, randomly, by similarity of their physical habitat and by dissimilarity of their physical habitat. These groupings produced varying levels of heterogeneity at different scales. We fitted species–area and species–volume relationships to the four groups of communities, and obtained z-values for each group or a portion of the group if the slope of the relationship varied. As predicted, we recovered a number of properties reported by others. More interestingly, we found that small- and large-scale habitat heterogeneity produced scale-dependent z-values while the random grouping of pool habitats produced z-values more robust across scales but also susceptible to initial values of habitat richness. Habitat area affected rate at which species accumulated much less than the mean degree of inter-habitat differences: increasing area that is heterogeneous at broader scales produces higher z-values than increasing an area that shows heterogeneity at small scale only. Our results, while from a microcosm system, rely on logic transferable to larger scale data sets.

Keywords Species–area relationships · Aquatic microcosms · Heterogeneity · Invertebrates · Rock pools

J. Kolasa (✉)
Department of Biology, McMaster University, 1280 Main Street, Hamilton, ON L8S 4K1, Canada
e-mail: kolasa@mcmaster.ca

L. L. Manne
Department of Ecology & Evolutionary Biology, City University of New York/College of Staten Island, 2800 Victory Blvd, Staten Island, NY 10314, USA

S. N. Pandit
Department of Biological Sciences, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B 3P4, Canada

Introduction

Species–area relationships, or SARs, play an important role in fundamental and applied biodiversity research because they capture an empirical generalization that increasingly larger areas (A) contain increasing numbers of species (S). Commonly, SARs are expressed as a power law $S = cA^z$ (but see Scheiner et al. (2000) and

the following debate by Gray et al. (2004a, b) for the whole range of criticisms), with z reflecting the logarithmic rate at which species richness increases with area sampled. In general, causal contribution of factors potentially affecting z is difficult to determine (Gentile & Argano, 2005). A number of explanations have been offered for the particular form that the increase that S with area takes: number of habitats sampled (Lack, 1976; Connor & McCoy, 1979), patch shape (Condit et al., 1996; Harte et al., 1999b), length of time taken to conduct sampling (Adler & Lauenroth, 2003; White, 2004), random versus non-random distribution of samples in space (Gray et al., 2004a), self-similarity in species distributions (Harte et al., 1999a), complete versus incomplete sampling (Cam et al., 2002), and grain size (sampling area relative to overall region of interest (He & Legendre, 2002; Hortal et al., 2006). A meta-analysis by Drakare et al. (2006) indicates that scale and habitat, among several other factors, affects the shape of the SARs (and particularly z) but does not provide specific evaluation of how habitat diversity at any single scale may modify z. Similarly, Shen et al. (2009) found that habitat heterogeneity affects distribution of tree individuals, which, in conjunction with rates of dispersal, explains the SAR pattern on Barro Colorado Island, Panama. Neither study examined the effects of heterogeneity changes on SAR as a function of scale. This gap is particularly relevant to aquatic systems where studies are often limited by the number and density of samples representing local communities.

Thus, the most obvious potential predictor of z, that arising from the relationship between species number and the (possibly nested) habitat structure, has not been rigorously tested (Allen & White, 2003). Habitat heterogeneity should affect SARs over a broad range of scales (Turner & Tjørve, 2005), although not all combinations of regions and taxa demonstrate a relationship between z and habitat heterogeneity (Cam et al., 2002).

Landscapes with diversified habitat types, and higher levels of natural fragmentation (heterogeneous landscapes), should maintain higher species number for the same surface area than homogeneous landscapes (Chust et al., 2003; Triantis et al., 2005). In aquatic systems, this trend has been demonstrated for stream algae (Passy & Blanchet, 2007). Consequently, in heterogeneous landscapes, species–area curves should be initially steeper; with their shapes strongly affected by the interaction between the scale of observation and the scale of heterogeneity. Connor & McCoy (1979) suggested that a direct test of the heterogeneity hypothesis as the sole factor responsible for SAR as opposed to the null model (area alone) would require contrasting the effects of heterogeneity against a homogeneous habitat. This is an impractical requirement for field studies although some aspects of it were examined by Shen et al. (2009) via modeling. An alternative and more feasible approach to data from natural systems might be to contrast z from natural habitats sampled according to the degree of heterogeneity and homogeneity.

General expectations of how heterogeneity may affect SAR shape (ISAR and SARcum, i.e., isolated SAR and cumulative SAR) need to consider three possibilities (Fig. 1). Regions may be highly heterogeneous, highly homogeneous or, most likely, with a landscape of mixed heterogeneity composed of peaks and valleys of high and low heterogeneity, respectively. Specifically, if one samples progressively larger areas in the direction indicated by arrows or, if one adds species lists along transects indicated by the arrows, one will (i) continue sampling high heterogeneity (Fig. 1a), (ii) start with high heterogeneity but later include areas of only low heterogeneity and vice versa (Fig. 1b), and (iii) sample only low heterogeneity (Fig. 1c). Each of these relationships between sampling regime and the configuration of heterogeneity in space is likely to affect species–area relations, z-values, and our inferences about rates of species accumulation (but see Tjørve & Tjørve (2008) who prefer to focus on proportion of species added with doubling of area) differently (Fig. 1, rightmost panels). Thus, Fig. 1 can be seen as graphical formulation of testable hypotheses.

