Part I

Introduction to Community Ecology

Theory and Methods

1 · *Historical Development of Community Ecology*

In this first chapter we give a brief overview of the history of community ecology, starting from the early twentieth-century debates on how communities should be defined, and continuing until the modern conceptual frameworks. The aim is not to review every single theory, model or framework that has been developed in community ecology – that would call for an entire book! Instead, we give an overview of how this field has developed through history. Most importantly, this chapter is needed to introduce the concepts and ideas that underline the ecological assumptions behind species distribution models (SDMs) in general, and Hierarchical Modelling of Species Communities (HMSC) in particular. Here we will briefly mention how some of the theoretical concepts relate to HMSC, but more thorough discussions on how HMSC ties to ecological theory will be given later in the book, under each of the relevant chapters where the different components of HMSC are introduced.

The reader may wonder why a statistically orientated book starts with a historical tour of the development of community ecology. Many readers interested in figuring out how to fit a joint species distribution model (JSDM) in R might be tempted to completely skip this chapter and jump straight to where the equations and scripts start. While this is understandable, we strongly recommend that you keep reading. In our view, ecologists should think about the theoretical context in which their study questions are framed, before starting to fit any model. We start by recalling what community ecology is about (Section 1.1) and how an ecological community may be defined (Section 1.2). We then briefly review the developments in community ecology from the foundational ideas during the twentieth century up to the current frameworks (Sections 1.3–1.5).

1.1 What Is Community Ecology?

Community ecology is a cross-disciplinary field that aims to describe and understand the spatio-temporal structure and dynamics of ecological

communities. Although nowadays community ecology is well rooted within the broader scope of ecology, this has only recently become the case.

One of the most influential papers in community ecology is Lawton (1999), which critically questions the entity of community ecology as a field. In his own words, 'community ecology is a mess with so much contingency that useful generalizations are hard to find'. What Lawton found problematic was that conclusions from studies in this field were mostly case-specific and lacked general or unifying conceptual frameworks. This was indeed the case, as the conceptual and theoretical developments in community ecology have lagged behind other fields, such as population ecology and population genetics. Since the influential 'community ecology is a mess' statement, the past two decades have experienced a proliferation of unifying theory and general conceptual frameworks for community ecology (for books on community ecology theory see Leibold & Chase 2018; Morin 2011; Vellend 2016).

In the next sections we will review the most important early debates that formed the basis for the current conceptual and theoretical frameworks in community ecology.

1.2 What Is an Ecological Community?

Nowadays, the term 'ecological community' is generally understood as the assemblage of at least two potentially interacting species at a given time and location. However, throughout history this term has acquired disparate meanings for different scientists (Fauth et al. 1996; Stroud et al. 2015). For some early ecologists, the basic feature of a community was that species must interact. Whittaker (1975) defined an ecological community as 'an assemblage of populations of plants, animals, bacteria and fungi that live in an environment and interact with one another, forming together a distinctive living system with its own composition, structure, environmental relations, development, and function'. Others did not put such emphasis on interactions, but rather on the spatial co-occurrence among species. Along these lines, for Krebs (1972) a community is 'an assemblage of populations of living organisms in a prescribed area or habitat', and for Ricklefs (1990) a community reflects 'associations of plants and animals that are spatially delimited and that are dominated by one or more prominent species or by a physical characteristic'.

Because of the tradition of studying different taxa separately, community ecologists often work with communities of species that are

phylogenetically related (e.g. insects, birds, fungi, plants, etc.). Although we normally use the term 'community' to refer to these (e.g. insect community, bird community, fungal community, plant community), the technical word for referring to communities of taxonomically similar species is 'taxocene'. Other terms that are often used in place of 'ecological community' are 'guild' and 'assemblage'. The term 'guild' is used when the ecological community is formed by species that use resources in similar ways (Root 1967). For instance, all grazers (either mammals or insects) or saprotrophs (either fungi or bacteria) form their own guilds. The term 'assemblage' refers to species that exist in a given area, but do not necessarily interact. In the ecological literature, 'assemblage' usually refers to the species pool present in a large spatial area, and when the interspecific relationships among species are not so clear (Stroud et al. 2015). As an example, atlas data on species' distributions are considered 'assemblage' data rather than community data: information about a species' occurrence has often been recorded at different time points, and the size of the spatial unit at which the data are recorded (i.e. grid size) is not necessarily related to the spatial scale of the ecological processes, and is usually quite large (e.g. tens of km).

