Common Ecology

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In contrast to their rarity, the commonness of species has historically received surprisingly little explicit attention from ecologists. However, this situation is changing. Here I review the current understanding of the nature of commonness, with particular emphasis on the dynamics and causes of this state, as well as on its ecological and evolutionary implications. Depending on the focal issue, common species can variously have lower, greater, or similar per capita influences compared with rare ones. Importantly, however, these influences almost invariably remain strong because of the high numbers of individuals and local occurrences in taxonomic assemblages contributed by the relatively few species that are common. The importance of these species highlights the significance of deepening concerns over the declines of many common species and the vital need for a balanced approach to maintaining their commonness while also addressing the more familiar conservation issue of preventing the loss of rare species.

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The majority of species within a higher taxon are rare; they have low abundances and are narrowly distributed. The reasons for, and the consequences of, this phenomenon have long fascinated biologists; staple research questions include, why are there so many such species (and thence why are there the overall numbers of species that there are), what are their evolutionary and ecological (including ecosystem) effects, and how do they persist? Indeed, arguably, much of the history of the field of ecology has de facto been that of the study of rare species.

The corollary of most species being rare is that only a minority are therefore common. Put another way, although common species are those with which we are inevitably most familiar, the state of being common is itself rare. This, of course, belies the numerical significance of common species. They account for a very high proportion of the total numbers of individuals in taxonomic assemblages and, to a lesser degree, of the total numbers of area or locality occurrences. Not unusually, across a spectrum of spatial extents (from local to continental), 50% of the individuals in an assemblage are accounted for by less than 10% of the species, the most abundant 25% of species account for more than 80% of the individuals (figure 1), and the most widespread 25% of species account for more than 50% of the locality records (Gaston and Fuller 2008). As the resolution at which spatial distributions are recorded becomes finer, these lower percentage values for occurrences will grow and converge with those for abundances. Unfortunately, the level of numerical dominance by common species is often somewhat obscured in the presentation of abundance and occurrence data for assemblages because the between-species variation it gives rise to makes the use of logarithmic scales more convenient. However, even among tropical assemblages, which have traditionally been characterized as being dominated by rarity, the commonest species typically still account for high proportions of the total numbers of individuals and locality records (e.g., Pitman et al. 2001).

Local abundance and regional occupancy also tend to be positively correlated within taxonomic assemblages, such that the species that have the largest overall populations are among the most widespread and have higher local densities where they do occur; that is, species that are common in terms of abundance are often also common in terms of distribution (Gaston 2003). This correlation somewhat simplifies the discussion of commonness, although it remains the case that species can be locally abundant but narrowly distributed or locally scarce but widely distributed; thus, there are multiple routes to being common on either one of these axes.

Although the commonness of species has not been especially well studied (box 1), in recent years there has been an increased focus on the ecology and evolutionary biology of common species. In part this has been driven simply by a recognition of key gaps in understanding, but it has also followed from deepening concerns over declines of many common species and the consequences these declines might have (Gaston 2010). In this article I review what is known about the nature of commonness. In so doing, I particularly highlight what is arguably the key issue that common ecology has to address: whether the ecological and evolutionary dynamics of assemblages are influenced to a greater or a lesser extent by common species than one would predict on the basis of their abundance and distribution alone. That is, are common species more than just rare species writ large? Throughout, I focus foremost on taxonomically constrained assemblages (e.g., the fern, moth, or bird species of a given study area or region).

