CHAPTER ONE

Speciation and patterns of biodiversity

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There are many more species of insects (>850 000) than of their putative sister taxon (Entognatha, 7500 species) (Mayhew 2002). More than 1600 species of birds have been recorded near the Equator in the New World compared with 300–400 species at latitudes around 40° North or South (Gaston & Blackburn 2000). Mammalian families with average body sizes around 10 g have nearly 10 times as many species as those with average body sizes around 3 kg (Purvis *et al.* 2003). In a catch of 15 609 moths of 240 species over 4 years of light trapping at Rothamsted, England, the majority of species (180) were represented by 50 individuals or less (Fisher *et al.* 1943). These observations illustrate the highly uneven distribution of the world's biological diversity. They are examples of four well-known patterns: species richness varies among clades; it varies spatially, with the latitudinal gradient being a classic example; it is higher in small animals than large ones; and rare species are more numerous than common ones. Documenting and explaining such patterns is a major enterprise of ecology (Gaston & Blackburn 2000).

In their introduction to a previous British Ecological Society (BES) Symposium Volume, Blackburn and Gaston (2003) identified three evolutionary processes that underlie large-scale patterns of biodiversity: speciation, extinction and range changes. Anagenetic change might also contribute to some patterns, for example if there is a general tendency for size increase among mammalian lineages (Alroy 1998). The 2002 BES Symposium dealt mainly with rates of extinction and the ecological processes limiting the distributional ranges of species, but had relatively little to say about speciation. Therefore, our intention in this volume is to examine the thesis that mechanisms and rates of speciation are key determinants of biodiversity patterns. Since ecological factors, including the current diversity of a community, may influence speciation and this in turn may alter ecological relationships, there is a rich web of interactions to explore. This volume, like the Symposium from which it is derived, aims to foster communication among the various disciplines that can contribute to this exploration, especially evolutionary ecologists interested in the speciation process and macroecologists interested in

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explanations for patterns of diversity. In this first chapter we highlight some of the key issues.

How many species are there?

Diversity is measured by counting species. This is not a straightforward process for several reasons, and the complexities should be kept in mind when analysing patterns of diversity. Counting species is relatively easy when there is a tight association between species identity and easily measured traits such as plumage or floral morphology. This is one reason why many studies of the distribution of biodiversity focus on the best-known groups, such as birds (Gaston & Blackburn 2000; Phillimore *et al.*, this volume; Ricklefs, this volume), mammals (Alroy, this volume; Purvis, this volume) and angiosperms (Schemske, this volume). However, even in these taxa, it is likely that northern temperate diversity is better documented than tropical diversity.

Analyses of biodiversity patterns make the necessary simplification that species in all taxa, whether prokaryote or eukaryote, plant or animal, can be treated as equivalent units and counted. One reason why this is inadequate relates to the genetic diversity contained within species. This can be highly variable across taxa, partly because some speciation mechanisms generate very unequal products. One could argue that a highly polymorphic species represents more diversity than a monomorphic one (Tregenza & Butlin 1999). This is akin to the argument for weighting the conservation value of species according to phylogenetic distinctiveness (Mace *et al.* 2003) but has been less-widely discussed.

Establishing the diversity of microorganisms is a special challenge. Morphology is often a useless guide to species identity, and genetics might be the only way. Only recently have large-scale sequencing projects started to clarify the number of distinct types of bacteria present in environmental samples and to allow extrapolations to global diversity. The resulting numbers are very large (Bell, this volume). Explaining this diversity and its distribution in terms of ecological processes, such as colonization and local adaptation, remains a major challenge (Curtis, this volume). Aside from possible differences in the criteria used to define ‘species’ in the two groups, protist diversity is much lower than bacterial diversity and this cannot be readily explained by differences in body size or total number of individuals (Bell, this volume). Besides being relatively new on the face of the earth (about 2 billion years), compared to prokaryotes (>3.5 billion years), protists typically have sexual reproduction, at least occasionally. Perhaps the high frequency of sexual reproduction and recombination in protists might oppose niche specialization and speciation. In prokaryotes, gene exchange does occur by non-sexual means but recombination rates are much lower, which may allow greater diversity to evolve. Objectively definable units of diversity exist in at least some asexual taxa (Barraclough, this volume), but the units may not be equivalent to sexual species.

