Lecture 1b. Macroecology

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Table of contents

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This material must be reviewed by BCB743 students in Week 1 of Quantitative Ecology.

1 Ecological Concepts

When we talk about 'ecology', central to our discussion is the concept of biodiversity. The Convention on Biological Diversity defines biodiversity as:

> "The variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems."

In this lecture, we will work towards an understanding of macroecology by working through these topics:

- ‘Traditional’ ecology—focus on the ‘local’ scale.
- The distinction between populations and communities.
- A definition for what ecology is.
- The concept of the ‘niche’ (fundamental and realised).
- The concept of ‘species’.
- Describe the properties of communities, viz. mainly structure and function.
- Using measures of diversity to understand structure.
- Arrive at the concept of macroecology.

In this module, we’ll rely on thinking emerging from a unifying field of ecology called macroecology. According to Keith et al. (2012), macroecology is:

> “…the study of the mechanisms underlying general patterns of ecology across scales.”

2 Macroecology: Ecology Across Scales

For a deeper dive into macroecology, please see the paper Shade et al. (2018). I provide some additional views on macroecology to supplement the insights you extract from this publication.

Macroecology explores ecological patterns and processes across a wide range of scales (from microbes to blue whales, from the Cape Flats Nature Reserve to the whole of Earth, and from the Pleistocene to 2100). To the best of my knowledge, the term ‘macroecology’ was coined by Brown and Maurer (1989), who used it to study continental biotas. The term has since then undergone much growth and evolution in recent decades. More recently, it has led to attempts to develop unified theories of ecology (Keith et al. 2012), driven by a convergence of technological and methodological advancements, building upon earlier foundations laid by disciplines such as ‘phytosociology.’

Phytosociology (phytocoenology or plant sociology) studies and classifies plant communities. It has greatly influenced modern ecological research. Phytosociologists emphasise systematic vegetation classification and the understanding of plant community structure, which prepared the ground for many concepts in macroecology. For example, the Braun-Blanquet method, a cornerstone method in phytosociology since its development by Josias Braun-Blanquet (1884-1980) (Dengler et al. 2008, Dengler 2016), still forms a standardised approach to vegetation sampling. The method has been adapted and expanded in the study of, amongst other things, benthic (limnetic and marine) communities, as it is well suited to sampling communities comprised mainly of sessile organisms.

Recent progress in macroecology was achieved through advances in several key areas. Molecular phylogenetics provided new insights into evolutionary relationships, while high-resolution datasets of abiotic and biotic variables offered unprecedented detail about environmental conditions and species distributions. Today’s vast (and rapidly growing) computational power allows the processing and analysis of these complex datasets, and novel numerical approaches and a robust statistical framework provide tools to extract insightful patterns from the data.

Increased knowledge sharing and access to open data have further accelerated the growth of macroecology. Wider collaborative networks of ecologists now provide a more integrated understanding of ecological systems across broad spatial and temporal scales. We can now tackle complex questions that were previously out of reach.

Some of these fundamental questions include inquiries about variations in body size across species and regions, the patterns of biodiversity at global spatial scales and over geological timescales, abundance distributions across size classes of organisms, geographical range dynamics as we experience the various pressures of global change and the role of neutral processes in shaping ecological communities.

While 'traditional' ecology primarily focuses on describing natural patterns, macroecology has shifted towards finding mechanistic explanations for the processes resulting in observed biodiversity patterns. This transition advances our understanding of ecological systems, moving beyond mere description to explanation and prediction. Ecological systems are also increasingly coupled with Earth system models to offer projections of ecological structure and function in the future.

Today's ecology students must reconcile their biological observations and knowledge with hypotheses about patterns and processes and understand the statistical models used to explain them. New frameworks are being developed to integrate biological theory with sophisticated statistical techniques, and we can conduct more robust and meaningful analyses of large-scale ecological data.

A key insight from this approach is the recognition that local species interactions can explain broad-scale patterns in species distributions. This understanding bridges the gap between small-scale ecological studies and large-scale macroecological patterns and provides a more cohesive view of how ecosystems function across different spatial scales.

This growing recognition that links local processes to global patterns has led some ecologists to try and find unified theories of ecology. These theories aim to be predictive by offering explanations for observed patterns and the ability to forecast future ecological scenarios. Such unified theories represent a holy grail in ecology and potentially provide an integrated framework for understanding and predicting ecological phenomena across scales and systems.

