Biological diversity of fish communities: pattern and process[§]

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For over 150 years, ecologists have been striving to explain fundamental patterns of biological diversity, such as the observation that communities invariably consist of common and rare species, and to unravel the processes that underpin these patterns. This task is increasingly urgent given the accelerating loss of biological diversity. Although fishes are the most diverse vertebrate taxon and fish communities occur in a wide range of habitats, they have been relatively little studied in the quest to elucidate the processes that shape patterns of biological diversity. Here, some of the topics that investigations of fish assemblages can illuminate are highlighted. These include the characteristics of ecological communities and the role that dispersal limitation plays in structuring them, the distinction between core and occasional species, the insights that evaluating abundance in different currencies can bring and the assessment of community capacity. Questions are identified that future investigations of fish communities might tackle and a case study of a biodiverse ecoregion (Thailand and Peninsula Malaysia) is used to illustrate the need for better links between these ecological questions and effective conservation practice. © 2011 The Authors

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INTRODUCTION

Fishes are the most diverse of all vertebrate taxa. Nelson (2006) estimates the total number of species of fish as 32 500. Of these some 28 400 are considered valid species, where a valid species is one that consists of groups of interbreeding populations that are assumed to be reproductively isolated from other taxa (Nelson, 1999). It is likely that the numbers of valid species will increase as candidates are more thoroughly documented (Nelson, 2006). On the other hand molecular tools, such as barcoding (Ward *et al*., 2009; Ardura *et al*., 2010), can offer different answers to the question of how many fish species there are. For example, Zemlak *et al*. (2009) argued that about one-third of the fish species thought to be common to South Africa and Australia are probably two taxa rather than one. But irrespective of how fish species are delineated and counted, it is clear that this is a highly diverse group. To put

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it in context, there are around 10 000 bird species and 5000 mammal species. What is particularly striking, however, is that although fresh waters make up only *c*. 0·01% of the water on the planet, they support *c*. 40% of fish species (Nelson, 2006).

Given this variety, fishes offer rich opportunities to study a wide range of fundamental questions about biological diversity. Moreover, because rarity and richness go hand in hand, understanding the processes that underpin this diversity is crucial if effective policies for conservation are to be developed. The intertwining of pattern and process in ecology was recognized over 60 years ago (Watt, 1947). New theoretical developments combined with empirical studies now allow a much better understanding of the processes that underpin patterns of biological diversity. This paper focuses on one of the oldest patterns in ecology, which is the observation that communities are composed of species that vary in abundance. How investigations of fish assemblages can lead to new insights into the distribution of commonness and rarity and into the processes that shape these patterns are discussed. The paper concludes by considering how the insights that emerge from this work can aid conservation. The emphasis here is on ecological patterns rather than evolutionary ones but it is recognized that there is a large body of work exploring the origins of biological diversity, and the role of natural and sexual selection, and that fishes have been extensively and productively used in this context.

BACKGROUND

A universal feature of ecological communities is that some species are common, and others, typically the majority, are rare. Figs 1 and 2 provide an example of the type of species abundance distributions typically seen in fish communities. The observation that species vary in their proportional abundances with most taxa being rare was reported by Darwin (1859) and other 19th century naturalists, and was surely obvious to the earliest hunters and gatherers. There is a single known exception to this rule, and this is a case where a bacterium is the sole organism in a gold mine some 2·8 km below the Earth's surface (Chivian *et al.*, 2008). Despite the universality of the pattern of commonness and rarity, it was not until the 20th century that researchers began to quantify the distribution of species abundances (Motomura, 1932; Raunkaier, 1934; Fisher *et al.*, 1943; Preston, 1948). In essence, there are four approaches to quantifying and exploring species abundance distributions: visual and graphical methods, statistical models, tests of biological processes and neutral models. Although in principle these techniques can be separated into those that describe patterns and those that explain processes, in practice the same approach may be used in both contexts.

Visual and graphical methods are widely used to describe the pattern of diversity in communities. Often researchers simply want to plot a graph of the species abundance data and use the shape of this graph to draw conclusions about an assemblage. There are a number of methods of doing this and visual approaches to understanding species abundances have been widely used in the past and remain popular today (May, 1975; Magurran, 2004; McGill *et al.*, 2007). One method that is frequently adopted is the rank−abundance plot (MacArthur, 1957; Whittaker, 1960; Fig. 1). The *k*-dominance plot (Lambshead *et al.*, 1983) and *Q* statistic (Kempton & Taylor, 1978) are alternative ways of presenting species abundance data (Magurran, 2004). McGill *et al.* (2007) and McGill (2011) argue that an empirical cumulative density function
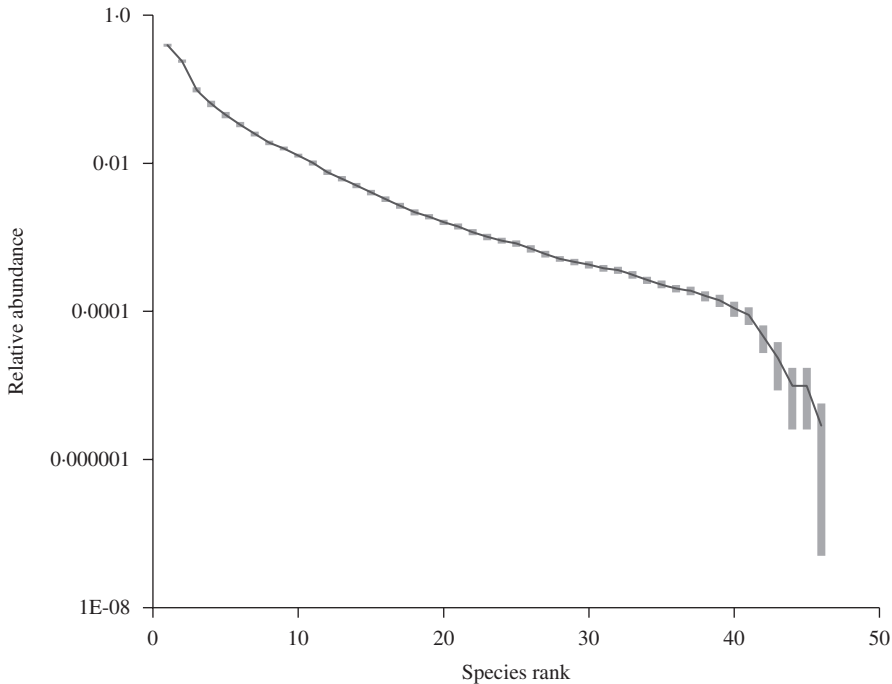
FIG. 1. Ecological communities typically have some common and many rare species. This figure illustrates the relative abundances of species in the Hinkley Point (Bristol Channel, U.K.) estuarine community of fishes that have been surveyed for three decades (Henderson, 2007; Henderson & Bird, 2010). The rank abundance plot summarizes the pattern across the time series. Values for first ranked species disregarding species identity, second ranked species, third ranked species and so on, have been averaged for each year of the time series. The 95% C.L. around these mean values are given (▪). The figure has been re-drawn from Magurran & Henderson (2010).

