FORUM is a lighter channel of communication between readers and contributors; it aims to stimulate discussion and debate, particularly by presenting new ideas and by suggesting alternative interpretations to the more formal research papers published in ECOGRAPHY and elsewhere. A lighter prose is encouraged and no summary is required. Contributions should be concise and to the point, with a relatively short bibliography. Formal research papers, however short, will not be considered.

Parasites and the neutral theory of biodiversity

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At a time when biodiversity is under threat from human encroachment upon, and destruction of, natural habitats, we are in a dire need of a theory of biodiversity that integrates what we know of the processes responsible for the origin and maintenance of species diversity in a predictive framework. Hubbell (2001) proposes such a theory, analogous to the neutral allele theory of molecular evolution (Kimura 1983). The latter theory proposes that selectively neutral alleles arise by mutation and fluctuate randomly in relative abundance; in this scenario, natural selection is not necessary to explain the substantial genetic variation observed in natural populations. Similarly, assuming that all individuals in a community, whatever their species, have roughly identical per capita probabilities of birth, death, dispersal and speciation, Hubbell (2001) shows that ecological drift coupled with random speciation and dispersal are sufficient to explain observed patterns of species richness and relative species abundances on a range of spatial and temporal scales. The theory is neutral because it postulates no differences among species in a community in key per capita demographic parameters, and involves no competitive interactions. The only other central assumption of Hubbell's theory is that the community is saturated with individuals, with community members thus engaged in a zero-sum game: an increase in the abundance of one species must coincide with a decrease in the collective number of individuals of all other species. From these two basic assumptions, the neutral theory of biodiversity predicts many patterns already documented in nature, especially in tropical tree communities (Hubbell 2001; see also Bell 2000, 2001). For example, the neutral theory predicts that there will always be more rare species in local communities than expected from a lognormal distribution of species abundance. Still, the quantitative fit between predicted and observed patterns remains a matter of controversy (McGill 2003, Volkov et al. 2003), and the future of the neutral theory of biodiversity will depend on how its assumptions fare compared to those of competing models (Nee and Stone 2003).

The neutral theory is in fact a theory of within-trophic-level diversity. It makes predictions relevant to ecological communities consisting of trophically-similar, sympatric species that actually or potentially compete for the same or similar resources. It thus applies to species at the same trophic level but not necessarily belonging to the same feeding guilds. This aspect of Hubbell's (2001) neutral theory could make it relevant to many parasite communities. For instance, gastrointestinal helminths in a vertebrate host population, although belonging to different higher taxa, all live in the same general habitat (the digestive tract of the host), all feed on the same or similar food resources, and all potentially compete for one basic limiting resource: attachment space. A community of parasitic helminths (or component community, following the terminology of ecological parasitologists; Bush et al. 1997) is spatially fragmented; each host individual represents a suitable patch for adult worms, separated from others by an inhospitable environment. However, all host individuals are exposed to the same pool of infective larvae, with the probabilities of infection depending on characteristics of the hosts and on chance. This is no different from many communities of free-living organisms, where the habitat is patchy, such as boulders on a beach used as substrate by intertidal marine invertebrates settling in as planktonic larvae. The determinants of species richness in communities of parasitic helminths have been the focus of much research over the past two decades (see reviews in Poulin 1997, 1998, Morand 2000). Early predictions were derived from the theory of island biogeography (MacArthur and Wilson 1967, Kuris et al. 1980); host features presumed to promote high rates of parasite colonization or speciation were expected to explain much of the variation in parasite species richness among host species. More recently, epidemiological theory has been providing a new perspective on the diversity of parasite communities (Roberts et al. 2002). Epidemiological models make predictions about the conditions necessary for new parasite species to invade and persist in a host population. For instance, each parasite species has a threshold host population density above which the transmission rate of infective stages is sufficient to maintain the parasite locally. Recent empirical tests show that epidemiological processes may indeed be important in determining local parasite species richness (Morand and Poulin 1998, Arneberg 2002).