Dynamics of commonness

Central to understanding many issues about commonness are the dynamics of this state. Not only are a minority of
Figure 1. The percentage of individuals in assemblages contributed by the commonest species. (a) Woody plants on a 50-hectare (ha) forest plot on Barro Colorado Island (10-millimeter diameter at breast height and above); (b) benthic invertebrates in samples from the southern Irish Sea; (c) Scarabaeidae dung beetles caught in human dung–baited traps in Abokouamekro, Ivory Coast; (d) birds on a 104-ha forest plot in Panama; (e) land birds of North America; and (f) mammals of Britain. In all cases the percentage cumulative number of individuals (filled circles) is plotted against the percentage cumulative growth in number of species, with species ranked from most to least abundant. For each plot the percentage of species that contribute 50% of the individuals and the percentage of individuals contributed by the 25% most abundant species are, respectively, (a) 3% and 90%, (b) 6% and 90%, (c) 4% and 94%, (d) 11% and 73%, (e) 5% and 88%, and (f) 5% and 97%. Where data sources allowed, percentage cumulative growth is also given for biomass (open circles; calculated as the product of abundance and body mass), also plotted against the percentage cumulative growth in number of species, with species ranked from most to least abundant. Data sources: (a) Hubbell and colleagues (2005), (b) Mackie and colleagues (1995), (c) Hanski and Cambefort (1991), (d) Robinson and colleagues (2000), (e) Rich and colleagues (2004), (f) Battersby (2005).
species common at any one time but most species never become common, and those that do remain common only for a relatively short period of their existence (i.e., commonness is geologically transient). A variety of possible trajectories have been suggested for the overall population, occupancy, or geographic range size of a species through its lifetime, from speciation to extinction (Gaston 2003). Although many more such studies are needed, recent intraspecific analyses of the fossil record have suggested that these trajectories are generally best characterized as hump shaped, with species becoming most widespread either relatively early (Liow and Stenseth 2007) or toward the midpoint of their existence (Foote et al. 2007). A pattern in which the temporal rise in abundance and distribution is more rapid than is the fall would fit a mechanistic model in which initial expansion is relatively easily achieved but is subsequently undermined by the ecological and evolutionary responses of prey, competitors, and predators or parasites. How widespread a species becomes appears to be important to the rate of range size decline, and, as the theory of risk spreading would predict, species with larger geographic ranges persist for longer periods (Gaston 2003). Although the relationship between persistence and the range size that is achieved is nonlinear (i.e., persistence slows at large range sizes), this correlation may also explain the trend that has been reported in several studies—that present range size and evolutionary age are positively correlated across the extant species in a higher taxon (e.g., Böhning-Gaese et al. 2006).

One result of the marked long-term dynamics of the population and geographic range sizes of individual species is that in comparison with some other traits (e.g., body size), these variables exhibit relatively little phylogenetic conservatism (although just how much conservatism in population and range size is actually generated by species-level selection is the subject of substantial debate; Webb and Gaston 2003). This lack of phylogenetic conservatism has some unfortunate practical consequences; for example, for species for which population and distribution status is unknown, this information cannot usefully be inferred from that of any better-known close relatives.

Although the abundances and distributions of species show marked changes on evolutionary timescales, on ecological timescales they may exhibit much greater stability. Thus, within an assemblage, common species tend often to remain common, and rare ones tend to remain rare, for long
periods (i.e., abundances and range sizes show high cross-species temporal concordance), subject to anthropogenic pressures (see below) and marked stochastic and directional shifts in environmental conditions (Lawton 2000). This is not to say that abundances and range sizes of species do not change on ecological timescales—naturally, they do—but rather that the changes may often be small relative to the differences in these variables between those species that are common and those that are rare at any one time.

**Causes of commonness**

Attempts to understand why at any given time some species in a given higher taxon are common but most are not have been rooted in two principal paradigms. In the first, the distribution of individuals among species essentially is considered a consequence of stochastic processes, and in the second, it is considered a consequence of differences in ecological traits (through their interaction with prevailing environmental conditions). Species-abundance and species-range-size distributions (the frequency distributions of species with different abundances or range sizes) can be well characterized by a diversity of stochastic models (e.g., Hubbell 2001, Harte et al. 2005, Storch et al. 2008). These models do not include any taxon- or environment-specific information, but assume that everything is essentially random, subject to some general principles and constraints. These constraints typically concern the spatial structure of individual species distributions. The details of particular models or classes of models can be criticized, and they will doubtless continue to be developed, but it is now clear that the simple assumption that species distributions are aggregated on hierarchical spatial scales is sufficient to predict much not only about the observed shapes of species-abundance and species-range-size distributions but also those of other associated macroecological patterns (e.g., species-area relationships; Storch et al. 2008). By definition, of course, such models cannot predict which particular species in an assemblage are common at any one time, or even averaged over time; indeed, here, common species are in many senses quite literally treated simply as rare species writ large.

