Lecture 3. Ecological Gradients

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

> ℹ **BDC334 Lecture Transcript**
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> **Please see the BDC334 Lecture Transcript for the main content of all lectures.**

> 💡 **This Lecture is Accompanied by the Following Lab**
>
> - Lab 2a. R & RStudio
> - Lab 2b. Environmental Distance

1 Robert H. Whittaker's Role in Understanding Community Formation

Robert H. Whittaker (1920-1980) was instrumental in shaping our understanding of ecological gradients and their role in species community formation. He challenged the prevailing Clementsian view of his time of communities as discrete, interdependent units, and instead proposed the "individualistic hypothesis" (Whittaker 1953). This hypothesis posited that species respond individually to environmental gradients, resulting in gradual shifts in community composition along these gradients.

Whittaker undertook extensive field research in diverse ecosystems, from the Great Smoky Mountains to the Siskiyou Mountains. This work provided strong empirical support for his hypothesis (Whittaker 1967). He developed the "gradient analysis" method, a quantitative approach to studying species distributions along environmental gradients, which became a cornerstone of modern community ecology.

Whittaker's placed community ecology onto a new trajectory and shifted the focus from discrete community types to the continuous variation of species along environmental gradients. This shift is continuing to have deep implications for our understanding of biodiversity patterns, ecosystem functioning, and conservation strategies.
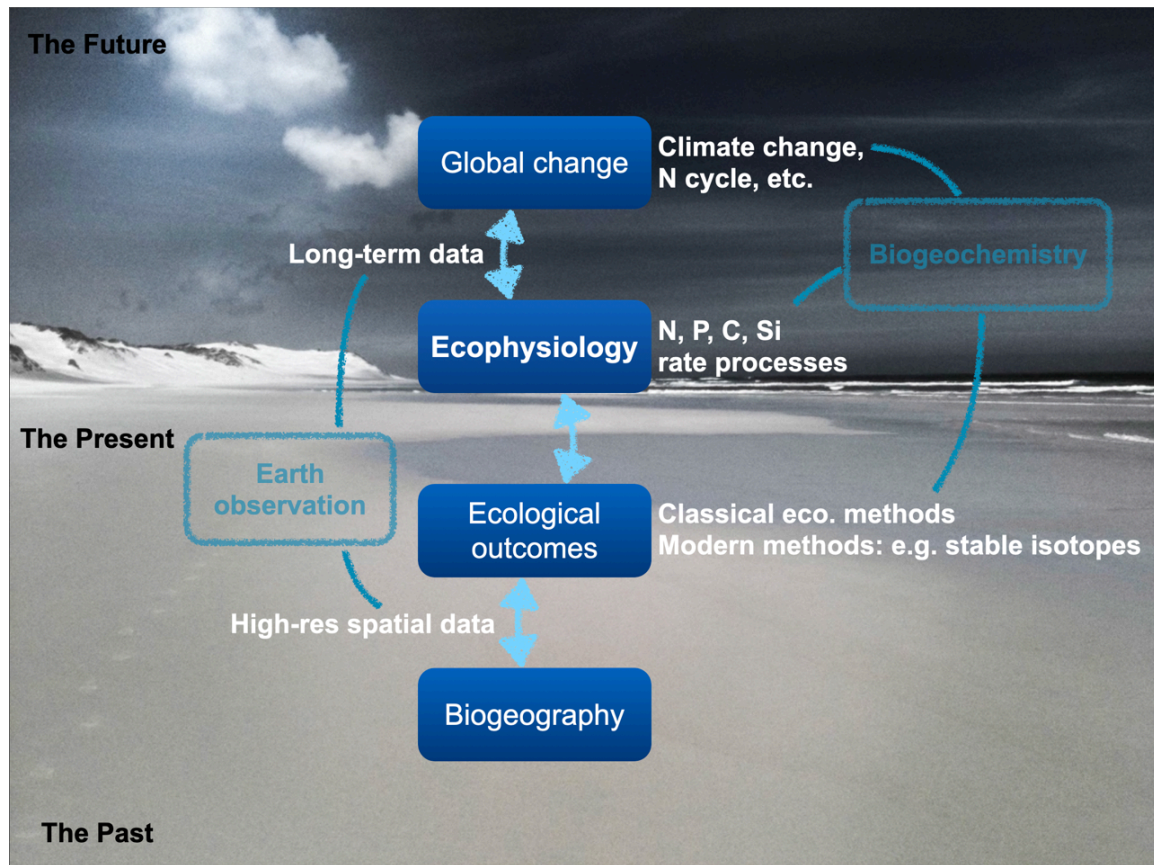
2 Environmental Gradients

