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Biodiversity and extinction: species and people

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I Introduction

The most important agent of change in the spatial patterns of much of biodiversity at present is ultimately the size, growth and resource demands of the human population (Vitousek *et al*., 1997; Sala *et al*., 2000). This is giving rise to: (i) levels of global species extinction largely unprecedented outside periods of mass extinction (e.g., Lawton and May, 1995; Pimm *et al*., 1995; C.D. Thomas *et al*., 2004); (ii) levels of net losses of populations and individuals which may both absolutely and proportionately be several times greater than rates of species loss (e.g., Hughes *et al*., 1997; 1998; Chan, 1998; Hobbs and Mooney, 1998; Ceballos and Ehrlich, 2002; Gaston *et al*., 2003; J.A. Thomas *et al*., 2004); (iii) levels of dispersal of organisms, associated with the movements of people and goods, that routinely overcome long-standing barriers to natural movement and which in some areas have become more important than natural dispersal mechanisms (e.g., Hodkinson and Thompson, 1997; Pimentel, 2001); and (iv) humans having become among the greatest evolutionary forces on Earth, shaping the tolerances and capacities of numerous organisms (Palumbi, 2001). Such pervasive effects have led some to term the present era the 'anthropocene' (Crutzen and Stoermer, 2000).

While the large 'ecological footprint' of major sectors of the human population is undoubtedly important, generating pressures in areas often far removed from where the people responsible reside (Rees, 2001; Wackernagel *et al*., 2002), the extent of the conflicts between people and other components of biodiversity also depends in large part on the degree to which the two spatially co-occur. Nonetheless, until recently, surprisingly little explicit work had been conducted on the relationships between human population size or density in areas and the structure and dynamics of the ecological assemblages present. This is now changing rapidly and in this paper I selectively review these contributions.

II Species richness

To many, one of the more surprising discoveries in recent biodiversity research has been that, at broad geographic scales, the total numbers of species in different groups of organisms occurring in an area tend often to be positively correlated with the numbers of people; there is a positive species-humans relationship. This pattern has been documented, with varying degrees of statistical

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and biological significance (depending, for example, on the strengths of the relationships, and whether spatial autocorrelation, variation in area and other confounding variables have been accounted for), for birds and mammals in different countries worldwide (Kerr and Currie, 1995), birds in different countries in Europe (Gaston and Evans, 2004), butterflies, amphibians, reptiles, birds and mammals in North America at an ecoregion scale (Luck *et al.*, 2004), plants in the USA at a state scale (McKinney, 2001b), amphibians, snakes, birds and mammals, separately and summed, in sub-Saharan Africa at a one-degree resolution (Balmford *et al.*, 2001b), plants in sub-Saharan Africa at a one-degree resolution (Balmford *et al.*, 2001a), butterflies, amphibians, birds and mammals in Australia at a one-degree resolution (Luck *et al.*, 2004), mammals in Mexico at a half-degree resolution (Vázquez and Gaston, 2005), birds in South Africa at quarter-, half- and one-degree resolutions (Chown *et al.*, 2003; van Rensburg *et al.*, 2004), plants, reptiles, amphibians and mammals in Europe at a 50 km resolution (Araújo, 2003), mammals in Argentina at a provincial scale (Real *et al.*, 2003), plants on Southern Ocean islands (Chown *et al.*, 1998; Selmi and Boulinier, 2001), and bird and mammal species in Nepal in different altitudinal bands (Hunter and Yonzon, 1993). In a similar vein, the human population has been shown to be distributed such that more than 1.1 billion individuals (about a sixth of the global total) live within the 25 global biodiversity hotspots which constitute some of the most important and threatened areas for other forms of life but which cover only 1.4% of the land surface (Cincotta and Engelman, 2000; Cincotta *et al.*, 2000); the density of people in hotspots is about 73 per km^2, compared with a global average of 42 per km^2.