(eCDF) is a better method of presenting species abundance data (Fig. 2). This is because rank abundance plots are strongly influenced by species richness. Moreover, the eCDF approach is mathematically more powerful than the rank–abundance plot (McGill, 2011).

Alternatively, the investigator can fit a known distribution to the data, or calculate metrics that can be used to evaluate an assemblage. For example, the log-normal distribution, which was first proposed by Preston (1948), and the log-series distribution, which was introduced by Fisher (Fisher *et al*., 1943), provide a good fit to many natural communities. Diversity indexes linked to these models, such as Fisher's α statistic, are a convenient way of summarizing a community's diversity. Although inherently descriptive, it has been common practice to use these methods to make inferences about the processes that shape the patterns.

Biological models are the third method of approaching species abundance data. Here, the key idea is to model the ecological processes that determine the relative abundance of species. Competition is usually regarded as the primary driver of this; consequently, these models typically ask how niche space will be divided amongst competing species. The very first biological model was proposed by Motomura (1932). Later contributions include those by Sugihara (1989) and Tokeshi (1993,
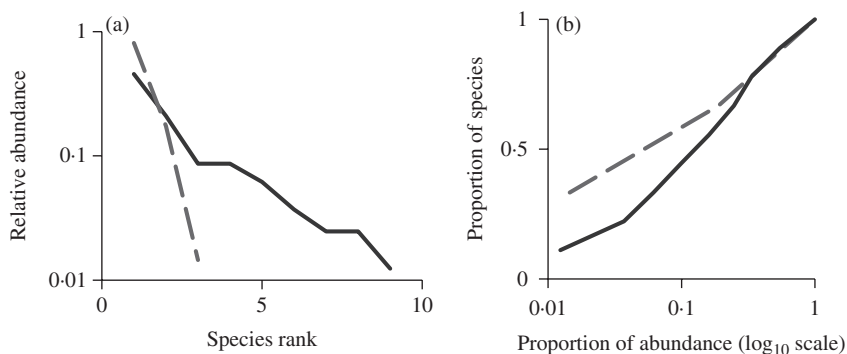
FIG. 2. (a) Rank abundance plots are a traditional method of illustrating species abundance data. Here, the figure contrasts the pattern of fish diversity seen in two localities in Trinidad's Northern Range. One site (Upper Aripo) (barrier; ----) is upstream of a barrier waterfall and thus experiences a high level of dispersal limitation. The other (Upper Tacarigua) (no barrier; ——) is in a river that is similar in terms of size and elevation but where there is no barrier waterfall. The site above the barrier has fewer species, and the pattern on the rank abundance figure suggests that this is a very uneven community with one species dominating. The impression of evenness is confounded by the differences in species richness. (b) The data are replotted in the form of an empirical cumulative distribution function (eCDF). Here, the species are sorted from least to most abundant. The cumulative abundances are then calculated and plotted (using a $\log_{10}$ scale) on the *x*-axis. The *y*-axis standardizes species richness (S) (by dividing each species rank by total richness) and plots the values S^{-1} to 1. This standardization makes it possible to directly compare assemblages that differ in species richness. In this example, this method of plotting shows that the barrier site has a higher proportion of rare species relative to its richness. This is evident from the fact that the line for the barrier assemblage lies above that of the no barrier assemblage at the left-hand (rare) side of the graph (A. E. Magurran, unpubl. data).

1996). By definition, these types of models are likely to be most relevant to small groups of species exploiting a common resource.