Can the neutral theory of biodiversity also be applied to parasite communities? As emerging diseases are becoming a growing problem for wildlife and domesticated animals (Daszak et al. 2000, Dobson and Foufopoulos 2001, Friend et al. 2001, Harvell et al. 2002), it is becoming imperative to understand just what drives parasite and pathogen biodiversity. Here, I first take a brief look at patterns of relative species abundance in intestinal parasite communities of vertebrates to see whether they show a qualitative fit to those expected from the neutral theory. I then discuss the two central assumptions of the neutral theory, the equivalence of individuals regardless of species and the saturation of individuals leading to zero-sum community dynamics, within the context of parasite communities.

Relative species abundance in parasite communities

To illustrate general patterns of relative species abundance, I chose three communities of intestinal helminths in bird hosts with very different species richness. These may not be representative of all helminth communities, but there is no reason to believe that they are unusual in any way. The first is the community of helminths from lesser scaup ducks *Aythya affinis* in Alberta, Canada (Bush and Holmes 1986). A total of almost one million worms were recovered from 45 adult birds; these belong to 52 different helminth species, making it one of the most diverse helminth communities reported in the literature. The second helminth community is that of cattle egrets *Bubulcus ibis* in Alabama (Stuart et al. 1972). Over 5000 worms belonging to 10 species were recovered from 30 individual birds; this sort of species richness is more typical of that observed in aquatic birds in general. Finally, the third helminth community considered here is that found in the red-necked grebe *Podiceps grisegena* in Alberta, Canada (Stock and Holmes 1987). A sample of 33 birds yielded almost 90 000 worms belonging to 23 species, giving it a helminth diversity intermediate between those of the two other communities.

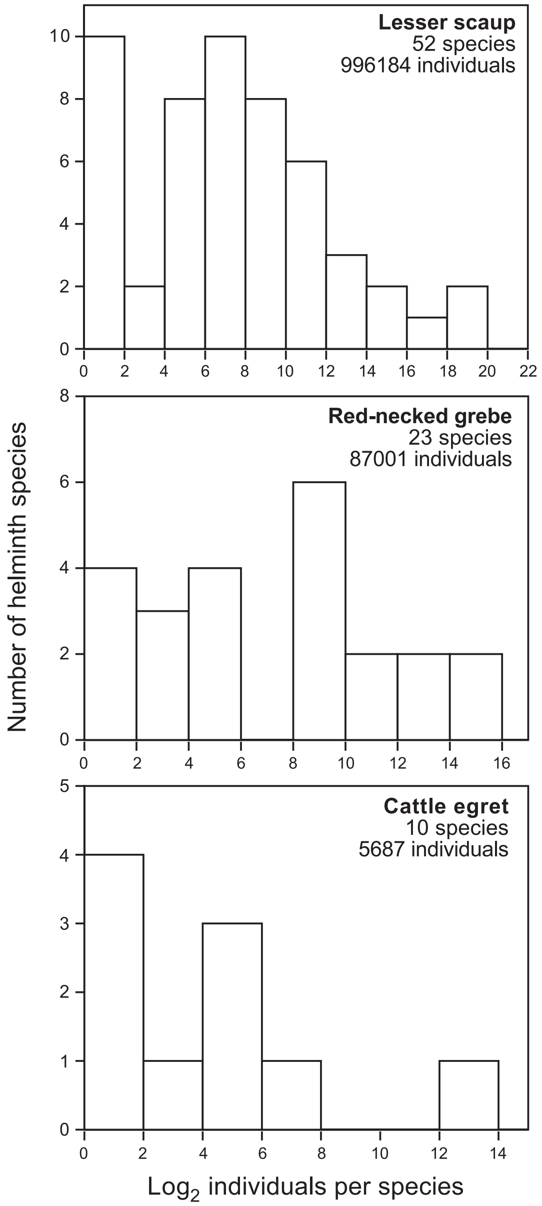

Fig. 1. Frequency distribution of the abundances of gastrointestinal helminth parasite species in three different bird species. Note that abundance (number of individuals per species) is $\log_2$-transformed, as in Hubbell (2001).

The frequency distributions of species abundance for these three helminth communities are shown in Fig. 1. The distributions all have an internal mode, but all show an excess of rare species, too. Had many more individual worms been recovered from much larger samples of bird individuals, the shape of the distribution would be different: the peaks on the left would probably be replaced by a very long tail of very rare species. Hubbell's (2001) neutral theory predicts that species abundances should follow a statistical distribution known as the zero-sum multinomial, which differs from the lognormal distribution in usually having a long tail of rare species. The presence or length of that tail depends on the magnitude of dispersal limitation of species in the metacommunity (i.e. among communities within a region). Thus, at a glance, data from the three bird communities agree with this expected pattern.