For the purpose of analysing data with HMSC, it does not matter whether the data are community data or assemblage data. In both cases, the input data matrices will have the same structure, and the results will look the same, in the sense that the output from the model will be in the same format. Yet, for the ecological interpretation, the distinction between these two can be critical. For example, empirical community ecologists are often interested in studying how species interact with each other, which can be described as interaction networks or food webs. Interaction networks are essentially communities in which all interactive relationships among the species are depicted, whereas food webs focus on the feeding relationships (i.e. food chains) among species (Elton 1927). In the case of assemblage data, the species-to-species association matrices (on which we focus in Chapter 7) may have nothing to do with species interaction networks, while for community data they might.

As seen from those pioneering definitions of ecological communities, some of the early scientists emphasised the taxonomical identity of the species as a characteristic to form an ecological community. Most early community ecologists worked on terrestrial plant and animal communities, as these contain the most conspicuous study organisms. Consequently, pioneering conceptual frameworks in community ecology were developed using terrestrial plant and animal communities as model

systems. Many modern community ecologists consider it equally import-
ant to work with any taxonomical group from any environment, includ-
ing for example microorganisms from the air (Barberán et al. 2015) or
from the digestive tract (Burns et al. 2015). Molecular species identifica-
tion methods now allow us to study many more kinds of communities
than before. This is greatly facilitating the detection and identification of
less conspicuous and highly diverse organisms.

In the context of HMSC, what we call an 'ecological community'
follows the definition by Fauth et al. (1996): a collection of species
occurring in the same place and at the same time, the species not being
necessarily restricted by phylogeny or resource use, and allowing
the spatial boundaries to be either natural (e.g. islands) or arbitrary
(e.g. study plots).

1.3 Early Community Ecology: A Descriptive Science

In the beginning community ecology was a merely descriptive scientific
field. After Linnaeus' work, naturalists began building species inventories,
i.e. identifying and listing species from given localities. They soon started
to realise that there are predictable differences in the numbers and
abundances of species among localities that differ in their environmental
conditions. This inspired scientists to classify communities according to
the species composition patterns and environmental variation (Köppen
1884; Wallace 1876; Whittaker 1962).

Some of the community classifications developed in the 1960s and
1970s are still currently used. Perhaps the most remarkable example is
Whittaker's (1975) classification of terrestrial communities according to
the dominant plant species and environmental conditions. Whittaker
borrowed from previous biome classifications (e.g. Clements 1916) and
assigned them to annual precipitation and average temperature condi-
tions. Although this classification has undergone several modifications
since its original publication, it still represents a basic system for under-
standing biodiversity organisation globally.

Furthermore, Whittaker provided the first definition of one of the
most popular concepts for assessing between-site variation in species
composition: beta diversity (Whittaker 1972). Whittaker defined beta
diversity as an index to measure the 'extent of differentiation of commu-
nities along habitat gradients'. Currently known as Whittaker's multi-
plicative law, he postulated that the total gamma diversity (total number
of species) of a geographic area is a product of the alpha diversity (average

number of species in a single locality) and the beta diversity (variation in species composition between localities). Since Whittaker's seminal work on beta diversity, this concept has been redefined in a number of ways, and a multitude of indices and methods for measuring beta diversity have been developed (Anderson et al. 2011; Tuomisto 2010).

In spite of the modernisation of the concept of beta diversity since its origin, community ecologists assessing beta diversity essentially aim to do what Whittaker did, i.e. to assess the variation in species composition among sites. Indeed, classifying communities according to the species composition patterns and environmental variation is still of central interest in community ecology. Novel sampling methods and species identification techniques are revolutionising the amount and accessibility of information about biodiversity, yet there is still a large gap in our knowledge about how communities are distributed on Earth. Describing the community composition patterns along environmental, spatial and temporal gradients is an indispensable step towards understanding the structure of species communities.

As mentioned above, the justification of community ecology as a proper discipline was highly debated in the end of the twentieth century. In the early twentieth century, the debate was centred on whether ecological communities are self-organised and delineable systems, or collections of populations with unclear boundaries. These contrasting views are known as the *organismic concept of communities* and the *individualistic continuum concept*, and were advocated by botanists Clements (1916) and Gleason (1926), respectively. Under the organismic view, Clements believed that ecological communities form static and definable units that can be classified, similar to the Linnaean taxonomical system for species. On the contrary, according to Gleason, a community can be seen as an assemblage of populations of different species whose traits allow them to persist in a given area. Therefore, opposed to Clements' view, Gleason thought that communities result from species-specific responses to the environment, rather than from the associations among species. Under Gleason's view, the spatial boundaries of ecological communities are not so sharp, and the composition of communities may change over time and space.