Speciation is a process, and this too can make it difficult to apply a species criterion. It can be very rapid, as in the origin of hybrid and polyploid species, but it may take hundreds of thousands or even millions of years from the initial restriction of gene flow to its complete elimination. During this transition time, boundaries between species are blurred and it is difficult to find objective criteria for species enumeration (Hey, this volume). For divergent, allopatric, closely related populations, there is no adequate criterion, as Mayr himself recognized (Mayr 1942), and this makes it difficult to measure beta- and gamma-diversity in consistent and meaningful ways.

Speciation mechanisms and biodiversity

Speciation in sexual taxa is the evolution of reproductive isolation – genetically based barriers to gene flow between populations. Coyne and Orr (2004, p. 57) argue that the central problem of speciation is to understand the evolutionary forces that create the *initial* reduction in gene exchange between populations. The emphasis is on the initial barriers because genetic changes that affect hybrid production or hybrid fitness continue to accumulate long after speciation is over, yet have little to do with the process of speciation itself. For this reason, most research on speciation focuses on incompletely isolated taxa or on young, very recently formed species.

Speciation can, and probably does, occur by a variety of mechanisms (reviewed in Coyne & Orr 2004). It can occur in a single step, such as by polyploidy, or it may occur by a gradual series of allelic substitutions at multiple loci. It can happen as a by-product of adaptation to contrasting niches or environments, or it can happen without any adaptation at all. Speciation is inevitable when populations are separated for a long time by a geographic barrier, but it might also happen in the face of considerable gene flow between populations inhabiting the same small geographic region. Many speciation mechanisms have been shown to be plausible, but there remains considerable uncertainty over which of these scenarios are responsible for most of the species on earth.

For our perspective in this book, the question is whether the mechanisms of speciation – the processes that underlie the evolution of reproductive isolation – have played a role in establishing the uneven distribution of global biodiversity. One way to attempt an answer to the question is to explore whether common mechanisms of speciation affect the probability that the resulting species coexist. If so, then the number of species in a given community (alpha diversity) will increase. If not, then the derived species replace one another geographically and only beta or gamma diversity will increase. To this end, we address what speciation yields from an ecological standpoint. In particular, we compare mechanisms of speciation whose products – species – are ecologically different. Ecological divergence facilitates long-term coexistence and increases the numbers of species along environmental gradients.

Polyploidy is a mechanism of speciation that is relatively common in plants. Here, reproductive isolation evolves instantaneously upon the accidental doubling of chromosome number, because triploid hybrids between ancestral diploid and derived tetraploid individuals are sterile. When polyploids are formed from within a species, the derived form contains a subset of alleles already present in the ancestor and so is not much different genetically from the original. Nevertheless, physiological and life history differences associated with having twice the number of chromosomes can influence ecological tolerances and possibly affect niche use (Levin 2002). Functional diversification is even more likely when the polyploids are formed by hybridization between two species, because in this case entirely new gene combinations are produced. This can have two immediate ecological consequences. Firstly, the new gene combinations might code for unique ecological traits. Secondly, the polyploids might immediately be exposed to strong natural and sexual selection to purge the population of incompatible or unfit gene combinations, and favour specific gene combinations in the environments in which the polyploids occur. Polyploidy is actually one of the few speciation mechanisms for which it is possible to estimate its contribution to the generation of diversity: it accounts for about 7% of speciation events in ferns and 2–4% of speciation events in angiosperms (Otto & Whitton 2000). The same cannot be said for other types of chromosomal rearrangements, the importance of which remains unclear. Although many pairs of species differ in chromosome number or form, the evidence for a causal association with speciation is very limited (Coyne & Orr 2004; Butlin 2005).