Figure 1: Environmental gradients exist across space and time and link biodiversity outcomes (structure and function) to environmental properties.

Environmental gradients exist across space and time and link biodiversity outcomes, which we may measure as structure and function, to environmental properties {Figure 1). These gradients can be observed through Earth observation technologies, such as satellite remote sensing, which provide high-resolution spatial data essential for understanding biogeography. Biogeographical patterns help us discern how species distributions and community compositions vary in response to different environmental factors such as temperature, precipitation, and nutrient availability. We refer to these environmental factors as *drivers* when they affect ecological—and ultimately, biogeographical—outcomes.

As we move from present to future scenarios, the data collected enable us to use ecophysiological principles: that is, we use our understanding of physiological processes of organisms and how they adapt to changing environments. Long-term data are crucial for understanding global change processes, such as climate change and nutrient cycles such as those involving N, P, C, and Si, for example. These processes impact ecological outcomes by altering ecosystem structure and function, and can be studied using both

classical ecological methods and modern techniques like stable isotopes. These outcomes feed back into biogeochemistry, linking the cycles of key elements to broader ecological and environmental changes. This interconnected approach can help us predict how ecosystems might respond to future environmental shifts, emphasising the importance of integrating data across temporal and spatial scales.

3 The Unimodal Model

The 'unimodal' model (Whittaker 1967) is a core concept in ecology. It provides a framework for understanding how species and communities are distributed along environmental gradients and offers an intuitive explanation for the patterns we observe in nature.

The unimodal model posits that the relationship between a species' abundance (or other measures such as biomass or relative frequency) and its position along an environmental gradient follows a unimodal function. This means that the abundance of a species typically peaks at a specific point along the gradient where the conditions are 'just right' (to quote Goldilocks) and decreases as conditions deviate from this optimum in either direction.

