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Models of Functional Redundancy in Ecological Communities

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MODELS OF FUNCTIONAL REDUNDANCY IN ECOLOGICAL COMMUNITIES

A Dissertation
Presented to
the Graduate School of
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In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Mathematical and Statistical Sciences

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by
Sandra Annie Tsiorintsoa
May 2024

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Abstract

Functional redundancy is the number of taxa that perform a given function within a given community. In most systems, high levels of functional redundancy are important, because they contribute to ecosystem stability. However, we currently have very little understanding of why functional redundancy varies among communities. One possible factor that could affect functional redundancy is environmental complexity. Many studies show that simplified ecosystems harbor communities with lower taxon diversity. What is less clear is if this simplicity and lower taxon diversity also affects functional redundancy. To answer this question, we use metacommunity models to explore the connection between environmental complexity and functional redundancy, focusing on resource diversity as our measure of environmental complexity. Specifically, we consider two paradigms for local community assembly within a larger metacommunity: environmental filtering and niche partitioning. We then use these paradigms to develop null expectations for how functional redundancy should scale with the number of resources available in a local community. Our model for environmental filtering indicates that functional redundancy of local resources is constant with respect to local resource complexity, while it increases for niche partitioning. These findings suggest that different modes of community assembly yield different relationships between resource complexity and functional redundancy. We explore these findings as they pertain empirical ecosystems and management strategies for maintaining high functional redundancy—a first step towards protecting ecosystem stability and resilience.

Dedication

"So whether you eat or drink or whatever you do, do it all for the glory of God."

1 Corinthians 10:31

"Koa na mihinana na misotro hianareo, na inona na inona ataonareo, dia ataovy ho voninahitr'Andriamanitra izany rehetra izany."

1 Korintiana 10:31

This dissertation is dedicated to the Almighty God who has been my source of knowledge, strength, grace and wisdom (Ho an'Andriamanitra irery anie ny voninahitra sy ny dera). To my family and friends who have stood by me throughout this journey. In memory of my Dad, Ranaivosolo, whose foresight into my mathematical journey laid the bedrock for my pursuit in this field (Misaotra Dada!). To my Mom, Rasoamanalina, your boundless love, care, prayers, patience, and sacrifices have been the pillars of my strength (Mankasitraka Mama!). To my fiancée, Tolotriniray, who has steadfastly supported me through every challenge. To my nephews, Alexandro, Christiano, Ricardo and Luciano, whose presence always brings me joy. To my sister, Maria, and brother, Alain, who have continuously believed in me and have been proud of my endeavors. Despite the physical distance separating us over the years, your unwavering support, sacrifices, and steadfast belief in my abilities have fueled my pursuit of excellence.

To my advisors, Dr. Sharon Bewick and Dr. Matthew Macauley, your genuine commitment to my success transcends mere mentorship, and I am profoundly grateful for the opportunities you have provided me to flourish in my career.

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Chapter 1

Introduction

1.1 Functional redundancy in ecological communities

Functional redundancy is a measure of the number of different taxa that perform similar roles within an ecological community or ecosystem [54, 16]. Often, redundancy is defined based on what happens when a species is removed. In particular, the removal of a redundant species must leave the system intact. What constitutes an intact community or ecosystem, however, is often subjective. Possible criteria include [46, 25]: (1) that the abundances of the remaining species do not change, (2) that no new species colonize the community and fill the niche of the redundant species, (3) that ecosystem function is maintained or (4) that at least some members of the community persist. In practice, the definition of redundancy is strongly dependent on the focus of the study. If, for example, the focus of the study is bird community composition, then a redundant bird species would be one whose removal does not significantly impact the abundances or relative abundances of the remaining bird populations [15]. By contrast, if the focus of the study is how insects affect wetland nutrient cycling, then a redundant insect species would be one whose removal does not impact nitrogen or carbon pools, irrespective of whether or not its removal alters population abundances of other insect species [17]. Historically, there has been debate over whether and how functional redundancy persists in ecological communities [54]. This is because basic Lotka-Volterra competition models predict that stable coexistence of truly redundant species is not possible [54]. However, these models fail to account for factors like spatial and temporal variability and nonlinearity that may underlie functional redundancy in real systems [54]. Further, individual species do not have to be identical—an assumption of the Lotka-Volterra predictions—for there to be functional redundancy at the ecosystem scale. This has led some researchers to propose use of the term 'functional similarity' rather than 'functional redundancy' to capture the fact that species can coexist while still exhibiting niche overlap [21]. Alternately, true functional redundancy may be possible if competition is not a dominant factor governing community assembly. This is the assumption of both neutral theory [35] and the theory of environmental filtering [45], with the former positing that dispersal limitation and drift structure communities, and the latter suggesting that community structure is primarily dependent on tolerance to abiotic conditions. In reality, ecological communities are likely structured by a combination of factors, with competition and niche theory lying at one end of the spectrum and environmental filtering and neutral theory lying at the other. Meanwhile, true communities likely emerge as combinations of the various forces, with the relative importance of competition versus dispersal, drift and tolerance depending on both the community and the timescale considered. This, in turn, likely determines both the degree to which functional redundancy is possible and how functional redundancy is maintained.

Strictly based on empirical evidence, many communities – including communities comprised of both macro- [24, 15, 6] and microorganisms [31, 79, 64]—exhibit at least some level of functional redundancy. For instance, in plant-pollinator communities, the understory herbs *Costus allenii* and *C. laevis* (Zingiberaceae) use the same pollinator (*Euglossa imperialis*) and occupy the same habitats [76]. Likewise, amongst gut microbiota, *Salmonella enterica serovar typhimurium* and *Clostridium difficile* both catabolize the same mucosal carbohydrates, apparently in the same way [67]. In other communities, however, functional redundancy is less apparent. Many gut bacteria, for instance, have evolved unique enzymatic pathways to degrade specific carbohydrates. As an example, *Bifidobacterium* species have specialized in the breakdown of *oligosaccharides* from breast milk, and their presence is of critical importance during infancy when these carbohydrates are abundant. That *Bifidobacterium* cannot be replaced by alternate bacterial taxa suggests limited intergeneric redundancy in their ecological niche [56], though there may be substantial interspecific redundancy among *Bifidobacterium* strains.

One ecosystem characteristic that likely impacts both the potential for and level of functional redundancy is *environmental complexity*—the diversity of underlying resources or conditions that support the focal community or ecosystem. As with functional redundancy, the appropriate definitions of complexity and its measurement are not universally consistent [53]. Broadly speaking, there are two types of environmental complexity: *habitat complexity* [13, 44], and *resource complexity* [75]. Habitat complexity reflects the number of patches of different habitat types present in a particular region [13, 44]. In agroecosystems, for example, habitat complexity often refers to the diversity of habitats surrounding a farm [59, 39, 84]. Likewise, in aquatic systems, density and fractal dimension of macrophytes, variation in water velocity, structural density (e.g.: rocks, woody debris, leaf litter), and substrate rugosity are often used to characterize habitat complexity [85, 43]. By contrast to habitat complexity, resource complexity reflects the variety of resources available within a community [75]. In rocky shore communities, for example, the onshore flow of cool nutrient-rich waters from upwelling can increase invertebrate recruitment, raising resource complexity for the benthic and epiphytic algae community [74, 63]. Similarly, for a pollinator community, resource complexity could be measured as the number of different flower species, which then determines nectar diversity [1, 73, 18]. In this thesis, I define environmental complexity as the diversity of the set of resources that are used by a community of consumers, henceforth, "species".

In most communities and ecosystems, positive outcomes are associated with higher environmental complexity [81]. This is particularly true for ecological patterns like ecosystem function and resilience [53, 66, 68, 9, 50, 30, 55, 33, 11, 71, 40]. Higher foliage height diversity, for example, supports a higher richness of bird species [58]. Likewise, more heterogeneous habitats support a higher richness of lizards [6]. Environmental complexity impacts community and ecosystem characteristics by altering species interactions. Prey richness (i.e., resource complexity for the predator community), for instance, shapes predator-prey interactions, food-web complexity, ecosystem stability, and the provision of ecosystem services [86, 69, 5]. Typically, complexity modifies species interactions by buffering prey against consumption, or consumers against competition, thereby facilitating greater species diversity within the community [32]. Said differently, greater complexity inflates the number of available niches, thereby allowing for increased species diversity, as well as increased partial niche overlap.

Broadly speaking, the resources that shape resource complexity within a community or ecosystem can be substitutable or nonsubstitutable. nonsubstitutable resources satisfy different species requirements that cannot be exchanged for one another. A carbon source and a nitrogen source, for example, are nonsubstitutable. By contrast, substitutable resources satisfy the same species requirement. For instance, although glucose and sucrose are chemically different sugars, both can be used exchangeably as carbon sources. Even when resources are substitutable, it is possible, and indeed probable, that only a subset of consumer species can exploit any given resource. A macroscopic example would be nectar provided by a variety of different flower species to a pollinator community. Although nectar is largely substitutable (water and sugars) from one flower species to another, not all pollinators can access nectar from all flowers. Hummingbirds, for example, require a certain flower size and shape to acquire nectar based on their beak size. A similar microscopic example would be a set of different carbon sources available to a bacterial community. Whereas different carbon sources are largely substitutable, not all bacterial taxa have the enzymes required to break down all carbon sources. Both the complexity of substitutable and nonsubstitutable resources have the potential to impact community and ecosystem characteristics, including functional redundancy, in a positive manner.

Unfortunately, although environmental complexity is typically viewed as a positive contributor to ecological communities and ecosystems, human activities tend to simplify environmental complexity. Fishing, for example, has been associated with the degradation or loss of complex structure of coral reefs [2, 78]. Similarly, deforestation has a negative effect on species richness, community structure and functional diversity of birds, small mammals and lizards [77, 28, 29]. This simplification is thought to be one of the major causes of biodiversity loss [22, 4] in ecosystems today. While the impacts of complexity loss are already apparent in many ecosystems, an increasing fear is that some level of ecosystem damage is being masked by functional redundancy. Although biodiversity is being lost, ecosystem services are maintained because the historical communities had high levels of functional redundancy. Consequently, when one species goes locally extinct, another species is available to fill its functional niche. However, even though ecosystem function may be retained temporarily, the end result is a 'thinner' ecological community that is less stable and less resilient to perturbation. Indeed, at some point, there will be only a single species covering critical ecosystem functions. Thus, when a perturbation (e.g., disease, a flood, a fire) wipes that species out, ecosystem services will collapse. For this reason, it is imperative that I understand how complexity impacts functional redundancy and how the destruction of complexity is putting us at a precipice for potential failure of ecosystem services that we have come to rely on.

In this dissertation, I consider the effect of resource complexity on functional redundancy of resource use. More specifically, I use metapopulation models to develop theoretical predictions for the relationship between resource complexity and functional redundancy under two limiting theories of community assembly—niche partitioning and environmental filtering.

This dissertation has six chapters. In the first chapter, I cover background ecological terminology, and lay out mathematical notation and methodology. In Chapter 2, I develop of the environmental filtering model for substitutable resources. In Chapter 3, I develop the niche partitioning model for substitutable resources. In Chapter 4 I extend both the environmental filtering and the niche partitioning models to consider nonsubstitutable resources. Finally, in Chapter 5 I present some applications on empirical data and in Chapter 6 I summarize the conclusions from my dissertation.

1.2 Ecological terms

In this section, I will define and summarize the important ecological terms that will be used throughout this thesis. Many of these, despite being common words, have field-specific meanings. In some cases, these terms are my own definitions (e.g., high- and low-use resource) and are not broadly used elsewhere in ecological literature.

- *Abiotic:* having to do with non-living components like water, sunlight, inorganic elements and molecules, etc.
- *Biotic:* having to do with living organisms.
- *Population:* a group of interacting organisms of the same species that reproduce and live together in a given place at a given time.
- *Community:* all of the populations of different species that occur together in the same place at the same time.
- *Ecosystem:* a combination of a community and all of the abiotic factors in a given place at a given time.
- *Local community:* an ecological community that resides in a relatively small local region. Often, the size of the region is such that all individuals of all species could conceivably interact with one another over their lifetimes, as depicted in Figure 1.1.
- *Metacommunity (or global community):* a set of local communities that are linked by dispersal of some of the interacting species.

- *Metacommunity framework:* a concept that integrates local and regional dynamics wherein species and resources in the metacommunity are divided into a set of local communities linked by dispersal. While individuals can disperse from one local community to another, local communities need not be identical (e.g., different resources may be present). Depending on the metacommunity framework adopted, there is often a focal local community that is the subject of study which is then linked to a broader metacommunity from which species are recruited (i.e., not all individual local communities are considered in the same detail).

- *Local species:* species that lives in the focal local community.

- *Nonlocal species:* species that lives in the metacommunity, but not in the focal local community.

- *Species richness:* a count of the number of species in a community. For instance, a plant community consisting of four individual *Noccaea caerulescens* trees and two white poplar (*P. alba*) trees has a species richness of two.

- *Local species richness:* a count of the number of species in the focal local community.

- *Species abundance:* a count of the number of individuals of a given species in a population or community. In the above example, the species *Noccaea caerulescens* has a species abundance of four and the species *P. alba* has a species abundance of two.

- *Species diversity:* species richness with some degree of accounting for the evenness of species abundances.

- *Resources:* elements (biotic or abiotic) that an organism consumes or otherwise requires in order to grow, survive, and reproduce. Examples of resources include food, shelter, light, etc. [82].

- *High-use resources (HR):* resources with a high probability of being used by a given species. These are resources that are used by the majority of species in the metacommunity.

- *Low-use resources (LR):* resources with a low probability of being used by a given species. These are resources that are used by only a few species in the metacommunity.

- *Substitutable resources:* resources that satisfy the same requirements for survival and reproduction [49]. That is, a species can survive using any one of the substitutable resources. As an example, two different sugars like glucose and sucrose satisfy the same requirement—they provide carbon—necessary for microbial growth and survival.

- *Nonsubstitutable or complementary resources:* resources that do not satisfy the same requirements for survival and reproduction [49]. That is, a species cannot survive using only one of the nonsubstitutable resources. As an example, plants require both light to provide energy and CO_2 to provide carbon, thus, light and CO_2 are nonsubstitutable.
- *Local resources (or present resources):* resources that are present in the focal local community.
- *Nonlocal resources (or absent resources):* resources that are present in the metacommunity but that are absent from the focal local community.
- *High-use local species richness:* a count of the number of local species using at least one local high-use resource.
- *Low-use local species richness:* a count of the number of local species using at least one local low-use resource.
- *Environmental complexity (or local resource complexity):* the number of resources available in the focal local community.
- *Functional redundancy (FR) of resources:* the average number of local species that use a given resource.
- *Local functional redundancy:* the average number of local species using local resources.
- *Nonlocal functional redundancy:* the average number of local species using nonlocal resources.
- *Total functional redundancy:* the average number of local species using all resources (i.e., both local and nonlocal resources).
- *Ecological niche:* a concept used to define where a particular species can live and why.
- *Eltonian niche:* a definition of the *ecological niche* based on species competition (i.e., biotic interactions) [23]. According to Charles Elton, each species occupies a particular role in a community and there can only be one species that occupies that role because there will always be one winner if two species occupy the same role.