A fourth way of explaining inequalities in species abundances is to invoke neutral models. These models (Caswell, 1976; Bell, 2001; McGill, 2010) assume that biological differences between species play no role in shaping the pattern of abundance; in this they resemble the neutral theory of molecular genetics (Kimura, 1968). The model that has received the most attention is Hubbell's (2001) unified neutral theory of biogeography and biodiversity. Hubbell (2001) argues that species are functionally equivalent, at least as far as biodiversity is concerned, and that the pattern of species relative abundance in a local community is a result of both the species abundance distribution in the metacommunity (the source of colonists) and the extent of dispersal limitation (that is, how isolated the local community is relative to the metacommunity). Because neutral models seek to expose the processes that shape species abundances, they differ from the classical null-model approach in which a statistical test attempts to account for the influence of random chance (Gotelli & McGill, 2006). Hubbell's (2001) model is called a unified model because it attempts to bring together patterns that historically have been treated separately, such as the species abundance distribution and the species area relationship, in a common framework. As McGill (2010) notes, there are six of these models, and although they are formulated in different ways, they make similar assumptions about nature. Specifically, all six argue that individuals in the same species tend to be clumped, that species

abundances across large scales such as a region are inequitable (some common and many rare species), and that spatial (and temporal) interactions between species are unimportant in explaining the diversity patterns that the models seek to explain.

These approaches have contributed many new insights into the pattern of biological diversity in ecological communities and the processes that shape this pattern. Nonetheless, models based on contrasting and even mutually exclusive assumptions can generate predictions that match empirical data sets well (Chisholm & Pacala, 2010). Thus, while a good fit between model predictions and observed data is essential, this in itself is not sufficient to prove that a particular model can account for the processes that underpin a species abundance distribution (Magurran, 2004; McGill *et al*., 2007; Connolly & Dornelas, 2011; McGill, 2011). Stronger tests are needed (McGill *et al*., 2007).

There are a number of reasons why it has proved challenging to get a definitive explanation for the fundamental ecological pattern of commonness and rarity. As noted above, competing models can generate the same species abundance distribution, so fit alone is not enough to separate them. In addition, when models do make distinct predictions about abundance, this usually concerns the rare species (for example, the log-series distribution assumes a larger fraction of rare species than the log-normal model does). It is, however, the abundances of the rare species that are most vulnerable to sampling error (Preston, 1948). For example, any difference in catchability (Buckland *et al*., 2011) amongst species is likely to have the greatest effect on the detection of species that naturally occur at low frequencies. A related factor is that the extent of sampling in space, and its duration and frequency in time, influences the perception of the community structure (Loehle, 2006). When an assemblage is sampled repeatedly through time, the numbers of rare species encountered will increase (Magurran & Henderson, 2003; McGill, 2003). Similarly, increasing the spatial extent of the sampling will change the view of how the assemblage is structured (May, 1975; Tokeshi, 1993, 1999; Magurran, 2011). The shape of the species area relationship is important here too (Tjørve, 2003, 2009; Tjørve & Tjørve, 2008).

WHERE FISH STUDIES CAN HELP

Investigations of fish assemblages have the potential to increase the understanding of biological diversity, both through sharpened thinking on how communities are structured, and by providing data that will help tease apart the different explanations for patterns of commonness and rarity. Fishes are particularly useful subjects for exploring biodiversity patterns, as they live in habitats that range from temporary puddles (Costa & Brasil, 1990) to vast oceans, can vary by many orders of magnitude in abundance and body size and exhibit a wide range of life histories and behaviours. Because the taxon also includes many species that are commercially important, fisheries biologists routinely collect data that are invaluable for testing ideas. Here, some of the insights that investigations of fish communities have delivered are explored, and the opportunities that such studies offer for improving the understanding of patterns of biological diversity in nature are discussed. Inevitably the focus is on the most familiar examples and case studies to the authors, but that should not detract from the central message, which is that investigations of fish communities have the potential to move this research field forward.
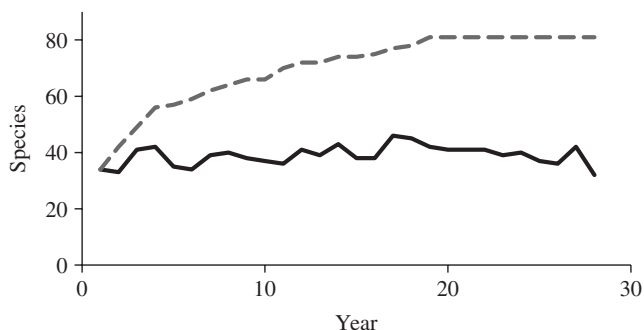
F<small>IG</small>. 3. The number of species caught each year at Hinkley Point estuarine assemblage (Bristol Channel, U.K.; see Fig. 1) (——) and the cumulative number of species through the three decade time series (‒ ‒ ‒) are shown.

WHAT IS MEANT BY A LOCAL COMMUNITY?

One question that researchers and policy makers often ask concerns the number of species that are present in a particular locality or habitat. Ecologists who are trying to quantify the pattern of species abundances would also like to know how many species there are. Although the question seems straightforward, the answer rarely is. There are two issues here. The first is the difficulty of completely censusing the species present and the second, the observation that all communities experience turnover. A new generation of statistics, developed by Chao (1987), Colwell & Coddington (1994), Chao *et al*. (2000) and Gotelli & Colwell (2011), provide a means of estimating species richness and has proved a very useful technique. Comments on these methods and other approaches are given by Ugland *et al*. (2003, 2005), Ugland & Gray (2004) and Reichert *et al*. (2010). These methods draw on the frequencies or abundances of rarely sampled species to deduce the total number of species. The usual metaphor applied to this is that a local community resembles a sweet or candy jar; with sufficient sampling, it should be possible to get an exact idea of how many species are present. The total number of taxa recorded in any natural system, however, will continue to rise through time, even given perfect sampling, because new species colonize and existing ones become locally extinct (Fig. 3).