Although most ecologists believe that ecological trait differences among species are fundamental in shaping their abundance and distribution, explicitly trait-based models have been rather unsuccessful in characterizing this variation in general terms. Statistically significant interspecific relationships between abundance or geographic range size and life-history or niche characteristics have frequently been documented, with those for range size tending to be stronger than those for abundance, and measures of niche position (which capture the availability of resources or conditions that are suitable for a species) often perform best (e.g., Blackburn et al. 1996, Murray et al. 2002, Heino 2005). However, although more (and more comparable) studies would be valuable, such relationships tend to be relatively weak, inconsistent, and highly dependent on the spatial scale of analysis, and they may be open to variable interpretations (e.g., over directions of causality, compounded by the difficulty of discriminating effects particularly among the more abundant and widely distributed species). Even in combination these relationships usually do not explain the vast majority of the variance in abundance or geographic range size. Thus, again, rare and common species cannot readily be distinguished by ecological characteristics beyond their rarity and commonness (exemplified by the frequent difficulty in understanding why pairs of sister species apparently sharing very similar ecologies, one may be rare and the other common). This conclusion should not be particularly surprising given that, by comparison with variation in ecological traits, the relative importance of different abiotic and biotic factors (including natural enemies) in limiting the density of an individual species shifts markedly across its geographic range, varies with spatial resolution, and changes substantially through time (historical contingency; Gaston 2003). Consequently, even though such traits may have profound ramifications for the abundances and distributions of individual species, stochastic processes may nonetheless characterize patterns of interspecific abundance and range-size variation reasonably well. Indeed, concerns about the failure of ecology to predict precisely which species become common may be fundamentally misplaced.

Further support for the conclusion that the identity of common species may often be essentially unpredictable can be drawn from the previously mentioned relatively low phylogenetic conservatism of abundance and range size. Conversely, tendencies for the abundance or occupancy achieved by species in their native geographic ranges to be positively correlated with those that they attain when intentionally or accidentally introduced elsewhere by human agency (Duncan et al. 2001) would seem to provide evidence for greater predictability, although it is difficult to disentangle the effects of the greater likelihood that individuals of naturally abundant and widespread species have of being dispersed anthropogenically.

**Evolutionary consequences of commonness**

Whatever its particular causes, commonness has a variety of evolutionary consequences. First, because of the frequent distribution of common species across broad positional (e.g., latitude, elevation, depth) and environmental gradients (e.g., temperature, precipitation, salinity)—which may be several orders of magnitude larger than the typical dispersal distances of individuals—many classical ecogeographic patterns are disproportionately or solely exhibited by such species. These include systematic trends in body size and reproductive traits (e.g., clutch size; Gaston et al. 2008). Indeed, for birds the best biogeographic predictor of interspecific variation in phenotypic divergence, as reflected by subspecies richness, is geographic range size (Phillimore et al. 2007). Such phenotypic variation often reflects genetic adaptation of local populations, as has been demonstrated for a growing number of common species (e.g., Joshi et al. 2001), which also tend to show greater genetic diversity and genetic variation than do rare ones (Frankham 1996).

It has long been held that common species are important sources of evolutionary novelty, because their broad
geographic ranges are more likely to be broken by barriers to dispersal, and because they extend over a greater diversity of environments, with the associated potential for local adaptive divergence (Rosenzweig 1995). However, models suggest that species with relatively small, although not the smallest, range sizes have higher speciation rates because the effects of the greater probability of subdivision of larger ranges as a result of their extent are offset by the typically greater local densities of individuals and frequently greater dispersal abilities (Gavrilets et al. 2000). Data from fossil assemblages have also revealed an inverse relationship between range size and speciation rate (Jablonski and Roy 2003), which implies that commonness may actually place something of a brake on evolutionary diversification. However, the relationship between range size and the number of species produced during a parental species’ lifetime varies from weakly negative to positive, indicating that the effects of geographic range size per se may to some extent be offset by the greater persistence of species with larger ranges (e.g., Jablonski and Roy 2003). In other words, rare and common species may be broadly equivalent in terms of their net contribution to diversification (i.e., common species are not rare ones writ large), although they make this contribution through different routes.

