

Chapter 1. Introduction and conceptual approach

1.1 Will we live with or without biodiversity?

Humans have ‘conquered’ the world (Figure 1.1), and now it is time to face the consequences. The world is changing:

‘...Fossil-fuel combustion and deforestation have increased the concentration of atmospheric carbon dioxide (CO₂) by 30% in the past three centuries... We have more than doubled the concentration of methane... In the next century ... greenhouse gases are likely to cause the most rapid climate change that the Earth has experienced since the end of the last glaciation 18,000 years ago... Humans have transformed 40–50% of the ice-free land surface, changing prairies, forests and wetlands into agricultural and urban systems... We use 54% of the available fresh water... [The] mobility of people has transported organisms across geographical barriers that long kept the biotic regions of the Earth separated...’ (p. 234, Chapin III *et al.* 2000)

Overpopulation, pollution, thinning of the ozone layer, global warming (or cooling), toxic wastes, new deadly diseases, and a rapidly growing number of extinct species: these are some of the challenges for humans to overcome. In biological disciplines, science has made giant steps, such as evolutionary theory, the human genome project, and heart transplants. However, we are still unable to control the common cold, predict the weather, or assess the damage caused by species extinctions. Some of these questions are more pressing than others. Species extinction was recognised as a potential problem only in the last few decades. There is evidence that human impact on the rate of species extinction may be great: ‘...recent calculations suggest that rates of species extinction are now on the order of 100 to 1000 times those before humanity's dominance of Earth... At present, 11% of the remaining birds, 18% of the mammals, 5% of fish, and 8% of plant species on Earth are threatened with extinction’ (Vitousek *et al.* 1997).

Why is it important to have diversity? There are several reasons, among them the medicinal value of plants in disappearing tropics, diversity's stabilising effect on