Another way of looking at these data consists of plotting relative species abundance, expressed as a percentage of all individuals in the community, against the rank in abundance of the species (Fig. 2). The curve for cattle egret, in which helminth species richness is lowest, is steeper than for the other two bird species, indicating that one or very few helminth species achieve numerical dominance in the community when the community is species-poor. The general shape of these dominance-diversity curves, and the way in which it changes with increasing species richness, are also in general accordance with expectations of the neutral theory (Hubbell 2001).

Qualitatively, therefore, these patterns fit what is expected under the neutral theory. Whether a quantitative fit can also be achieved will become clearer once tables for the zero-sum multinomial distribution are published, as promised by Hubbell (2001). But I have no doubt that the theory's expectations can be fitted to the patterns observed in parasite communities. The question will be then whether the fit is coincidental or whether it truly reflects the operation of the ecological processes postulated by the neutral theory.

Parasites and the assumptions of the neutral theory

The neutral theory of biodiversity appears quite robust to violations of its assumptions (Hubbell 2001). Still, one would expect the assumptions to be generally correct, or at least a caricature of reality.

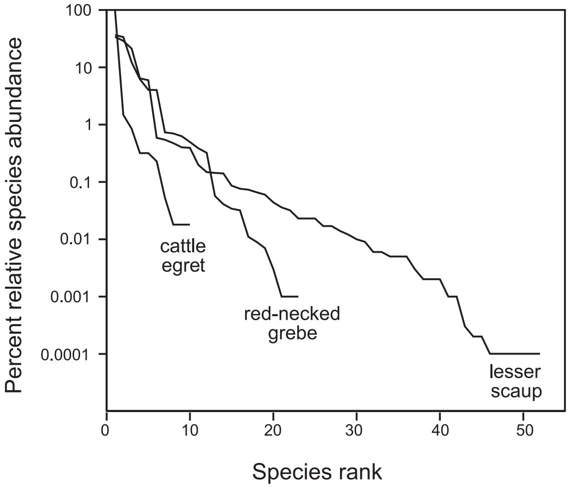

Fig. 2. Patterns of relative species abundance in the gastrointestinal helminth parasite communities of three different bird species. Helminth species in each community are ranked in percentage relative abundance from commonest (left) to rarest (right). Note that the percentage relative abundance on the y-axis is on a logarithmic scale.

One of the two fundamental assumptions of the neutral theory of biodiversity is that communities are saturated with individuals engaged in a zero-sum game competing for some limiting resource (Hubbell 2001). There has been a debate in the parasitology literature regarding whether or not helminth parasite communities are saturated with species (Kennedy and Guégan 1996, Rohde 1998). However, with respect to individual helminths, there is no debate: host populations (i.e. parasite component communities) are not saturated with individual parasites. For instance, in the lesser scaup mentioned above, the number of individual worms per bird host ranged from <100 to $>100\,000$ (Bush and Holmes 1986). All birds sampled were breeding adults, and this huge variation is not merely the outcome of gross differences in host age or body mass. There are always many lightly-infected host individuals in natural systems. Although a few host individuals may be saturated with worms, many more are far from full. There must therefore always be numerous empty spaces potentially available for parasite settlement in a helminth community. The reason for this is the tendency for metazoan parasites to be aggregated among their hosts (Poulin 1998, Wilson et al. 2002). The distribution of individuals of the same helminth species among host individuals is far from even or random: it follows a negative binomial distribution characterised by most individual hosts being free of parasites and a few hosts harbouring the majority of parasites. Aggregation results from a combination of slight differences in susceptibility among individual hosts and stochastic processes (Poulin 1998, Wilson et al. 2002). Summing up the aggregated distributions of the different helminth species co-occurring in a host population generates a complex distribution pattern, but one that still leaves many unexploited spaces in the digestive tracts of host individuals. The global distribution of all worms (all species combined) within a host population may be less intensely aggregated than that of any given helminth species, but it may also be much more aggregated: positive pairwise associations between the abundances of helminth species are very common (see Bush and Holmes 1986, Lotz and Font 1994). The point of the above arguments is that helminth communities in vertebrate hosts are generally not saturated with individual helminths. The population dynamics of different helminth species are to some extent independent of one another, and the community members are not locked in a zero-sum game.