These two disparate views mainstreamed the avenue of plant community ecology. Clements' organismic view of communities represents the foundation of phytosociology, i.e. the science that aims at classifying plant communities into fixed units. Following Clements' idea, plant communities reach a steady state after the process of ecological succession

occurs (Clements 1936). Phytosociology culminated in the beginning of the twentieth century, when botanists around the globe developed their own classification systems and most plant communities were assigned to vegetation types. The current view on how communities are structured is more dynamic, and therefore closer to Gleason's view. The current emphasis is not on classifying species assemblages into a discrete set of archetypal communities, but rather on understanding the mechanisms allowing species coexistence within communities (Götzenberger et al. 2012).

Another debate began in the twentieth century, about the spatial scale at which ecological communities should be described. Partially reflecting the Clementsonian vs. Gleasonian view of communities, the debate was focussed on the extent to which communities are spatially bound. The definitions of ecological community always implied a spatial aspect: an assemblage of populations of living organisms *in a prescribed area* (Krebs 1972); an assemblage of populations of plants, animals, bacteria and fungi that live *in an environment* and interact with one another, forming together a distinctive living system (Whittaker 1975); associations of plants and animals that are *spatially delimited* and that are dominated by one or more prominent species or by a physical characteristic (Ricklefs 1990). As an implicit consensus, communities were conceptually delimited at the spatial scale that interspecific interactions physically take place. But often the spatial scale at which an observational study is conducted is decided quite arbitrarily, partially because the true spatial scale at which species interactions operate (or even the interactions themselves) are usually unknown beforehand. As such, the uncertainty about the spatial scale at which communities should be defined continued gaining much attention, especially after Ricklefs' influential work on the importance of spatial scale on the processes structuring communities (Ricklefs 1987, 2008).

Another early line of research in community ecology focused on patterns of accumulation of species and individuals across space and time, such as the species–area relationship, species–time relationships and species abundance distribution (Arrhenius 1921; Fisher et al. 1943; Preston 1948, 1960). Since the first descriptions of these relationships, community ecologists and macroecologists have been fascinated by the high consistency of their shapes across ecosystems and taxonomical groups. For example, the species–area curve is often found to follow a power-law (Arrhenius 1921; Dengler 2009), whereas the species abundance distribution tends to show great variation among species, in particular a long tail of many rare species (Fisher et al. 1943; McGill et al.

2007; Preston 1960). The question of what mechanisms underpin these patterns has been a major inspiration for the development of theories about the drivers of community assembly (McGill et al. 2007).

1.4 Emergence of the First Theories

By the end of the twentieth century, two controversial theories about community assembly were formalised, namely the *Niche Theory* (Hutchinson 1959; MacArthur & Levins 1967) and the *Neutral Theory* (Hubbell 2001). The early ideas of the concept of ecological niche had already emerged in the beginning of the twentieth century, when an ecological niche was considered the place that a species occupies in an ecological community. During these early years, the concepts of Grinnellian and Eltonian niches originated, which were later formalised as the concepts of fundamental and realised niches. For Grinnell (1917), the ecological niche was 'the sum of habitat requirements and behaviours that allow a species to persist and produce offspring'. Elton (1966) defined the ecological niche as 'the place of an animal in the abiotic environment, its relations to food and enemies'.

These ideas persisted for decades, but it was not until the end of the twentieth century that the concept of ecological niche was formalised. Hutchinson (1959) developed a formal notion of the ecological niche as a n-dimensional hypervolume, and this concept has remained to the present day (Blonder 2018). The n dimensions of the hypervolume are the environmental and resource characteristics that the species requires to persist. Hutchinson also formally introduced the ideas of fundamental and realised niches. Specifically, the fundamental niche of a species is represented by the hypervolume defined by the environmental and resource characteristics that the species require to persist, whereas the realised niche is what remains from the hypervolume after interactions with other species are taken into account. Another important contribution to the Niche Theory was provided by MacArthur and Levins (1967), who implemented Hutchinson's niche concept into a mathematical model. The consumer-resource model of MacArthur and Levins (1967) illustrates the overlap in resource use among species.