Hybridization between species can have similar effects on the speciation process regardless of whether the resulting hybrid is polyploid or diploid, because in both cases new gene combinations are produced that are immediately distinct ecologically or immediately subjected to strong selection in their environments, provided hybridization is associated with a restriction of gene flow from their parental species. The best examples are again from plants (Rieseberg *et al.* 2007), but examples of hybrid species are also known in animals (Mallet, this volume; Mavarez *et al.* 2006).

Over the past decade evidence has been accumulating that many, and possibly most, speciation events involve some form of natural and sexual selection. The evidence comes from both genetics and ecology. First, the few genes, which have been discovered to date, that underlie reproductive isolation between species tend to exhibit statistical signatures of selection, such as rapid rates of nucleotide substitution in coding sequences (Noor 2003). Second, a growing number of studies find that reproductive isolation evolves most quickly between species when ecological differences also accumulate (Schluter 2001; Funk *et al.*, this volume). Third, a number of studies have found evidence of gene flow having occurred during the speciation process (Via 2001; Barluenga *et al.* 2006; Savolainen *et al.* 2006; Gavrilets and Vose, this volume). This provides indirect evidence for selection because without it gene flow would have prevented the evolution of reproductive isolation.

Natural and/or sexual selection can bring about the evolution of new species by a variety of mechanisms that have very different ecological consequences. We can group these mechanisms into two broad categories: reproductive isolation driven by divergent natural selection between environments or niches ('ecological speciation') and reproductive isolation resulting from divergent genetic responses to the same environmental selection pressures ('non-ecological speciation'). A key difference between the two categories of mechanisms is that whereas ecological speciation yields species that are ecologically different and can coexist, non-ecological speciation produces forms that are ecologically equivalent. Coexistence of ecologically equivalent taxa is possible, at least for considerable time periods (Hubbell 2001), but establishing sympatry may be slowed. Divergent selection is also likely to produce reproductive isolation more rapidly than uniform selection. Furthermore, divergent selection continues to select against hybrids if they have an intermediate phenotype (extrinsic postzygotic isolation), and this might allow species to coexist relatively soon after they formed, and to persist in sympatry in the face of gene flow. In other respects, the types of reproductive isolation that evolve are not necessarily different between the two categories of speciation mechanisms. Both mechanisms can lead to intrinsic postzygotic isolation due to genetic incompatibilities and prezygotic isolation due to divergence in mating cues. Reinforcement of prezygotic isolation can also occur under either category of mechanism.

The threespine sticklebacks, *Gasterosteus aculeatus*, inhabiting postglacial lakes and streams of the northern hemisphere provide multiple examples in which divergent natural selection has led to both extrinsic reproductive isolation and incidental assortative mating by body size (Rundle *et al.* 2000; McKinnon *et al.* 2004; Vines & Schluter 2006). There is also evidence for reinforcement of premating isolation in sympatry (Rundle & Schluter, 1998; Albert & Schluter 2004). In general, divergence driven by selection may occur more rapidly the greater the number of ecological dimensions that are involved (Nosil & Harmon, this volume).

Cases of speciation by non-ecological mechanisms are difficult to confirm. The evolution of intrinsic postzygotic isolation between *Drosophila melanogaster* and *Drosophila simulans* involving nucleotide substitutions at *Nup96* might represent an example (Presgraves & Stephan 2007). The gene interacts with an unknown factor on the X chromosome to create sterility of F1 hybrid males. It

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codes for a protein in the nuclear pore complex. Excessive non-synonymous substitutions in the coding sequence of the gene indicate that *Nup96* was under selection, but as it functions in the nuclear pore complex it is not easy to see how a change of environment could be the driving mechanism.

Divergent sexual selection may also drive the evolution of reproductive isolation (Lande 1981; Gavrilets 2004). Comparative evidence suggests that sexual selection indeed plays a role in generating species diversity. For example, sexual dichromatism in bird clades is positively correlated with number of species in the clade (Barraclough *et al.* 1995). Beta, rather than alpha diversity, is mainly affected (Price 1998). Direct evidence for a primary role of sexual selection in speciation is more equivocal (Panhuis *et al.* 2001; Ritchie 2007).