Our general approach is to compare rates of species accumulation (z-values) for species collections from the same areas but different habitat heterogeneities, to examine habitat heterogeneity as a source of variation in species–area curves. We use the same data set for all analyses. While this approach compromises some statistical power, it avoids confounding the effects of area size and those of habitat heterogeneity, both of which might vary in response to diversity of different regions, history of colonization, or speciation. This setup provides us with a distinct advantage relative to other attempts at assessing the role of habitat heterogeneity on patterns

Fig. 1 Region or habitat heterogeneity and its expected effect on species accumulation curves. If patterns on the left symbolize (**a**) high heterogeneity, (**b**) a mixture of heterogeneity patterns with high on the left and low on the right and (**c**) low heterogeneity, the measured heterogeneity values would differ if assessed along directions indicated by the *arrows* (central panels). Corresponding SARs are on the *right*. Note that in (**b**), two different SARs are possible depending where one starts sampling (transect direction). If sampling begins in a heterogeneous area, the curve is initially steeper
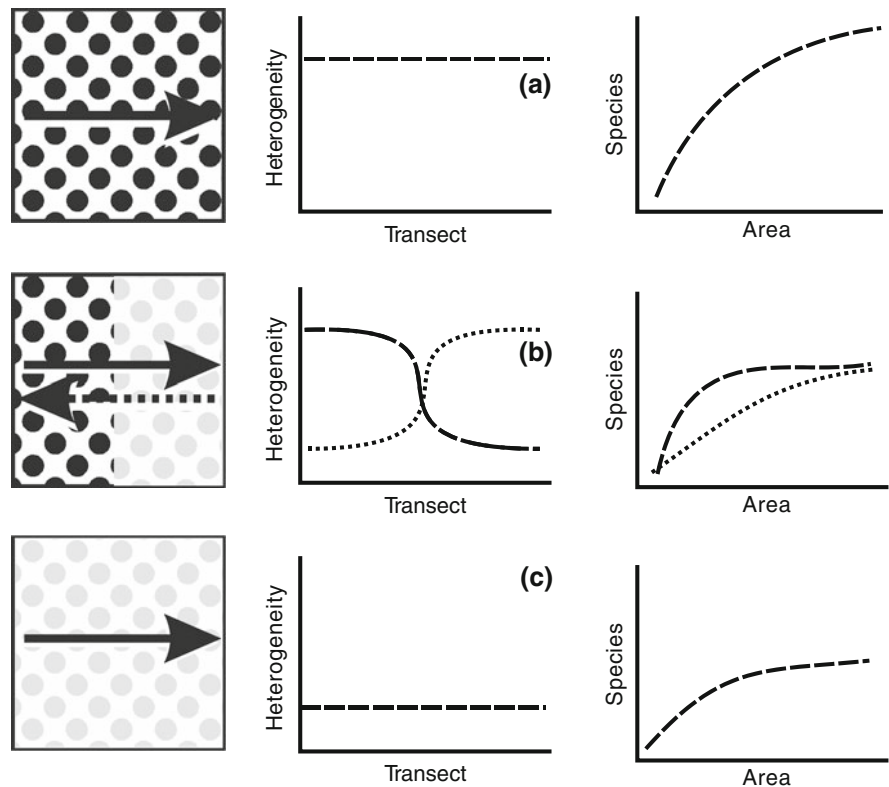
of species richness and species accumulation across habitat islands.

Data and methods

Study site

We use aquatic microcosm data on aquatic invertebrates inhabiting the supratidal zone rock pools near the Discovery Bay Marine Laboratory (18°28′N, 77°25′W) on the north coast of Jamaica (Schuh & Diesel, 1995; Kolasa et al., 1996, 1998; Therriault & Kolasa, 1999; Therriault & Kolasa, 2000; Romanuk & Kolasa, 2001, 2002; Pandit et al., 2009) collected from a system of rock pool communities. These pools differ in their salinity (0–32 ppt), temperature, pH, oxygen concentrations, conductivity, and nutrient contents from each other, and individual pools show biologically meaningful levels of temporal variability. The study site covered an area 50 m in diameter of mixed land and sea habitat. Forty-nine pools were randomly chosen (Kolasa et al., 1996) and sampled in late December or early January in 1989–1993, 1997–2000,

2002, and in June 1997. Pools ranged from 14 to 100 cm in length (mean ± SD = 52 ± 20.0 cm), 10 to 61 cm in width (30 ± 14 cm), and 1 to 37 cm in depth (12.8 ± 8.3 cm). Correspondingly, pool areas varied from 0.019 to 0.47 m^2 (0.18 ± 0.12 m^2) and pool volumes (measured by emptying the pools) ranged from 0.5 to 78.4 l (16.8 ± 18.5 l), a maximum difference of over two orders of magnitude. The areas of individual pools are much less variable than the volumes because of generally steep pool walls. Volume, by contrast, is highly variable and depends on the time elapsed since the last rain fall or inflow from the sea. Both sources of pool water are intermittent. Elevation above sea level ranged from 1 to 235 cm (76.6 + 80.1 cm) at high tide, with the tide rarely exceeding 30 cm. Seven pools were tidal (although tidal flooding is irregular). The remaining 42 pools were maintained by rainwater and, very occasionally, wave splash or storm water.