- *Grinnellian niche:* a definition of the *ecological niche* based on environmental conditions (i.e., abiotic interactions) [27]. According to Joseph Grinnell, each species occupies locations where the habitat or environment is suitable.

- *Hutchinson niche:* a definition of the *ecological niche* based on both biotic and abiotic conditions. Hutchinson captured the multivariate nature of the *ecological niche* by proposing an *n-dimensional hypervolume* (e.g., food size, temperature, branch density, etc.) that defines where a species can persist [36].

- *Fundamental niche:* the *ecological niche* that a species could occupy without considering interactions with other species (e.g., predation competition, mutualisms).

- *Realized niche:* the *ecological niche* that a species actually occupies after interactions with other species are considered.

- *Competitive exclusion principle:* a theory based on Lotka-Volterra models that states that two identical species cannot coexist. One species will always be slightly stronger than the other and, over long time-scales, will drive the weaker species extinct.

- *Limiting similarity:* a theory that defines the minimal niche difference required for two competing species to coexist [57]. For simple models, coexistence requires that the mean difference in resource use between species is approximately equal to the standard deviation in resource use of each species [62, 61].

- *Niche partitioning (NP):* a mechanism by which species coexist because they inhabit different regions of niche space; in my models, this means that each species needs to outcompete all other species for at least one resource in order to persist.

- *Environmental filtering (EF):* a mechanism wherein species can only exist where environmental conditions meet their survival requirements; in my models, this means that each species needs to use at least one of the resources in the community to persist.

- *Community assembly:* the process by which species come together to live and persist in a community. There are two different baseline assumptions for community assembly: niche partitioning (NP), and environmental filtering (EF).

Figure 1.1 shows a simple example of a metacommunity, where the resources are shown in red, the species are shown in black and the local populations are shown as dark blue patches.

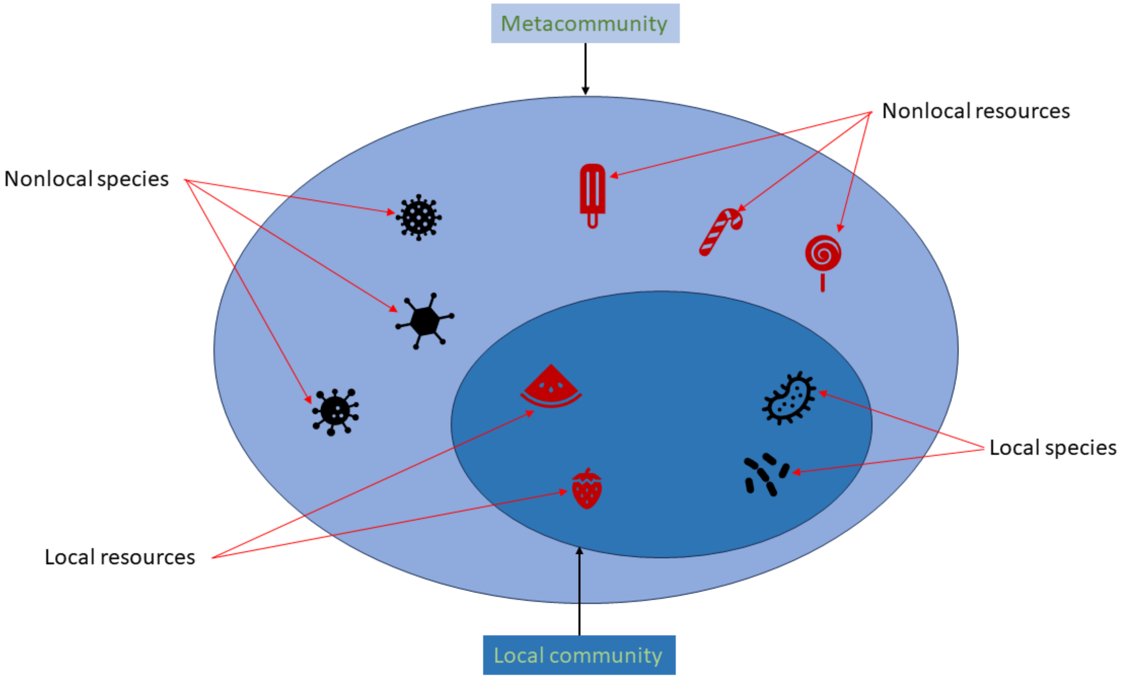

Figure 1.1: Depiction of a metacommunity, illustrating resources (red), species (black) and local community (dark blue patches).

1.3 Mathematical Notation

The following notation will be used throughout the dissertation, unless explicitly stated otherwise. The details of these definitions will be described later; this is only meant as a summary and quick reference guide.

- R: the number of resources in the metacommunity.
- r: the number of resources in the focal local community, $1 \leq r \leq R$.
- R_h: the number of high-use resources in the metacommunity.
- r_h: the number of high-use resources in the focal local community.
- R_ℓ: the number of low-use resources in the metacommunity.

- r_ℓ: the number of low-use resources in the focal local community.

- S: the number of species in the metacommunity; the *species richness* of the metacommunity.

- b: the number of resources that each species uses in the metacommunity, henceforth referred to as the *resource breadth*, $1 \leq b \leq R$.

- p_k: the probability that a given species with resource breadth $b \leq S$ will use exactly k resources in the local community, under an uniform distribution.

- p: the probability that a given species will persist in the local community, assuming an uniform distribution. This is the probability that at least one of its b resources can be found in the local community.

- s: the expected number of species that can persist in the local community; the *species richness* of the local community.

- s_h: the expected number of species that persist in the local community and use at least one high-use resource (i.e., high-use local species richness) for the environmental filtering; and outcompete others for at least one high-use resource for the niche partitioning.

- s_ℓ: the expected number of species that persist in the local community and use at least one low-use resource (i.e., low-use local species richness) for the environmental filtering; and outcompete others for at least one low-use resource for the niche partitioning.

- Ω_p: the *functional redundancy* of each resource present in the local community. This is the expected number of local species that use each resource in the local community.

- Ω_a: the *functional redundancy* of resources present in the metacommunity but absent from the local community (henceforth: "absent resources"). This is the expected number of local species that can use each resource outside the local community.

- Ω_t: the total *functional redundancy* of resources in the metacommunity. That is, a weighted average of Ω_p and Ω_a. This is the expected number of species in the local community that can use any resource in the metacommunity.

- Ω_p^h: the *functional redundancy* of each high-use resource present in the local community. This is the expected number of local species that can use each high-use resource in the local community.

- Ω_a^h: the *functional redundancy* of each absent high-use resource. This is the expected number of local species that can use each high-use resource outside the local community.

- Ω_p^ℓ: the *functional redundancy* of each present low-use resource. This is the expected number of local species that can use each low-use resource in the local community.

- Ω_a^ℓ: the *functional redundancy* of each absent low-use resource. This is the expected number of local species that can use each low-use resource outside the local community.

Figure 1.2 shows a simple example of a metacommunity of $S = 4$ species and $R = 5$ resources, where the species are microbes, and the resources are sugars. Although there are $R = 5$ sugars in the metacommunity, there are only $r = 2$ of the metacommunity sugars present in the local community—glucose and xylose. Each microbial species has a resource breadth of $b = 2$, which means that each microbial species can use two different sugars. One of the two sugars that any given microbial species uses must be present in the local community for that microbial species to persist. Thus, for example, coccus microbial species cannot persist in the local community because neither fructose nor lactose are present in the local community. In the absence of competition (i.e., according to the environmental filtering model), the remaining three microbes should be able to persist in the local community because they can use at least one of the sugars present in the local community. In practice, though, whether or not the remaining three species persist depends on the extent to which competition shapes community assembly. Assuming a model with competitive exclusion (niche partitioning), a maximum of two microbial species will coexist in the local community, because one microbial species will outcompete the other two for glucose while either that same microbial species or a different microbial species will outcompete the other two for xylose.

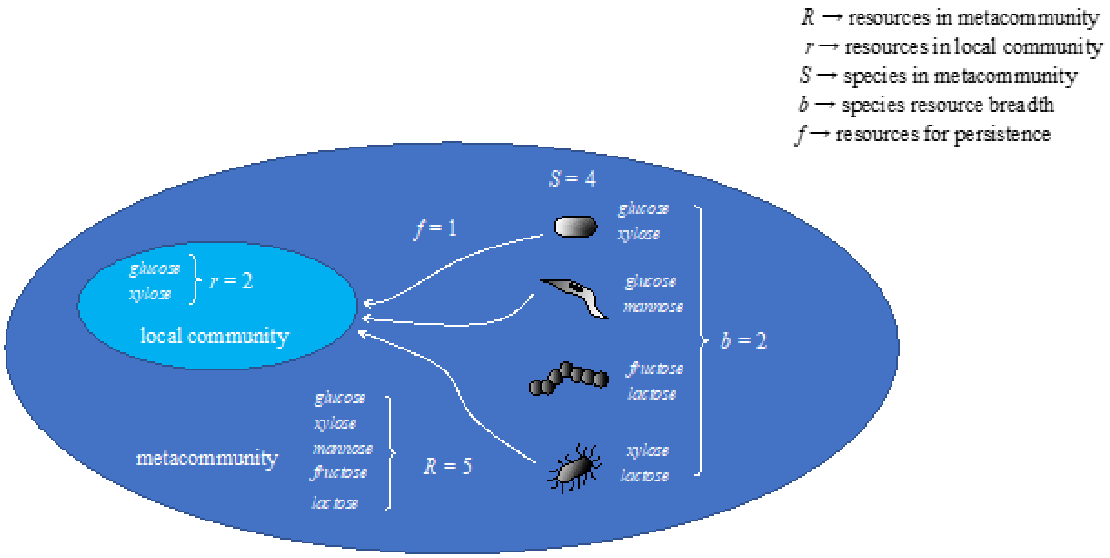

Figure 1.2: A simple example of community of $S = 4$ microbes (species) competing for $r = 2$ sugars (resources) in a local community. Each species has a resource breadth of $b = 2$, from the $R = 5$ sugars in the metacommunity.

1.4 Methodology

In the thesis that follows, I assume that a more complex environment is one with more types of resources. To explore how environmental complexity impacts functional redundancy, I consider a focal local community which is nested within a broader metacommunity. Whereas there are R resources in the metacommunity, only $r < R$ of these are present in the local community. Consequently, of the S consumer species present in the metacommunity, only $s < S$ can persist in the local community, and it is this subset that is used to determine the functional redundancy. By keeping R and S fixed in the metacommunity while varying r in the local community, I can calculate the expected number of species within the local community that can use any given resource. Notably, this can be done for the Ω_p resources *present* in the local community, the Ω_a resources *absent* from the local community, and the Ω_t *total* resources (regardless of their status in the local community). I then use the expected number of species that can use a particular type of resource as my measure of functional redundancy. Below, I outline heuristics for modeling local communities given two limiting models for community assembly: environmental filtering (persistence in the local community is fully determined by the resources present) and niche partitioning (persistence in the local community is fully determined by the ability to outcompete other species for the resources present). I also briefly summarize several other assumptions that I consider regarding the number of resources any consumer species can use, as well as the number of consumer species that use any given resource.

For both the environmental filtering and niche partitioning scenarios, I begin by considering an empty local community with only resources present. The particular resources present are selected, at random, from the set of resources available in the broader metacommunity using a stochastic modelling approach (see [72] for an overview of stochastic models). I then 'fill' the local community by considering whether or not each species present in the metacommunity can persist in the local community. To decide whether species from the metacommunity can persist in the local community, I use a rule based probability approach. More specifically, I look at the distribution of resource use across a large number of species and use this to determine the expected number of species that can use each resource in the local community. From this information, I then assess the relationships between functional redundancy and the resource complexity within a local community.

In Chapters 2 and 3 I build models that consider fully substitutable resources (e.g., carbon sources). Chapter 2 develops models that assume communities assemble under an environmental filtering mechanism while Chapter 3 develops models that assume communities assemble under a niche partitioning mechanism. I refer to both of these models as *one-dimensional* because they consider a single dimension of the 'Hutchinsonian niche'. Later on, in Chapter 4, I extend the environmental filtering and niche partitioning models by considering *nonsubstitutable resources* (e.g., carbon and nitrogen sources).

Chapter 2

Environmental filtering

The models in this section assume *environmental filtering* (EF) assembly. More specifically, for a species to persist in the local community, it must find at least one resource that it can utilize. The species does not, however, need to outcompete any other species for this resource. The presence of a usable resource in the local community is enough for species persistence. Briefly, I use a metacommunity framework for my model. Starting from the pool of all of resources present in the metacommunity, I randomly select a subsample of these resources to be present in the focal local community. I then use probability and combinatorial techniques to determine which species from the metacommunity can persist in the focal local community. This allows me to compute the number of different local species that use any given local and/or metacommunity resource.

2.1 Equal resource use

To begin, I suppose that all R resources in the metacommunity are equally likely to be used and that any given species, i, is able to use exactly b_i of these resources, where b_i is the *resource breadth* of species i.

2.1.1 Delta distribution

For the simplest EF model, I assume equal resource breadth across all species. Thus, $b_i \equiv b$ and all species are able to use the same number of resources. I call this a "delta distribution" of resource breadths, because it resembles the Dirac delta function (see Figure 2.1 for examples of this distribution for both $b = 1$ and $b = 2$). In what follows, I consider different scenarios based on different possible values of b and use this to derive an expression for *local species richness*, s, in the local community. This is the expected number of species that will persist in the local community, as a function of the number of resources r present in the local community, as well as the total number of species, S, and resources, R in the metacommunity. I then use my expression for local species richness to derive equations for functional redundancy.

2.1.1.1 Case studies for $b = 1$ and $b = 2$

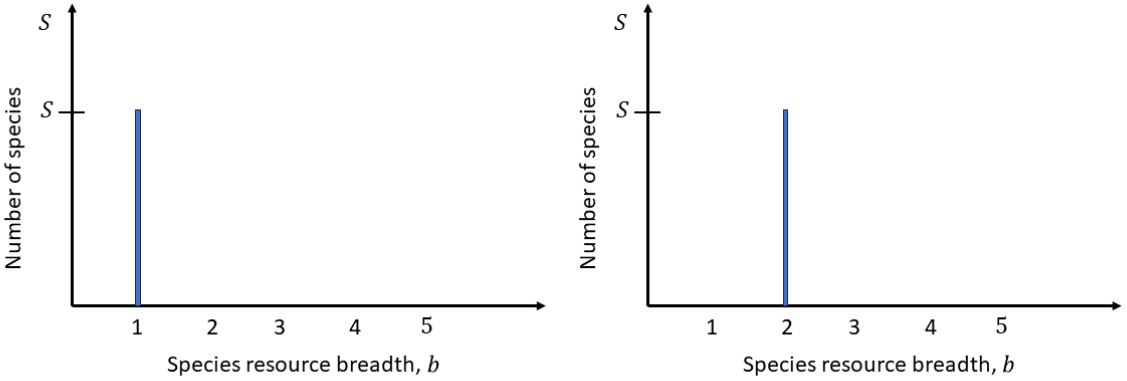

Figure 2.1: Delta distribution for $b = 1$ (left) and $b = 2$ (right).