Mechanisms of sexual selection can be grouped under the ecological or non-ecological categories of speciation mechanism depending on the ultimate cause of genetic divergence in the mating preferences. For example, mating signal transmission may be strongly affected by environment, which can bring about the evolution of divergent signals between populations inhabiting different environments (Endler 1992; Boughman 2002). A powerful example of this interaction between natural and sexual selection is provided by Lake Victoria cichlids in the genus *Pundamilia* (Seehausen, this volume). This case is particularly significant because previous explanations for the exceptionally rapid diversification of these fish have put the central driving role on sexual selection, whereas divergent natural selection was overlooked (Turner & Burrows 1995). In general, signal-response systems are likely to diverge along with ecological divergence rather than independently (but see Irwin *et al.* 2008). On the other hand, divergent mating preferences arising from sexual conflict can happen independently of the environment. It is difficult to find clear-cut examples in nature but experimental manipulation of sexual conflict in laboratory populations of *Sepsis* dung flies showed increased isolation in response to high levels of conflict (Martin & Hosken 2003). The process of sexual conflict might still be influenced by the environment, for example through the impact of population density on remating rate.

The possibility of speciation without selection, by mutation and genetic drift alone, is hotly debated. There can be no doubt that, given sufficient time and strong enough extrinsic barriers, mutation and genetic drift will result in speciation through the fixation of incompatible alleles in separate populations. However, the time required is probably too long for this mechanism of speciation to be a major contributor to biodiversity. Much more attention has focused on the role of drift in very small populations that colonize new areas: the 'founder effect'. According to theory there are serious obstacles to founder-effect speciation (Barton & Charlesworth 1984). In addition, colonization of new areas is very likely to involve a habitat difference and hence strong selection. It is therefore difficult to separate effects of drift and selection in driving divergence and speciation following colonization of new environments. The evidence for a role of founder effects in nature is weak (Coyne & Orr 2004). For example, the radiation of Hawaiian *Drosophila* has been thought of as an example of rapid speciation by repeated founder events. Yet, genetic diversity within these *Drosophila* species is typically high, which seems inconsistent with repeated bottlenecks during speciation events (Hunt *et al*. 1989).

Ecology can play a role in driving speciation apart from its influence on selection. For example, successful colonization of new areas, a prerequisite for allopatric speciation, might be easier if diverse resources are present and few other species utilize them (Mayr 1942; Phillimore & Price, this volume). At the same time, reproductive interference might prevent species from coexisting even if they are ecologically different (Goldberg & Lande 2006). This is clear from the large number of sharp parapatric boundaries between populations at hybrid zones (Barton & Hewitt 1985). For example, incomplete assortative mating and low hybrid fitness may prevent sympatry in *Bombina* toads despite clear ecological differences (Vines *et al*. 2003). In other hybrid zones, the interacting populations have no detectable ecological differentiation and yet show significant pre- and postzygotic isolation. For example, in the meadow grasshopper *Chorthippus parallelus* there is some evidence that the colonization process promoted the evolution of incompatibilities (Butlin 1998; Tregenza *et al*. 2000, Tregenza *et al*. 2002).

Generation of distinct and persistent taxa that coexist is clearly a crucial endpoint of speciation from the point of view of diversity patterns. Speciation driven by divergent selection is likely to make a qualitatively different contribution to diversity patterns compared with speciation driven by other 'non-ecological' forces, including drift, some forms of sexual selection, and divergent response to uniform natural selection. Ecological speciation generates species that have distinct ecological roles, in contrast to other forms of speciation. Perhaps the ecological mechanisms of speciation are also more likely to occur in the presence of high ecological opportunity and to be dependent on the number of species already present in the community. Therefore, it would be helpful to understand the contributions of different mechanisms to speciation rates and their variation. Unfortunately, as Coyne and Orr (2004) have emphasized in their thorough review of the literature, this is a question about which we know rather little. Until recently, empirical speciation research has concentrated on case studies and one can find well-supported examples of many different modes of speciation. The approach of Barraclough and Vogler (2000) to sympatric and allopatric speciation is a notable exception, although it is not clear if a similar approach can distinguish speciation mechanisms. Recently, comparative analysis of diversification rates has provided an alternative approach to finding general patterns and one that clearly has the potential to forge links between speciation process and macroecological pattern.