Biota

The pool communities consisted of aquatic meio- and micro-invertebrates, with the cumulative number of

species exceeding 70. The full list of taxa included Turbellaria (7), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (20), Copepoda (6), Cladocera (4), Decapoda larvae and various shrimps (4), Amphipoda (1), Isopoda (1), and Insecta (18). Apart from the 70 species that were included in our primary data set, some transient visitors were found, including gastropods (Littorinidae and Neritidae), hermit crabs, and the brachyuran crabs *Pachygrapsus* sp. (Schuh & Diesel, 1995).

Physical parameters

We collected data on each rock pool temperature, oxygen concentration, pH, salinity, conductivity, water level, volume, shape, surface area, chlorophyll concentration, and turbidity. Most of the temporal data were collected at multiple time scales over 14 years of observations. As a rule, several measurements were taken over a single annual visit of 14 days. On three occasions each of the pool parameters were measured over 24 h, with a 2 h interval between measurements. Spatial data were collected at two scales: that of a single pool, and on a grid of 5×5 cm within each pool. In addition, when applicable, the grid measurements were taken at depth of 1, 10 cm, and at the bottom of the pool. For pools <10 cm deep only 1 cm depth measurements were used.

Analytical treatment

We quantified the habitat size as either water volume of the pool (mean volume of several measurements) or maximum pool surface area obtained from the pool outline available in ArcMap GIS (ESRI) photographic maps. These pools are true "isolates" (Gray et al., 2004b). We characterized SARs in the rock pool system in a traditional manner, regressing species richness, log S, against the log of habitat size. Here, z-values represent a relationship between the pool size and species richness and may have little to do with the species accumulation curve (Gray et al., 2004b). Species richness was represented as mean pool richness over the 10 sampling dates. In addition, we checked for a relationship between cumulative species richness, S_{cum}, which was richness of combined communities from 1, 2, …, 49 pools, and area. In this procedure, we used the number of pool communities as a variable equivalent to area on the assumption that an addition of a discrete habitat (pool) community has an analogous effect on the total number of species recorded in a sample as addition of a unit of area. We checked whether accumulating pool areas as compared to pools significantly altered our results.

To determine the effects of intra- and inter-habitat heterogeneity on the rate of species accumulation, we accumulated richness of pool communities in several ways (see Scheiner (2004) for a review of available approaches and their interpretation). Gray et al. (2004b) argued, in contrast to Scheiner, that similar SARs form even when different sampling protocols are used (e.g., nested vs. non-nested). Therefore, while recognizing that the distinctions made by Scheiner are subject to debate as points raised by Gray et al. (2004a, b) imply, it is useful to clarify that our procedures fall into two main categories. One involves deriving SARs from areas of different sizes (individual rock pools) and is termed ISARs, and the other is most akin to sampling of the nested areas, although we manipulate the "nestedness" and use counts of sampled habitats as equivalents of area. Under this protocol, an addition of a single pool community implies some (albeit non-uniform) increase in the area from which S is sampled. As we show later, this introduced variability has no meaningful effect on the results.

For the purpose of hypothesis testing, the pool faunae were combined either randomly or according to a "habitat heterogeneity" protocol. To maximize initial heterogeneity, we accumulated faunae of the most different pools first and more similar pools were added in the later steps, with the most similar pools added last. Thus, the pool faunae were added in order of decreasing heterogeneity of environmental characteristics (see below for more information on the process by which we ordered the pools). To minimize initial heterogeneity, we accumulated faunae from pools in order of increasing heterogeneity (least different pools added first). To each of the data sequences we fitted $S = cA^z$, where S is richness, c is a constant, and z is the exponent proportional to the rate of species accumulation (fitted as linear regressions to log-transformed y and x axes).

To create the gradients of heterogeneity mentioned above, we ordered pools according to either increasing or decreasing differences in their physical characteristics or distance separating the pools. We used

spatial difference (pools located in close or far from one another, with the expectation that pools near one another are more likely to contain similar faunae) and difference in physiographic and environmental conditions within the pool. To identify the latter differences we used a principal component analysis (PCA) on the range of pool attributes (surface area, perimeter, maximum volume, mean depth, location coordinates, pH, the number of desiccation events, mean oxygen concentration, mean salinity, maximum salinity, mean turbidity, mean chlorophyll, and mean temperature) and then, using cluster analysis, we created a gradient of pools from those with most similar to most different PCA scores. To check whether the PCA/cluster analysis based orderings produced an acceptable characterization of inter-pool differences, we created an alternative basis for pool ordination: We used geometric means of products of the above variables and used those means to determine the order of pool entry in the species accumulation procedure.