Resource breadth $b = 1$

I begin with the simplest example, where each species only uses one resource, $b = 1$. First, I find the probability that a randomly selected species from the metacommunity uses one of the r resources present in the local community. Because every species uses exactly $b = 1$ resource, and because all resources are used with equal probability, the probability that a randomly selected species i from the metacommunity will be able to use at least one of the $r \leq R$ resources present in the local community is

$$p = P\left(|\varsigma_i \cap \varsigma_\ell| \geq f \mid b = 1\right) = \frac{r}{R}, \tag{2.1}$$

where ς_i is the set of all resources used by species i, and ς_ℓ is the set of all resources present in the local community. If there are a total of S species in the metacommunity, then the expected number of species that can persist in the local community is

$$s = Sp = \frac{Sr}{R}. \tag{2.2}$$

This is the *local species richness.* Since each species is only be able to use $b = 1$ resource, and there are $r \leq R$ resources present in the local community, the expected number of local species using any single local resource is

$$\Omega_p = \frac{s}{r} = \frac{S}{R}. \tag{2.3}$$

This is the *local functional redundancy.* Likewise, the number of species using any single resource that is present in the metacommunity but absent from the local community is

$$\Omega_a = 0. \tag{2.4}$$

This is the *nonlocal functional redundancy* and follows from the fact that each species can only use a single resource ($b = 1$); thus, for species to persist in the local community, the single resource that the species use must be a local resource.

In summary, for the "delta distribution" with $b = 1$, the species richness, s, of the local community, scales linearly with the resource complexity, r, of the local community. However, both the local, Ω_p, and nonlocal, Ω_a, functional redundancies are independent of the resource complexity of the local community. Figure 2.2 shows a simple example of this scenario for S microbial species and $R = 3$ sugars, of which $r = 1$ is present in the local community.

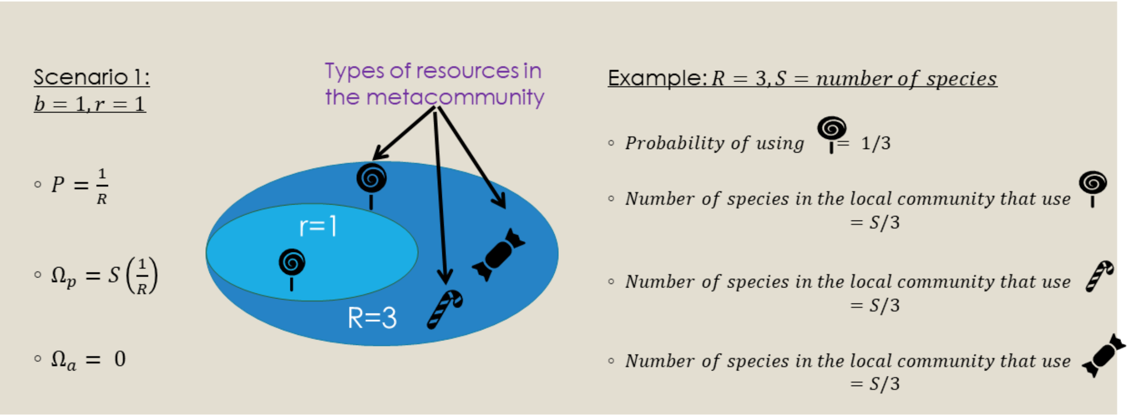

Figure 2.2: Example of breadth $b = 1$ with $R = 3$ and $r = 1$.

Resource breadth $b = 2$

As my second example, I assume that each species can use exactly $b = 2$ resources. There are three possible scenarios: (i) both resources that a species can use are present in the local community, (ii) neither of the resources that a species can use are present in the local community, or (iii) only one of the two resources that a species can use is present in the local community. Consistent with my assumption of equal resource use, I assume that all $\binom{R}{2}$ combinations of resources are equally likely to be used by any given species. The number of ways of choosing two resources from R with at least one of those resources being present in the local community is $\binom{R}{2} - \binom{R-r}{2}$. Therefore, the probability, p, that any given species can persist in the local community is

$$\begin{aligned} p = \frac{\binom{R}{2} - \binom{R-r}{2}}{\binom{R}{2}} &= \frac{\frac{R!}{2(R-2)!} - \frac{(R-r)!}{2(R-r-2)!}}{\frac{R!}{2(R-2)!}} = \frac{\frac{R(R-1)}{2} - \frac{(R-r)(R-r-1)}{2}}{\frac{R(R-1)}{2}} \\ &= \frac{R\,(R-1) - (R-r)\,(R-r-1)}{R\,(R-1)} = \frac{2rR - r^2 - r}{R\,(R-1)}. \end{aligned} \tag{2.5}$$

In Equation (2.5), $\frac{\binom{R}{2}-\binom{R-r}{2}}{\binom{R}{2}} = \frac{\binom{r}{2}+r(R-1)}{\binom{R}{2}}$, where $\frac{\binom{r}{2}}{\binom{R}{2}} = \frac{r(r-1)}{R(R-1)}$ is the probability of a species using two of the resources that are present in the local community, and $\frac{r(R-r)}{\binom{R}{2}} = \frac{2r(R-r)}{R(R-1)}$, is the probability of a species using only one of the resources that is present in the local community. If there are a total of S species in the metacommunity, then the expected number of species that can persist in the local community is

$$s = Sp = \frac{\left(2rR - r^2 - r\right) S}{R\,(R-1)}. \tag{2.6}$$

This is the *local species richness.* Of the species that can use only one local resource, the number that use any particular focal local resource, Ω_{p_1}, is

$$\Omega_{p_1} = \frac{1}{r} \cdot \frac{2r\,(R-r)\,S}{R\,(R-1)}. \tag{2.7}$$

Likewise, of the species that can use two local resources, the number that use any particular focal local resource, Ω_{p_2}, is

$$\Omega_{p_2} = \frac{2}{r} \cdot \frac{r\,(r-1)\,S}{R\,(R-1)}. \tag{2.8}$$

Combining Equations (2.7) and (2.8) gives

$$\Omega_p = \frac{2}{r} \cdot \ \frac{r\,(r-1)\,S}{R\,(R-1)} + \frac{1}{r} \cdot \frac{2r\,(R-r)\,S}{R\,(R-1)} = \frac{2S\,(r-1+R-r)}{R\,(R-1)} = \frac{2S\,(R-1)}{R\,(R-1)} = \frac{2S}{R}. \tag{2.9}$$

This is the *local functional redundancy.*

Next, I derive an expression for the expected number of local species that use a particular nonlocal resource. Species that use two local resources do not use any nonlocal resources. Species that use only one local resource, however, also use one nonlocal resource. Combining Equation (2.7) with the probability that any particular nonlocal resource is chosen from the total $R - r$ nonlocal resources in the metacommunity gives

$$\Omega_a = \frac{1}{R-r} \cdot \frac{2r\,(R-r)\,S}{R\,(R-1)} = \frac{2rS}{R\,(R-1)}. \tag{2.10}$$

This is the *nonlocal functional redundancy*

In summary, for the "delta distribution" with $b = 2$, the species richness, s, of the local community, scales non-linearly with local resource complexity; the nonlocal functional redundancy, Ω_a, scales linearly with the local resource complexity; and local functional redundancy, Ω_p remains independent of local resource complexity.

2.1.1.2 Exact expressions for functional redundancy

Species richness in the local community

Extending my previous two examples to the case where each species uses $b > 2$ resources, there are $\binom{R-r}{b}$ ways of choosing b nonlocal resources, leaving $\binom{R}{b} - \binom{R-r}{b}$ ways of choosing b resources with at least one being a local resource. Thus, the probability that a given species can live in the local community is

$$
\begin{aligned}
p = \frac{\binom{R}{b} - \binom{R-r}{b}}{\binom{R}{b}} &= \frac{\frac{R!}{b!\,(R-b)!} - \frac{(R-r)!}{b!\,(R-r-b)!}}{\frac{R!}{b!\,(R-b)!}} \\
&= \frac{\frac{R\,(R-1)\,(R-2)\cdots(R-b+1)}{b!} - \frac{(R-r)\,(R-r-1)\cdots\;(R-r-b+1)}{b!}}{\frac{R\,(R-1)\,(R-2)\cdots(R-b+1)}{b!}} \\
&= \frac{R\,(R-1)\,(R-2)\cdots(R-b+1) - (R-r)\,(R-r-1)\cdots\;(R-r-b+1)}{R\,(R-1)\,(R-2)\cdots(R-b+1)},
\end{aligned}
\tag{2.11}
$$

which can be partitioned into individual probabilities, p_k, that persistence is based on finding exactly $k > 0$ usable resources in the local community, where $\max(1, b{+}r{-}R) \leq k \leq \min(r, b)$. An expression for p_k can be derived based the number of ways of choosing k resources that are present in the local community and $b-k$ resources that are not present in the local community

$$
\begin{aligned}
p_k = \frac{\overbrace{\binom{r}{k}}^{\substack{\text{\# ways to choose}\\ k\text{ resources from }r\\ \text{in local comm.}}}\qquad\overbrace{\binom{R-r}{b-k}}^{\substack{\text{\# ways to choose}\\ b-k\text{ resources from }R-r\\ \text{outside local comm.}}}}{\underbrace{\binom{R}{b}}_{\substack{\text{\# ways to choose}\\ b\text{ resources from }R\\ \text{in metacommunity}}}} &= \frac{\frac{r!}{k!\,(r-k)!}\cdot\frac{(R-r)!}{(b-k)!\,(R-r-b+k)!}}{\frac{R\,(R-1)\,(R-2)\cdots(R-b+1)}{b!}} \\
= \frac{b\,(b-1)\,(b-(k-1))\,r\,(r-1)\cdots(r-(k-1))\,(R-r)\,(R-r-1)\cdots(R-r-(b-k-1))}{k!R\,(R-1)\,(R-2)\cdots(R-b+1)}&.
\end{aligned}
\tag{2.12}
$$

The *local species richness* is

$$
s = Sp = S \sum_{k=\max(1,b+r-R)}^{\min(b,r)} p_k. \tag{2.13}
$$

Functional redundancy of local resources: Ω_p

Each species that can live in the local community must be able to use at least one local resource. Of the species that use one and only one local resource, the number that use any particular focal local resource is

$$\frac{1}{r} \cdot \frac{S\binom{r}{1}\binom{R-r}{b-1}}{\binom{R}{b}} = \frac{\frac{(R-r)!}{(b-1)!(R-r-(b-1))!}}{\frac{R(R-1)(R-2)\cdots(R-b+1)}{b!}} S = \frac{b\,(R-r)\cdots(R-r-(b-2))\,S}{R\,(R-1)\,(R-2)\cdots(R-b+1)}.$$

Likewise, of the species that use exactly two local resources, the number that use any particular focal local resource is

$$\begin{aligned}\frac{2}{r} \cdot \frac{S\binom{r}{2}\binom{R-r}{b-2}}{\binom{R}{b}} &= \frac{2}{r} \cdot \frac{\frac{r!}{2(r-2)!} \cdot \frac{(R-r)!}{(b-2)!(R-r-(b-2))!}}{\frac{R(R-1)(R-2)\cdots(R-b+1)}{b!}} S = \frac{2}{r} \cdot \frac{b\,(b-1)\,r\,(r-1)\,(R-r)\cdots(R-r-(b-3))}{2R\,(R-1)\,(R-2)\cdots(R-b+1)} S \\ &= \frac{b\,(b-1)\,(r-1)\,(R-r)\cdots(R-r-(b-3))}{R\,(R-1)\,(R-2)\cdots(R-b+1)} S.\end{aligned}$$

More generally, of the species that use k local resources, the number that use any particular focal local resource is,

$$\begin{aligned}\frac{k}{r} \cdot \frac{S\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} &= \frac{k}{r} \cdot \frac{\frac{r!}{k!(r-k)!} \cdot \frac{(R-r)!}{(b-k)!(R-r-(b-k))!}}{\frac{R(R-1)(R-2)\cdots(R-b+1)}{b!}} S \\ &= \frac{k}{r} \cdot \frac{b\,(b-1)\cdots(b-(k+1))\,r\,(r-1)\cdots(r-(k+1))\,(R-r)\cdots(R-r-(b-(k+1)))}{k!R\,(R-1)\,(R-2)\cdots(R-b+1)} S \\ &= \frac{b\,(b-1)\cdots(b-(k+1))\,(r-1)\cdots(r-(k+1))\,(R-r)\cdots(R-r-(b-(k+1)))}{(k-1)!R\,(R-1)\,(R-2)\cdots(R-b+1)} S.\end{aligned}$$

Summing the number of species that use any particular focal local resource across all values of k gives

$$\Omega_p = \sum_{k=\max(1,b+r-R)}^{\min(b,r)} \frac{k}{r} \cdot \frac{S\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}. \tag{2.14}$$

This is the *local functional redundancy.* The expression for local functional redundancy in Equation (2.14) can be simplified considerably. In what follows, I will give two proofs of the simplified expression: one combinatorial, and one probabilistic using a hypergeometric distribution.

Proposition 1 *Consider an ecological community under the assumption of equal resource use, a delta distribution for resource breadth* $b, r \le R$ *and all other parameters as defined above. In this case, the functional redundancy of local resources is*

$$\Omega_p = \sum_{k=\max(1,b+r-R)}^{\min(b,r)} \frac{k}{r} \cdot \frac{S\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} = \frac{bS}{R}. \tag{2.15}$$

Proof 1 (Combinatorial) *Each species uses b resources, thus the probability of using each local resource is $\frac{b}{R}$. The number of species that use each local resource is $\frac{bS}{R}$. Equation* (2.14) *gives the number of species that use each local resource, which is the functional redundancy of each local resource. Thus*

$$\Omega_p = \sum_{k=\max(1,b+r-R)}^{\min(b,r)} \frac{k}{r} \cdot \frac{S\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} = \frac{bS}{R}.$$

Proof 2 (Hypergeometric distribution) *A random variable X on $\{1,\ldots,b\}$ follows a* hypergeometric distribution *with probability mass function (pmf)*

$$P(X=k) = \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}$$

and mean [38]

$$\sum_{k=1}^{b} k \cdot \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} = \frac{br}{R}.$$

Hence,

$$\Omega_p = \sum_{k=1}^{b} \frac{k}{r} \cdot \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} S = \frac{bS}{R}.$$

Once again, note that the functional redundancy of local resources, Ω_p, is independent of local resource complexity, r.