Ecological consequences of commonness

As well as its evolutionary consequences, commonness has a variety of ecological consequences. Indeed, these have generally been found to be much more profound than was previously suspected.

Macroecological patterns. It has long been asserted that geographic patterns of species richness and species spatial turnover (change in species composition) are driven foremost by the large numbers of rare species. However, although yet small in number, recent empirical studies have shown that at a breadth of spatial scales it is actually common species that principally contribute to determining these patterns (e.g., Jetz and Rahbek 2002, Lennon et al. 2004, Gaston et al. 2007). There is also evidence that this finding extends to patterns of covariance of species richness with environmental variables (e.g., Jetz and Rahbek 2002). Where examined, these outcomes do not appear generally to be a consequence of the distributions of common species comprising greater volumes of information than the same number of rare species—as might happen, for example, if rare species were rarer than common species were common (e.g., more species occurred in just 0% to 10% of sites than in 90% to 100%)—but appear instead to be robust to attempts to control for such effects (Lennon et al. 2004). For species-richness patterns, at least, the dominant influence of common species is a consequence of the shape of the frequency distribution of species richness among sites, and is promoted by the fact that species-occupancy distributions (the numbers of species with different levels of occupancy) tend to be markedly right skewed (Sitzing et al. 2009).

Food-web structure. On average, within a taxonomic assemblage, common species are exploited by larger numbers of species of natural enemies (including, variously, herbivores, predators, and parasites). Studies have shown that these effects persist when controlling for sampling effort and the phylogenetic nonindependence of species (e.g., Kelly and Southwood 1999). Moreover, the development of quantitative food webs, in which species-species interactions are not simply identified but the numbers of individuals involved are estimated, has also demonstrated that common species are exploited by larger numbers of individual natural enemies (figure 2). Importantly, here, as with their overall species richness, the increase in abundance of natural enemies

Figure 2. The relationship between the abundances of herbivores and parasitoids. (a) Moth caterpillars from a forest study plot on Kauai, Hawaii, and the parasitoids reared from them (note that the most abundant host is a species complex). (b) Leaf-mining Diptera, leaf-mining Lepidoptera, and externally feeding Lepidoptera from an organic farm study plot in southwest England, and the parasitoids reared from them. The solid lines indicate the 1:1 relationship (note the data transformations). Data sources: (a) Henneman and Memmott 2001, (b) Macfadyen and colleagues (2009).
Ecosystem structure. Unsurprisingly, common species often provide the larger part of the biologically generated physical structure of ecosystems. Principally this results from their contribution to overall biomass. Within taxonomic assemblages, the 25% most abundant species frequently contribute at least 50% of the biomass (figure 1). The percentage may, however, be much higher (Gaston and Fuller 2008), dependent in large part on the level of interspecific variation in body mass. Because abundance tends broadly to decline with body mass, where this interspecific variation is low, there is a higher contribution of common species to biomass.

If common species make up a disproportionate amount of assemblage biomass, then they most likely also do so for energy use. This finding is at odds with the energetic equivalence hypothesis, which predicts that within a taxonomic assemblage, the local populations of species of different body size should have similar energy use, with declines in population density with increasing body size offset by the lower per-unit mass metabolic demands of larger organisms (i.e., rare and common species are energetically similar; Damuth 1981). However, interspecific density–body size relationships are often rather weak, particularly locally and when density estimates are generated in strictly comparable fashion, such that marked differences in energy use can result among species (White et al. 2007). Moreover, these relationships vary greatly in slope, removing any simple trade-offs.