Next, we assessed heterogeneity within pools (intra-pool heterogeneity), and contrasted this against the between-pool heterogeneity (inter-pool heterogeneity) measures described above. This appeared a necessary step because internal heterogeneity of a pool could affect its richness, which in turn could affect calculated SARs. We examined both spatial and temporal within-pool heterogeneity. For the assessment of spatial heterogeneity, we scored the within-pool spatial heterogeneity as variance in measurement of pH, salinity, oxygen, and temperature on the 5×5 cm grid described earlier. We scored the temporal heterogeneity as variance in the same variables across sampling dates (where spatial data were not used).

The length of time of data collection can potentially affect the form of SARs, because a longer sampling effort will yield a higher species richness (Adler & Lauenroth, 2003; White, 2004). In addition, species distribution patterns can sufficiently change over time so that local SARs also change (Manne et al., 2007). For these reasons, we last examined the effect of time on behavior of z. We constructed a species accumulation curve from a random ordering of pool communities, and then repeated this process for each year (using the same ordering as for the first year) to quantify the possible year-to-year variation in z.

Results

Overall, pool size emerged as a poor predictor of local richness when we created an isolate species–area relationship (ISAR). Different measures of habitat size may produce different relationships between species richness and size of habitat. For three-dimensional habitats such as lakes, rock pools, or stratified vegetation, volume is often used as an alternative to area. We compared species–area (surface area) relationships to species–volume relationships. Surprisingly, surface area explained almost twice as much variation in S than volume (Fig. 2a, b), though neither variable showed a strong relationship with S ($r^2 = 0.09$ for volume vs. $r^2 = 0.15$ for surface area).

Pool surface area may be a stronger correlate of richness than volume due to the relationship between area and pool perimeter. The relationship between pool area and the area/perimeter ratio is an insignificantly decelerating line ($r^2 = 0.568$ for the function $y = a + bx^{0.5}$ as compared to $r^2 = 0.555$, $P < 0.00001$, for the straight line) implying that convolution of the pool shape does not decline with its size or it may even slightly increase. Thus, greater pool edge development in larger pools may be fostering microhabitat diversification, a condition that facilitates species survival and coexistence to a greater degree than increase in volume alone. This assumption is corroborated by a significant although modest increase of within pool heterogeneity as a function of the surface area (a decelerating curve fitted by $y = a + b \ln(x)$; $r^2 = 0.098$; $P < 0.04$). By contrast, volume shows a marginally significant declining effect on pool heterogeneity. While neither pool volume nor area was strong predictors of richness, the number of pools used for accumulations was a strong predictor (Fig. 2c) when accumulation sequence was randomized.

More importantly, we were interested to find out if changing patterns of landscape heterogeneity affected z-values. Thus, in the next step, we have created two cumulative SARs from a single set of 49 pools. We have added species of the first 25 pools and then remaining 24 pools under one of the two scenarios. In the first scenario, we combined faunae of the most similar pools first (based on differences in PCA scores on physical variables characterizing the pools). In the second scenario, we combined faunae of the most different pools first. When we accumulated S of pools that were most similar in their PCA scores first, we found steep

(a)

(b)

(c)
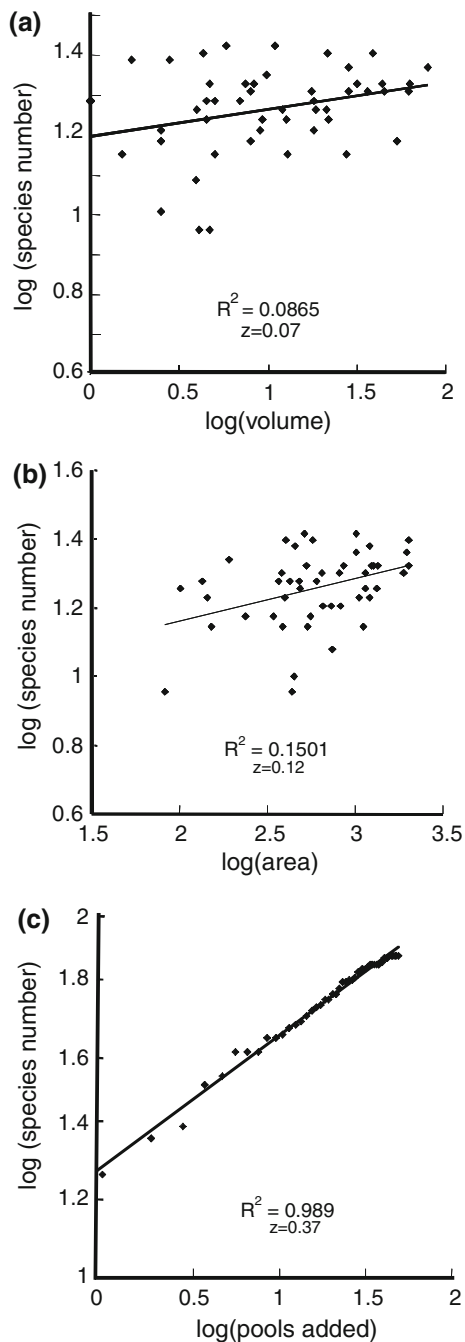
Fig. 2 Species diversity as a function of maximum rock pool volume in liters (**a**) and surface area in cm² (**b**) or random addition of faunae of individual pools (**c**). Graphs (**a**) and (**b**) thus represent relations observed across individual pools (species–area sensu Gray et al., 2004b), while graph (**c**) represents one of many possible accumulation curves that can be constructed from the available data (the relationship chosen has z close to the average from 100 curves)

SAR in both groups of pools, with $z = 0.338$ and $z = 0.519$, respectively (Fig. 3; "Most similar first"). This acceleration of species accumulation during combining the remaining 24 sites can be attributed to the "loading" of the most different pools into the model last (by design heterogeneity is greatest in this set). In other words, the potential species overlap (sensu Tjørve & Tjørve, 2008) is greater at the beginning of the accumulation and lower later in the process.