The second cornerstone assumption of the neutral theory is that individuals of all species are identical, on a per capita basis, in their probabilities of birth, death or dispersal (Hubbell 2001). Although this statement will certainly raise objections, Hubbell (2001) does a great job in supporting it. With respect to parasites, however, I see at least one way in which inequalities among individuals of all species can greatly affect the predictions of the neutral theory. I am not referring to inequalities in competitive abilities between parasite species. This has been demonstrated by the asymmetrical nature of competition between many helminth species, the obvious positional shift shown by one or both species in a pair when co-occurring in the same host individual, and the possible exclusion of one species by another (see Poulin 1998 for review). Instead, I want to address the huge inequalities in body size among and within helminth species. Based on his experience with close-canopy forests, Hubbell (2001) visualizes a community as a multidimensional matrix in which each cell is occupied by one individual. When this individual dies, the cell is then taken up by a recruit from the same species or from another species. In this situation, where all individuals have roughly the same size (i.e., they all fit in one cell), probabilities of colonizing the cell may well be similar across the different species in the community. Helminths of different species, however, are not similarly-sized. Some species of cestodes, or even acanthocephalans and nematodes, are several orders of magnitude larger than other community members in the same feeding guild. If helminth communities were saturated with individuals, then the death of a small-bodied worm would create a vacancy that could not equally be filled by any species (and again under saturation, the death of a large-bodied worm could open up spaces for many small-bodied worms, violating the rules of the zero-sum game). To complicate matters further, there is also much intraspecific variability in the adult sizes of certain helminth species, such as some cestodes and nematodes parasitic in fish (Shostak and Dick 1987, Szalai and Dick 1989). In any event, with or without saturation of individuals in helminth communities, huge inequalities in body sizes among species in the same community defy the assumption of equivalence among all individuals.

The neutral theory of biodiversity asserts that communities are dispersal-assembled rather than niche-assembled (Hubbell 2001). Recently, Mouillot et al. (2003) attempted to fit the relative abundance patterns of species in helminth communities from fish hosts to niche-assembly models using biomass rather than abundance data. This approach took into account the inequalities in size mentioned above. Mouillot et al. (2003) found support for the random assortment model, which suggests that different species apportion resources independently from one another (Tokeshi 1999). This agrees with the view that most parasite communities are non-saturated with species or individuals, with many empty spaces, and with interspecific competition not playing a major structuring role. Dispersal-assembly models, such as the neutral theory, could possibly fit these data well, but they will need to be based on realistic assumptions about parasites to achieve broad acceptance.

Concluding remarks

Time will tell whether the neutral theory of biodiversity can be applied successfully to parasite communities. It would not surprise me if its predictions prove a good quantitative fit to observed patterns of parasite species richness and relative abundance. However, this accuracy may be based on biological assumptions that are invalid. Several centuries ago, when the geocentric view of the universe was accepted by all, good mathematical models allowed one to predict the movement of celestial bodies across the heavens. These models were replaced by new ones once it became accepted that the Earth orbited the Sun. The new models provided only marginally more accurate predictions of the planets' movements, but they were immensely preferable because they were based on what had become accepted facts. The neutral theory's predictions regarding patterns of species richness and relative abundances in parasite communities may prove accurate enough, but their biological foundation clashes with evidence coming from several fronts. The challenge ahead will be to reconcile its mathematics with biological reality.

Acknowledgements – I thank the Royal Society of New Zealand for supporting me via a James Cook Research Fellowship.

References

Arneberg, P. 2002. Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. – Ecography 25: 88–94.

Bell, G. 2000. The distribution of abundance in neutral communities. – Am. Nat. 155: 606–617.

Bell, G. 2001. Neutral macroecology. – Science 293: 2413–2418.

Bush, A. O. and Holmes, J. C. 1986. Intestinal helminths of lesser scaup ducks: patterns of association. – Can. J. Zool. 64: 132–141.