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Biodiversity and speciation rates

Speciation is the ultimate source of new species, in the same way that mutation is the ultimate source of genetic variation within species (and extinction is analogous to loss of alleles). Inequities in the rates of speciation are thus likely to contribute to large scale biodiversity patterns. It has often been proposed, in cases where some parts of the globe have excessive numbers of species, that the taxa in those regions have experienced unusually high speciation rates. Conversely, regions of the globe with fewer species are inferred to be speciation-limited.

For example, to explain the latitudinal gradient in species diversity, Dobzhansky argued that speciation rates were higher in the tropics than in the temperate zone, because of the greater opportunity for co-evolution (Schemske, this volume). However, diversity is the outcome of the *difference* between speciation and extinction, not just speciation alone. New estimates of speciation rates in birds and mammals in the recent past suggest that they are actually highest at temperate latitudes (Weir & Schluter 2007), even while net diversification appears to be highest in the tropics (Cardillo 1999; Ricklefs 2006). The implication is that lower extinction, not higher speciation, is behind the faster accumulation of species in the tropics (Weir & Schluter 2007). On the other hand, these estimated rates might be a temporary outcome of the turmoil of the Pleistocene glaciations, and speciation rates may really have been higher in the tropics over the longer term. This example indicates that the extent to which diversity patterns reflect speciation rates is an open question for research.

It is possible to model how speciation rates might impact biodiversity patterns. In his ‘neutral theory’ Hubbell (2001) showed that metacommunity diversity depends only on community size (the total number of individuals) and speciation rate. Extinction occurs as a consequence of stochastic variation in population sizes, which are on average lower the more species are present. In these models, quantitative features of the species-abundance relationship, and species’ longevities, depend on the mode of speciation: if new species result from random fission of the ancestral species then they begin with relatively large population sizes and so have relatively long persistence times. Under the alternative ‘point mutation’ mode of speciation, each new species begins as a single individual, in which case they are expected to be very short-lived. In response to criticism by Ricklefs (2003) that these extreme patterns are unrealistic, Hubbell and Lake (2003) introduced a third mode of speciation into the Hubbell neutral model, called ‘peripheral isolate speciation’. This allows speciation to occur in an isolate of variable population size and has two parameters: the mean and the variance of isolate size. By varying these parameters, a wide range of species-abundance relationships and persistence distributions can be obtained, thus overcoming Ricklefs’ objection.

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This exchange is instructive for two reasons. First, it demonstrates that, in the simplest of models, both the rate and the mode of speciation influence patterns of diversity. Second, it emphasizes our ignorance because even these models require parameters for which we have few, if any, good estimates (the rate of speciation and the mean and variance of the population size in which speciation is initiated). Without limits on these parameters, the model lacks heuristic value because it can produce too wide a range of outcomes. This is partly why Chave (2004) concluded that neutral models are unlikely to benefit from more complex models of speciation.

Neutral models are based on the neutrality assumption: all species are assumed to be ecologically equivalent, which is the expectation only if all speciation is non-ecological (and species fail to diverge ecologically post-speciation). But if speciation is commonly ecological (or species diverge ecologically post-speciation) then species persistence is affected by niche differences, and the stage is set for a much more complex set of interactions between the mode and rate of speciation on the one hand and patterns of diversity on the other. The first steps in unravelling these interactions must be to document speciation rates and, where they vary, test for ecological correlates of that variation.