Predictably, when the communities of physically most different pools were accumulated first, we found a shallower SAR in general, with $z = 0.296$ for the "First 25" set of pools and $z = 0.246$ for the last set of pools.

We then checked the effect of heterogeneity internal to the rock pools on SAR. When we analyzed data by adding communities of internally heterogeneous pools first and contrasted SAR so obtained with one produced by adding least heterogeneous pools first, the results were qualitatively the same as with the inter-pool analysis. Accumulation process that started with high internal heterogeneity yielded a steeper SAR with z-value 1.43 times higher than the z-value associated with low initial (internal) heterogeneity (Fig. 4).

It was not immediately clear why the initial S values were lower in the SAR based on the addition of more heterogeneous pools first (cf., Fig. 4). To generate a baseline of SARs for comparison, we randomized the data one hundred times and created new a SAR for each randomization (Fig. 5a). The variance in z-values so generated provides a null model of expected variance in z-values for the data set we use. The simulated SARs produced z-values ranging from $z = 0.26$–0.45, distributed normally (Kolmogorov–Smirnoff test, $P > 0.2$).

Finally, we constructed a species accumulation curve from a random ordering of pool communities, and then repeated this process for each year (we used the same order of entry by which communities were combined to avoid the effect of arbitrary order that the range of values in Fig. 5a suggest). We found substantial variation in the estimated values (which ranged from 0.32 to 0.55; Fig. 5b).
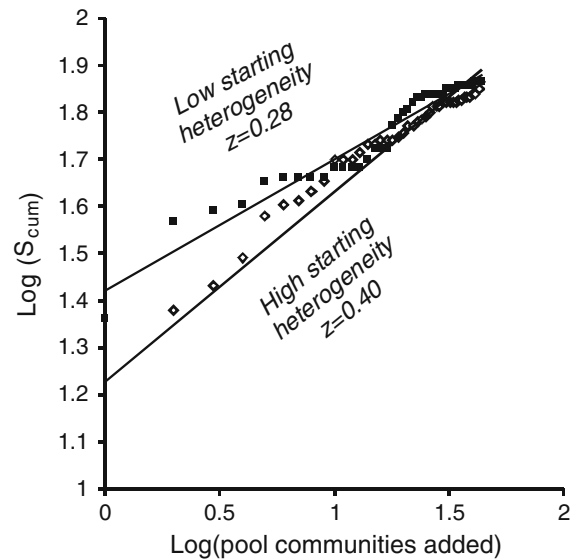
Discussion

As hypothesized, the analyses show that (1) heterogeneity among pools and within pools affects
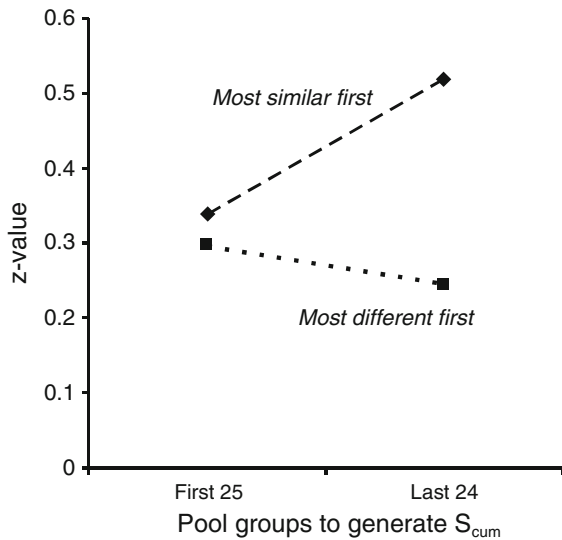
Fig. 3 Changes in the rate of species accumulation (z-values) in response to habitat. Pools were added starting with the most different (most different first) or with the most similar (most similar first); z-values are for SARs generated by combining species of most similar (25) or most different (24) pools first and SARs generated by combining species of the 24 remaining pools, respectively. This exercise corresponds to and contrasts situations with habitats/areas showing greater heterogeneity at small spatial scale (most different first) and habitats/areas showing greater heterogeneity at larger spatial scale (most similar first). The abbreviation "First 25" stands for the first 25 (most similar or different) pools used to generate z-value; "Last 24" stands for the remainder of the pool set of a total of 49 pools used in the analyses. Thus, the highest point on the graph represents z-value for the second portion of the accumulation curve that began with "most similar pools first" and it indicates a steep curve because it adds the most different communities at the end