This constant inflow and loss of species are the ideas that underpin MacArthur & Wilson's (1967) theory of island biogeography. The rate at which new species colonize will be related to how leaky an assemblage is. Fish assemblages very nicely illustrate how leakiness varies. Thus, an isolated lake receives colonists only occasionally whereas a section of ocean will be open to a constant stream of new species. Indeed, fish assemblages can be viewed as distributed along a continuum of open to closed assemblages. This is an important resource to ecologists seeking to explain patterns of diversity. Variation in leakiness provides an opportunity to link changes in structure to the level of dispersal limitation, a key element of Hubbell's (2001) neutral theory. A classic example is the contrast in the structure of stream communities in Trinidad's Northern Range above barrier waterfalls, compared with equivalent streams in rivers that lack these barriers (Magurran, 2005; Fig. 2). Another instance would be the lakes in Canada's Experimental Lakes Area (Beamish *et al*., 1976) as these vary in size and connectedness. There are many other possibilities.

To date, most tests of biodiversity models have used only a very limited number of datasets, with the tree communities in Barro Colorado Island (BCI) being one of the most thoroughly analysed (McGill, 2010). Any theory that seeks to offer general explanations for patterns of diversity needs to be demonstrably applicable to different community types, and it is here that fish communities have considerable and as yet barely exploited potential. Recent analyses have begun to explore the consequences of different types of dispersal. For example, Rosindell & Cornell (2009) extend spatially explicit neutral models to include long-distance dispersal and test their predictions using the BCI data. The range of dispersal scenarios offered by fish communities could be invaluable to researchers working in this area.

There are other aspects of community ecology that are taking increasing note of dispersal limitation and the openness of assemblages. For instance, leakiness provides an opportunity to distinguish an established core community of species from the occasional or vagrant species that colonize and then become locally extinct. This concept, and its implications, is now explored.

THE CORE COMMUNITY

Within any local community some species are persistent, that is, they occur repeatedly when the community is resampled through time, while others appear only occasionally. This pattern is evident at Hinkley Point (51° 13′ N; 03° 08′ W), an estuarine fish assemblage in the Bristol Channel, U.K., that has been sampled monthly for 30 years (Henderson, 2007; Henderson & Bird, 2010). The tempo of the pattern will obviously be linked to the leakiness of the community with open ones receiving a stream of arriving species. In the Hinkley estuarine community, species can be distinguished that are almost always present (the core species) from those that make occasional appearances (Fig. 4). This persistence is linked to abundance; core species are generally abundant, while occasional species are often rare. Importantly, this distinction is underlain by differences in the ecology of the species. Core species are typically those associated with estuarine habitats, while occasional species are often adapted to other environments such as deep water or the open sea (Magurran & Henderson, 2003). Moreover core species will be the ones responsible for much of the function (*e.g.* biomass production). If the species abundance distribution at Hinkley Point is divided (based on data accumulated across three decades) into core and occasional species, abundances of core species resemble a log-normal distribution, while the abundances of occasional species are more similar to a log-series distribution. This finding is interesting because it shows that it makes biological sense to partition a species abundance distribution and fit different models to the different parts. It also helps explain why some communities have an excess of rare species (Nee *et al*., 1991; McGill, 2003). Similar partitions have been applied to other communities, including insects (Ulrich & Ollik, 2004; Ulrich & Zalewski, 2006). Incidentally, the observation that there are subsets of species leads to interesting questions about what a local community actually is. Traditionally ecologists have considered communities to be groups of interacting species, although the extent of these interactions is probably a lot more limited than people often assume (Magurran & Henderson, 2010; McGill, 2010). Assemblage is an alternative term that makes fewer assumptions about species interactions (Fauth *et al*., 1996).
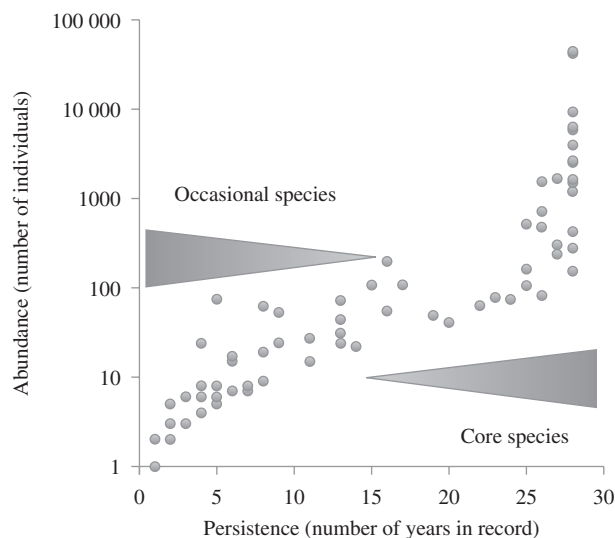
FIG. 4. Species that are more persistent in the record are also more abundant. This figure plots the numerical abundance of species in the Hinkley Point estuarine assemblage (Bristol Channel, U.K.), against number of years the species are present. Persistent species are regarded as core species and infrequent species as occasional ones. There are ecological differences between the two sets of fishes, with the persistent ones typically more adapted to estuarine habitats. This conclusion is not greatly affected by the position of the separation point (Magurran & Henderson, 2003).