Functional redundancy of nonlocal resources: Ω_a

Taking a similar approach to derive an expression for nonlocal functional redundancy, a species that uses $b-k$ local resources will use k nonlocal resources. Thus, the probability that a local species that uses k nonlocal resources will use any focal nonlocal resource is given by

$$\begin{aligned}\frac{k}{R-r} \cdot \frac{S\binom{r}{b-k}\binom{R-r}{k}}{\binom{R}{b}} &= \frac{k}{R-r} \cdot \frac{\frac{r!}{(b-k)!(r-(b-k))!} \cdot \frac{(R-r)!}{k!(R-r-k)!}}{\frac{R(R-1)(R-2)\cdots(R-b+1)}{b!}} S \\ &= \frac{b\,(b-1)\ldots(b-(k-1))\,r\,(r-1)\ldots(r-b+k+1)\,(R-r-1)\cdots(R-r-(k-1))}{(k-1)!R\,(R-1)\,(R-2)\cdots(R-b+1)} S.\end{aligned}$$

Again, summing over all possible values of k gives

$$\begin{aligned}\Omega_a &= \sum_{k=\max(1,b+r-R)}^{\min(b-1,r)} \frac{k}{R-r} \cdot \frac{S\binom{r}{b-k}\binom{R-r}{k}}{\binom{R}{b}} = \sum_{k=\max(1,b+r-R)}^{\min(b-1,r)} \frac{b-k}{R-r} \cdot \frac{S\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} \\ &= \sum_{k=\max(1,b+r-R)}^{\min(b-1,r)} \frac{b\,(b-1)\cdots(b-(k-1))\,r\,(r-1)\cdots(r-(b-k-1))\,(R-r-1)\cdots(R-r-(k-1))}{(k-1)!R\,(R-1)\,(R-2)\cdots(R-b+1)}\,S.\end{aligned} \tag{2.16}$$

This is the *nonlocal functional redundancy.* Unfortunately, unlike local functional redundancy, the exact expression for nonlocal functional redundancy cannot be simplified in any straightforward manner. However, it can be reduced to a more concise form using the gamma function, Γ, as follows.

$$\Omega_a = \frac{Sb}{R} - \frac{(R-b)bS\Gamma(R-r)\Gamma(R-b)}{\Gamma(R-r+1-b)\Gamma(R+1)}, \tag{2.17}$$

where Γ is defined by the improper integral

$$\Gamma(z) = \int_0^\infty t^{z-1}e^{-t}, \qquad \Re(z) > 0; \qquad \text{and} \qquad \Gamma(n) = (n-1)! \qquad \forall n \in \mathbb{N}.$$

2.1.1.3 An approximate expression for nonlocal functional redundancy: Ω_a

Equation (2.17) can be simplified by recognizing that $\frac{\Gamma(n)}{\Gamma(n-m)} = \frac{(n-1)!}{(n-1-m)!} = (n-1)(n-2)\cdots(n-m)$ for all $n, m \in \mathbb{N}$. Thus, when $n \gg m$, $\frac{\Gamma(n)}{\Gamma(n-m)} \approx n^m$. Applying this approximation to our expression for the functional redundancy of nonlocal resources, Ω_a, gives

$$\begin{aligned}
\Omega_a &= \frac{Sb}{R} - bS \cdot \frac{\Gamma(R-r)}{\Gamma(R-r+1-b)} \cdot \frac{(R-b)\Gamma(R-b)}{\Gamma(R+1)} \\
&= \frac{Sb}{R} - bS \cdot \frac{(R-r-1)!}{(R-r-b)!} \cdot \frac{(R-b)!}{R!} \\
&= \frac{Sb}{R} - bS \cdot [(R-r-1)\cdots(R-r-(b-1))] \cdot \frac{1}{R(R-1)\cdots(R-(b-1))} \\
&\approx \frac{Sb}{R} - bS \cdot \frac{(R-r)^{b-1}}{R^b} \\
&= \frac{Sb}{R} - \frac{bS}{R} \cdot \frac{(R-r)^{b-1}}{R^{b-1}} \\
&= \frac{Sb}{R} \cdot \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \\
&= \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \Omega_p.
\end{aligned} \tag{2.18}$$

Figure 2.3 illustrates the approximation of Ω_a given by Equation (2.18).

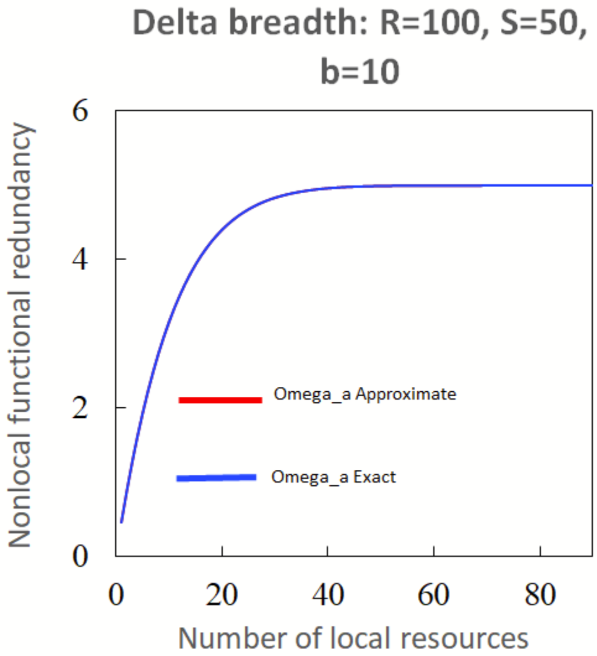

Figure 2.3: Approximations of Ω_a for a breadth delta distribution with $R = 100$ number of metacommunity resources, $S = 50$ number of metacommunity species with resource breadth $b = 10$.

2.1.1.4 An approximate expression for total functional redundancy: Ω_t

Recall that Ω_t denotes the *total functional redundancy*, which is the expected number of local species that use any resource in the metacommunity, regardless of whether the resource is local or nonlocal. Ω_t is a weighted average of the local functional redundancy, Ω_p, and the nonlocal functional redundancy, Ω_a.

Using Equation (2.15) and the approximation in Equation (2.18), the total functional redundancy is

$$\begin{aligned}\Omega_t = \frac{R-r}{R} \cdot \Omega_a + \frac{r}{R} \cdot \Omega_p &\approx \frac{R-r}{R} \cdot \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \cdot \Omega_p + \frac{r}{R} \cdot \Omega_p \\ &= \left(\frac{R-r}{R} \cdot \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) + \frac{r}{R}\right) \Omega_p \\ &= \left(1 - \frac{R-r}{R}\left(1 - \frac{r}{R}\right)^{b-1}\right) \Omega_p \\ &= \left(1 - \left(1 - \frac{r}{R}\right)^{b}\right) \Omega_p.\end{aligned}$$

2.1.2 Other resource breadth distributions

In Section 2.1.1, I assumed that species resource breadths followed a *delta distribution* with probability mass function (pmf), $\varphi_b = \begin{cases} 1 & b_n = b \\ 0 & b_n \neq b \end{cases}$, where $b_n = 1, \ldots, R$ are the potential resource breadths of species in a metacommunity with R resources. Though not biologically realistic, the delta function is useful because it can be used to derive expressions for a range of other discrete distributions. In this section, I will consider some of these other distributions, such as a uniform distribution and several triangular distributions.

For the uniform distribution, I assume that any randomly selected species, i, in the metacommunity is equally likely to use any number of resources in the range $b_i \in (b_{\min}, b_{\max})$. Some species, for example, may only use one resource. If that resource is not present in the local community, the species cannot survive there. Other species could use every resource present in the metacommunity, guaranteeing their survival in the local community. Figure 2.4 shows an example of the uniform resource breadth distribution. Each integer in $b_{\min} = 1, \ldots, 6 = b_{\max}$ is the resource breadth of the same number of species, $\frac{S}{6}$. To be a truly discrete uniform distribution, $\frac{S}{b_{\max} - b_{\min} + 1}$ must be an integer. In reality, this is rarely the case. However, the uniform distribution serves as an idealized model that can be compared to the delta distribution as well as the triangular distributions that I will discuss in the next sections.

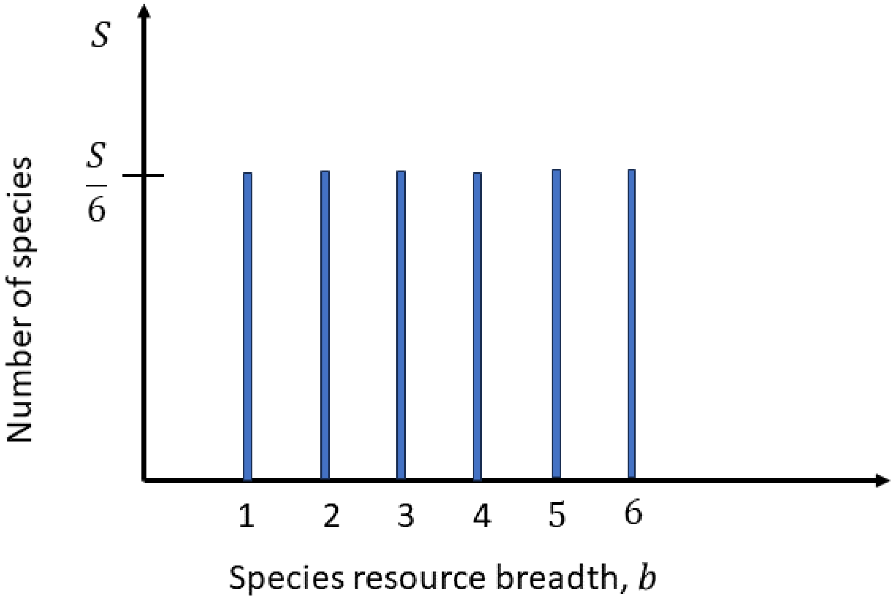

Figure 2.4: Uniform distribution of the resource breadth over $\{1, \ldots, 6\}$.

In some sense, the delta and uniform distributions serve as idealized models on opposite ends of the spectrum. Between these two extremes lie a range of distributions with a most common, or modal, value of b but also a range of additional b values around the mode. This motivates me to consider three common triangular distributions:

- *left*; when the mode is equal to $b_{\min}$,
- *right*; when the mode equal to $b_{\max}$, and
- *center*; when the mode is at the midpoint of the range between $b_{\min}$ and $b_{\max}$ and the distribution is symmetric.

Classically, a triangular distribution is continuous. In my model, however, resource breadth distributions are discrete. For this reason, I use discrete versions of triangular distributions developed in [42]. In a left triangular distribution, most species are specialists (use a small number of resources), while a small number are generalists (use a large number of resources). Figure 2.5–A gives an example of a left triangular resource breadth distribution, where there are $\frac{S}{21}$ species that use 6 resources and $\frac{6S}{21}$ species that use one resource. Conversely, in a right triangular distribution, most species are generalists, while a small number are specialists. Figure 2.5–B gives an example of a right triangular resource breadth distribution, where there are $\frac{6S}{21}$ species that use 6 resources, but only $\frac{S}{21}$ species that use one resource. In a center triangular distribution, most species use an intermediate number of resources, while a small number of species are generalists, and a small number of species are specialists. Figure 2.5–C gives an example of a center triangular distribution, where $\frac{11S}{21}$ species use 3 resources, while $\frac{S}{21}$ species use 1 or 5 resources and $\frac{4S}{21}$ species use 2 or 4 resources. Ideally, the number of species using each different number of resources (e.g., $\frac{S}{21}$) would be an integer in all cases; however, this is not always possible. Fortunately, non-integer values are less problematic for larger values of S and R, which is the case for most of our models.

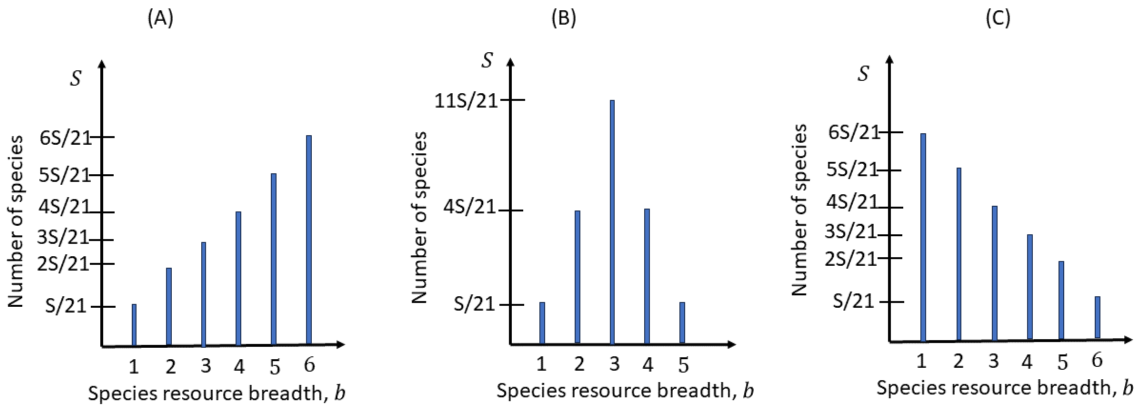

Figure 2.5: Triangular distributions of the resource breadth. A: Left triangular distribution over $\{1, \ldots, 6\}$; B: Center triangular distribution over $\{1, \ldots, 5\}$; and C: Right triangular distribution over $\{1, \ldots, 6\}$.

From the analysis developed in Section 2.1.1, the functional redundancies of local and nonlocal resources, given a general distribution with pmf φ_b, are

$$\begin{aligned}
\Omega_p &= \sum_{b=b_{\min}}^{b_{\max}} \varphi_b S \sum_{k=\max(1,b+r-R)}^{\min(r,b)} \frac{k}{r} \cdot \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} = \sum_{b=b_{\min}}^{b_{\max}} \varphi_b \frac{Sb}{R}, \\
\Omega_a &= \sum_{b=b_{\min}}^{b_{\max}} \varphi_b S \sum_{k=\max(1,b+r-R)}^{\min(r,b-1)} \frac{b-k}{R-r} \cdot \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} \\
&\approx \sum_{b=b_{\min}}^{b_{\max}} \varphi_b \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \cdot \frac{bS}{R},
\end{aligned} \tag{2.19}$$

where $b_{\max} \leq R$ is the maximum resource breadth used by species in the community, and $b_{\min} \geq 1$ is the minimum resource breadth. The total functional redundancy is then the following weighted average

$$\begin{aligned}
\Omega_t = \frac{r}{R} \cdot \Omega_p + \frac{R-r}{R} \cdot \Omega_a &= \sum_{b=b_{\min}}^{b_{\max}} \varphi_b \left(\frac{r}{R} \cdot \frac{Sb}{R} + \frac{R-r}{R} S \sum_{k=\max(1,b+r-R)}^{\min(r,b-1)} \frac{b-k}{R-r} \cdot \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} \right) \\
&\approx \frac{r}{R} \cdot \frac{S}{R} \sum_{b=b_{\min}}^{b_{\max}} b\varphi_b + \frac{R-r}{R} \cdot \frac{S}{R} \sum_{b=b_{\min}}^{b_{\max}} b \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \varphi_b \\
&= \frac{S}{R} \left[\frac{r}{R} \sum_{b=b_{\min}}^{b_{\max}} b\varphi_b + \frac{R-r}{R} \sum_{b=b_{\min}}^{b_{\max}} b \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \varphi_b \right] \\
&= \frac{S}{R} \left[\sum_{b=b_{\min}}^{b_{\max}} b\varphi_b - \frac{R-r}{R} \sum_{b=b_{\min}}^{b_{\max}} b \left(1 - \frac{r}{R}\right)^{b-1} \varphi_b \right] \\
&= \frac{S}{R} \sum_{b=b_{\min}}^{b_{\max}} \left(1 - \frac{R-r}{R} \left(1 - \frac{r}{R}\right)^{b-1}\right) b\varphi_b \\
&= \frac{S}{R} \sum_{b=b_{\min}}^{b_{\max}} \left(1 - \left(1 - \frac{r}{R}\right)^{b}\right) b\varphi_b.
\end{aligned} \tag{2.20}$$