Fig. 4 Rate of species accumulation depends on whether habitats added to produce larger samples are heterogeneous. Here, by contrast to Fig. 3, heterogeneity refers to within-pool heterogeneity as measured by the mean of standard deviations in physical characteristics of the pools: temperature, salinity, etc.). *Open diamonds*—highly heterogeneous pools added first, from the most heterogeneous to the least heterogeneous; *black squares*—highly heterogeneous pools added last (order reversed as compared to the previous accumulation curve)

cumulative SARs—specifically, higher heterogeneity (higher differences at small sampling scales, i.e., among adjacent habitats), produces z-values that decline as the larger scale, inclusive of less diversified habitat, is added (cf., Fig. 1b); (2) this is true whether habitats are added to create SARs for larger samples of the same habitat type or whether individual, different habitats are accumulated to generate SARs (cf., Figs. 3, 4); (3) SARs produced from single sequences of area sizes show great variability; and (4) this variability appears to be heavily dependent on the initial species number (as hypothesized in Fig. 1b; also see Gray et al. (2004b) for similar suggestions). Biologically, this means that highly diversified habitat conditions at small spatial scales may "sample" regional pool of species more effectively and thus

increasing the sampling effort to include larger scales (more sites or area) does not translate in a substantial increase in species number. However, when differences among adjacent habitats are small, given a fixed number of species as in this study, the accumulation gain is more prominent when larger areas are sampled (as seen in Fig. 3; "Most similar first").

As far as the findings 3 and 4 are concerned, the important point is that most published species–area curves represent a single set of data, with no re-sampling attempted. Thus, we suggest that z-values reported in the literature may often reflect the nature of regional faunae and florae at a single snapshot in time, and re-sampling should be conducted before they are used for conservation planning or management.

As we have fitted a single type of formula (i.e., $S = cA^z$), a question arises whether all the relationships we observed follow this model. Two aspects of the study may provide justification for this approach. First, fits of the power model to the data were generally very good, with the variation primarily in the coefficients but less in the r^2 values. Second, the
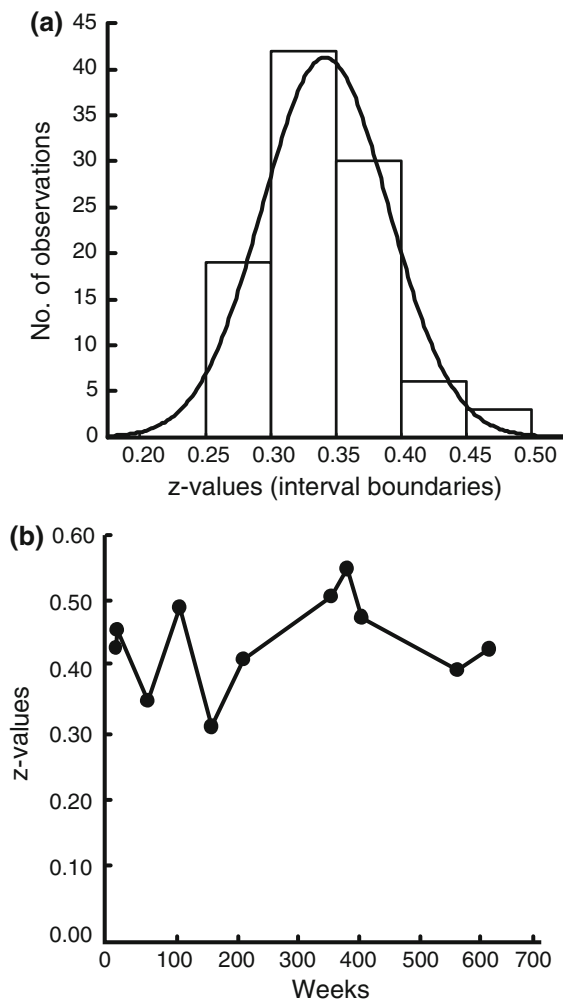
Fig. 5 Distribution of *z*-values for SARs derived from one hundred randomizations of rock pools (1–5; physical heterogeneity effects and spatial autocorrelations are removed in the process of randomization) (**a**). Time series of *z*-values for 10 (mostly annual) samples of 49 rock pool systems. Species accumulation curves were constructed using the one random sequence (the same each year) of pool communities for each of the 10 sampling dates (**b**)

primary motivation for our study was to examine one of the possible and important reasons for the variation in the scaling exponent *z* because it is broadly reported in the literature. Notwithstanding, it is quite possible that the power model is inappropriate in many situations for biological or mathematical reasons (Tjørve & Tjørve, 2008).

A legitimate question arises of whether a small metacommunity system (a set of local communities connected by dispersal) can represent and thus be fruitfully investigated to answer questions of macroecology and biogeography. We believe it can: natural microcosms are a strong candidate model system for ecology (Srivastava et al., 2004) where one can use a small model system to represent and examine phenomena usually examined at much larger spatial scales. Indeed, if the effects of heterogeneity are general, then they should be detectable at small and large scales. Consequently, our results should apply, qualitatively, to other situations. Earlier we showed (Kolasa et al., 1998) that the system of rock pool communities is an informative model for large-scale diversity gradients. We do not see any methodological reason not to consider this model as appropriate for SARs analysis.