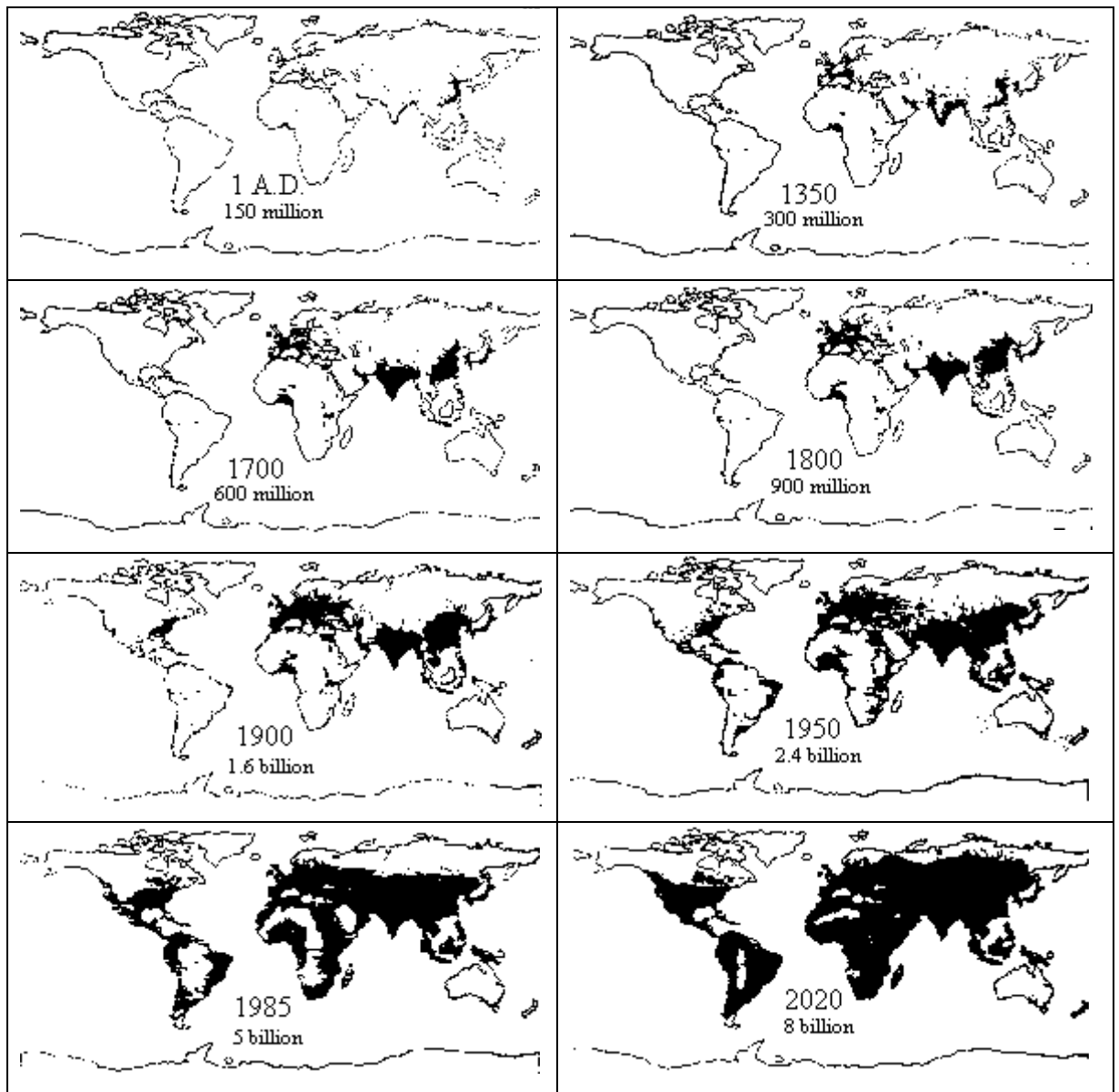


Figure 1.1 The spread of humanity from 1 A.D. to 2020 (from Tanton 1995).

ecological systems, uses of wild species for agriculture, and ethical and esthetic considerations. But more importantly, we are not sure how and when diversity is important. Such an answer, while policy makers do not usually accept it as an urgent call for action, should be taken extremely seriously. If the role that diversity plays in ecosystem functioning and health is not understood, it might not be possible to estimate the dangers. Perhaps much of diversity is redundant – but perhaps it is not. Perhaps, tomorrow or next year it will be too late. Because we do not have a precise understanding of our impact on ecosystems, it is important to realise the necessity of research, in the face of the gravity of the possible consequences. ‘In view of the genuine possibility of a global collapse of biodiversity in the near future, it is unconscionable that we still have no serviceable general theory of biodiversity.’ (p. x), wrote Hubbell in his book on the theory of biodiversity (Hubbell 2001). Can we understand the consequences of our actions to ourselves and our environment? Can we understand other ecological systems so that we may manage them prudently? These questions may be vital to our survival, and are tests of whether human intelligence - which makes us ‘so special’ - can help us to use our environment wisely.

1.2 Explaining biodiversity

1.2.1 Measuring biodiversity

The incredible diversity of natural communities is apparent to even the most uninformed observer. The multitude of shapes, colours and sizes that exist in ecosystems, ranging from the rainforest to our backyard, is striking. However, in order to study diversity in communities, it is necessary not only to observe but to measure diversity. Measures of diversity can incorporate a range of information such as simply the number of species in an area, or the kinds of species present in a community and their abundance.

The available measures of diversity are 1) measures of the species number, 2) species indices (which incorporate information about the distribution of species in a community), and 3) diversity patterns (such as the species abundance distribution or the species-area relationship). The first type includes three measures which express the number of species, defined by Whittaker (1970). The α diversity is the number of species at a particular location. The β diversity is the rate at which species accumulate

as the observer moves away from a point, in a line. The γ diversity is the number of species in a particular region (Rosenzweig 1995).