The niche concept has been surrounded by confusion since its foundation, and the controversy about how exactly to define it still continues (Pocheville 2015). This problem arises from the fact that different ecologists have meant slightly different things when referring to a niche (Leibold 1995). Additionally, it is difficult to distinguish between the effect of the

environment on a species and the effect of the species on the environment
(Chase & Leibold 2003). In spite of this, the Niche Theory remains a
central principle in ecology, and one of the fundamental theoretical pillars
in species distribution modelling (Peterson et al. 2011). As in most SDMs,
the species niche in HMSC is the relationship between species occurrence
or abundance and the environmental conditions, and thus refers more to
realised rather than fundamental niche. The niche of a particular species is
thus measured by regression parameters that describe how the occurrence
or abundance of that species depends on the environmental conditions that
are included in the analyses (Chapter 5). The distribution of species-
specific niches describes how the entire community responds to environ-
mental variation (Chapter 6).

A milestone for the development of predictive community ecology
research was the *Equilibrium Theory of Island Biogeography* by MacArthur
and Wilson (1967). This theory was originally developed for explaining
the species richness patterns in oceanic islands, and was later empirically
validated by Simberloff and Wilson (1969). This theory predicts that on an
island the number of species is determined by a balance between immigra-
tion and extinction. The 'equilibrium' part of the theory comes from the
assumption that immigration rate decreases and extinction rate increases
with an increasing number of species that already occupy the island. Thus,
the number of species that can persist will converge to an equilibrium. The
number of species on islands that are large or near the mainland is predicted
to be larger than the number of species on distant small islands, because
there is higher immigration to large islands near the mainland, and higher
extinction on small islands. Many kinds of suitable habitats within a matrix
of less suitable habitats can be conceptually viewed as an island. As such,
this theory represents a baseline for understanding species diversity far
beyond true island systems (Hanski 2016). For example, for forest-
dwelling organisms, forest fragments embedded within an agricultural
matrix would be analogous to islands distributed within the ocean. Simi-
larly, for aquatic organisms, lakes embedded within terrestrial habitats
could be considered as islands. For species with low tolerance to anthro-
pogenic disturbance, the islands could be protected natural areas embedded
within the matrix of human-modified areas.

By the end of the twentieth century, a new ground-breaking theory on
how communities are assembled emerged: The *Unified Neutral Theory of
Biodiversity and Biogeography* (Hubbell 2001). Inspired by the incredibly high
plant diversity in tropical environments – which is very difficult to relate to
variation in environmental conditions – Hubbell proposed that biodiversity

arises and is organised at random. From the Neutral Theory perspective, all individuals are ecologically identical and niche differences are not needed to explain biodiversity patterns. Highly diverse communities of equivalent species (i.e. species with identical niches) arise solely because of random events (i.e. chance extinctions balanced by chance speciations). More specifically, stochastic random processes that include birth, death and immigration of individuals, as well as speciation, can lead to species-rich communities. Because of the extreme point of view that biodiversity originates solely from random processes, the Neutral Theory of biodiversity provoked a wave of criticism. This resulted in the development of tests in which the predictions of niche-based and the neutral theories were compared against empirical data, for example in terms of species abundance distributions (e.g. McGill 2003; McGill et al. 2006a; McGill et al. 2007; Wootton 2005). While these empirical tests failed to find general support for Hubbell's Neutral Theory, they did establish its position as a highly useful null model for evaluating the roles of non-neutral processes such as adaptation and natural selection in shaping ecological communities.

The proliferation of mathematical models in population ecology during the 1960s and 1970s (see Kingsland 1986) greatly influenced the field of community ecology. Single-species population models started incorporating the influences of other competing species, and linking the patterns of resource use to competitive abilities. Extensions of the original Lotka-Volterra two-species competition model and consumer–resource models allowed modelling networks of interacting species (e.g. Levine 1976; MacArthur 1972; Tilman 1994). The development of multi-species models of interacting species also raised one of the central issues in community ecology today: the relationship between network stability and complexity (May 1971). Furthermore, the emergence of Neutral Theory motivated the development of more complex and realistic niche-based modelling frameworks (e.g. Chave et al. 2002). One important conclusion from such modelling studies was that many contrasting types of community assembly processes can result in surprisingly similar patterns, for example in terms of species abundance relationships (Chave et al. 2002).

1.5 Current Community Ecology: Search for the Unifying Theory

The turn of the 21st century saw a change in community ecology research, where the interest switched from describing community