The model implies that each species has a unique set of optimal conditions under which it thrives and attains maximal abundance. This 'sweet spot' represents the ideal combination of environmental factors for that particular species. As conditions move away from this optimum, whether becoming too hot or too cold, too wet or too dry, the species' abundance decreases. This creates a characteristic bell-shaped curve (Figure 2) when plotting abundance against the environmental gradient.

```r
library(coenocliner)
set.seed(666)
M <- 3                                    # number of species
ming <- 3.5                               # gradient minimum...
maxg <- 7                                 # ...and maximum
locs <- seq(ming, maxg, length = 100)     # gradient locations
opt  <- runif(M, min = ming, max = maxg)  # species optima
tol  <- rep(0.25, M)                      # species tolerances
h    <- ceiling(rlnorm(M, meanlog = 3))   # max abundances
pars <- cbind(opt = opt, tol = tol, h = h) # put in a matrix

mu <- coenocline(locs, responseModel = "gaussian", params = pars,
                 expectation = TRUE)

matplot(locs, mu, lty = "solid", type = "l", xlab = "pH", ylab =
"Abundance")
```
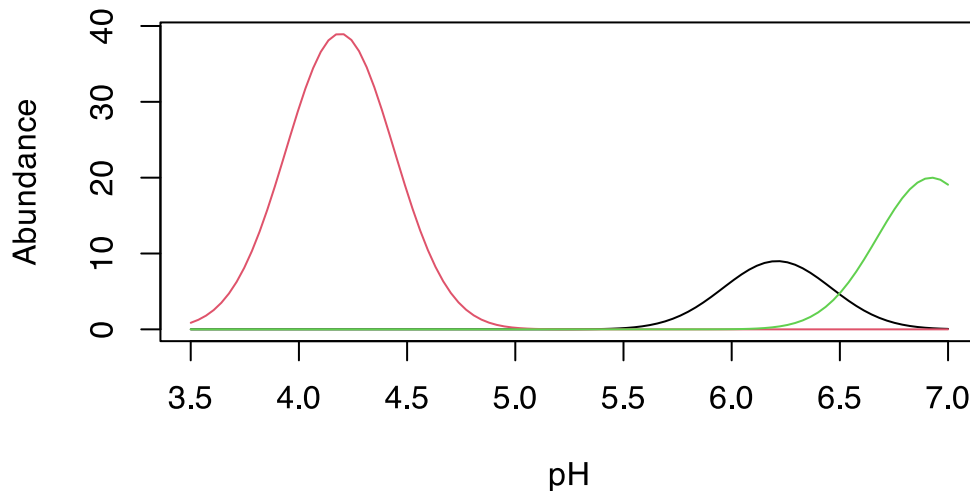
Figure 2: A coenocline representing the unimodal model of abundance of three species along a hypothetical environmental gradient.

The unimodal model is simple to understand and has a broad applicability. It's trivial to conceptualise how species come to be arranged or sorted along gradients based on their individual optimal conditions and tolerance ranges. This sorting effect explains why we often observe distinct changes in species composition as we move along environmental gradients, such as elevation in mountains or moisture in transitions from wetlands to uplands, or even across wider regional gradients such as along a coastline influenced by a western boundary current (e.g. Agulhas Current) or east to west across South Africa. This gives rise to the ideas of distance-decay relationships, community structuring along elevation gradients, and species turnover, for all of which the outcome can be measured as β-diversity.

In real-world ecosystems, however, multiple gradients co-exist simultaneously and the situation may be more complex than alluded to in Figure 2. Species are responding not just to one environmental factor, but to a complex interplay of various gradients. These might include temperature, precipitation, soil pH, nutrient availability, and many others. As a result, communities—collections of species coexisting in a given area—are formed within this multidimensional 'space' of gradients. Please see the section on coenoplanes and coenospaces for more information. To complicate things further, many types of biotic inter-actions (e.g. competition, predation, mutualism) can also influence species distributions and community assembly.

4 Fundamental and Realised Niches

The formation of communities in this gradient space can be conceptualised as the outcome of multiple interacting unimodal species-environment relationships, modulated by complex biological interactions. Each species in the community occupies a position that reflects its response to various environmental gradients, shaped by its physiological tolerances, competitive abilities, and other biotic factors. This interplay leads to the complex patterns of species composition and diversity we observe in nature.

To fully understand this process, we must consider the concepts of fundamental and realised niches. The fundamental niche represents the full range of environmental conditions under which a species could potentially thrive in the absence of biotic interactions. In the context of the unimodal model, this would correspond to the species' theoretical response curves along various environmental gradients.

However, in real ecosystems, species rarely occupy their entire fundamental niche. Instead, they occupy a realised niche, which is typically a subset of the fundamental niche. The realised niche is shaped by biotic interactions such as competition, predation, and mutualism, as well as by dispersal limitations and historical factors. In the gradient space, a species' realised niche is represented by its actual measurable distribution and abundance patterns.

The interaction between fundamental and realised niches adds layers of complexity to community formation. Competition may lead to niche compression, where species occupy narrower niches than they are physiologically capable of. Conversely, in the absence of competitors or predators, species might experience niche expansion. Over time, niche differentiation can occur as species evolve to reduce competition, potentially altering their response to environmental gradients.