The advancements in macroecology have significantly enhanced our comprehension of biodiversity, ecosystem functioning, and ecological responses to global change. Notably, macroecology has exerted a remarkably wide-ranging and transformative impact at the intersection of scientific research and policy-making. This influence is especially evident in land-use management, climate change mitigation and adaptation strategies, and efforts to address biodiversity loss.

Lecture Transcript: Macroecology

3 Definition of Macroecology

I have already spoken a bit about this, but let me say a bit more. What is macroecology? If you were to summarise it in a sentence or two, it is the study of the mechanisms underlying general patterns in ecology, across scales. There are words there worth unpacking—'patterns' is probably one, and patterns in ecology across scales. The two important ideas—patterns and scales—we'll be unpacking further, if not today then in due course. I'll show you what "patterns" in ecological space can look like. But that's the essence of macroecology.

Let's examine the definition in a little more detail.

4 Traditional Approaches in Ecology (Slide Reference: Early Slides)

To understand macroecology, you first need to understand how ecology has traditionally been practised. Going back perhaps a hundred years or more, even to Darwin's era, ecology was about observing and investigating individual species. That is, the study of populations—a collection of individuals of the same species, occupying a specific space and time. The focus was to examine the dynamics of a species within a population: how it is affected by the environment, by other species sharing the same space, and so on. Traditional ecology, then, was very local in scale—limited to what you could see, for instance, standing at Cape Point and surveying the kelp forest before you. The boundaries of that study would be as far as your eye could discern the kelp—very much a local scale.

But this ignores that kelp occurs not only at Cape Point, but also in Norway, Iceland, and elsewhere worldwide. Macroecology would look at kelp not only in South Africa, but also Norway, Iceland, the United States, Canada, and everywhere kelp occurs. The aim is an integrated understanding of the processes that make kelp forests work, regardless of whether they are found in South Africa or New Zealand. Traditional ecology, by contrast, kept its focus strictly local.

Now, due to advances in technology, data processing, and the sorts of questions we're able to ask, the scope—the scale—of our enquiry has greatly expanded. Today, macroecology can examine patterns at the global level. Darwin embarked on a voyage round the world in the Beagle, observing numerous locales—it took him two, perhaps three years. Today, in just 24 hours, we can obtain a 'snapshot' of the entire Earth and collect sufficient ecological data world-wide, something previously unimaginable [attention: Darwin's ability to analyse global ecology in a single synthesis was much more limited than described here]. Thus, new technologies have altered our perspective.

5 Biodiversity: Definitions and Scales

Biodiversity is another key concept—it appears throughout this module, including in its very name. The traditional definition, as described by the International Union for Conservation of Nature (IUCN), defines biodiversity as "the variability among living organisms from all sources, including terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part. This includes diversity within species, between species, and of ecosystems."

Again, the question of scale becomes evident—diversity within species, for example, means taking humans: within Homo sapiens there is great diversity, all the way down to genetic differences. That's a scale we can go down to—though Dr Stephen Boatwright will cover genetics; I won't get into that aspect here.

Diversity also exists between species—species occupying the same ecosystem. In a kelp forest you might have Ecklonia maxima, Laminaria pallida, Macrocystis pyrifera, various red baits, fish, sharks, and so on—all interacting within the kelp forest. Then, there is diversity at the ecosystem level—kelp forests interact with pelagic ecosystems nearby, with the rocky shore, with coastal dunes on the land, and so forth. Globally, a diversity of ecosystems exists, each with its own species assemblages and modes of environmental interaction.

So, biodiversity is essentially all life on Earth, at all the various scales in which we observe it, and in all the different configurations, forming habitats or ecosystems regardless of location—from $11,000\,\mathrm{m}$ below the ocean surface to the summit of Mount Everest.

6 Populations, Communities, and the Move to Macroecology

So, we've mentioned populations (collections of one species) and communities (collections of multiple species). Ecology studies the processes by which species relate to their environment, to each other, and how the environment influences both populations and communities.

Macroecology naturally starts from population and community ecology: it makes sense to move from the local scale, to groups of communities, and then ultimately to encompass the whole Earth, which is the domain of global ecology and macroecology.

A proper understanding of the effects of scale, and of various scaling processes and gradients—as they occur from local to global levels—is absolutely crucial. This knowledge helps explain why certain species exist in particular locales but not in others. For example, why do kelp forests thrive in Cape Town, but not off Durban in KwaZulu-Natal? It's because the environmental conditions differ: Cape Town's seawater is much colder throughout the year, making it suitable for kelp, while Durban's warmer temperatures exclude kelp from surviving there.