2.1.2.1 Uniform distribution

For the discrete uniform distribution with $1 \leq b_{\min} \leq b \leq b_{\max} \leq R$, the pmf is

$$\varphi_b = \frac{1}{b_{\max} - b_{\min} + 1}. \tag{2.21}$$

From the general formula in Equation (2.19), and using the pmf for a uniform distribution in Equation (2.21), the exact expression of local functional redundancy is

$$\Omega_p = \frac{S}{R} \sum_{b=b_{\min}}^{b_{\max}} b \cdot \frac{1}{b_{\max} - b_{\min} + 1} = \frac{S\left[b_{\max}(b_{\max}+1) - (b_{\min}-1)b_{\min}\right]}{2(b_{\max} - b_{\min} + 1)R}. \tag{2.22}$$

Likewise, the approximate expression of nonlocal functional redundancy is

$$\begin{aligned}
\Omega_a &= \sum_{b=b_{\min}}^{b_{\max}} \frac{1}{b_{\max} - b_{\min} + 1} S \sum_{k=\max(1,b+r-R)}^{\min(r,b-1)} \frac{b-k}{R-r} \cdot \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} \\
&\approx \frac{S}{R} \sum_{b=b_{\min}}^{b_{\max}} b \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \frac{1}{b_{\max} - b_{\min} + 1} \\
&= \frac{S}{R} \left[\frac{\left[b_{\max}(b_{\max}+1) - (b_{\min}-1)b_{\min}\right]}{2(b_{\max} - b_{\min} + 1)} - \sum_{b=b_{\min}}^{b_{\max}} b \left(1 - \frac{r}{R}\right)^{b-1} \frac{1}{b_{\max} - b_{\min} + 1} \right].
\end{aligned} \tag{2.23}$$

Finally, the total functional redundancy is given by a weighted average of Equation (2.26) and Equation (2.27):

$$\begin{aligned}
\Omega_t &= \sum_{b=b_{\min}}^{b_{\max}} \frac{1}{b_{\max} - b_{\min} + 1} \left(\frac{r}{R} \cdot \frac{Sb}{R} + \frac{R-r}{R} S \sum_{k=\max(1,b+r-R)}^{\min(r,b-1)} \frac{b-k}{R-r} \cdot \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} \right) \\
&\approx \frac{S}{R} \left[\sum_{b=b_{\min}}^{b_{\max}} b \cdot \frac{1}{b_{\max} - b_{\min} + 1} - \frac{R-r}{R} \sum_{b=b_{\min}}^{b_{\max}} \left(1 - \frac{r}{R}\right)^{b-1} \frac{1}{b_{\max} - b_{\min} + 1} \right] \\
&= \frac{S}{R} \left[\frac{\left[b_{\max}(b_{\max}+1) - (b_{\min}-1)b_{\min}\right]}{2(b_{\max} - b_{\min} + 1)} - \frac{R-r}{R} \sum_{b=b_{\min}}^{b_{\max}} b \left(1 - \frac{r}{R}\right)^{b-1} \frac{1}{b_{\max} - b_{\min} + 1} \right] \\
&= \frac{S}{R} \left[\frac{\left[b_{\max}(b_{\max}+1) - (b_{\min}-1)b_{\min}\right]}{2(b_{\max} - b_{\min} + 1)} - \sum_{b=b_{\min}}^{b_{\max}} b \left(1 - \frac{r}{R}\right)^{b} \frac{1}{b_{\max} - b_{\min} + 1} \right]
\end{aligned} \tag{2.24}$$

Figure 2.6 illustrates the exact expression and the approximation of the nonlocal functional redundancy for a uniform distribution.

2.1.2.2 Triangular distribution

In order to describe a wide range of left, center, and right triangular distributions, I will use the following parameters:

- $b_{\max}$: the maximum resource breadth of across a set of species,

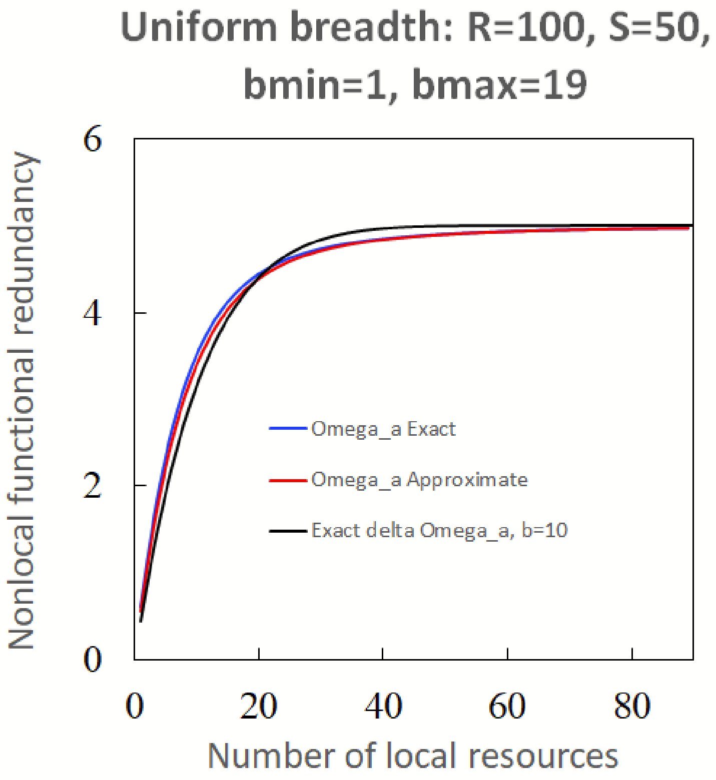

Figure 2.6: Functional redundancy of nonlocal resources, Ω_a, with $R = 100$ number of metacommunity resources, $S = 50$ number of metacommunity species, calculated using our exact expression for the delta resource breadth distribution with resource breadth $b = 10$ (black), and the uniform resource breadth distribution over $(b_{\min}, b_{\max}) = (1, 19)$ (blue), as well as our approximation for the uniform resource breadth distribution (red).

- $b_{\min}$: the minimum resource breadth across a set of species,
- c: the modal resource breadth of across a set of species.

A triangular distribution is

- *left* if $b_{\max}$ is the modal resource breadth,
- *right* if $b_{\min}$ is the modal resource breadth,
- *center* if $b_{\min} = c - h$ and $b_{\max} = c + h$, for some integer $h \geq 1$.

I will start with the expressions of functional redundancies of a discrete center triangular distribution. The pmf of a discrete center triangular distribution [41] is

$$\varphi_b = \frac{(b_{\max} - c) + 1 - |b - c|}{((b_{\max} - c) + 1)^2}. \tag{2.25}$$

By combining Equation (2.19) with the pmf for a discrete center triangular distribution in Equation (2.29), the functional redundancy of local resources is

$$\begin{aligned}
\Omega_p &= \frac{S}{R}\left[\sum_{b=b_{\min}}^{c} b \cdot \frac{(b_{\max} - c) + 1 + (b - c)}{((b_{\max} - c) + 1)^2} + \sum_{b=c}^{b_{\max}} b \cdot \frac{(b_{\max} - c) + 1 - (b - c)}{((b_{\max} - c) + 1)^2}\right] \\
&= \frac{S}{R}\left[\frac{(b_{\max} - c) + 1 - c}{((b_{\max} - c) + 1)^2} \cdot \frac{c(c+1) - b_{\min}(b_{\min} - 1)}{2} + \frac{(b_{\max} - c) + 1 + c}{((b_{\max} - c) + 1)^2} \cdot \frac{b_{\max}(b_{\max} + 1) - c(c-1)}{2}\right. \\
&\qquad \left. + \frac{c(c+1)(2c+1) - (b_{\min} - 1)b_{\min}(2b_{\min} - 1)}{6((b_{\max} - c) + 1)^2} - \frac{b_{\max}(b_{\max} + 1)(2b_{\max} + 1) - (c-1)c(2c-1)}{6((b_{\max} - c) + 1)^2}\right] \\
&= \frac{S}{R}\left[\frac{((b_{\max} - c) + 1)(2c - b_{\min}(b_{\min} - 1) + b_{\max}(b_{\max} + 1)) - c(2c^2 + b_{\min}(b_{\min} - 1) + b_{\max}(b_{\max} + 1))}{2((b_{\max} - c) + 1)^2}\right. \\
&\qquad \left. + \frac{4c^3 + 2c - (b_{\min} - 1)b_{\min}(2b_{\min} - 1) - b_{\max}(b_{\max} + 1)(2b_{\max} + 1)}{6((b_{\max} - c) + 1)^2}\right]
\end{aligned} \tag{2.26}$$

Similarly, the functional redundancy of nonlocal resources is

$$\begin{aligned}
\Omega_a &= \sum_{b=b_{\min}}^{b_{\max}} \frac{(b_{\max} - c) + 1 - |b - c|}{((b_{\max} - c) + 1)^2} S \sum_{k=\max(1,b+r-R)}^{\min(r,b-1)} \frac{b - k}{R - r} \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} \\
&\approx \frac{S}{R}\left[\sum_{b=b_{\min}}^{c} b\left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \frac{(b_{\max} - c) + 1 + (b - c)}{((b_{\max} - c) + 1)^2} + \sum_{b=c}^{b_{\max}} b\left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \frac{(b_{\max} - c) + 1 - (b - c)}{((b_{\max} - c) + 1)^2}\right] \\
&= \frac{S}{R}\left[\frac{((b_{\max} - c) + 1)(2c - b_{\min}(b_{\min} - 1) + b_{\max}(b_{\max} + 1)) - c(2c^2 + b_{\min}(b_{\min} - 1) + b_{\max}(b_{\max} + 1))}{2((b_{\max} - c) + 1)^2}\right. \\
&\qquad + \frac{4c^3 + 2c - (b_{\min} - 1)b_{\min}(2b_{\min} - 1) - b_{\max}(b_{\max} + 1)(2b_{\max} + 1)}{6((b_{\max} - c) + 1)^2} \\
&\qquad \left. - \sum_{b=b_{\min}}^{c} b\left(1 - \frac{r}{R}\right)^{b-1} \frac{(b_{\max} - c) + 1 + (b - c)}{((b_{\max} - c) + 1)^2} - \sum_{b=c}^{b_{\max}} b\left(1 - \frac{r}{R}\right)^{b-1} \frac{(b_{\max} - c) + 1 - (b - c)}{((b_{\max} - c) + 1)^2}\right].
\end{aligned} \tag{2.27}$$

Finally, the total functional redundancy is given by a weighted average of Equation (2.26) and Equation (2.27):

$$\begin{aligned}
\Omega_t &= \frac{r}{R}\cdot\frac{S}{R}\sum_{b=b_{\min}}^{b_{\max}} b\cdot\frac{(b_{\max}-c)+1-|b-c|}{((b_{\max}-c)+1)^2} + \frac{R-r}{R}\sum_{b=b_{\min}}^{b_{\max}}\frac{(b_{\max}-c)+1-|b-c|}{((b_{\max}-c)+1)^2}\, S\sum_{k=\max(1,b+r-R)}^{\min(r,b-1)}\frac{b-k}{R-r}\frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}\\
&\approx \frac{S}{R}\left[\sum_{b=b_{\min}}^{c} b\cdot\frac{(b_{\max}-c)+1+(b-c)}{((b_{\max}-c)+1)^2} + \sum_{b=c}^{b_{\max}} b\cdot\frac{(b_{\max}-c)+1-(b-c)}{((b_{\max}-c)+1)^2}\right.\\
&\qquad\left. -\left(\sum_{b=b_{\min}}^{c} b\left(1-\frac{r}{R}\right)^b\frac{(b_{\max}-c)+1+(b-c)}{((b_{\max}-c)+1)^2} + \sum_{b=c}^{b_{\max}} b\left(1-\frac{r}{R}\right)^b\frac{(b_{\max}-c)+1-(b-c)}{((b_{\max}-c)+1)^2}\right)\right]\\
&= \frac{S}{R}\left[\frac{((b_{\max}-c)+1)(2c-b_{\min}(b_{\min}-1)+b_{\max}(b_{\max}+1))-c(2c^2+b_{\min}(b_{\min}-1)+b_{\max}(b_{\max}+1))}{2((b_{\max}-c)+1)^2}\right.\\
&\qquad+\frac{4c^3+2c-(b_{\min}-1)b_{\min}(2b_{\min}-1)-b_{\max}(b_{\max}+1)(2b_{\max}+1)}{6((b_{\max}-c)+1)^2}\\
&\qquad\left. -\left(\sum_{b=b_{\min}}^{c} b\left(1-\frac{r}{R}\right)^b\frac{(b_{\max}-c)+1+(b-c)}{((b_{\max}-c)+1)^2} + \sum_{b=c}^{b_{\max}} b\left(1-\frac{r}{R}\right)^b\frac{(b_{\max}-c)+1-(b-c)}{((b_{\max}-c)+1)^2}\right)\right].
\end{aligned}\tag{2.28}$$

Figure 2.7 illustrates the exact expression and the approximation of the nonlocal functional redundancy for a center triangular distribution.