A fairly weak relationship between the pool area and pool species richness (Fig. 2b) makes it possible for *z*-values to vary stochastically in response to species richness of pool community that initiates construction of the accumulation curve. Thus, the strong variation of *z*-values shown during the random generation of the curves can be explained partly by the nature of data. A lesson from this converges with Lomolino's (Lomolino, 2000) observation that idiosyncratic effects increase as the range of area samples shrinks (the range covered in this study was slightly over two orders of magnitude). This indeed applies to regression models in general. More important, however, is the finding that in regions of uneven heterogeneity (a case with most regions at most scales) specific location of the initial area strongly affect *z*-values. This finding is robust and most likely general, particularly since there is a considerable degree of idiosyncrasy of species richness at the pool community level. Our cautionary note resonates well with observations that spatial scale at which studies are carried out largely predetermines the outcome of analyses (Dumbrell et al., 2008).

One additional concern with our study is a possible small island effect (SIE) (MacArthur & Wilson, 1967), often known as the minimum area effect (Turner & Tjørve, 2005), which arises when the minimum required area size is not met for all species in the sample. While the "islands" and their archipelago that we studied are indeed small in absolute terms (the study area was 50 m in diameter), it is important to remember that the rock pools are not small relative to the organisms inhabiting them. It appears that the SIE is either absent or negligible here, as the rock pool communities displayed a

normal albeit modest effect of habitat size (Fig. 2) and, more importantly, no species has been identified to be present in large pools but systematically absent from small pools. Such an exclusion is a condition of SIE to occur (Triantis et al., 2006). Indeed, given that area and spatial heterogeneity within rock pools are slightly correlated, we cannot exclude the possibility that a SIE contributes to variation observed in species richness. This effect might influence SARs constructed from individual pools of different areas but not the accumulation curves that add up individual pool faunae (Fig. 2c, 3, 4).

A wide range of *z*-values may result from differences in rates at which new species migrate into the system (Durrett & Levin, 1996). An earlier experiment (Kolasa, unpublished data) showed that virtually all species originally present returned to their respective pools within 12 months or less after pools were emptied and cleared of propagules. Thus, while there is little doubt that pools are recolonized differentially, a pool's species number appears to stabilize in a fairly short period of time, even when starting from 0 species. The time period examined here is much greater than 12 months, so we should not be hampered by this sort of bias.

In general, our findings suggest possible applications of SARs, as well as caveats associated with their use. Furthermore, the findings indicate that the theoretical meaning attached to *z*-values and the recurring message that these values may represent a scaling law is clearly inappropriate. Assuming that our results are general and apply to other systems and across scales (as has been shown for South African *Proteaceae*, Manne et al., 2007), SARs could be seen as unique indices of local conditions and convenient summaries of species density over the landscape they have been derived for. They should not be seen, though, as transferable between regions or habitats without prior verification that *z*-values do not differ through time and space, a rather unlikely proposition (Adler & Lauenroth, 2003; Manne et al., 2007).

References

Adler, P. B. & W. K. Lauenroth, 2003. The power of time: spatiotemporal scaling of species diversity. Ecology Letters 6: 749–756.

Allen, A. P. & E. P. White, 2003. Effects of range size on species–area relationships. Evolutionary Ecology Research 5: 493–499.

Cam, E., J. D. Nichols, J. E. Hines, J. R. Sauer, R. Alpizar-Jara & C. H. Flather, 2002. Disentangling sampling and ecological explanations underlying species–area relationships. Ecology 83: 1118–1130.

Chust, G., J. L. Pretus, D. Ducrot, A. Bedos & L. Deharveng, 2003. Identification of landscape units from an insect perspective. Ecography 26: 257–268.

Condit, R., S. de Loo, J. V. LaFrankie, R. Sujumar, N. Monokaran, E. G. Leigh, R. P. Foster, P. S. Ashton & S. P. Hubbell, 1996. Species–area and species–individual relationships for tropical trees—a comparison of three 50 ha plots. Ecology 84: 549–562.

Connor, E. F. & E. D. McCoy, 1979. The statistics and biology of the species–area relationship. American Naturalist 113: 791–833.

Drakare, S., J. J. Lennon & H. Hillebrand, 2006. The imprint of the geographical, evolutionary and ecological context on species–area relationships. Ecology Letters 9: 215–227.

Dumbrell, A. J., E. J. Clark, G. A. Frost, T. E. Randell, J. W. Pitchford & J. K. Hill, 2008. Changes in species diversity following habitat disturbance are dependent on spatial scale: theoretical and empirical evidence. Journal of Applied Ecology 45: 1531–1539.

Durrett, R. & S. Levin, 1996. Spatial models for species–area curves. Journal of Theoretical Biology 179: 119–127.

Gentile, G. & R. Argano, 2005. Island biogeography of the Mediterranean Sea: the species–area relationship for terrestrial isopods. Journal of Biogeography 32: 1715–1726.