CURRENCIES OF ABUNDANCE

Much of the literature on species abundance distributions treats abundance as synonymous with numbers of individuals. This is a practical decision as it is generally easier to count individuals than to measure biomass or energy. For communities of similar sized organisms, such as guilds of birds, it probably does not matter greatly. There is a growing appreciation, however, that examining how species abundance distributions are structured when abundance is measured in different currencies can help in the understanding of processes that shape diversity (Morlon *et al*., 2009). Indeed, some authorities (Tokeshi, 1993) argue that biomass is a much more informative measure of abundance if the goal is to test the veracity of niche partitioning models, while other researchers have pointed out that different impressions community structure emerge when different measures are used (Saint-Germain *et al*., 2007). As fish ecologists and fisheries scientists often measure both number of individuals and biomass, these data sets lend themselves well to establishing new perspectives in biodiversity research (Morlon *et al*., 2009).

An example of this is again provided by the Hinkley Point data [Fig. 5(a)]. If the log-numerical abundance is plotted against log-biomass, the data will form a roughly triangular shape (Henderson & Magurran, 2010). The boundaries of this triangle are determined by simple considerations. The left-hand side represents the biomass (*i.e.* body size) of singleton species, the lower line is set by body size multiplied by abundance while the upper line represents the maximum total biomass for any species. Species are distributed within this triangle approximately at random; this pattern is consistent with the hypothesis that a community consists of a number of spatial

guilds (Henderson & Magurran, 2010). Spatial guilds are composed of species that use the structural habitat in a particular way (Lawton, 1990). Two examples of these in the Hinkley Point community are benthic species and open-water fishes. Crucially, the species that make up these spatial guilds are distributed along axes that bisect the triangular space, and are visible because abundance is viewed in both currencies simultaneously (Henderson & Magurran, 2010). Thus, the community is composed of a number of spatial guilds, overlain one on the other. Temporal variation in abundance helps randomize the regular patterns of species with their spatial guilds. Now, because the distribution of species within the triangle approximates to random, the shape of the triangle can be used to infer the form of the species abundance distribution in both currencies (a regular distribution of species in biomass–numerical abundance space would also allow deduction of the shape of the species abundance distribution, but temporal variability in species abundances makes a strictly regular pattern unlikely). In many communities, such as Hinkley Point, the polygon represented by biomass–numerical abundance space will resemble an obtuse triangle. In such cases the distribution of biomass will be log-normal in form, while the distribution of numerical abundance will be more similar to a truncated log-normal (or log-series) distribution (Henderson & Magurran, 2010). This is exactly the pattern detected by Connolly *et al*. (2005) in their investigation of Pacific reef fishes and coral communities.

These observations allow predictions about communities. For example, if a group of organisms exploit a single spatial resource (such as fishes in a leaf-litter bank) the distribution of species in biomass-numerical abundance space will fall around a single line, rather than in a triangle (Henderson & Magurran, 2010). Another variant is illustrated by Malaysian stream fishes [Fig. 5(b)]. Here, the pattern resembles a roughly kite-shaped polygon. The sharp cut-off point on the lower edge suggests that smaller fishes may not have been captured. In this instance, both species abundance distributions (of biomass and numerical abundance) are roughly log-normal (Henderson & Magurran, 2010).

A further application of this approach is that the probable consequences for community structure can be predicted of the removal of top predators, or of overfishing of certain size classes or of different sampling protocols. As long as the distribution of species in biomass–numerical abundance space is indeed approximately random, as is the case in the examples known to date, it can be seen how changes in the body size distribution will lead to changes in community structure.

THE SIZE OF A COMMUNITY (EXPLAINING *S* AND *N*)