Although there are other possibilities (e.g., coincidence, disturbance, extinction filters, geomorphology; see Araújo, 2003; Kühn *et al.*, 2004), the most generally accepted explanation for this pattern of positive covariance is that species richness and numbers of people both respond positively to levels of environmental energy availability. Species numbers often increase with energy (the species-energy relationship) at a geographic scale, at least over a wide range of values of energy availability, for a variety of reasons (Evans *et al.*, 2005a). But foremost they have been thought to do so because more energy enables more biomass and greater numbers of individuals to be sustained, which enables more species to maintain viable populations within an area (the so-called 'more individuals' hypothesis; Wright, 1983; Rosenzweig and Abramsky, 1993; Kaspari *et al.*, 2003). If this mechanism were correct, then one would expect to find more biomass and individuals of given taxonomic groups in areas in which more of their species occur and, although it is extremely difficult to test, there is some evidence that this is indeed so (Kaspari *et al.*, 2000; Gaston and Evans, 2004; Meehan *et al.*, 2004).

Why numbers of people are positively correlated with environmental energy availability at broad geographic scales has been less well explored, at least in the biodiversity literature. However, this relationship may exist because early human populations established more readily in warm and productive areas, and perhaps grew more rapidly there, with present patterns of abundance reflecting this historical signal – a significant level of historical consistency in the pattern of human populations has been assumed in modelling long-term changes in the influences of those populations on land use (Klein Goldewijk, 2001), although there are many exceptions and the relationship is scale-dependent. The effect may have been enhanced at global scales by the distribution of wealth and its consequences for population growth rates, although the patterns of wealth and its effects have changed through human history. Regardless, the similarity of the responses exhibited by humans and other biota to energy availability is underlined by numerous strong parallels between how species richness and human populations are structured in space (Mace and Pagel, 1995; Cashdan, 2001; Collard and Foley, 2002; Moore *et al*., 2002; Manne, 2003), and in how these variables respond to current environmental change (Sutherland, 2003).

If positive relationships between numbers of other species and numbers of people are a consequence of the two covarying in a similar way with a third variable (energy availability), then the puzzling question is how more direct effects of human density on species numbers fit into this picture. An intuitive expectation would seem to be that species richness would decline when human densities are high, as a consequence of the loss and fragmentation of natural habitat, and pressures of exploitation, pollution and introduced species (with all of these effects potentially being amplified through extinction cascades). There are three possible reasons why this has not been observed in many (though not all) of the analyses of relationships between species richness and human population listed earlier. First, these analyses have been conducted at rather coarse spatial resolutions. It may thus be that even within those areas in which human densities are high there is still sufficient natural habitat and refuges from other threatening processes. If this were correct, then one would predict that at finer spatial resolutions the relationship between species richness and human density would be hump-shaped or possibly negative. There is some empirical evidence that suggests this is indeed so (Araújo, 2003; Turner *et al*., 2004).

In a similar vein, the second possible explanation for why a positive relationship between species richness and human density is observed at geographic scales is that human density *per se* is not an important determinant of levels of species richness. Rather, in an increasingly human-dominated world, species richness depends much more on the existence of effective mechanisms for the maintenance of species numbers (or at least for reducing impacts upon them) than on the actual numbers of people. This suggests that the form of the observed relationship between numbers of species and numbers of people will vary systematically between regions, dependent on the strength of conservation, and broader environmental, action (see also Huston, 1993; Margules and Gaston, 1994). This would be an interesting idea to test.

The third possible reason that a positive relationship between species richness and human density is observed at geographic scales is that there is an effect of human density on species richness across the full range of variation in the former, the outcome of which is to lower the overall slope of the species richness-human density relationship rather than simply to invert it or make it hump-shaped. The potential for such a mechanism is evidenced by the fact that humans seem to have caused extinctions, both in palaeontological and historical times, even when the densities of people have been rather low (e.g., Martin and Steadman, 1999; Miller *et al*., 1999; Linnell *et al*., 2001; Laliberte and Ripple, 2003; Lyons *et al*., 2004). Although the influences of anthropogenic factors on the observed form of macroecological patterns has not generally been well explored (Gaston and Blackburn, 2003; Gaston, 2004), there is some evidence that variation in human densities influences observed species-energy relationships (Evans and Gaston, 2005). It also makes a great deal of sense, in as much as impacts of humans on patterns of species richness are known to be extremely widespread.

Of course, these explanations for positive geographic-scale relationships between species richness and human density are not mutually exclusive. For example, at high human densities, the majority of native species recorded from an area may be sustained in remnant patches of natural or semi-natural habitat, protected by conservation measures, but still markedly depleted in diversity.