Gray, J. S., K. I. Ugland & J. Lambshead, 2004a. On species accumulation and species–area curves. Global Ecology and Biogeography 13: 567–568.

Gray, J. S., K. I. Ugland & J. Lambshead, 2004b. Species accumulation and species area curves—a comment on Scheiner (2003). Global Ecology and Biogeography 13: 473–476.

Harte, J., A. Kinzig & J. Green, 1999a. Self-similarity in the distribution and abundance of species. Science 294: 334–336.

Harte, J., S. McCarthy, K. Taylor, A. Kinzig & M. L. Fischer, 1999b. Estimating species–area relationships from plot to landscape scale using species spatial-turnover data. Oikos 86: 45–54.

He, F. & P. Legendre, 2002. Species diversity patterns derived from species–area models. Ecology 83: 1185–1198.

Hortal, J., P. A. V. Borges & C. Gaspar, 2006. Evaluating the performance of species richness estimators: sensitivity to sample grain size. Journal of Animal Ecology 75: 274–287.

Kolasa, J., J. A. Drake, G. R. Huxel & C. L. Hewitt, 1996. Hierarchy underlies patterns of variability in species inhabiting natural microcosms. Oikos 77: 259–266.

Kolasa, J., C. L. Hewitt & J. A. Drake, 1998. The Rapoport's rule: an explanation or a byproduct of the latitudinal gradient in species richness? Biodiversity and Conservation 7: 1447–1455.

Lack, D., 1976. Island Biology: Illustrated by the Land Birds of Jamaica. University of California Press, Berkeley.

Lomolino, M. V., 2000. Ecology's most general, yet protean pattern: the species–area relationship. Journal of Biogeography 27: 17–26.

MacArthur, R. H. & E. O. Wilson, 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Manne, L. L., P. H. Williams, G. F. Midgley, W. Thuiller, T. Rebelo & L. Hannah, 2007. Spatial and temporal variation in species–area relationships in the Fynbos biological hotspot. Ecography 30: 852–861.

Pandit, S. N., J. Kolasa & K. Cottenie, 2009. Contrast between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. Ecology 90: 2253–2262.

Passy, S. I. & F. G. Blanchet, 2007. Algal communities in human-impacted stream ecosystems suffer beta-diversity decline. Diversity and Distributions 13: 670–679.

Romanuk, T. N. & J. Kolasa, 2001. Simplifying the complexity of temporal diversity dynamics: a differentiation approach. Ecoscience 8: 259–263.

Romanuk, T. N. & J. Kolasa, 2002. Environmental variability alters the relationship between richness and variability of community abundances in aquatic rock pool microcosms. Ecoscience 9: 55–62.

Scheiner, S. M., 2004. A mélange of curves—further dialogue about species–area relationships. Global Ecology and Biogeography 13: 479–484.

Scheiner, S. M., S. B. Cox, M. Willig, G. G. Mittelbach, C. Osenberg & M. Kaspari, 2000. Species richness, species–area curves and Simpson's paradox. Evolutionary Ecology Research 2: 791–802.

Schuh, M. & R. Diesel, 1995. Breeding in a rock pool: larvae of the semiterrestrial crab *Armases [=Sesarma] miersii* (Rathbun) (Decapoda: Grapsidae) develop in a highly variable environment. Journal of Experimental Marine Biology and Ecology 185: 109–129.

Shen, G. C., M. J. Yu, X. S. Hu, X. C. Mi, H. B. Ren, I. F. Sun & K. P. Ma, 2009. Species–area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. Ecology 90: 3033–3041.

Srivastava, D. S., J. Kolasa, J. Bengtsson, A. Gonzalez, S. P. Lawler, T. E. Miller, P. Munguia, T. Romanuk, D. C. Schneider & M. K. Trzcinski, 2004. Are natural microcosms useful model systems for ecology? Trends in Ecology and Evolution 19: 379–384.

Therriault, T. W. & J. Kolasa, 1999. Physical determinants of richness, diversity, evenness and abundance in natural aquatic microcosms. Hydrobiologia 412: 123–130.

Therriault, T. W. & J. Kolasa, 2000. Explicit links among physical stress, habitat heterogeneity and biodiversity. Oikos 89: 387–391.

Tjørve, E. & K. M. C. Tjørve, 2008. The species–area relationship, self-similarity, and the true meaning of the *z*-value. Ecology 89: 3528–3533.

Triantis, K. A., M. Mylonas, M. D. Weiser, K. Lika & K. Vardinoyannis, 2005. Species richness, environmental heterogeneity and area: a case study based on land snails in Skyros archipelago (Aegean Sea, Greece). Journal of Biogeography 32: 1727–1735

Triantis, K. A., K. Vardinoyannis, E. P. Tsolaki, I. Botsaris, K. Lika & M. Mylonas, 2006. Re-approaching the small island effect. Journal of Biogeography 33: 914–923.

Turner, K. A. & E. Tjørve, 2005. Scale-dependence in species–area relationships. Ecography 28: 1–10.

White, E. P., 2004. Two-phase species–time relationships in North American land birds. Ecology Letters 7: 329–336.