A feature common to the various attempts to explain the shape of species abundance distributions is that researchers take the empirical values of *S* (observed species richness) and *N* (total numerical abundance; biomass can be used here too), and use these inputs to predict the relative abundance of *S* species (McGill, 2010). One of the largest unanswered questions in this research field (McGill, 2010) is what drives these values of *S* and *N*. The global level variation in species richness, for example, along latitudinal gradients, is usually explored through correlations with factors such as productivity (Mittelbach *et al*., 2001). Environmental gradients, such as those of altitude and disturbance, are also probed to explain variation in *S*. Although *S* and *N*
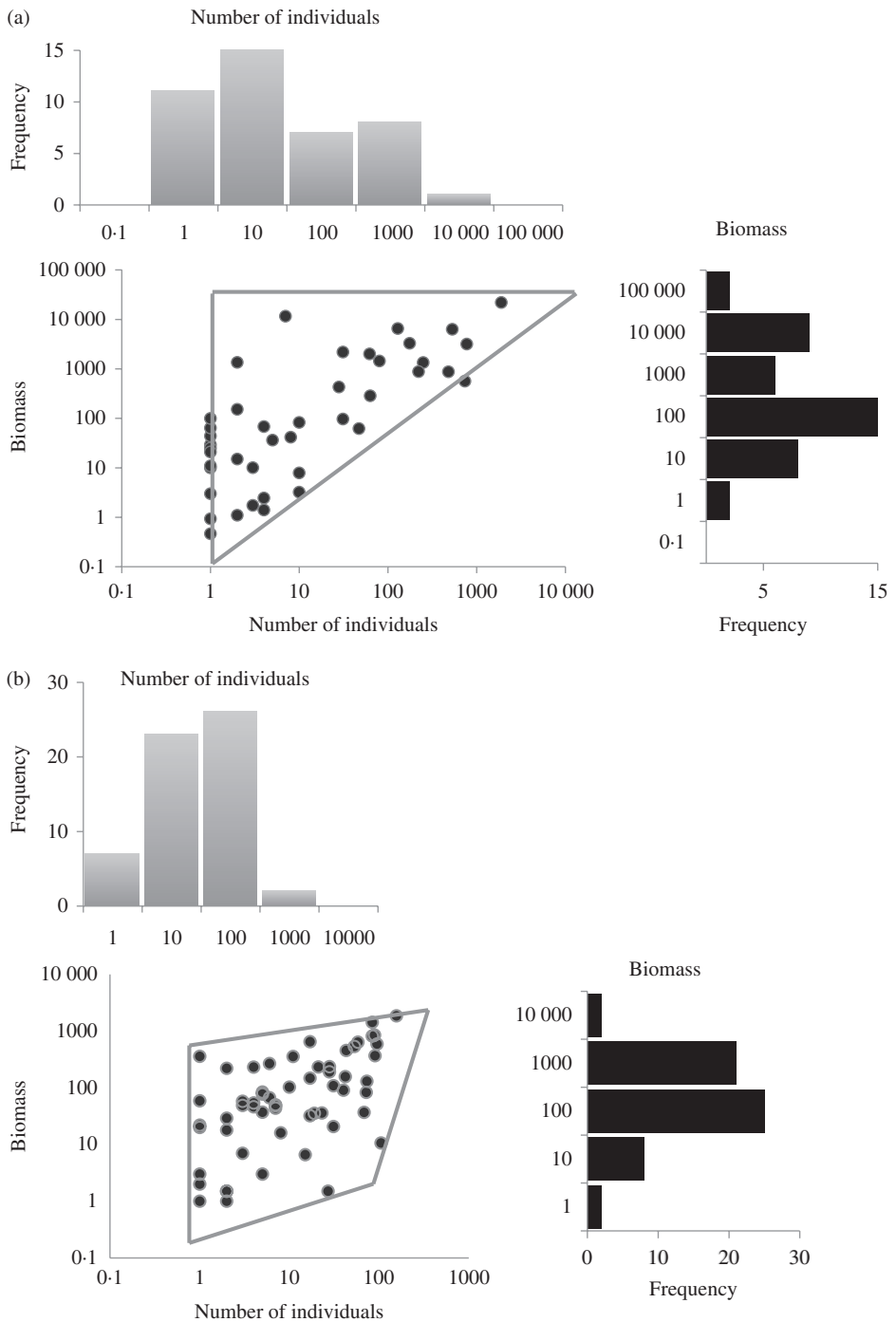
FIG. 5. Figure legend on next page.

can covary, (May, 1975; Srivastava & Lawton, 1998), S and N are rarely examined in tandem in such studies.

One way of thinking about this problem is to assume communities have a capacity; that is, they can support a certain number of individuals (or biomass). This idea is similar to the notion of saturation, which suggests that communities have a maximum size and all the available slots for individuals are occupied or saturated. Saturation is one of the assumptions of Hubbell's (2001) neutral model, but the extent to which ecological communities are saturated remains controversial. Nonetheless, communities not undergoing directional change (such as succession or disturbance) reveal that overall abundance is conserved through time (Fig. 6) even though the abundances of the individual species vary markedly. Indeed, the argument can be flipped around to show that community properties, such as total abundance or biomass, are preserved because the abundances of the individual species shift independently of one another (Magurran & Henderson, 2010). As long as there are a reasonable number of species in the assemblage these changes will cancel one another out (Cottingham et al., 2001).

Dornelas et al. (2011) used Trinidadian fish communities to ask how total abundance varies across a species richness gradient. Total abundance was estimated in three ways: as numerical abundance, as biomass and as energy use. They found that, on average, each measure of total abundance increases with increasing species richness, but that the upper limit of abundance remains constant. This shows that the relationship between S and N is more predictable as S increases. It also suggests communities have a maximum size in terms of N (this holds when abundance

Fig. 5. The relationship between biomass and numerical abundance (number of individuals) in two fish communities. These figures show how the species abundance distributions of biomass and numerical abundance are related to this relationship. Indeed, the shapes of these species abundance distributions can be deduced from the bounded area (usually triangular in shape) within which the points fall, as long as the distribution of species within this area is approximately random (an assertion supported by empirical data and grounded in the theory of spatial guilds; Henderson & Magurran, 2010). In the case of (a), where the Hinkley Point estuarine assemblage was sampled over 12 months in 2008, the pattern resembles an obtuse triangle, probably the most common configuration. The biomass species abundance distribution resembles a log-normal, while the species abundance distribution based on numbers of individuals has an excess of rare species. In contrast, in (b), Malaysian stream communities of fishes, the polygon has a sharp cut-off point at the lower edge and forms a roughly kite-shaped polygon. This pattern can occur when very small individuals are not included in a sample (for example, if the mesh size of a seine allows the smaller fishes through) and was predicted by Henderson & Magurran (2010), and is based on data from nine small streams in Peninsular Malaysia. Fish samples were obtained using a battery-powered backpack electroshocker (Smith-Root model LR-25; www.smith-root.com). Sampling reaches were blocked using stop-nets at both the ends to prevent fishes from entering or escaping the site. Fishes were collected by moving upstream and carefully sampling all microhabitats present within the reach (Henderson & Magurran, 2010). To minimize mortality, all captured fishes were placed in collapsible loop-nets and immersed in flowing water. Small fishes were placed in a bucket separately. All fishes were identified to species in the field, counted, measured for total and standard length and weighed before being released at the end of each sampling. Any unidentified species were preserved in 10% formalin in the field and were left in fixative for 2 weeks. These were later soaked in the tap water to remove excessive formaldehyde for further identification before transferring the specimens into 70% ethanol for long-term preservation. All specimens were classified and identified using relevant taxonomic keys (Alfred, 1969; Roberts, 1989; Kottelat et al., 1993; Rainboth, 1996; Ng & Ng, 1998; Ng & Kottelat, 2000; Kottelat, 2005).
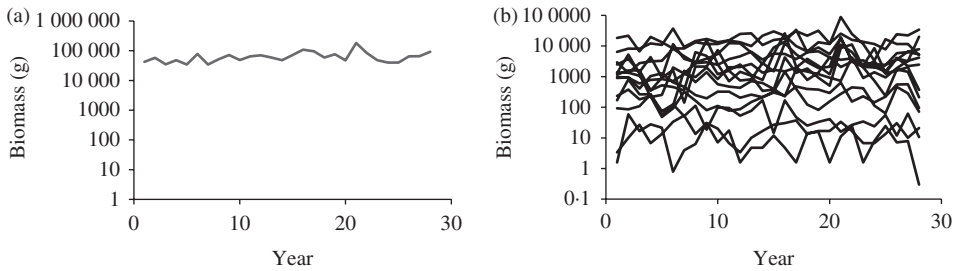
FIG. 6. Temporal trends in the abundance of the fish community at Hinkley Point. (a) Overall biomass, through a three decade time series. (b) Year-to-year variation in the abundance of species (biomass, that are always present; Magurran & Henderson, 2010).