III Threat and extinction

Even if at broad spatial resolutions species richness and human population sizes or densities are typically positively correlated, this is not to say that at such scales there is no evidence for adverse effects on biodiversity of those populations or densities, and the activities that are associated with them. Thus, paralleling these relationships, positive correlations have also been documented between the numbers of species and the proportions of species in different groups of organisms occurring in an area that are presently threatened with extinction and the numbers of people living there. This pattern has been documented, again with varying degrees of statistical and biological significance, for plants, birds and mammals in different countries (Kerr and Currie, 1995; McKinney, 2001a; 2002a), butterflies, amphibians, reptiles, birds and mammals in North America at an ecoregion scale (Luck *et al*., 2004), birds in Australia at a one-degree resolution (Luck *et al*., 2004), mammals in Mexico at a half-degree resolution (Vázquez and Gaston, 2005), birds in South Africa at quarter-, half- and one-degree resolutions (Chown *et al*., 2003), mammals in the USA at a state scale (Kirkland and Ostfeld, 1999) and reptiles in the USA at a county scale (Dobson *et al*., 1997); some studies have also found no marked species-humans relationships for threatened species in some groups and regions (e.g., Dobson *et al*., 1997; McKinney, 2002a; Araújo, 2003).

All else being equal, if overall numbers of species are higher in areas with greater numbers of people, then by chance the numbers of threatened species would be expected to be higher. Thus, the observation that the proportions of threatened species are often also higher is considerably more important. The logical consequence of heightened numbers and proportions of threatened species in areas with higher human population sizes and densities is that extinction rates will also be greater in these areas. Thus, the number of scarce plant species that have not been recorded from areas of Britain since 1970 is an increasing function of the human population density of those areas (Thompson and Jones, 1999), and the occurrence and persistence of a number of, predominantly large-bodied, vertebrate species declines with human population density and urbanization, even when these species are in protected areas and this density is measured in the surrounding areas (Hoare and du Toit, 1999; Woodroffe, 2000; Brashares *et al*., 2001; Germaine *et al*., 2001; Parks and Harcourt, 2002; Laliberte and Ripple, 2003; 2004; Liley and Clarke, 2003; Walsh *et al*., 2003; Cardillo *et al*., 2004; Jędrzejewski *et al*., 2004; but see Harcourt *et al*., 2001; Linnell *et al*., 2001). Of course, in the extreme, levels of extinction may become sufficient to remove, or even invert, any relationship between the numbers and proportions of threatened species and the numbers of people, a form of extinction filter (Balmford, 1996).

As mentioned earlier, threats to other species from higher human population sizes and densities may come from a variety of directions. Thus, although the interaction may be modified by social and environmental context, human population sizes and densities have been found to be positively correlated with levels of forest loss and fragmentation (e.g., Meyer and Turner, 1992; Cohen, 1997; Laurance *et al*., 2002; Wikramanayake *et al*., 2002; Jędrzejewski *et al*., 2004), overall land transformation (e.g., Chown *et al*., 2003; Vázquez and Gaston, 2005) and numbers of introduced species (see below).

IV Introductions

The emphasis thus far has been on regional and local declines in native species numbers that often follow from human activities. However, such activities may also lead to increases in species numbers as a consequence of the introduction of species to areas in which naturally they would not occur. It is thus perhaps unsurprising that a number of analyses have documented positive relationships between the numbers or proportions of species that have been introduced to an area and the size of the human population established or visiting that area. This pattern has been documented for plants in the Azores and in the USA (McKinney, 2002b; Silva and Smith, 2004; see also Withers *et al.*, 1998), plants, insects and mammals on Southern Ocean islands (Chown *et al.*, 1998; 2000; Selmi and Boulinier, 2001), plants and fish in the USA at a state scale (McKinney, 2001b), plants in national parks in the USA and in South Africa (Lonsdale, 1999), and plants in nature reserves in the Czech Republic (Pyšek *et al.*, 2002). Such movements of species have been brought about by a multiplicity of routes, including intentional introduction for cultivation or sport, the transport of soil and ballast, the connection of waterways through canals, and the release or escape of pets. They reflect our choices as consumers, travellers, gardeners and so on (Baskin, 2002).