Speciation rates do seem to be highly variable across taxa (Fig. 1.1). One can imagine many conditions that might favour local adaptation and so increase the

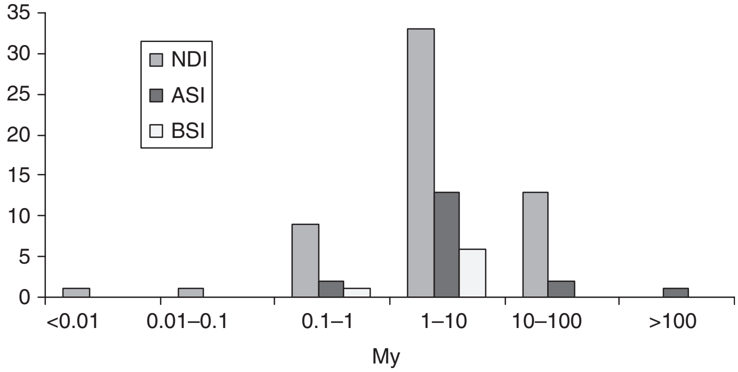

Figure 1.1 Variation in speciation intervals among taxa. NDI is 'net diversification interval', which is the average time between the origin of a lineage and the next branching event on that lineage assuming a pure birth model (i.e. without extinction); ASI is 'apparent speciation interval', which includes a correction for extinction, estimated either from a phylogeny or from fossil data; and BSI is 'biological speciation interval', estimated from extant taxa by determining divergence times between sister taxa or extrapolating the observed increase in reproductive isolation with time to the point of complete isolation. Data from Coyne and Orr (2004), Table 12.1. See their discussion, pp. 416–425, for further details.

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rate of ecological speciation, such as new ecological opportunities, selection along multiple dimensions (Nosil & Harmon, this volume), high productivity, wide dispersal, or fragmented habitats (especially host associations). Conversely, there are clearly factors that limit the ability of populations to respond to selection, especially where the environment changes too quickly in time or space (Bridle *et al.* this volume). Diversity itself is one potential driver for speciation, although one can make arguments in either direction: high diversity creates more ways of making a living and so favours speciation, but it also tends to decrease population sizes, working against speciation and in favour of extinction. For example, evidence that speciation rate is positively correlated with diversity on islands (Emerson & Kolm 2005) is controversial (Cadena *et al.* 2005). A different set of factors might be expected to enhance, or depress, rates of non-ecological speciation. Large ranges, limited dispersal and environmental change all increase the opportunities for extrinsic isolation and so for accumulation of genetic incompatibilities, for example, while frequent remating increases sexual conflict and so the opportunity for conflict to drive speciation (Arnqvist *et al.* 2000).

However, speciation rates are very difficult to estimate and this makes it hard to test hypotheses about the causes of rate variation. Some of the wide variation in estimated speciation intervals is, undoubtedly, due to methodological limitations. The most problematic of these is disentangling speciation from extinction. This problem exists for interpretation both of the fossil record (Alroy, this volume) and of molecular phylogenies (Phillimore & Price, this volume; Ricklefs, this volume). Estimating speciation and extinction rates requires finding appropriate models for diversification if interesting questions are to be addressed.

For example, Ricklefs (this volume) and Alroy (this volume) both ask whether diversity is at a steady state, with extinction rate approximately equal to speciation rate. Alroy, analysing fossil mammals, demonstrates that alpha diversity is more stable than expected from observed rates of species turnover, suggesting that diversity is bounded. Ricklefs, analysing phylogenetic trees of birds and plants, finds a poor fit across taxa to the expectations of constant birth–death models. He suggests that a steady-state model in which speciation roughly matches extinction fits the data best. These results are inconsistent with previous phylogenetic studies showing that speciation always outpaces extinction, leading to a rise in diversity. Ricklefs suggests that the phylogenetic methods are biased. We tend to work on taxa with a reasonable number of species, which dooms us to find that speciation has outpaced extinction. Declines in diversity are also undetectable in phylogenetic trees. Similar methodological problems plague tests of apparent changes in speciation and extinction rate, such as a decrease in diversification rate towards the present (Phillimore & Price, this volume). These problems need to be overcome before important ecological questions can be addressed.