The great abundance and biomass of common species frequently make them significant ecosystem engineers—modifying, maintaining, and creating habitats. They can be both autogenic engineers (changing the environment through their own physical—living or dead—structures) and allogenic engineers (changing the environment by transforming living or nonliving materials from one physical state to another by mechanical or other means; as defined by Jones et al. 1994). Their effects on ecosystems may play out on very large scales. For example, a number of studies have shown that tree cover is important to regional temperature and rainfall patterns (e.g., Webb et al. 2006). Recent models suggest that natural forests may act as biotic pumps, sustaining the ocean-to-land transport of atmospheric water, and thus precipitation, for thousands of kilometers inland to the interior of continental systems (Makarieva and Gorshkov 2007). The pumps are generated by the concatenated evapotranspiration of water from many closely packed individual trees, a high proportion of which belong to just a small number of common species.

Ecosystem function. Numerous experimental and field studies have sought to document relationships between levels of species richness and ecosystem function (Cardinale et al. 2006, Worm et al. 2006). Frequently reporting positive effects of richness, these studies also highlight the importance of species composition. In particular, common species are disproportionately significant in ecosystem function (whether the same species remain common at different levels of richness or not), formalized as the mass–ratio hypothesis (albeit, given the potentially great variation in body mass, with abundance here interpreted explicitly in terms of biomass; Grime 1998). Although this is widely understood to be the case, explicit empirical studies remain surprisingly scarce. Those that have been conducted show that common species can be responsible for the bulk of primary production and carbon storage (Smith and Knapp 2003, Bunker et al. 2005) and consumption (Dangles and Malmqvist 2004), and can also have a major influence on other ecosystem properties such as bioturbation (biogenic mixing of sediment; Solan et al. 2004), carbon flows (Taylor et al. 2006), functional stability (Polley et al. 2007), and invasion resistance (e.g., Emery and Gross 2007). Meta-analyses of the results of experiments that have manipulated species richness have also found that the standing stock (total abundance or biomass) and resource depletion of the most speciose treatments tend to be similar to those of treatments including just the single most productive species (Cardinale et al. 2006). What is not well understood is how the contributions of common and rare species to ecosystem function scale with the differences in their abundances, although presumably this is highly dependent on the particular function of concern.

This is not to say that rare or less abundant species may not also be important, perhaps most obviously where they strongly interact with other species, have high per-individual resource demands (e.g., because they are very large bodied), or are major ecosystem engineers (Soulé et al. 2005). However, in terms of delivering ecosystem function, the significance of rare species seems to lie principally in buffering changes in that function (the insurance hypothesis) by providing other species to become common when environmental conditions change.

Applied dimensions of commonness

Despite their evident evolutionary and ecological significance, species that were once naturally common are now in widespread decline throughout much of the world. Indeed, although the major threats to biodiversity are almost invariably described in terms of their impacts on rare species, common species lie at the very heart of the biodiversity crisis (Gaston 2010). First, common species are the principal victims of land-use change. Although this change is typically quantified in terms of areal losses, it constitutes the death of large numbers of individuals. Land-use change may dramatically increase the abundances of other species, most notably those that are able to exploit farmlands and urban areas. However, the intensification of agriculture and the densification of urban areas in much of the developed world have been associated with subsequent systematic declines of species that had
previously become common in response to human activities (e.g., PECBMS 2007, Van Dyck et al. 2009).

Second, by definition, large-scale overexploitation of natural living resources concerns previously common species. For example, the 10 species (out of a large number) that contributed most to global marine fisheries catches by tonnage in 2006 accounted for more than 30% of those catches (FAO 2009), and both the 3 and the 10 most common forest tree species constitute more than 50% of the average growing stock in at least 40 of the 82 countries for which data are available (FAO 2006). The collapse of many marine fisheries, the marked loss of old-growth forests from logging, and "empty forest syndrome" (in which forests are drained of vertebrate populations by some combination of extraction for bushmeat, traditional medicine, and the pet trade) all constitute examples of the major declines that can result from large-scale overexploitation. In addition to the immediate impacts on the continued supply of key goods and services, of particular concern is the potential for significant overharvesting to contribute to systems flipping to alternative states, with the prospect, for example, that marine communities previously dominated by fishes will become jellyfish dominated (Richardson et al. 2009).