The pmf of a discrete left triangular distribution [41] is

$$\varphi_b = \frac{(b_{\max}-b_{\min})+1+(b-b_{\max})}{2((b_{\max}-b_{\min})+1)^2}. \tag{2.29}$$

Similar to what I did for the center triangular distribution, the functional redundancies of a discrete left triangular distribution are

$$\begin{aligned}
\Omega_p &= \frac{S}{R}\left[\frac{((b_{\max}-b_{\min})+1-b_{\max})(b_{\max}(b_{\max}+1)-b_{\min}(b_{\min}-1))}{2(2((b_{\max}-b_{\min})+1)^2)}\right.\\
&\qquad\left.+\frac{b_{\max}(b_{\max}+1)(2b_{\max}+1)-(b_{\min}-1)b_{\min}(2b_{\min}-1)}{2(6((b_{\max}-b_{\min})+1)^2)}\right]\\
\Omega_a &= \sum_{b=b_{\min}}^{b_{\max}}\frac{(b_{\max}-b_{\min})+1+(b-b_{\max})}{2((b_{\max}-b_{\min})+1)^2}\, S\sum_{k=\max(1,b+r-R)}^{\min(r,b-1)}\frac{b-k}{R-r}\frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}\\
&\approx \frac{S}{R}\left[\frac{((b_{\max}-b_{\min})+1-b_{\max})(b_{\max}(b_{\max}+1)-b_{\min}(b_{\min}-1))}{2(2((b_{\max}-b_{\min})+1)^2)}\right.\\
&\qquad+\frac{b_{\max}(b_{\max}+1)(2b_{\max}+1)-(b_{\min}-1)b_{\min}(2b_{\min}-1)}{2(6((b_{\max}-b_{\min})+1)^2)}\\
&\qquad\left.-\sum_{b=b_{\min}}^{b_{\max}} b\left(1-\frac{r}{R}\right)^{b-1}\frac{(b_{\max}-b_{\min})+1+(b-b_{\max})}{2((b_{\max}-b_{\min})+1)^2}\right]
\end{aligned}\tag{2.30}$$

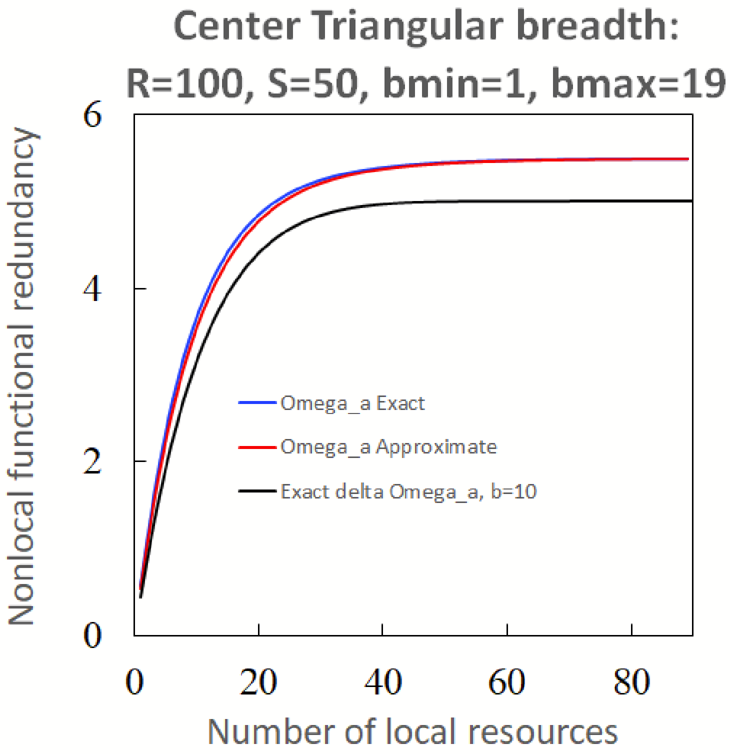

Figure 2.7: Functional redundancy of nonlocal resources, Ω_a, with $R = 100$ number of metacommunity resources, $S = 50$ number of metacommunity species, calculated using our exact expression for the delta resource breadth distribution with resource breadth $b = 10$ (black), and the center triangular resource breadth distribution over $(b_{\min}, c, b_{\max}) = (1, 10, 19)$ (blue), as well as our approximation for the center triangular resource breadth distribution (red).

$$
\begin{aligned}
\Omega_t = {} & \frac{r}{R} \cdot \frac{S}{R} \left[\frac{((b_{\max} - b_{\min}) + 1 - b_{\max})(b_{\max}(b_{\max} + 1) - b_{\min}(b_{\min} - 1))}{2(2((b_{\max} - b_{\min}) + 1)^2)} \right. \\
& \left. + \frac{b_{\max}(b_{\max} + 1)(2b_{\max} + 1) - (b_{\min} - 1)b_{\min}(2b_{\min} - 1)}{2(6((b_{\max} - b_{\min}) + 1)^2)} \right] \\
& + \frac{R - r}{R} \sum_{b=b_{\min}}^{b_{\max}} \frac{(b_{\max} - b_{\min}) + 1 + (b - b_{\max})}{2((b_{\max} - b_{\min}) + 1)^2} S \sum_{k=\max(1,b+r-R)}^{\min(r,b-1)} \frac{b-k}{R-r} \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} \\
\approx {} & \frac{S}{R} \left[\frac{((b_{\max} - b_{\min}) + 1 - b_{\max})(b_{\max}(b_{\max} + 1) - b_{\min}(b_{\min} - 1))}{2(2((b_{\max} - b_{\min}) + 1)^2)} \right. \\
& + \frac{b_{\max}(b_{\max} + 1)(2b_{\max} + 1) - (b_{\min} - 1)b_{\min}(2b_{\min} - 1)}{2(6((b_{\max} - b_{\min}) + 1)^2)} \\
& \left. - \sum_{b=b_{\min}}^{b_{\max}} b \left(1 - \frac{r}{R}\right)^b \frac{(b_{\max} - b_{\min}) + 1 + (b - b_{\max})}{2((b_{\max} - b_{\min}) + 1)^2} \right].
\end{aligned}
$$

Figure 2.8 illustrates the exact expression and the approximation of the nonlocal functional redundancy for a right triangular distribution.

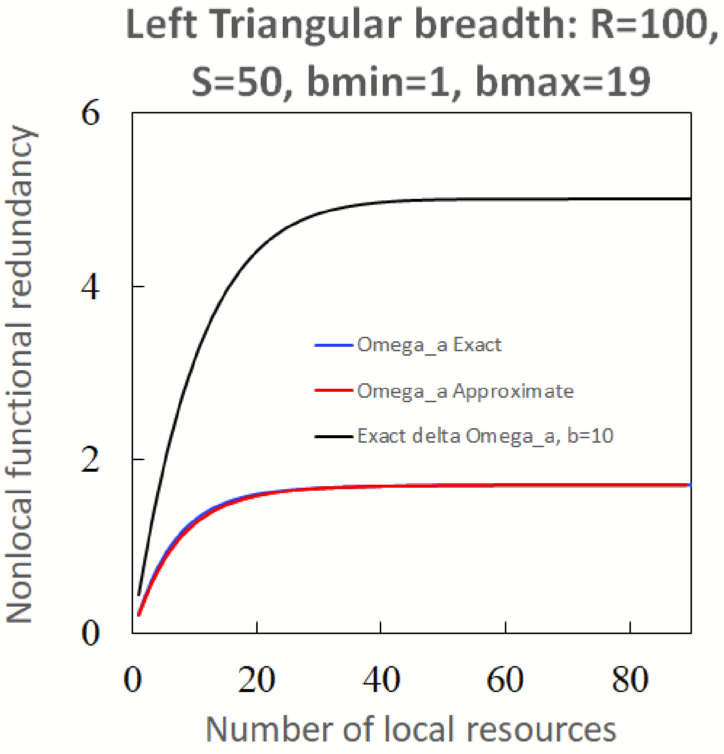

Figure 2.8: Functional redundancy of nonlocal resources, Ω_a, with $R = 100$ number of metacommunity resources, $S = 50$ number of metacommunity species, calculated using our exact expression for the delta resource breadth distribution with resource breadth $b = 10$ (black), and the left triangular resource breadth distribution over $(b_{\text{min}}, b_{\text{max}}) = (1, 19)$ (blue), as well as our approximation for the left triangular resource breadth distribution (red).

The pmf of a discrete right triangular distribution [41] is

$$\varphi_b = \frac{(b_{\text{max}} - b_{\text{min}}) + 1 - (b - b_{\text{min}})}{2((b_{\text{max}} - b_{\text{min}}) + 1)^2}. \tag{2.31}$$

Similar to Equation (2.30), the functional redundancies of a discrete right triangular distribution are

$$
\begin{aligned}
\Omega_p &= \frac{S}{R}\left[\frac{((b_{\max}-b_{\min})+1-b_{\min})(b_{\max}(b_{\max}+1)-b_{\min}(b_{\min}-1))}{2(2((b_{\max}-b_{\min})+1)^2)}\right.\\
&\qquad\left.-\frac{b_{\max}(b_{\max}+1)(2b_{\max}+1)-(b_{\min}-1)b_{\min}(2b_{\min}-1)}{2(6((b_{\max}-b_{\min})+1)^2)}\right]\\
\Omega_a &= \sum_{b=b_{\min}}^{b_{\max}}\frac{(b_{\max}-b_{\min})+1-(b-b_{\min})}{2((b_{\max}-b_{\min})+1)^2}S\sum_{k=\max(1,b+r-R)}^{\min(r,b-1)}\frac{b-k}{R-r}\frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}\\
&\approx \frac{S}{R}\left[\frac{((b_{\max}-b_{\min})+1-b_{\min})(b_{\max}(b_{\max}+1)-b_{\min}(b_{\min}-1))}{2(2((b_{\max}-b_{\min})+1)^2)}\right.\\
&\qquad-\frac{b_{\max}(b_{\max}+1)(2b_{\max}+1)-(b_{\min}-1)b_{\min}(2b_{\min}-1)}{2(6((b_{\max}-b_{\min})+1)^2)}\\
&\qquad\left.-\sum_{b=b_{\min}}^{b_{\max}}b\left(1-\frac{r}{R}\right)^{b-1}\frac{(b_{\max}-b_{\min})+1+(b-b_{\min})}{2((b_{\max}-b_{\min})+1)^2}\right]\\
\Omega_t &= \frac{r}{R}\cdot\frac{S}{R}\left[\frac{((b_{\max}-b_{\min})+1-b_{\min})(b_{\max}(b_{\max}+1)-b_{\min}(b_{\min}-1))}{2(2((b_{\max}-b_{\min})+1)^2)}\right.\\
&\qquad\left.-\frac{b_{\max}(b_{\max}+1)(2b_{\max}+1)-(b_{\min}-1)b_{\min}(2b_{\min}-1)}{2(6((b_{\max}-b_{\min})+1)^2)}\right]\\
&\quad+\frac{R-r}{R}\sum_{b=b_{\min}}^{b_{\max}}\frac{(b_{\max}-b_{\min})+1-(b-b_{\min})}{2((b_{\max}-b_{\min})+1)^2}S\sum_{k=\max(1,b+r-R)}^{\min(r,b-1)}\frac{b-k}{R-r}\frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}\\
&\approx \frac{S}{R}\left[\frac{((b_{\max}-b_{\min})+1-b_{\min})(b_{\max}(b_{\max}+1)-b_{\min}(b_{\min}-1))}{2(2((b_{\max}-b_{\min})+1)^2)}\right.\\
&\qquad-\frac{b_{\max}(b_{\max}+1)(2b_{\max}+1)-(b_{\min}-1)b_{\min}(2b_{\min}-1)}{2(6((b_{\max}-b_{\min})+1)^2)}\\
&\qquad\left.-\sum_{b=b_{\min}}^{b_{\max}}b\left(1-\frac{r}{R}\right)^{b}\frac{(b_{\max}-b_{\min})+1+(b-b_{\min})}{2((b_{\max}-b_{\min})+1)^2}\right].
\end{aligned}
\tag{2.32}
$$

Figure 2.9 illustrates the exact expression and the approximation of the nonlocal functional redundancy for a right triangular distribution.

The analytical approximations of the functional redundancy of nonlocal resources and total resources, Ω_a and Ω_t, of other distributions is not straightforward since it contains $\sum_{b=b_{\min}}^{b_{\max}} b\left(1-\frac{r}{R}\right)^b$, which won't be covered in this thesis.

2.2 Unequal resource use

Thus far, I have assumed that all resources are equally likely to be used. In general, this is not biologically realistic. For example, in a most microbial communities, a simple sugar like glucose

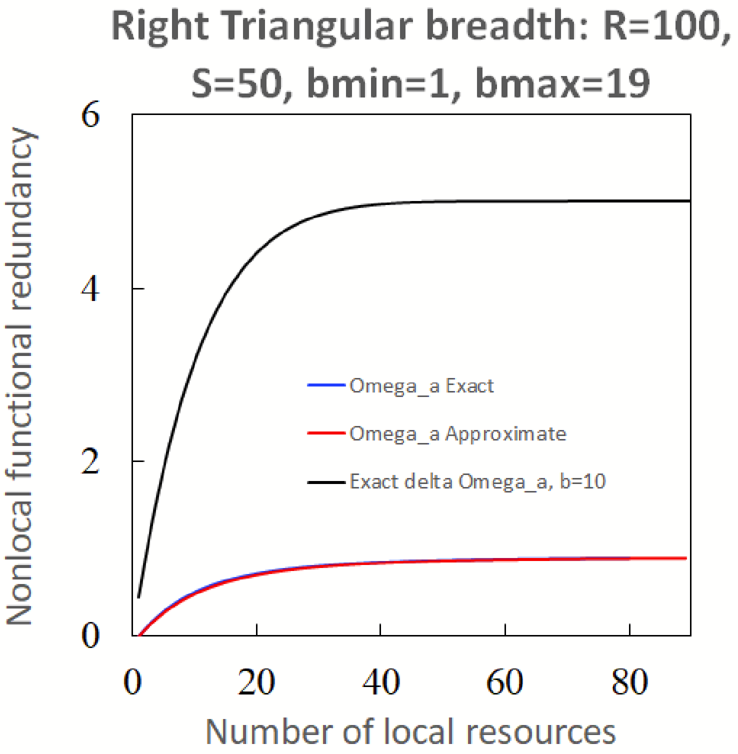

Figure 2.9: Functional redundancy of nonlocal resources, Ω_a, with $R = 100$ number of metacommunity resources, $S = 50$ number of metacommunity species, calculated using our exact expression for the delta resource breadth distribution with resource breadth $b = 10$ (black), and the right triangular resource breadth distribution over $(b_{\text{min}}, b_{\text{max}}) = (1, 19)$ (blue), as well as our approximation for the right triangular resource breadth distribution (red).

is far more likely to be used than a complex sugar like glycogen. Indeed, in many systems, one or two resources are used by most members of a community, while the vast majority of resources are only used by one or a handful of specialists. In this section, I will extend my EF model to include unequal resource use. In particular, will consider the special case where resources fall into one of two classes:

- *high-use resources* (HR): those used by a majority of species in the metacommunity
- *low-use resources* (LR): those used by only a few species.

I will model the functional redundancy of resources from each class separately. My goal is to determine whether relationships between functional redundancy and environmental complexity hold for cases where resource use is unequal. As in Section 2.1, I will continue to assume that resources are substitutable, meaning that a species can survive as long as it can find any of its b resources in the local community, regardless of whether they are high-use or low-use resources.

2.2.1 Definition of high- and low-use resources

For R_h, R_ℓ (high- and low-use resources in the metacommunity), r_h and r_ℓ (high- and low-use resources in the local community), the following equalities must hold:

$$0 \leq r_h \leq R_h, \qquad 0 \leq r_\ell \leq R_\ell, \qquad \text{and} \qquad 0 \leq r = r_h + r_\ell \leq R_h + R_\ell = R.$$

Similar to the scenario for equal resource use in Section 2.1, the requirement for a species to persist in the local community is the presence of at least one of its resources. Figure 2.10 shows an example that illustrates this criterion when there are low- and high-use resources present.

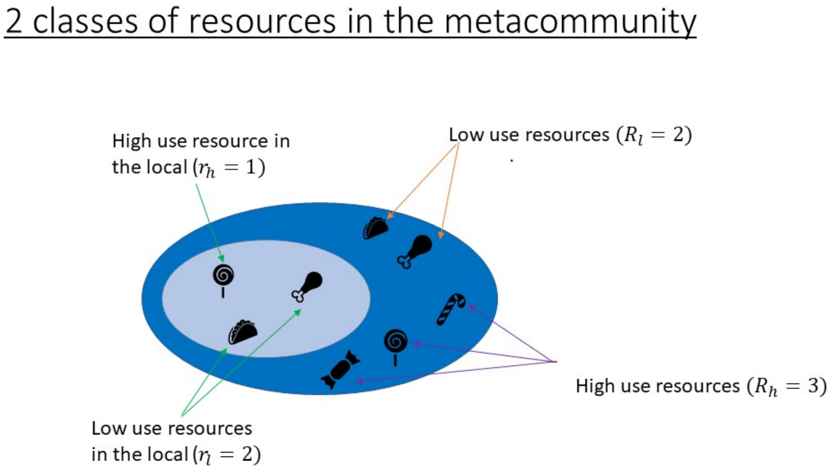

Figure 2.10: Example of two classes of resources.