Bush, A. O. et al. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. – J. Parasitol. 83: 575–583.

Daszak, P., Cunningham, A. A. and Hyatt, A. D. 2000. Emerging infectious diseases of wildlife: threats to biodiversity and human health. – Science 287: 443–449.

Dobson, A. P. and Foufopoulos, J. 2001. Emerging infectious pathogens of wildlife. – Philos. Trans. R. Soc. Lond. B 356: 1001–1012.

Friend, M., McLean, R. G. and Dein, F. J. 2001. Disease emergence in birds: challenges for the twenty-first century. – Auk 118: 290–303.

Harvell, C. D. et al. 2002. Climate warming and disease risks for terrestrial and marine biota. – Science 296: 2158–2162.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press.

Kennedy, C. R. and Guégan, J.-F. 1996. The number of niches in intestinal helminth communities of *Anguilla anguilla*: are there enough spaces for parasites? – Parasitology 113: 293–302.

Kimura, M. 1983. The neutral theory of molecular evolution. – Cambridge Univ. Press

Kuris, A. M., Blaustein, A. R. and Alió, J. J. 1980. Hosts as islands. – Am. Nat. 116: 570–586.

Lotz, J. M. and Font, W. F. 1994. Excess positive associations in communities of intestinal helminths of bats: a refined null hypothesis and a test of the facilitation hypothesis. – J. Parasitol. 80: 398–413.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.

McGill, B. J. 2003. A test of the unified neutral theory of biodiversity. – Nature 422: 881–885.

Morand, S. 2000. Wormy world: comparative tests of theoretical hypotheses on parasite species richness. – In: Poulin, R., Morand, S. and Skorping, A. (eds), Evolutionary biology of host-parasite relationships: theory meets reality. Elsevier, pp. 63–79.

Morand, S. and Poulin, R. 1998. Density, body mass and parasite species richness of terrestrial mammals. – Evol. Ecol. 12: 717–727.

Mouillot, D., George-Nascimento, M. and Poulin, R. 2003. How parasites divide resources: a test of the niche apportionment hypothesis. – J. Anim. Ecol. 72: 757–764.

Nee, S. and Stone, G. 2003. The end of the beginning for neutral theory. – Trends Ecol. Evol. 18: 433–434.

Poulin, R. 1997. Species richness of parasite assemblages: evolution and patterns. – Annu. Rev. Ecol. Syst. 28: 341–358.

Poulin, R. 1998. Evolutionary ecology of parasites: from individuals to communities. – Chapman and Hall.

Roberts, M. G. et al. 2002. Parasite community ecology and biodiversity. – In: Hudson, P. J. et al. (eds), The ecology of wildlife diseases. Oxford Univ. Press, pp. 63–82.

Rohde, K. 1998. Is there a fixed number of niches for endoparasites of fishes? – Int. J. Parasitol. 28: 1861–1865.

Shostak, A. W. and Dick, T. A. 1987. Individual variability in reproductive success of *Triaenophorus crassus* Forel (Cestoda: Pseudophyllidea), with comments on use of the Lorenz curve and Gini coefficient. – Can. J. Zool. 65: 2878–2885.

Stock, T. M. and Holmes, J. C. 1987. Host specificity and exchange of intestinal helminths among four species of grebes (Podicipedidae). – Can. J. Zool. 65: 669–676.

Stuart, J. J., Dismukes, J. F. and Dixon, C. F. 1972. Endoparasites of the cattle egret (*Bubulcus ibis*) in Alabama. – J. Parasitol. 58: 518.

Szalai, A. J. and Dick, T. A. 1989. Differences in numbers and inequalities in mass and fecundity during the egg-producing period for *Raphidascaris acus* (Nematoda: Anisakidae). – Parasitology 98: 489–495.

Tokeshi, M. 1999. Species coexistence: ecological and evolutionary perspectives. – Blackwell.

Volkov, I. et al. 2003. Neutral theory and relative species abundance in ecology. – Nature 424: 1035–1037.

Wilson, K. et al. 2002. Heterogeneities in macroparasite infections: patterns and processes. – In: Hudson, P. J. et al. (eds), The ecology of wildlife diseases. Oxford Univ. Press, pp. 6–44.