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ECOLOGICAL SOUNDING

Island ecology and contingent theory: the role of spatial scale and taxonomic bias

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ABSTRACT

Scale, the scale dependency of patterns and processes, and the ways that organisms scale their responses to these patterns and processes are central to island and landscape ecology. Here, we take a database of studies in island ecology and investigate how studies have changed over a 40-year period with respect to spatial scale and organisms studied. We demonstrate that there have been changes in the spatial scale of islands studied and that there is taxonomic bias in favour of vertebrates in island ecological studies when compared to scientific publications as a whole. We discuss how such taxonomic bias may have arisen and discuss the implications for ecology and biogeography.

Key words invertebrates, island area, island biogeography, island ecology, plants, spatial scale, vertebrates.

> *Ecological patterns and the laws, rules and mechanisms that underpin them are contingent on the organisms involved and their environment* (Lawton, 1999, p. 177).

There is an increasing recognition of the importance of scale and the scale dependency of patterns and processes in ecology, and the ways that organisms scale their responses to these patterns and processes (Levin, 1992; Wiens *et al*., 1993; Hubbell, 2001). Here, we investigate how studies in island ecology have changed over a 40-year period with respect to spatial scale and the organisms studied. Island ecology has a long pedigree in ecology and biogeography, stretching at least as far back as the work of Alfred Russel Wallace (1880), although in recent years island ecology has been dominated by island biogeography *sensu* MacArthur & Wilson (1967) (Whittaker, 1998). The MacArthur–Wilson model is based on the assumption that the numbers of species found on islands is a balance between the opposing rates of immigration and extinction, the latter influenced by island area acting on population size and the former influenced by distance from the mainland. As such, a common methodological approach has been to count numbers of species on a sample of islands (oceanic or habitat) of differing sizes and relate patterns of species richness to geographical (e.g. area, isolation) or physical (e.g. habitat diversity, altitude) attributes of islands (e.g. McCollin, 1993; Báldi & Kisbenedek, 2000). Alternative approaches, using more intensive studies on a smaller range of islands (e.g. Blondel *et al*., 1999), can also be very informative but tend to be much less common.

We ask whether there are trends in the spatial scales chosen by researchers working in island ecology over time and whether there are trends in taxa studied. If any such trends exist we ask what are their causes and query whether they are exclusive to island ecology or whether they reflect a more fundamental bias or lack of rigour in ecological method. These are important questions not just for island ecology, but potentially have wider implications for landscape ecology and biogeography.

We use a pre-existing dataset assembled by Wright *et al*. (1998) for their analysis of nestedness in ecological communities. The spread of papers in this dataset is not comprehensive, but it does represent a large sample of studies published between 1933 and 1993. The 163 independent data matrices used by Wright *et al*. (1998) include useful information for such an analysis including taxon, location and island size, among others (see www.aics-research.com/nested). In order to test this dataset for trends with respect to spatial scale, data for numbers of species, numbers of islands, minimum and maximum area were entered into correlation

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Table 1 Correlation matrix between year of publication and number of islands, number of species and area (km^2) of the smallest and largest islands. Pearson's correlation coefficient, *N* and two-tailed significance are given. Year: year of publication; No. islands and No. species are the number of islands and species per study, respectively; Min. area and Max. area are the size of the smallest and largest island per study, respectively

	No. islands	No. species	Min. area	Max. area
Year	0.287	−0.148	−0.080	0.032
	150	150	50	63
	< 0.001	0.071	0.580	0.805
No. islands		−0.053	−0.480	−0.036
		150	50	63
		0.520	< 0.001	0.778
No. species			−0.021	−0.065
			50	63
			0.885	0.611
Min. area				0.791
				50
				< 0.001

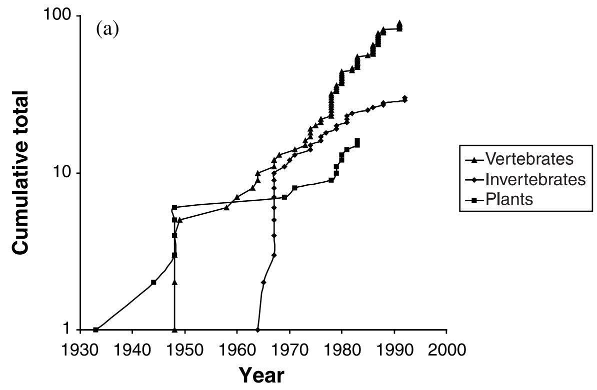
analyses. All variables were $\log_{10}$-transformed to normalize their distributions.

This analysis showed that the numbers of islands used in studies increased with time (Pearson's $r = 0.29$, $P < 0.001$, $n = 150$). However, while there appeared to be no significant trend to sample larger islands ($r = 0.03$, NS), or smaller islands with time ($r = -0.080$, NS), there was a tendency for larger datasets to include smaller islands ($r = -0.48$, $P < 0.001$, $n = 50$) but not larger islands ($r = -0.036$, NS) (Table 1).