Diversity indices are commonly used in field ecology. One of the earliest indices is Fisher's α (Rosenzweig 1995), which is a measure that does not depend on sample size. It is based on the assumption that species abundance fits a log-series distribution, *i.e.* if the total number of individuals, in a community is N , then, for a constant proportion p , the most common species has pN individuals, the next common $p(1-p)N$ individuals, the next $p(1-p)^2N$, etc. If the species abundance in a community fits such a distribution, then the number of species S in a sample is:

$$S = -\alpha \ln(1 - x)$$

where α is a constant that depends on diversity, and x is a variable that depends on the size of the sample, and satisfies:

$$\frac{S}{N} = \left(\frac{x-1}{x} \right) \ln(1-x).$$

There are many other indices of diversity: for example Shannon's index, Simpson's index, McIntosh's index, and others (Rosenzweig 1995). These indices incorporate the number of species and their distribution in various ways. Currently, the importance of incorporating differences between species in terms of their contribution to community functioning was highlighted (Nijs and Roy 2000). Progress towards this was made by Shimatani (2001), who described a diversity index incorporating species differences in terms of their genetic relatedness to each other. Diversity indices are useful for tracking the evolution of diversity in a community. However, those that have been devised to date do not provide insight into the underlying community processes that lead to diversity.

One of the remarkable characteristics of diversity is that, in various communities, it exhibits consistent patterns, such as the species-area relationship and the species abundance distribution. For a detailed treatment of diversity patterns see Rosenzweig (1995). One of the most well known ecological studies is the study of species richness (the number of species in a particular sampling area) on islands of different sizes conducted by MacArthur and Wilson (1963, 1967). They found a linear relationship on a log-log scale between the island size and the number of species found on the island. Since then, this relationship has been observed in many other communities and contexts. The same linear relationship on a log-log scale was observed if mainland plots of different sizes were considered. However, the slope of the linear relationship

changes with the scale of considered. Crawley and Harral (2001) analysed data for plants in Great Britain, and found that the slope was small (around 0.1 to 0.2) at small scales (less than 100 m²), larger (0.4 to 0.5) for the intermediate scales (less than 1 hectare), and low again (0.1 to 0.2) for the largest scales (regions of Great Britain). Rosenzweig (1995) presents Preson's species-area curve for land birds, in which the slope is higher (approximately 0.5) for the intermediate area (less than 0.5 km²), lower (approximately 0.2) for the regional areas (*e.g.* Pennsylvania), and high again (approximately 0.6) for the global scale (*e.g.* continents).

In a seminal paper, Preston (1948) collected ecological data on species abundances in communities, and formulated the theory of the canonical lognormal distribution of species abundance. He postulated that species number as a function of abundance is lognormally distributed. Moreover, it is canonical, *i.e.* there is a relationship between the parameters of the distribution. His work attracted attention, especially when some of the data sets were analysed to show that the lognormal distribution was not always evident. Instead, in some communities, the distribution of species abundances appeared to fit a geometric distribution better, and some exhibited distributions somewhere in between (Pielou 1977). MacArthur in 1957 formulated the 'broken-stick' theory of species abundance. In this theory, the species abundance distribution was assumed to arise from randomly splitting the total population into S segments, where S is the number of species in a community (MacArthur 1957). The lognormal distribution on log scale is a normal curve, and the geometric distribution is a horizontal line, MacArthur's distribution had a shape flatter than a normal curve, but not quite a horizontal line. Another species abundance theory was proposed by Whittaker (1965). This theory, dubbed 'niche pre-emption', assumes that each species, in order of decreasing competitive dominance, takes a fraction of the remaining resource available in the system. Sugihara (1980) put forward yet another theory of abundance distribution, the sequential breakage theory. This theory assumes that the species abundance distribution can arise from the following process: the total number of individuals in a community is divided randomly into two parts, then one of these parts is picked randomly and randomly split in two again, etc. Hubbell (2001) developed a theory of biodiversity on large scales. He considered a community consisting of many populations which interact by migration. He connected his theory to the work of MacArthur and Wilson (1967) and showed that the resulting species abundance distribution could be lognormal or negatively skewed. In general, a comparison of different communities shows that geometric distribution is characteristic of a community under stress or disturbance, or a young community in the r -selection stage