To quantify the difference between the probability that a high-use resource will be used, q_h, and the probability that a low-use resource will be used, q_ℓ, I define the following multiplier:

$$\sigma := \frac{q_h}{q_\ell} \in \mathbb{Q}^+. \tag{2.33}$$

Thus, for example, if $\sigma = 3$, then a species is three times as likely to use any given high-use resource than it is to use any given low-use resource. For $\sigma = 1$, all resources are equally likely to be used, which was the assumption throughout Section 2.1. A simple example of unequal resource use is shown in Figure 2.11, for $\sigma = 2$. Here, there are $R_\ell = 6$ low-use resources, each of which is used with probability $q_\ell = 0.1$. By contrast, there are $R_h = 2$ high-use resources each of which is twice as likely to be used as the low-use resources, and thus each of which is used with probability $q_h = \sigma q_\ell = 2q_\ell = 0.2$.

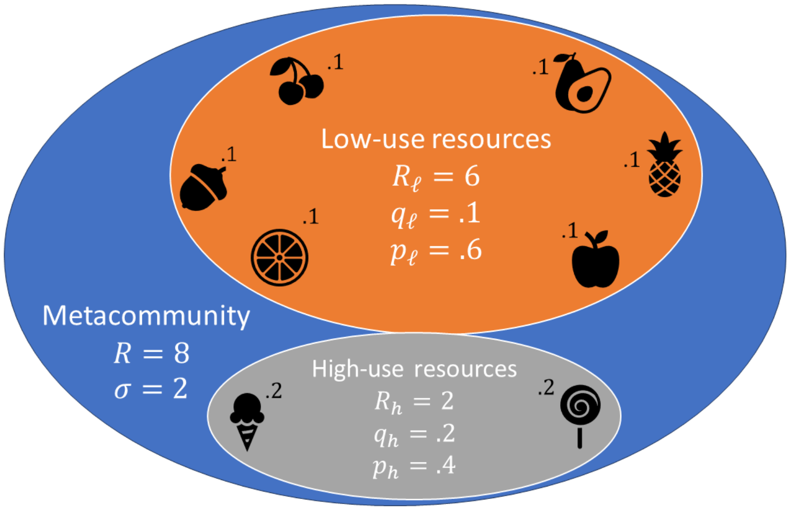

Figure 2.11: Example of a distribution of resource use with two classes of resources and $\sigma = 2$.

In addition to q_h and q_ℓ, I also define the quantities p_h and p_ℓ as follows:

$$p_h = \sum_{\substack{\text{high-use}\\\text{resources}}} \Pr\big(\text{randomly chosen species will use it}\big) = q_h R_h$$

$$p_\ell = \sum_{\substack{\text{low-use}\\\text{resources}}} \Pr\big(\text{randomly chosen species will use it}\big) = q_\ell R_\ell.$$

p_h and p_ℓ can be interpreted as the probability that any randomly selected resource is high-use and low-use respectively. In the example in Figure 2.11, for instance, $p_h = 0.2 \cdot R_h = 0.4$, and $p_\ell = 0.1 \cdot R_\ell = 0.6$. Notice that, because any given resource must be either high-use or low-use, $p_h + p_\ell = 1$. Further, because $q_h = \sigma q_\ell$, it follows that:

$$R_h q_h + R_\ell q_\ell = R_h(\sigma q_\ell) + R_\ell q_\ell = 1,$$

Solving for the individual probabilities q_ℓ and q_h in terms of R_ℓ and R_h gives:

$$q_\ell = \frac{1}{\sigma R_h + R_\ell}, \qquad \text{and} \qquad q_h = \frac{\sigma}{\sigma R_h + R_\ell}. \tag{2.34}$$

Using the definition of the multiplier $\sigma = q_h/q_\ell$ from Equation (2.33), with the definitions of $p_h = R_h q_h$ and $p_\ell = R_\ell q_\ell$ above, I derive

$$\frac{p_h}{p_\ell} = \frac{R_h q_h}{R_\ell q_\ell} = \frac{R_h}{R_\ell} \cdot \frac{q_h}{q_\ell} = \sigma \cdot \frac{R_h}{R_\ell}. \tag{2.35}$$

This has a simple interpretation: the ratio $\frac{p_h}{p_\ell}$ of the probability of a given resource being high-use versus low-use is equal to the multiplier, σ, times the ratio of high-use to low-use resources in the metacommunity. From these two equations, I can then obtain explicit formulas for p_h and p_ℓ:

$$p_h = \frac{\sigma R_h}{\sigma R_h + R_\ell} = R_h q_h, \qquad \text{and} \qquad p_\ell = \frac{R_h}{\sigma R_h + R_\ell} = R_\ell q_\ell. \tag{2.36}$$

Returning to the example in Figure 2.11, I can demonstrate the newly introduced terms by fixing the total number of metacommunity resources ($R = 8$), as well as the number of metacommunity resources that are high-use, $R_h = 2$, and low-use $R_\ell = 6$ respectively. I can then explore the effects of σ on q_h, q_ℓ, p_h and p_ℓ.

First, consider a scenarios with $\sigma = 1$, which means that all resources are equally likely to be used. Since $q_h = q_\ell$ and $2q_h + 6q_\ell = 1$, it follows that $q_h = q_\ell = \frac{1}{8}$. Thus, the probability of a given resource being high-use is $p_h = \frac{2}{8}$, and the probability of a given resource being low-use is $p_\ell = \frac{6}{8}$; see Figure 2.12. In this case, however, it does not matter, since high-use and low-use resources are used with the same probability. Thus they are high-use and low-use in name only. However, extending the same definitions to scenarios with $\sigma > 1$ allows me to define a fixed number of high-use and low-use resources set by the probabilities that a resource is high-use versus low-use:

$$p_h = \frac{2\sigma}{2\sigma + 6}, \qquad \text{and} \qquad p_\ell = \frac{6}{2\sigma + 6}.$$

This then also implies the probability that a species will use any given high-use resource relative to any given low-use resource.

$$q_h = \frac{\sigma}{2\sigma + 6}, \qquad \text{and} \qquad q_\ell = \frac{1}{2\sigma + 6}.$$

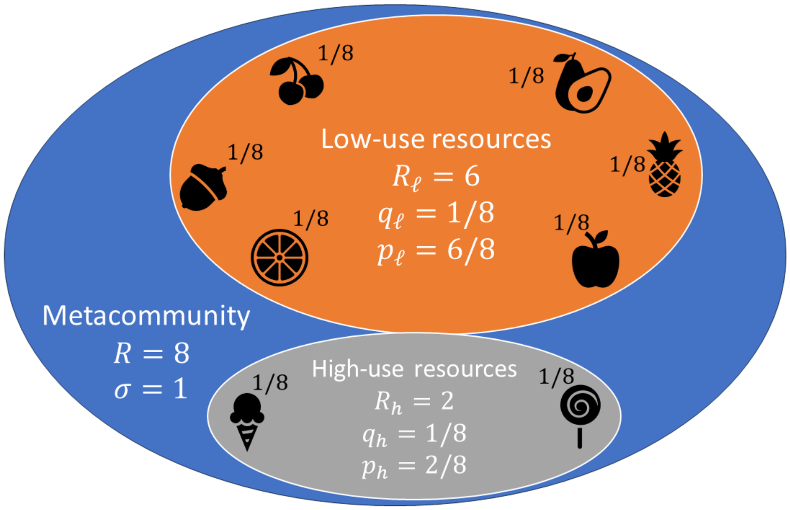

Figure 2.12: Example of a an equally distributed ($\sigma = 1$) of resource use with two classes of resources.

2.2.2 Species richness of the local community: s

In what follows, I derive expressions for species richness, s, in the local community, in the more general setting of unequal resource use. Recall that species richness is defined as the expected number of species that can persist in the local community. For the equal resource use models, I assumed that resources were allocated uniformly and at random to each species. In other words, all b-element subsets of resources were equally likely to be used by a particular species. For the unequal resource use models, I similarly assume that all high-use resources are used with equal probability and all low-use resources are used with equal probability. However, high-use and low-use resources are not used with equal probability.

Because my goal is to explore functional redundancy of high- and low-use resources separately, it is helpful to partition species richness into the species that use at least one local high-use resource, s_h, and the species that use at least one local low-use resource, s_ℓ. I now derive expressions for s_h and s_ℓ based on the resource breadth b of each species, assuming a delta distribution of resource breadths. Importantly, species richness will also depend on the number of high-use resources,

r_h, and the number of low-use resources, r_ℓ, in the local community. r_h can be thought of as the resource complexity of high-use resources, while r_ℓ can be thought of as the resource complexity of low-use resources. The overall environmental complexity is thus the sum of these two numbers, $r_h + r_\ell$.

Choosing b resources means choosing b_h high-use resources and b_ℓ low-use resources where $b_h + b_\ell = b$. Since a high-use resource is σ times likelier to be used by any given species than a low-use resource, the combination of b resources involving b_h high-use resources is weighted by σ^{b_h}. Let $C(b)$ denote a weighted total of the number of combinations by which it is possible to pick b resources from the set of R_h and R_ℓ resources. $C(b)$ can be defined by the following formula, which is a weighted sum of the binomial coefficients of $2^{R_h+R_\ell}$:

$$C(b) = \sum_{k=0}^{b} \overbrace{\sigma^k \binom{R_h}{k}}^{\substack{\#\text{ ways to choose} \\ k \text{ HR from } R_h}} \overbrace{\binom{R_\ell}{b-k}}^{\substack{\#\text{ ways to choose} \\ b-k \text{ LR from } R_\ell}} .$$

Using $C(b)$ it is possible to derive an expression for the probability of a given species using a particular high-use resource, ρ_{h_j}. Since this is one of the $b = b_h + b_\ell$ resources used by the focal species, the focal species should be able to use an additional $b_h - 1$ other high-use resources and b_ℓ low-use resources. Further, because each possible combination of resources used by the focal species should be weighted by σ^{b_h}, the probability of using ρ_{h_j} is

$$q_h(b) = \frac{\sum_{k=1}^{b} \sigma^{b-k+1} \binom{R_h-1}{b-k} \binom{R_\ell}{k-1}}{C(b)}.$$

By symmetry, the probability that the focal species uses any particular low-use resource out of its b resources is

$$q_\ell(b) = \frac{\sum_{k=1}^{b} \sigma^{b-k} \binom{R_h}{b-k} \binom{R_\ell-1}{k-1}}{C(b)}.$$

Therefore, the ratio of the probability of a given species using a particular high-use resource relative to a particular low-use resource is

$$\frac{q_h(b)}{q_\ell(b)} = \frac{\sum\limits_{k=1}^{b} \sigma^{b-k+1}\binom{R_h-1}{b-k}\binom{R_\ell}{k-1}}{\sum\limits_{k=1}^{b} \sigma^{b-k}\binom{R_h}{b-k}\binom{R_\ell-1}{k-1}} = \left(\frac{R_\ell}{R_h}\sum_{k=1}^{b}\frac{R_h-b+k}{R_\ell-k+1}\right)\sigma = \frac{p_h}{p_\ell}\sum_{k=1}^{b}\frac{R_h-b+k}{R_\ell-k+1}. \tag{2.37}$$

These four functional redundancies will be analyzed one by one, over the final four sections of the chapter.

2.2.3 Functional redundancy of local high-use resources: Ω_p^h

2.2.3.1 Case studies for $b = 1$ and $b = 2$

Resource breadth $b = 1$

Similar to my derivation of equal resource use models, I will again begin with the simplest scenario where every species uses exactly $b = 1$ resource. First, I will derive the probability that a randomly selected species can find its resource from the r present in the local community. Let ρ_{h_j} be a focal high-use resource. The probability of ρ_{h_j} being in the local community is $\frac{\binom{r_h}{1}}{\binom{R_h}{1}} = \frac{r_h}{R_h}$. For any given species, i, the resource used by species i is either a high-use resource or a low-use resource. The probability of the resource used by species i being a high-use resource is $p_h = \frac{\binom{R_h}{1}\sigma}{\binom{R_h}{1}\sigma+\binom{R_\ell}{1}} = \frac{R_h\sigma}{R_h\sigma+R_\ell}$. Therefore, the probability of species i using a high-use resource from the local community is

$$\frac{r_h}{R_h} \cdot \frac{\binom{R_h}{1}\sigma}{\binom{R_h}{1}\sigma + \binom{R_\ell}{1}} = \frac{r_h\sigma}{R_h\sigma + R_\ell}.$$

The expected number of species that can use a high-use resource in the local community (high-use local species richness), s_h, is

$$s_h = \frac{r_h}{R_h} \cdot \frac{\binom{R_h}{1}\sigma}{\binom{R_h}{1}\sigma + \binom{R_\ell}{1}} S = \frac{r_h\sigma}{R_h\sigma + R_\ell} S. \tag{2.38}$$

Since there are r_h high-use resources present in the local community, and each species uses only one resource, the functional redundancy of each high-use resource in the local community is

$$\Omega_p^h = \frac{1}{r_h} \cdot \frac{r_h\sigma}{R_h\sigma + R_\ell} S = \frac{\sigma}{R_h\sigma + R_\ell} S. \tag{2.39}$$

Because $b = 1$, no local species uses a high-use resource from the metacommunity that is not present in the local community. Therefore, the functional redundancy of nonlocal high-use resources is $\Omega_a^h = 0$.

Thus, I find that the high-use local species richness, s_h does not depend on the high-use resource complexity, r_h, of the local community. Similarly, the functional redundancy of local and nonlocal high-use resources, Ω_p^h and Ω_a^h, are also independent of the high-use resource complexity of the local community for $b = 1$.

Resource breadth $b = 2$

Next, I consider the scenario where each species uses $b = 2$ resources. Again, let ρ_{h_j} be a focal high-use resource in the local community. If a given species i uses ρ_{h_j}, then there are two general possibilities for the combination of resources that species i can use:

1. ρ_{h_j} is the only high-use resource that species i can use in the local community, or
2. species i uses ρ_{h_j} as well as another high-use resource from the local community.

When species i uses a single high-use local resource, it can persist in the local community, regardless of the identity of the second resource that it can use. That is, the second resource can be a nonlocal high-use resource, or a local or nonlocal low-use resource. Therefore, the probability of a species using a single high-use local resource is

$$\frac{\binom{r_h}{1}\binom{R_h - r_h}{1}\sigma^2 + \binom{r_h}{1}\binom{R_\ell}{1}\sigma}{C(2)} = \frac{\sigma r_h(\sigma(R_h - r_h) + R_\ell)}{C(2)}, \tag{2.40}$$

where $C(2) = \binom{R_h}{2}\sigma^2 + \binom{R_h}{1}\binom{R_\ell}{1}\sigma + \binom{R_\ell}{2}$.