In terms of taxa studied, there was a clear bias towards vertebrates (Fig. 1a). The rate of increase in vertebrate studies remained fairly constant, probably as a result of increases in different groups being investigated. After an initial rapid rise, rates of increase for invertebrates tailed off and studies of plants similarly failed to match other taxa. Given the most recent estimates of total global biodiversity in these groups one might expect the order to be reversed (Heywood, 1995).

Wright *et al.* used their dataset to test for nestedness, and it was compiled originally by Connor & McCoy (1979) for a critique of the species–area relationship. We are therefore compelled to ask whether any conclusions of these analyses are contingent upon the scales and organismal bias. Further, what are the reasons for any apparent biases, are they unique to island ecology, or are they simply a reflection of the inherent biases in ecology as a whole?

As a first step to addressing these questions we compared the results in Fig. 1a to the frequencies of studies in these taxonomic groups overall by carrying out an analysis using



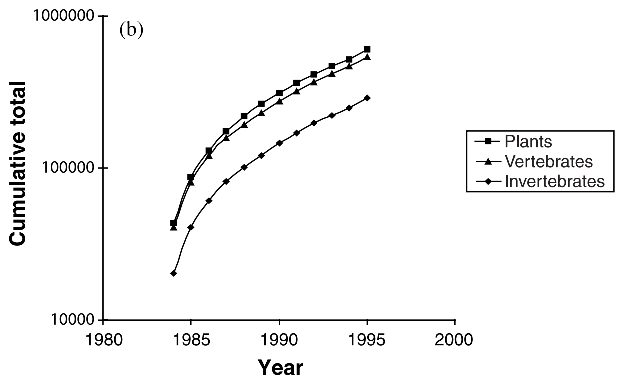


Fig. 1 Cumulative totals of numbers of published studies against time for (a) island studies from 1933 to 1993, and (b) for publications in CAB ABSTRACTS® 1982–96. See text for further explanation (NB: scales are not the same).

the bibliographic database, CAB ABSTRACTS®. We recognize that using the general search terms, 'vertebrate', 'invertebrate' and 'plant' will not necessarily pick up studies on specific taxonomic groups we would be interested in, although this is balanced by the comprehensiveness of the database, which includes over four million records added since its computerization in 1973. The database covers a wide range of fields, including agriculture, forestry, aspects of human health, human nutrition, animal health and the management and conservation of natural resources. (NB: it is not possible to search by publication year, so several years were combined. For example, there were 121 466 publications for vertebrates in the years 1984–86, hence a figure of 40 489 was used.)

There is an almost linear cumulative trend in publications (Fig. 1b). A visual comparison of Fig. 1a and b indicate that the cumulative rates of increase of the three taxonomic groups differ markedly between those for island ecology and for the background radiation. Studies of vertebrates dominate island ecology, plants show an initial rapid rise but soon tailed off, while studies of invertebrates entered the race later, showed a rapid rise, but again tailed off (Fig. 1a). In contrast, the background radiation shows steady rates of increase in plants, vertebrates and invertebrates (in order of numerical dominance) and the respective rates do not differ (i.e. the lines do not cross).

One possible explanation for these differences is that there exists a trade-off in island ecology between scientific requirements and practical pressures. Although the importance of including more larger islands and/or using a greater range of spatial scales in island studies has been stressed previously (MacArthur & Wilson, 1967; Whittaker, 1998) there are limitations to this, because much research is conducted by postgraduates or by established researchers with limited time in the field. Accordingly, there may be a tendency to choose sites and taxa to generate sufficient data to meet the requirements of the most commonly used statistical techniques (e.g. regression analysis) that can be reasonably accomplished by a single researcher (or at best, a small team of researchers) within the allotted time. The dominance of vertebrates in island ecology may be a result of choice of easy groups to work with (e.g. in terms of ease of sampling and of identification — especially relevant for relatively inexperienced postgraduates) as well as perceptions of which taxa are thought to be worthy of attention (particularly relating to questions in conservation biology) notwithstanding our inherent bias to flagship taxa that have intrinsic appeal for fellow *Homo sapiens*.

Recently, a decline in the number of publications in island biogeography in favour of metapopulation biology has been taken as evidence for a paradigm-shift taking place (Hanski & Simberloff, 1997). Metapopulation studies are not immune to taxonomic biases such as those shown here since there appears to be an overdominance of butterfly studies (Thomas & Hanski, 1997). We have demonstrated that there are biases in taxon choice and spatial scale with respect to island ecology. Returning to the key questions: what are the implications of such biases in terms of understanding the importance of scale, scale dependency and the ways that organisms scale their responses to these patterns and processes in island ecology? We are unable to answer these questions yet, as ecological patterns and the laws, rules and mechanisms that underpin them are not only contingent on the organisms involved and their environment (Lawton, 1999), but also on methodological biases. These are key questions that merit further attention, but until we can filter out the effects of potential methodological bias they will remain difficult to answer.

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