is measured in different ways) but that the patterns can be noisy, especially when S is low. Another intriguing observation is that N_{max}, the absolute abundance of the most abundant species, is independent of S. Once again, this holds for each of the measures of abundance. There is another interesting implication of these results. Although the absolute abundance of N_{max} does not change across the gradient, the relative abundance of N_{max} declines as S increases. The different behaviour of absolute and relative abundance measures is something that modellers of niche partitioning need to aware of, as they typically work with relative abundances. Taken together, the results suggest that each community has a certain capacity. This capacity will be set by factors such as the amount of physical space, the types of physical space, primary productivity and so on. Community capacity constrains the upper limit on abundance N as well as the number of species S. The exact number of species that do coexist in a community, however, will be determined by processes such as dispersal limitation. Thinking about this in the context of Trinidad it can be seen how two rivers, which are similar in terms of physical structure and productivity, might support similar numbers of individuals, but vary in species richness because one of them was isolated by a barrier waterfall and receives fewer colonists (Fig. 2).

FUTURE DIRECTIONS

This review has highlighted just a few of the topics under the general heading of community structure that are readily explored using data from fish assemblages. In doing so, this study has tried to link pattern and process. The sheer diversity of fishes and the large range of habitats in which they live make them an unusually interesting group to test these ideas. Furthermore, there are undoubtedly many untapped sources of data produced by the types of routine sampling that fish biologists and ecologists undertake. There are numerous themes that could be productively explored in future work. These include tests that evaluate the role of biological differences between species in structuring local communities, and how these differences result in species being common or rare. Such tests might take advantage of the life-history data that fish biologists routinely collect. It would also be interesting to ask how particular biological traits such as trophic position, mean body size and life form influence dispersal abilities (Drakare *et al.*, 2006). The extent to which dispersal

limitation influences community structure has already been mentioned, but it would be instructive to explore the interaction between dispersal limitation and disturbance as isolated assemblages will receive fewer colonists to balance local extinctions. Species turnover is also important (Harte & Kinzig, 1997; Arita & Rodríguez, 2002; Tjørve & Tjørve, 2008; Anderson *et al.*, 2011), but has been barely touched on here. The geometry of species distribution patterns is another topic that is receiving a lot of attention in the ecological literature (Storch *et al.*, 2008), but is one that may need to be approached in a different way when dealing with fish communities found in linear structures (such as river systems) or in isolated water bodies (such as lakes). Related to this are scaling issues. Various techniques for linking species occurrence to area now exist (Kunin, 1998; Ovaskainen & Hanski, 2003). Most of these are focused on terrestrial systems, but a growing number of investigators of fish communities now explicitly include scale in their analyses (Chick *et al.*, 2004; Higgins & Strauss, 2008; Flinders *et al.*, 2009; Kang *et al.*, 2009; Strecker *et al.*, 2011).

It is clear that fish studies have the potential to contribute to these and other fundamental ecological questions. Perhaps, the largest research gap that needs to be filled is how such investigations of the biological diversity of fish communities can help shape conservation policy at both local and regional scales.

A CASE STUDY

FISH DIVERSITY AND CONSERVATION CHALLENGES IN THE ECOREGION OF THAILAND AND PENINSULAR MALAYSIA

Thailand and west Malaysia are connected by a land bridge and have a total landmass of >1 000 000 km². Thailand and the western part of Peninsular Malaysia (western belt) are of Gondwanan origin (Rainboth, 1996; Yap, 2002), but the eastern region (eastern belt) is of Laurasian origin. Tectonic plates collided to create the landmass during the Lower Mesozoic period (Rainboth, 1996). The area is topographically varied. Central and south-western Thailand are relatively low lying while there are mountain ranges in the west, north and eastern part of the country. In Peninsular Malaysia, by contrast, mountain ranges run from north to south and divide the landmass into eastern and western coastal plains; these mountains are also the source of many streams and rivers. Subterranean streams and swamps add to the habitat diversity of this ecoregion, but natural lakes are absent.