(*i.e.* the population density is low, and the individuals with high growth rates are favoured). The lognormal distribution is characteristic of undisturbed long-existing communities. As May (1976) put it: ‘... [a] lognormally distributed community tends to be an egalitarian socialist society compared with the feudal hierarchy characteristic of early succession.’ (p.216)

1.2.2 Modelling approaches

Explanations of diversity in biological systems were sought in theoretical biology and mathematical population ecology. Theoretical biology characterised species in terms of their habitat space, both in terms of spatial distribution and resource requirements. The species’ habitat space is its niche, within which it competes with other species. Considered in these terms, species diversity is the sum of all the species that can pack themselves into the niches of the environment. While appealing on theoretical level, such an explanation is hard to test in real communities. Measuring a species niche is difficult since it is defined by many parameters (*e.g.* various environmental gradients, species resource preferences and responses to environmental conditions). However, attempts to measure a species niche have concentrated on measuring differences in one or a few properties, such as size or resource preferences (Gordon 2000).

Another area of ecology exploring diversity was mathematical population modelling. In this area, studies focused on coexistence mechanisms. Species coexistence studies began with Lotka-Volterra models defined in the 1920s. These models consisted of two coupled differential equations. They expressed the interactions of two species, predator and prey. The results showed that coexistence between the two species is possible when cyclic oscillations in both populations occur (Murray, 1989). To estimate the possible number of coexisting species in a community, a model was developed where the species were limited by different resources (Levin 1970). This model showed that the species number in a community is equal to the number of resources. However, this answer was unsatisfactory since many diverse communities are limited by just one resource, *e.g.* in grasslands (Gleason and Tilman 1990). Huisman and Weissing (1999) showed that under certain conditions coexistence of many species in an environment limited by few resources is possible in resource competition models.

In the 1970s, population dynamics turned to investigate the effect of spatial configurations on community diversity (influenced by the work of Turing (1952) on

morphogenesis, the generation of patterns from a uniform initial state). Levin (1974) wrote:

‘The distribution of a species over its range of habitats is a fundamental and inseparable aspect of its interaction with its environment, and no complete study of population dynamics can afford to ignore it. This point was emphasized over 20 years ago by Skellam (1951) and Hutchinson (1951); and yet, until recently, the mathematical theory of population dynamics has largely ignored spatial considerations.’ (p.207)

Levins was responsible for the introduction of spatial considerations into modelling. He defined an analytical model of species living in many habitat patches (Levins 1969). (This occurred around the same time as MacArthur and Wilson published their work on the species-area relationship.) This approach developed into an area of ecological modelling called ‘metapopulation modelling’ or ‘patch modelling’. Metapopulation models showed that coexistence between superior and inferior competitors is possible in a community consisting of many separated populations interacting with each other. This occurs through the emigration of the inferior species, which can ‘escape’ from the competition. This concept is sometimes referred to as ‘regional coexistence’ (Levins and Culver 1971 and Slatkin 1974, discussed in Levin 1974). These results have been confirmed more recently (Shmida and Ellner 1984). In a host-parasitoid system, Hasell *et al.* (1994) showed that spatial segregation occurs among the coexisting species.

To represent the diversity of individuals in a particular characteristic such as age on size, analytic models of physiologically structured populations were developed (Metz and today is Diekmann, 1986). These systems were defined with implicit space (i.e. there is no spatial dimension in the model, but spatial interactions are expressed through the formulation of the model, e.g. density dependent growth) and explicit space (where the model is defined with explicit definition of spatial dimensions and processes occurring in space). These models used a combination of analytical and numerical simulation approaches to explore population dynamics in these systems, and were used successfully to predict population dynamics in some systems, such as *Daphnia* communities (Metz *et al.* 1988). However, local interactions and spatial heterogeneity rendered the models too complicated for analysis (Metz and de Roos 1992).