Should these relationships be strong enough, then, given that at geographic scales overall species richness tends to be positively correlated with human density, one might expect that the numbers of native and introduced species in an area would also be positively correlated. There is some evidence that this is so (e.g., Lonsdale, 1999; Stohlgren *et al.*, 1999; Pyšek *et al.*, 2002; Sax, 2002; Houlahan and Findlay, 2004; Irz *et al.*, 2004; but see Case, 1996; Stohlgren *et al.*, 1999; McKinney, 2001b). Such patterns have attracted various interpretations, including that naturally more speciose assemblages are easier to invade, that native and introduced species richness respond to environmental factors (e.g., energy availability) in similar ways, and that because high numbers of other species tend to occur where there are large numbers of people greater numbers of species will tend to be successfully introduced into these areas (for discussion see, for example, Levine and D'Antonio, 1999; Stohlgren *et al.*, 1999; Duncan *et al.*, 2003; Evans *et al.*, 2005b). The relative importance of these possibilities is poorly understood and, despite the numerous weaknesses of such an approach, the simple existence of a positive relationship between numbers of native and introduced species in different areas has at some time been used to support each of them.

What is the relative balance of decreases in species richness through extinctions and increases through introductions? Global biodiversity is indisputably in decline, as a consequence of the global extinction of individual species. In contrast, at smaller spatial resolutions, net biodiversity seems commonly (though not exclusively) to be increasing, because the numbers of introductions outweighs the numbers of local or regional extinctions (e.g., Hobbs and Mooney, 1998; Rosenzweig, 2001; McKinney, 2002b; Sax *et al.*, 2002; Sax and Gaines, 2003). This is despite the fact that introductions themselves may drive local or regional extinctions (Williamson, 1996; but see Gurevitch and Padilla, 2004).

V Predictions for the future

The human population is predicted to grow by 2 to 4 billion people by 2050 (United Nations, 2001). While it took until about 1800 to attain a global population of 1 billion people, a medium projection is that it may take just 13 to 14 years to add another billion to the present total (Cohen, 2003). All else remaining equal, which it seldom does, a number of predictions would seem to follow from the work that has been conducted to date on the relationships between human densities and the numbers of native species, numbers or proportions of threatened species, and the numbers or proportions of introduced species. First, the spatial scale at which relationships between overall numbers of native species and human density become hump-shaped or at least gain marked negative phases seems likely to increase, even when species numbers and human density are mapped at a low spatial resolution. Increased human densification will mean that the maintenance and conservation of tracts of natural or semi-natural vegetation will become more difficult in areas of higher human density.

Secondly, the numbers and proportions of threatened species in different areas will tend to increase. McKee *et al*. (2003) have used existing relationships between numbers of threatened species and numbers of people in different areas to predict the consequences for biodiversity of continued increases in the human population. They found that the number of threatened bird and mammal species across 114 continental nations is expected to increase in the average nation by 7% by 2020 and 14% by 2050, on the basis of human population growth alone. Such aggregate estimates provide no indication of precisely what this is likely to do for the overall proportion of species that are globally threatened with extinction, but these increases can only serve to increase the 12% of bird species and the 23% of mammals currently listed as such (IUCN, 2003). Likewise, the proportion of species that have become globally extinct will increase.

Thirdly, the numbers and proportions of introduced species in different areas will tend to increase. Comparable analyses to those conducted by McKee *et al*. (2003) could also be conducted to predict the consequences for species introductions of continued increases in the human population. To my knowledge, this has not been done. However, the conclusions seem likely to be qualitatively, if not quantitatively, similar.

In combination, the loss of native species to extinctions and the establishment of nonnative species through accidental or intentional introductions leads to biotic homogenization, the reduction in the spatial variability of assemblage composition (McKinney and Lockwood, 1999; Rahel, 2000; Lockwood and McKinney, 2001; Olden *et al*., 2004). Albeit the relationship between biodiversity and human population growth is complex (Cohen, 1997), it is clear that, alongside other motivations for so doing, limiting this growth is essential for biodiversity conservation and management. Moreover, the explicit incorporation of spatial variation in the human population should come closer to the fore in schemes for prioritizing areas for that conservation and management (for examples see Fjeldså and Rahbek, 1998; Chown *et al*., 2003; Luck *et al*., 2004; van Rensburg *et al*., 2004).

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