Third, invasive species may often have major impacts on naturally common species. Some of the environmentally and economically most significant invasives are those that have directly or indirectly killed or replaced the natural dominants, typically through outcompeting, preying upon, or parasitizing them. Many common tree species in North America, for example, are in decline largely as a consequence of introduced pathogens and herbivorous insects (Ellison et al. 2005).

Finally, common species almost invariably lie at the heart of the most marked cascades of population declines. Because common species are involved in engineering environments and in large numbers of biotic interactions, their declines as a result of habitat loss, overexploitation, or nonnative species introductions have broad ramifications. Most obviously they particularly affect specialist consumers and parasites; in the extreme, coextinctions may occur (in which the loss of one species follows the loss of another), but many specialists will become extinct at much higher abundance thresholds of their hosts (Koh et al. 2004).

The impacts of each of these biodiversity threats are being played out against a background of ongoing global climate change. Attention has principally been focused on how climate change will alter the spatial distributions of species, but for common species, the effects on abundances will be more immediately significant. For example, recent population trends in European common birds are correlated with characteristics of their climatic niches, with species occurring at the lowest spring and summer temperatures in the hottest part of their breeding distribution showing the sharpest declines (Jiguet et al. 2010).

Concerns over the decline of common species, however these are driven, are particularly acute because in many cases they seem to be rather systematic patterns, with limited evidence that, at least within a given higher taxon, other species are growing in abundance and distribution to take their place. Indeed, declines in common species are often accompanied by declines in the overall abundance of assemblages. If other species become more common, they are typically rather different in their biological characteristics (e.g., they are smaller, and have shorter generation times and a greater propensity for boom-and-bust dynamics) and in the ecosystem services that they provide (e.g., Richardson et al. 2009).

Although there are already many known examples of declines in once naturally common species, instances of declines may be much more frequent than has been documented thus far because of the nature of the losses. There is a nonlinear relationship between the population size of a species and its geographic range, such that initially substantial reductions in population size can take place with relatively small impacts on geographic range (e.g., Gaston 2003). This is problematic because humans seem innately better able to detect the complete loss of an environmental feature than its progressive change. The recent dramatic decline of vultures on the Indian subcontinent, for example, was well advanced before it came to wide attention (Pain et al. 2008). Moreover, the severe nonlinearity of the relationship between population size and range size means that later declines can be extremely rapid.

There are examples of previously common species that have become globally extinct as a consequence of human activities (e.g., the rocky mountain grasshopper Melanoplus spretus, the passenger pigeon Ectopistes migratorius). However, with regard to common species the greater worry is not that these activities will lead to extinctions but that they will result in a loss of species’ commonness, and thus the loss of their influence on ecosystem structure and function. Moreover, the abundance profiles of assemblages often respond much more quickly to anthropogenic pressures than do species richness and other such measures of biodiversity.

The challenges of maintaining the abundances and distributions of naturally common species in the face of anthropogenic pressures are very different from those associated with doing the same for rare species. Locally directed conservation efforts, including the establishment and maintenance of protected areas, are often most appropriate for the latter. Indeed, in some parts of the world, such activities have led to an increase in the populations of many rare species, but this is not the case for common ones (Eaton et al. 2009). Protected areas undoubtedly have positive influences (Devictor et al. 2007), but schemes to improve the environmental quality of the wider landscape and seascape matrix (e.g., agri-environment schemes, urban greenspace planning) are much more important for maintaining the common status of species. There is growing evidence that such schemes can indeed lead to increases in the abundances of common species (e.g., Kleijn et al. 2006).

Conclusion
Substantial developments over the last decade have served foremost to detail the absolute importance of common species
to a wide variety of ecological and evolutionary processes, to
document widespread declines and their potential significance,
and thus to highlight the vital need for a balanced consider-
ation both of common and rare species. As described above,
evidence as to the relative per capita influence of common and
rare species has been mixed, with examples in which there is
more, less, or a similar amount of evidence for common spe-
cies. In order to improve understanding of the ecological and
evolutionary dynamics that are principally influenced in these
different ways we will require an increased body of case studies
specifically directed toward this issue and that pays particular
attention to the significance of spatial and temporal scales and
taxon.

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