Moreover, some species exhibit niche plasticity, adjusting their ecological roles in response to environmental changes or biotic pressures. Others engage in niche construction, actively modifying their environment and thereby altering the gradient space for themselves and other species.

Understanding these dynamics is important if we wish to interpret the complex patterns we observe and measure in nature. 'Community assembly' (note, not implying a deliberate act) is not simply a passive response to existing gradients, but a dynamic process involving adaptation, competition, and environmental modification. We must consider both abiotic factors, as emphasised in the unimodal model, and the various kinds of biotic interactions, as highlighted by the concept of realised niches.

5 The Unified Neutral Theory of Biodiversity

An alternative (or complementary?) hypothesis for community formation—which we will not cover too much but you are nevertheless required to understand the basic premise of—

is the Unified Neutral Theory of Biodiversity (UNTB). This theory posits that species in a community are functionally equivalent and that their relative abundances are determined by stochastic processes rather than by their individual traits or interactions. In other words, the UNTB suggests that all species are ecologically equivalent and that community composition is the result of random dispersal, speciation, and extinction events.

Please consult the following references for more information on the UNTB:

- Hubbell (2005)
- Hubbell (2011)
- Rosindell et al. (2012)
- Neutral Theory of Species Diversity

6 Lecture Transcript: Environmental Gradients

6.1 Ceonoclines, Ceonoplanes, and Ceonospaces

Okay, a question about coenoclines. Before I explain, as I said in earlier lectures, to best help you I need to understand what steps you have already taken and where exactly you're still struggling. Please, when you pose a question, indicate specifically what you've attempted and where you're getting lost.

One student says they've not read the specific article for now but, while reviewing topic two, could not find the corresponding figures described in the material—especially those about when the 'core inner space' is greater or less than two, which caused confusion.

Let me address this by first clarifying what a coenocline is. Typically, a coenocline is a visual, simplified representation of how a given species responds to a single environmental gradient. For instance, as you move across South Africa from east to west, rainfall typically decreases: there's more rain in the east than in the west. This gradient in rainfall is one example, and species are optimally distributed at some point along the gradient—where rainfall best fits their physiological needs.

However, rainfall isn't the only gradient influencing species distributions. Soil chemistry and physics, temperature fluctuations, atmospheric heat, and many other gradients also change simultaneously across a landscape. While a coenocline explains the distribution of a species along one gradient, real landscapes are far more complex: there might be ten, twenty, even forty gradients at play, all influencing species distributions at once.

A coenocline can be expanded to account for two or more gradients, and then we call it a ceonoplane. When even more gradients are considered, we refer to it as a ceonospace. The ceonospace defines a position in the landscape, specified by multiple interacting gradients, in which species are optimally distributed according to all their physiological tolerances.

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These are just modelling tools—quantitative ecology uses them to understand and predict distributions of individual species and community structures across landscapes.

For those considering Honours, we shall dive much deeper into these concepts, particularly quantitative ways of understanding community structure.

Essentially, what I want you to understand about coenoclines, ceonoplanes, and ceonospaces is that they allow us to model how multiple co-varying environmental variables sort and distribute species. Typically, species exhibit a unimodal distribution—their abundance peaks at the environmental conditions that most closely match their physiological optimum. Away from this 'sweet spot' (not a scientific term!), their abundance declines as conditions become less suitable.

Imagine a landscape gradient ranging from hot to cold. A species might be most abundant where temperatures align with its tolerance. But at every spot along that gradient, multiple factors—temperature, humidity, soil conditions—are also varying. Each species in the landscape responds similarly, preferring their own set of environmental optima, and this interplay shapes the overall vegetation and animal community structures that we observe.

So, to summarise: these tools—coenocline, ceonoplane, ceonospace—help us model, using mathematics or quantitative methods, the distribution of species and communities against the complexity of environmental gradients. Their use forms a core framework of how we understand community ecology.