The ecoregion of Thailand and Peninsular Malaysia forms part of the Indo-Burma and Sundaland biodiversity hotspot (Myers *et al.*, 2000). The region is thought to have well over a 1000 species of primary and secondary freshwater fishes (Yap, 2002) and its diversity has been recognized for years (Smith, 1945; Moshin & Ambak, 1983; Rainboth, 1996). Fish surveys and collections, which began in the 19th century, were initiated by ichthyologists such as G. Cuvier, A. Valenciennes, T. E. Cantor and P. Bleeker (pers. obs.). To date, over 800 freshwater fish species have been recorded in Thailand (S. Khachonpisitsak, unpubl. data) and *c*. 300 species (Lim & Tan, 2002) in Peninsular Malaysia. It is strongly believed that these figures are an underestimate not only because >10 new species or new records are being added to the list annually, but also due to observations which suggest that there are a

substantial number of species yet to be discovered from this region (unpubl. obs.). For instance, *c*. 25 species out of 72 rare and endemic species detected in Thailand are yet to be formally described (Vidthayanon, 2005).

The challenges of documenting fish diversity in Thailand and Peninsular Malaysia typify those often experienced in biodiverse but poorly studied regions. Paucity of research funding combined with limited taxonomic expertise is one reason why fresh-water fishes are not yet fully catalogued. High levels of uniqueness, endemicity and rarity are others. In Thailand, *c*. 8·5% of freshwater fishes are endemic; the equivalent figure for Peninsular Malaysia is *c*. 10%. Around 56% of the estimated 800 species in Thailand are unique species (species being restricted to a single watershed system) (S. Khachonpisitsak, unpubl. data). *Balitora*, *Homaloptera*, *Schistura* (Balitoridae) and *Akysis* (Akysidae) are examples of genera that are consistently unique. On the other hand, just 22 species are widely distributed across the country with high abundance. These include representatives of genera such as *Cyclocheilichthys*, *Puntius* and *Osteochilus* (Cyprinidae) (Howes, 1991). In Peninsular Malaysia, an example of a fish found throughout the region is *Poropuntius smedleyi* (de Beaufort 1933) (Cyprinidae) while those with restricted ranges include *Neolissochilus hendersoni* (Herre 1940) (Cyprinidae), reported on the island of Penang and Langkawi (Ahmad & Lim, 2006), and *Clarias batu* Lim & Ng 1999 and *Clarias sulcatus* Ng 2004 (Clariidae). Furthermore, every survey of local communities uncovers some abundant and many rare species and thus confirms the universal pattern discussed elsewhere in this paper (A. B. Ahmad, unpubl. data).

There may never be a reliable species count for this ecoregion since habitat loss and habitat modification is occurring at a rate that makes it probable that a substantial fraction of fish species will be lost before they are formally identified. Peat swamp is one type of habitat in Peninsular Malaysia that has only relatively recently been recognized as having a rich fish fauna (Ng *et al*., 1994). Unfortunately, large parts of the north Selangor peat-swamp forest have been cleared to make way for agriculture and other human activities. This has changed the groundwater hydrology and led to desiccation of the swamp forest, with the result that this habitat is now seriously threatened.

To date, there have been few attempts to draw on the insights from analyses of species abundance distributions, and to apply these to the conservation of freshwater fish communities in biodiverse ecoregions such as Thailand and Peninsular Malaysia.

CONSERVING BIOLOGICAL DIVERSITY

Research into patterns of biological diversity in the natural world has been given new impetus by the growing concern about accelerating extinction rates and increased awareness of the important functions that this diversity contributes. Fishes are important targets of conservation, not just because they are economically and recreationally important, but also because they make up such a large fraction of the vertebrate diversity on Earth. Much of the conservation effort to date, however, has focused on 'the furries and featheries' (May, 2002); most species for which there are formal conservation assessments are mammals and birds. A striking example is that 62 of the 81 species recorded at Hinkley Point have not yet been evaluated against IUCN criteria.

Geographical isolation is the engine of diversification in fishes, as in other taxa. The remarkable diversity of freshwater species is therefore, to a large part, linked to the fragmentation of freshwater systems into many isolated drainages, lakes and wetlands. Because the water bodies involved can be limited in extent, however, many freshwater fish species have small populations and restricted ranges. Diversity, in freshwater fishes at least, is a natural corollary of rarity, and *vice versa* (Magurran, 2009).

The case study above described the challenges of quantifying patterns of biological diversity of freshwater fishes in a rich, but poorly studied ecoregion (Thailand and Peninsular Malaysia). It shows that there is often only a limited understanding of how many species are present and what their distributional patterns are. Moreover, here, as in many other parts of the world, habitats are being lost before the fishes that live in them have been documented.

Although theories of biological diversity, such as the neutral model in its various forms, have been an intellectually exciting development in ecology, there is little evidence as yet that they have aided conservation managers (Clarke, 2009). There is nonetheless considerable potential for this to change (McGill & Collins, 2003; McGill, 2010). The idea that local communities are embedded in a metacommunity is central to neutral theory and is also relevant to conservation policy in ecoregions such as Thailand and Peninsular Malaysia. Many nature reserves conserve fragments of habitat, but pay little attention to how the species involved are located in relation to their range. Theory indicates that it would be wise to take this into account as populations towards the edge of a species' range tend to be smaller than those in the middle (McGill & Collins, 2003). Dispersal also needs to be considered. Analyses of fish communities also reveal that species abundance varies through time (Magurran & Henderson, 2010) and show how important it is that conservation policy heeds this natural change (Mace *et al*., 2010). Finally, the investigations of local communities indicates that rarity and local extinction are natural phenomena (Magurran, 2009). By linking patterns at the local community level with the processes shaping those patterns, conservation biologists will be able to develop management strategies that contribute the effective long-term conservation of biological diversity.

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