Another modelling approach of representing individual diversity in a population was developed by Caswell (1989). He developed age- or stage-structured models (also

known as matrix models). Matrix models consider a population consisting of groups of individuals varying in one particular parameter (*e.g.* age or weight). The dynamics of a population are simulated by defining source ('birth') rate, sink ('death') rate, and transition probabilities between the groups. Age- and stage-structured models are used widely as prediction tools for population dynamics (Hastings, 1997).

In the 1980's, technological advances in computational power led to the development of individual-based modelling (also known as agent-based modelling). In this approach, the behaviour of each individual in the modelled community is simulated explicitly. This became possible only when computers became powerful enough to simulate populations of individuals in a reasonable amount of time. Individual-based modelling was developed to relax two assumptions made in most mean-field models that a) all individuals are identical, and b) that all individuals are affected by each other and their environment in the same manner, in an effect called 'mixing' (Huston *et al.* 1988). In most biological communities, individuals interact with other individuals only within a certain neighbourhood. This neighbourhood can be of different sizes, include different number of various individuals, and can move if the individual in question is mobile. Individual-based models are used to explore the effects of individual interactions and variation on community dynamics, often in a spatially explicit environment (for further descriptions of this approach see Hogeweg and Hesper 1990, Uchmanski and Grimm 1996, Grimm 1999, Lomnicki 1999). Individual-based modelling has been used to investigate the dynamics of both animal and plant populations (for a general review see Grimm 1999; for a review of models of animal populations see Dunning *et al.* 1995; for a review of models of marine populations see Botsford 1992; for some examples of forest models see Mladenoff and W. Baker 1999, Köhler and Huth 1998, Kubo and Ida 1998, Shugart 1984).

The individual-based approach is especially relevant to modelling vegetation systems, since plants are sessile organisms, and neighbourhood interactions are restricted to individuals in the immediate area around the plant. Hence, neighbourhood interactions are especially pronounced and may affect ecosystem dynamics. Grassland individual-based models include models by Weiner and Conte (1981), Pacala and Silander (1985), Pacala (1986, 1987), Crawley and May (1987), Humphries *et al.* (1996), Warren and Topping (1999), Winkler *et al.* (1999), and Kleidon and Mooney (2000). Spatially explicit models allow explicit definition not only of the plant locations, but also of environmental variables for each of the locations. Therefore, environmental heterogeneity and disturbances can be simulated in individual-based

models. Individual-based models have been used to show that the introduction of description of spatial interaction in the models can have a strong impact on population dynamics (Tilman and Kareiva 1997). In particular, several studies showed that spatial arrangements of individuals, environmental heterogeneity, and environmental disturbances can alter interactions and, in some cases, promote the coexistence of species (Levin 1974, Weiner and Conte 1981, Green 1989, Chesson 1994, Tilman 1994, Lavorel and Chesson 1995, Weber *et al.* 1998, Winkler 1999).

1.2.3 The role of trade-offs in sustaining diversity

Spatial and temporal heterogeneity are the external environmental factors that can promote coexistence. What are the mechanisms within a community that promote coexistence? Why does a 'superspecies' (a species best at everything) not exist? Ecologists have noted that species superior in one aspect with respect to others are inferior in other aspects (for example, organisms which grow very fast do not have long life spans). This is believed to happen due to the existence of physical/physiological constraints on organisms. These constraints can be described in terms of trade-offs between traits of organisms.