If you're still unclear on any aspect, please do reflect on this answer. I will post the video of this session again for you to review. Listen to the explanation carefully, and if you get stuck, rephrase your question at the point where my explanation loses you, so I can pinpoint precisely where to build further understanding.

6.2 Environmental Gradients in South Africa

A student mentions that it gets drier from east to west across South Africa. Yes, this is the case: the eastern side of South Africa is adjacent to the warm Agulhas Current, which transports warm tropical or subtropical water down the coast into the higher latitudes. As this warm current flows past, evaporation adds heat and moisture to the atmosphere. This, in turn, brings rainfall to the adjacent land. That is why the eastern coast is so wet —characterised by tropical and subtropical vegetation, an abundance of rivers, and nutrient-rich soils leading to high productivity.

As you move westward into the centre of the country and then towards the west coast, the influence of the Agulhas Current diminishes. There is less moisture, less rainfall, fewer rivers, drier soil, and lower humidity—altogether favouring a different suite of plant and animal adaptations. By the time you reach the west, rainfall drops below 400 mm/year, and

only species adapted to very dry conditions are present. In KwaZulu-Natal, by contrast, you may get as much as $1,200$ mm/year, or thereabouts.

The two major currents on the country's east and west coasts bring different amounts of moisture into the atmosphere, exerting a strong influence on the environmental gradients across the region, which in turn mould distinctive ecological communities.

6.3 Ocean Currents and Regional Variation

Another question: "Do the two major currents mix at Cape Town?" They don't exactly mix at Cape Town itself, but rather in the region between Cape Point and Cape Agulhas —a stretch of coastline approximately 300 km long. There, the Indian and Atlantic oceans influence each other, resulting in a transition zone in both marine and terrestrial vegetation. The biological communities in this area reflect a blend of species from the comparatively warmer east coast and the colder west coast.

I authored a paper in 2017 entitled "Seaweeds in Two Oceans", which is part of your required reading, explaining precisely how and why these oceanic influences can be measured and how they shape biogeography. The area between Cape Agulhas (the southernmost tip of Africa) and Cape Point is where this mixing creates a transition—biogeographically, it marks the boundary between the Benguela and Agulhas marine provinces, each hosting distinct communities but with a measurable zone of overlap.

6.4 Atmospheric Pressure, Weather, and Climate

Another student asked whether humid conditions in the Western Cape are a consequence of the Agulhas Current. In short, not really—not on short timescales. While ocean currents set the broader climatic context and have significant influences over months and years, the day-to-day weather we feel (e.g., changes in humidity and temperature) is primarily due to changes in atmospheric pressure systems. The ocean's heat content changes slowly due to its high heat capacity, so it exerts a steady but slow influence.

Day-to-day weather variations are mostly driven by atmospheric fronts and systems. In the Western Cape, rain typically results from low-pressure systems in the southeast Atlantic south of South Africa, not directly from the Agulhas Current. The influence of the Agulhas Current is strongest on the east coast; by the time the current rounds the Agulhas Bank, most of its heat and moisture have already been released.

Longer-term shifts—over years or decades, such as those driven by El Niño or the displacement of large-scale atmospheric systems—do ultimately tie back to oceanic cycles, but for weather on the scale of days, it's mostly atmospheric.

For those interested in looking for longer-term patterns, analyses of sea temperature and atmospheric pressure in the Western Cape reveal subtle cycles up to 18 years long, which

influence both weather and biological communities, such as shifts in vegetation or fire frequency. However, these are subtle, and are not generally perceived on short timescales without data analysis.

6.5 Recap of Key Points

The key point for you to remember in this module is that environmental gradients—across rainfall, temperature, soil, and other variables—imprint themselves on the structure of biological communities. These gradients are frequently determined by major influences such as ocean currents, but it is the sum of these factors, and their interactions, that create the distinctive assemblages of species we see across landscapes.

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