Some organisms actually require kelp forests to survive or to reach their full productivity—certain species can only occur within kelp forests. So, the presence of kelp creates an environment that supports many other species. Thus, if kelp is absent (as off Durban), these organisms are also absent.

In short, global ecology seeks to understand how variations in temperature, light, soil characteristics, air quality, snow, rainfall, drought, humidity—all these environmental variables—combine to create a patchwork of suitable conditions for some species, but not others. Ecology, and especially macroecology, attempts to find global explanations for these broad patterns.

7 Lecture Transcript: Introduction to Macroecology

8 Revisiting Definitions and Scales

Regional to global scales — I've spoken about all of this already, so I don't need to go into regional to global scales again. You'll understand this in a little bit more detail once you read that paper that I've given you. There are going to be two other papers now which you're expected to read as well.

9 Patterns and Processes: Traditional vs Macroecology

Okay, patterns and processes. Traditional ecology essentially focused on patterns. It looked at the world and observed that there is a patchwork of different kinds of ecosystems, even on local scales and then regional scales. It noted that this ecosystem often appears different from the one next door, and described how it is different in terms of species present there, and in terms of the structure of the community. However, it didn't really attempt to explain the mechanism that created those differences in the first place.

In contrast, macroecology tries to add a mechanistic explanation for why and how things differ across the surface of Earth. To do this, we need to start treating ecology as a proper science, not merely as a form of natural history as it had been approached in the past. We need to ask questions about nature, to form hypotheses about nature that can be tested statistically, so that we can have a cause–effect explanation for why things are the way they are, or how things came to be as we observe them now.

This is, in fact, a very critical feature of modern-day ecology, particularly in macroecology, but also in contemporary population and community ecology at the local scale. We must ask testable hypotheses about nature—questions that we can actually go and test experimentally. Experimental assessment, experimental science, is the true test for whether something is so, or is not so. The necessity to measure things, and the necessity to have a statistical model or hypothesis, requires that we have data — that we go out into the world and measure things in specific ways, in order to have data that can be tested in a hypothesis setting via statistical models.

This is a very key part of modern ecology, and it's only something that has become feasible since about the 1970s. Before that, people did not look at ecosystems with the intention of asking hypotheses of them. They mostly described how things are, rather than why things became the way we observe them to be now.

10 From Local Interactions to Global Theories

We're going to examine local species interactions all the way up to global species distributions. Hence the necessity, once we have the entire earth in view, to develop unified theories. There are, of course, various applications.

11 Applications and Relevance of Macroecology

Why do we want to do macroecology? Because we want to create something for policymakers to help them understand the world better; to identify that certain regions of the world are of great importance, both strategically and ecologically, and for the benefit of people. It may be better not to have developments in such areas, or instead to conserve portions of biodiversity, to plan land use accordingly, and to understand what the future world is likely to be like as biodiversity is lost to an ever-greater extent.

So, understanding macroecological processes influences the way that policies unfold. One of the major visible policies in the world today is the tendency for nations to move away from fossil fuels towards renewable energy, because we know that fossil fuels cause climate change, and we know that climate change is having an effect on species globally. We want to minimise this effect, because if we do, the consequences for people will also be reduced, since humans are so strongly linked to the environment.

Additionally, explanations of epidemiology also become possible: understanding the ways in which diseases spread and operate around the world, their origins, and so forth. There are many reasons why macroecology is interesting and important. For me, it is important because people are making a living from the world around us, and we want to ensure that the way people are making a living from the world today will still be viable a century from now — for your children, perhaps, to make a similar kind of living from the world, if you indeed directly rely on natural systems. Even if you don't directly depend on ecosystems, you are indirectly supported by ecological goods and services.

12 Self-Study and Assignments

Anyway, that brings me to the end of what I needed to say today. There are two papers — or rather, one paper and one additional paper. There's the one you saw before, and another one, which I shall upload to the system shortly. I would like you to read them both by the end of this week, so that by Friday afternoon, if you have questions about them, you can ask me. I'll be available on Google Meet if you make an appointment to see me in groups of more than three.

So that's your self-study. Your assignments will also require that you understand these topics in quite a bit of detail.

13 Looking Ahead

Tomorrow, we shall move on to topic number two, and we're going to look at some of the questions that we can ask within the framework of macroecology.

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