Several trade-offs have been shown to lead to community diversity. One of these is a trade-off between competitive ability and dispersal, *i.e.* the superior competitors disperse at slower rates. This trade-off has been shown to make coexistence of species possible in the context of the metapopulation modelling (Levins and Culver 1971, Hastings 1990, Shmida and Ellner 1984). The same conclusion was reached by Weiner and Conte (1981) applying a different method - a spatial simulation model with neighbourhood competition. The model showed that a trade-off between competitive ability and dispersal rate can retard or prevent competitive elimination. Crawley and May (1987) modelled a two species community consisting of an annual plant species dispersing by seed and a perennial plant species invading only by lateral growth. They employed a spatially explicit neighbourhood model, and found that coexistence was possible due to the competition/colonisation trade-off, if the perennial species was a better competitor. Tilman (1994) further explored the role of trade-offs in coexistence mechanisms. He investigated coexistence in analytic models that assume local interactions on a homogeneous resource. Coexistence in these models was possible given two- or three-way interspecific trade-offs among competitive ability, colonisation ability, and longevity.

Lavorel and Chesson (1995) explored the effect that germination played in the coexistence mechanisms of ecological communities. They employed a two-species simulation model of annual plants with periodic disturbance. They found that a dispersal/germination strategy trade-off can lead to species coexistence. In other words, coexistence was possible if the species with shorter dispersal ranges had higher probabilities of germination. Diversity in seed production strategies was explored by Rees and Westoby (1997) and Geritz *et al.* (1999). In both studies, analytic models were considered in an evolutionary context. That is, plants' persistence was evaluated using a fitness function based on competitive ability and abundance. They showed that coexistence is possible due to a trade-off between seed size and seed number, provided that seedlings from large seeds were more competitive and viable. Evidence for the existence of this trade-off was examined by Guo *et al.* (2000), who inspected plant data in northern England and the Chihuahuan Desert of Arizona, USA. The results of the study show that a trade-off between seed number and size exists (species with small seeds produce more of them). However, they also show that small seeds have higher viability than large ones, contrary to the assumptions of the analytic models. In the study of a diverse grassland site with nitrogen as one limiting nutrient, Gleeson and Tilman (1990) stipulated that coexistence between species may be possible due to the trade-off in resource allocation to roots *vs.* reproduction.

1.3 Some open problems

‘... we do not know how many species inhabit the Earth or even a small part of it... We know even less about how and where most species on Earth originate, live and die.’

Hubbell (2001), p. ix

In addition to an incomplete catalogue of existing species, several other issues have been plaguing ecologists. One of them is the relationship between diversity and ecosystem functioning (*e.g.* its productivity and stability). This relationship has been a subject of an ongoing debate in ecology (Tilman 1999). Whether an increase in species diversity leads to an increase in ecosystem productivity, and whether diversity impacts system stability are two questions that have been much debated. The collection of studies on these topics (Loreau 2000, Schwartz *et al.* 2000, Hector *et al.* 1999, Tilman 1999, Tilman and Downing 1994, Naeem *et al.* 1994, Schulze and Mooney 1994) shows

that these questions have not been amenable to straightforward answers. These studies lead to the conclusion that ecosystem functions are related not to one, but to a collection of diversity characteristics (which include the number of species, types of species, and their proportion in a community). The exact effect of various diversity characteristics is unclear. Moreover, there is evidence that this effect depends on environmental conditions (Cardinale *et al.* 2000, Yachi and Loreau 1999). Therefore, understanding an ecosystem in terms of relationships between one property and one ecosystem function seems not to be possible.

While macroscopic patterns in diversity such as species abundance distribution and species-area relationship exist, the question of their origin is still unanswered. Their existence points to regular behaviour emerging from complexity at the individual level and offers constraints on proposed mechanisms. Most of the theories explaining the patterns are abstract, untestable, and do not explain the observed variation in patterns (see section 1.2.1). A recent book by Hubbell called *The Unified Neutral Theory of Biodiversity and Biogeography* (2001) describes a theory of the mechanisms on the metapopulation scale (*i.e.* a large scale of community consisting of many smaller populations). According to this theory, the species-area relationship and species abundance distribution are of the same form as those observed in ecological communities. However, the mechanisms generating diversity patterns on smaller scales are not yet known.

1.4 Challenges in understanding biodiversity

‘Variety is charming
and not at all alarming’

16th century English folk song

1.4.1 Complexity

It is not surprising that ecosystem dynamics have not yet been fully understood. An ecosystem is ‘all the interacting parts of the physical and biological worlds’ (Ricklefs and Miller 1999). It is a collection of entities sized from millimetres (*e.g.* micro-organisms) to kilometres (*e.g.* lakes). These all interact with each other in various ways: along and across scales, locally and globally. Moreover, several types of heterogeneity are present in ecosystems on various scales: in abiotic environmental

factors, in the spatial distribution of individuals, and between individuals themselves. It is difficult (an understatement!) to map out these interactions, decide which are important for the questions at hand, and capture them meaningfully in a model.

1.4.2 Defining diversity

To distill any understanding from the complexity of ecosystems, simplifications are necessary. One of these simplifications is in the definition of diversity. Most ecological models view ecosystems at the species scale. Originally, species were defined as ‘groups of populations that can actually or potentially exchange genes with one another and that are reproductively isolated from other such groups’ (Mayr 1942). This definition is convenient for evolutionary studies, which follow the genetic evolution of groups of populations in higher kingdoms (*e.g.* animals). In the plant and lower kingdoms, interspecific exchange of genetic material is common; this erases the genetic distinctions and makes the term ‘species’ unusable. However, describing diversity in terms of species is not informative if the question at hand is the relationship between the function of a community and the function of its subsets. Species are characterised genetically and often phenotypically, but genetic and phenotypic differences do not always correspond to differences in function. Functional variation between individuals within species is often great (Huston 1994, Briggs and Walters 1997). In addition, ecosystem processes affect all individuals, no matter what species. Huston (1994) expressed this point: ‘The basic rules of competition and predation among individuals are the same regardless of whether the individuals are of the same or of different species.’(p. 178)

On larger scales, this difficulty has been addressed by separating species into ‘functional groups’, which are groups of species that perform the same function in a community (Köhler and Huth 1998, Walker *et al.* 1999, Tilman 1999, Loreau 2000, Nijs and Roy 2000). Experimental studies have been done to assess the effect of different functional groups on ecosystem processes. The results are not consistent. Some studies found that functional groups were very important for ecosystem productivity, stability and other processes (Symstad and Tilman 2001, Tilman *et al.*, 1997). Other studies found no significant effect of removing functional groups (Hooper and Vitousek 1997). The major difficulty with the concept of ‘functional groups’ is in their definition, because it requires species to be related to functions. This is possible but difficult since species were not defined to be related to function.

1.4.3 Connecting models and reality

Most of the current ecological community models do not have much relevance to ecosystems, and offer, at best, qualitative results. The main reason for this is the difficulty in linking models to real ecological systems. In order to keep models manageable, they often lack much ecological detail and, therefore, relevance. The results of a highly simplified model are hard to relate to the ecological communities on which the model is based. It is also difficult to translate ecological observations and measurements into parameters of highly simplified models. Such parameters are, for example, competition or invasion coefficients and rates of replacement (Weiner and Conte 1981, Crawley and May 1987, and Sivertown *et al.* 1992). These describe the competitive effect that one species has on another. Experimental studies to determine these effects have been done (Naeem *et al.* 2000, Silvertown *et al.* 1992). However, as mentioned in the work by Naeem *et al.* (2000), the variation of this effect, which depends on environmental conditions and particular species arrangement, is likely to be great. As a result, there has been little connection between ecological models and experimental ecology (Schmitz 2000). This is now changing, particularly in the field of individual-based modelling, where individuals in the models are defined in terms of measurable characteristics (Warren and Topping 1999, Grimm 1999).

1.5 The conceptual approach of this work

‘After we reject the ideas of the identity of individuals within a species and of the homogeneity of ecological space, a different picture of natural communities emerges, in which individual variation, spatial heterogeneity, behavioural interaction between individuals, and migratory behaviour do determine the dynamics and stability of ecological systems.’

Lomniki (1988), p. 203

1.5.1 Re-defining diversity

In this work, diversity is defined in terms of individuals. Consider a community in which each individual is described by a set of basic traits (*e.g.* lifetime, fecundity etc.).

The traits define the functions and interactions of an individual with its environment and other individuals. The values of a trait for all individuals in a community define a distribution for that trait. The community diversity can then be defined as the range and distribution of the trait values in the community.

This idea can be conveniently expressed in mathematical notation. Suppose that individuals in a community are defined by n physiological traits, with each individual defined by a set of values for each of the traits. An individual can then be defined as a point in the n -dimensional space of traits. For example, Figure 1.2 shows a distribution of individuals in the 3-dimensional space of three traits: growth rate (g), death probability (d) and fecundity (b). The diversity of a population can then be defined as the frequency distribution of individuals (*i.e.* points) in the n -dimensional space of individual traits.

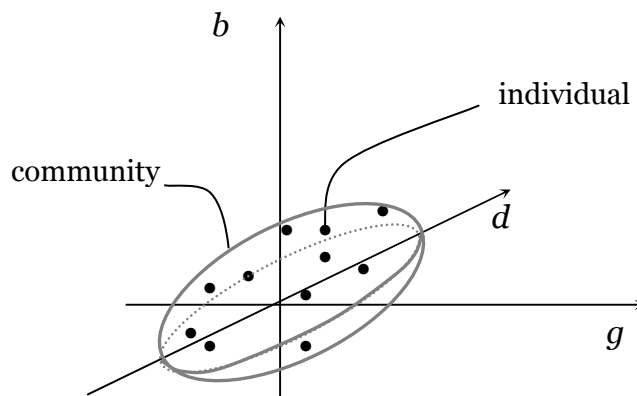


Figure 1.2 A representation of community as a collection of points in n -dimensional (3-dimensional in this case) space of physiological traits. Here, g is growth rate, b is fecundity, and d is death probability.

Using the described framework, the modelling is more closely tied to experimental ecology. Defining the community in terms of basic physiological traits has an advantage: the traits are measurable. It is experimentally feasible to measure the properties of individuals; however, it is much more difficult to measure individual interactions and other community-scale properties. Hence, a model with input

parameters that are physiological characteristics of individuals is more amenable to parameterisation (as shown in Ch. 3 of this work).

1.5.2 Questions addressed in this work

This work addressed the questions posed in section 1.3 of this chapter. Diversity patterns are consistent across a range of different life forms and environments. This suggests that the mechanisms responsible for these patterns are fundamental, and depend on characteristics that are common among different communities and conditions. This in turn implies that the key to understanding the patterns lies in the basic properties of the life cycle (*e.g.* birth, death, reproduction), and the basic properties of the environment (*e.g.* space, spatial interactions, and spatial variation). In this work the link between the properties of individuals to community properties is explored. This connection is then used to gain insight into the origins of diversity patterns.

Linking the properties of individuals and a community across scales offers an opportunity to gain insight into the nature of the relationship between community function and diversity. The simplistic view of relating community function to diversity by defining diversity as the number of species in a community can be modified. An alternate definition of diversity – as the range of values of physiological traits in a community – is linked to community productivity and stability. This definition incorporates the concepts of species richness, species evenness, and difference between species. All these diversity characteristics have been shown to have a significant effect on community dynamics (Nijs and Roy 2000). Since this definition of diversity (unlike species) describes community variability in terms of functional differences, it is possible in this work to elucidate the mechanisms -- on the scale of individual -- responsible for the generation of community behaviour.