Alternately, when species i uses two high-use local resources, those are the only two resources that it can use. Therefore, the probability of a species using two high-use local resources is

$$\frac{\binom{r_h}{2}\sigma^2}{C(2)}. \tag{2.41}$$

Combining Equations (2.40) and Equation (2.41), the expected number of species that live in the local community by using at least one local high-use resource is

$$s_h = \frac{S\sigma\left(\binom{r_h}{2}\sigma + r_h((R_h - r_h)\sigma + R_\ell)\right)}{C(2)}. \tag{2.42}$$

The functional redundancy of each high-use resource in the local community is a weighted average of the functional redundancy derived from species that use only one high-use resource from the local community and species that use two high-use resources from the local community. Hence, the functional redundancy of each high-use resource in the local community is

$$\Omega_p^h = S\left(\frac{1}{r_h}\cdot\frac{\sigma r_h(\sigma(R_h - r_h) + R_\ell)}{C(2)} + \frac{2}{r_h}\cdot\frac{\binom{r_h}{2}\sigma^2}{C(2)}\right) = \frac{S(R_h\sigma^2 + R_\ell\sigma - 1)}{C(2)}, \tag{2.43}$$

where $\frac{1}{r_h}$ is the probability that any given local high-use resource is used by a species that only uses one local high-use resource, and $\frac{2}{r_h}$ is the probability that my given local high-use resource is used by a species that uses two local high-use resources.

2.2.3.2 Exact expression for functional redundancy of local high-use resources: Ω_p^h

To derive a general formula of the functional redundancy of local high-use resources, I again let ρ_{h_j} be a focal high-use resource from the local community and i be a species that uses ρ_{h_j}. Of the b resources that species i uses, at least one and a maximum of $\min(b, r_h)$ must be local and high-use. This results in a range of possible scenarios:

1. ρ_{h_j} is the only local high-use resource used by species i. That is, the other $b-1$ resources are either nonlocal high-use resources, or local or nonlocal low-use resources.
2. species i uses ρ_{h_j} along with one additional local high-use resource; the remaining $b-2$ resources are either nonlocal high-use resources, or local or nonlocal low-use resources.

$$\vdots$$

k. species i uses ρ_{h_j} along with $k-1$ additional local high-use resources; the remaining $b-k$ resources are either nonlocal high-use resources, or local or nonlocal low-use resources.

$$\vdots$$

b. all b resources used by species i are local high-use resources.

The probability of any given species using a combination of resources consistent with the $(k)^{th}$

scenario—that is, where the species uses a focal local high-use resource, ρ_{h_j}, along with $k-1$ additional local high-use resources—is

$$\frac{\binom{r_h}{k}\sum\limits_{j=0}^{b-k}\binom{R_h-r_h}{j}\binom{R_\ell}{b-k-j}\sigma^{j+k}}{C(b)}.$$

Hence, the number of species that live in the local community and use at least one high-use resource is

$$s_h = S \cdot \frac{\sum\limits_{k=\max(1,b+r_h-R_h)}^{\min(b,r_h)} \overbrace{\binom{r_h}{k}\sigma^k}^{\substack{\text{\# ways to choose}\\ k \text{ HR from } r_h \text{ in}\\ \text{local comm.}}} \sum\limits_{j=0}^{b-k} \overbrace{\binom{R_h-r_h}{j}\sigma^j}^{\substack{\text{\# ways to choose}\\ j \text{ HR from } R_h-r_h\\ \text{in nonlocal comm.}}} \overbrace{\binom{R_\ell}{b-k-j}}^{\substack{\text{\# ways to choose}\\ b-k-j \text{ LR from}\\ R_\ell \text{ in metacomm.}}}}{C(b)}, \tag{2.44}$$

where $C(b) = \sum\limits_{k=0}^{b}\sigma^k\binom{R_h}{k}\binom{R_\ell}{b-k}$.

As was the case for $b = 2$, we can then express the functional redundancy of high-use local resources as a weighted average of the functional redundancies derived from species that use anywhere from one local high-use resource to $\min(b, r_h)$ local high use resources:

$$\Omega_p^h = S \sum_{k=\max(1,b+r_h-R_h)}^{\min(b,r_h)} \frac{k}{r_h} \cdot \frac{\binom{r_h}{k}\sigma^k \sum\limits_{j=0}^{b-k}\binom{R_h-r_h}{j}\binom{R_\ell}{b-k-j}\sigma^j}{C(b)}. \tag{2.45}$$

2.2.4 Functional redundancy of local low-use resources: Ω_p^ℓ

2.2.4.1 Case studies for $b = 1$ and $b = 2$

Resource breadth $b = 1$

As in Section 2.2.3.1, I will begin with the simple scenario where each species uses $b = 1$ resource. Let ρ_{ℓ_j} be a focal low-use resource. The probability of ρ_{ℓ_j} being in the local community is $\frac{\binom{r_\ell}{1}}{\binom{R_\ell}{1}} = \frac{r_\ell}{R_\ell}$. For any given species, i, the resource used by species i is either a high-use resource or a low-use resource. The probability of the resource used by species i being a low-use resource is $p_\ell = \frac{\binom{R_\ell}{1}}{\binom{R_h}{1}\sigma+\binom{R_\ell}{1}} = \frac{R_\ell}{R_h\sigma+R_\ell}$. Therefore, the probability of species i using a low-use resource from the local community is

$$\frac{r_\ell}{R_\ell} \cdot \frac{\binom{R_\ell}{1}}{\binom{R_h}{1}\sigma + \binom{R_\ell}{1}} = \frac{r_\ell}{R_h\sigma + R_\ell}.$$

The expected number of species that can use a low-use resource in the local community (low-use local species richness), s_ℓ is

$$s_\ell = S \cdot \frac{r_\ell}{R_h\sigma + R_\ell}. \tag{2.46}$$

Since there are r_ℓ low-use resources present in the local community, and each species uses only one resource, the functional redundancy of each low-use resource in the local community is

$$\Omega_p^\ell = \frac{1}{r_\ell} \cdot S \cdot \frac{r_\ell}{R_h\sigma + R_\ell} = S \cdot \frac{1}{R_h\sigma + R_\ell}. \tag{2.47}$$

Because $b = 1$, no local species uses a low-use resource from the metacommunity that is not present in the local community. Therefore, the functional redundancy of nonlocal low-use resources is $\Omega_a^\ell = 0$.

Thus, I find that the low-use species richness, s_ℓ, does not depend on the low-use resource complexity, r_ℓ, of the local community. Similarly, the functional redundancy of local and nonlocal low-use resources, Ω_p^ℓ and Ω_a^ℓ, are also independent of low-use resource complexity of the local community for $b = 1$.

Resource breadth $b = 2$

Next, I consider the scenario where each species uses exactly $b = 2$ resources. Again, let ρ_{ℓ_j} be a focal low-use resource in the local community. If a given species i uses ρ_{ℓ_j}, then there are two general possibilities for the combination of resources that species i can use:

1. ρ_{ℓ_j} is the only low-use resource that species i can use in the local community, or,
2. species i uses ρ_{ℓ_j} as well as another low-use resource from the local community.

When species i uses a single low-use local resource, it can persist in the local community, regardless of the identity of the second resource that it can use. That is, the second resource can be a nonlocal low-use resource, or a local or nonlocal high-use resource. Therefore, the probability of a species using a single low-use local resource is

$$\frac{\binom{r_\ell}{1}\binom{R_\ell - r_\ell}{1} + \binom{r_\ell}{1}\binom{R_h}{1}\sigma}{C(2)} = \frac{r_\ell(R_\ell - r_\ell + R_h\sigma)}{C(2)}, \tag{2.48}$$

where $C(2) = \binom{R_h}{2}\sigma^2 + \binom{R_h}{1}\binom{R_\ell}{1}\sigma + \binom{R_\ell}{2}$.

Alternately, when species i uses two low-use local resources, those are the only two resources that it can use. Therefore, the probability of a species using two low-use local resources is

$$\frac{\binom{r_\ell}{2}}{C(2)}. \tag{2.49}$$

Combining Equation (2.48) and (2.49), the expected number of species that live in the local community by using at least one local low-use resource is

$$s_\ell = \frac{S\left(\binom{r_\ell}{2} + r_\ell(R_\ell - r_\ell + R_h\sigma)\right)}{C(2)}. \tag{2.50}$$

The functional redundancy of each low-use resource in the local community is a weighted average of the functional redundancy derived from species that use only one low-use resource from the local community and species that use two low-use resources from the local community. Hence, the functional redundancy of each low-use resource in the local community is

$$\Omega_p^\ell = S\left(\frac{1}{r_\ell} \cdot \frac{r_\ell(R_\ell - r_\ell + R_h\sigma)}{C(2)} + \frac{2}{r_\ell} \cdot \frac{\binom{r_\ell}{2}}{C(2)}\right) = \frac{S(R_\ell + R_h\sigma - 1)}{C(2)}, \tag{2.51}$$

where $\frac{1}{r_\ell}$ is the probability that any given local low-use resource is used by a species that only uses one local low-use resource, and $\frac{2}{r_\ell}$ is the probability that the given local low-use resource is used by a species that uses two local low-use resources.

2.2.4.2 Exact expression for functional redundancy of local low-use resources: Ω_p^ℓ

To derive a general formula for the functional redundancy of local low-use resources, I again let ρ_{ℓ_j} be a focal low-use resource from the local community and i be a species that uses ρ_{ℓ_j}. Of the b resources that species i uses, at least one and a maximum of $\min(b, r_\ell)$ must be local and low-use. This results in a range of possible scenarios:

1. ρ_{ℓ_j} is the only local low-use resource used by species i. That is, the other $b-1$ resources are either nonlocal low-use resources, or local or nonlocal high-use resources.
2. species i uses ρ_{ℓ_j} along with one additional local low-use resource; the remaining $b-2$ resources are either nonlocal low-use resources, or local or nonlocal high-use resources.

$$\vdots$$

k. species i uses ρ_{ℓ_j} along with $k-1$ additional local low-use resources; the remaining $b-k$ resources are either nonlocal low-use resources, or local or nonlocal high-use resources.

$$\vdots$$

b. all b resources used by species i are local low-use resources.

The analysis here is completely analogous to what I did in Section 2.2.3.2, except that the h subscript (high) is now ℓ (low). I will omit the explanation, and refer the reader to Equation (2.44). Thus, the expected number of species that live in the local community and use at least one low-use resource is

$$s_\ell = S \cdot \frac{\sum_{k=\max(1,b+r_\ell-R_\ell)}^{\min(b,r_\ell)} \binom{r_\ell}{k} \sum_{j=0}^{b-k} \binom{R_\ell - r_\ell}{j} \binom{R_h}{b-k-j} \sigma^{b-k-j}}{C(b)}. \tag{2.52}$$

Meanwhile, the functional redundancy of low-use local resources is

$$\Omega_p^\ell = S \sum_{k=\max(1,b+r_\ell-R_\ell)}^{\min(b,r_\ell)} \frac{k}{r_\ell} \cdot \frac{\binom{r_\ell}{k} \sigma^{b-k} \sum_{j=0}^{b-k} \binom{R_\ell - r_\ell}{j} \binom{R_h}{b-k-j} \sigma^{-j}}{C(b)}. \tag{2.53}$$

Again, this equation is the same as Ω_p^h, for the functional redundancy of high-use local resources, but with the subscripts ℓ and h swapped, and with the scaling factor σ added.

2.2.5 Functional redundancy of nonlocal high-use resources: Ω_a^h

In the remaining two sections of this chapter, I will carry out a similar analysis for functional redundancy of nonlocal resources—in other words, resources that are used by local species, but that are only present in the metacommunity and not in the local community.

2.2.5.1 Case studies for $b = 1$ and $b = 2$

Resource breadth $b = 1$

Once again, I begin with the simplest scenario, where each species uses $b = 1$ resource. Any species that lives in the local community must use either a local high-use or local low-use resource. Because this is the only resource that they use, none of the species that persist in the local community can use a nonlocal resource. Therefore, when $b = 1$, the functional redundancy of nonlocal high-use resources is $\Omega_a^h = 0$.

Resource breadth $b = 2$

Next, I consider the scenario where each local species uses exactly $b = 2$ resources. Let P_{h_j} be a focal nonlocal high-use resource (i.e., it is present in the metacommunity but not the local community) used by local species i. For species i to persist in the local community, it must use at least one local resource. Therefore, species i can only use one additional resource, and P_{h_j} would be the only nonlocal high-use resource used by species i. The second resource used by species i could be either high-use or low-use, but it must be local. Hence, the probability of species i using P_{h_j} is

$$\frac{\binom{R_h - r_h}{1}\binom{r_h}{1}\sigma^2 + \binom{R_h - r_h}{1}\binom{r_\ell}{1}\sigma}{C(2)} = \frac{\sigma(R_h - r_h)(\sigma r_h + r_\ell)}{C(2)}.$$

In this scenario, only one nonlocal high-use resource can be used by any given local species. Thus, the nonlocal high-use resource is used with probability $\frac{1}{R_h - r_h}$ and the functional redundancy of nonlocal high-use resources is

$$\Omega_a^h = \frac{1}{R_h - r_h} \cdot \frac{\sigma(R_h - r_h)(\sigma r_h + r_\ell)}{C(2)} = \frac{\sigma^2 r_h + \sigma r_\ell}{C(2)}. \tag{2.54}$$

2.2.5.2 Exact expression for functional redundancy of nonlocal high-use resources: Ω_a^h

To derive a general formula for the functional redundancy of nonlocal high-use resources, I again let P_{h_j} be a focal nonlocal high-use resource and i be a local species that uses P_{h_j}. Of the b resources that species i uses, at least one and a maximum of $\min(b-1, R_h)$ can be nonlocal and high-use. This results in a range of possible scenarios:

1. P_{h_j} is the only nonlocal high-use resource used by species i. That is, the other $b-1$ resources are either local high-use resources, or local or nonlocal low-use resources.
2. species i uses P_{h_j} along with one additional nonlocal high-use resource; the remaining $b-2$ resources are either local high-use resources or local or nonlocal low-use resources.

$$\vdots$$

k. species i uses P_{h_j} along with $k-1$ additional nonlocal high-use resources; the remaining $b-k$ resources are either local high-use resources or local or nonlocal low-use resources.

⋮

$b-1$. all $b-1$ resources used by species i (i.e., every resource except the one require to persist in the local community) are nonlocal high-use resources.

Other than P_{h_j}, each of the $b-1$ resources used by species i, are either high-use or low-use. Of these, at least one must be a local resource in order for species i to persist in the local community. Denoting the local resource ρ_j, each of the remaining $b-2$ resources (excluding P_{h_j} and ρ_j) can be either local or nonlocal and either high-use or low-use. Let p_{h_k} be the probability that species i uses exactly k nonlocal high-use resources. This probability can be expressed as

$$p_{h_k} = \frac{\binom{R_h-r_h}{k}\sigma^k \left(\overbrace{\sum_{j=1}^{b-k}\binom{r_h}{j}\sigma^j\binom{R_\ell}{b-k-j}}^{\substack{\text{Total \# of ways using } j \text{ local HR} \\ \text{and any } b-k-j \text{ LR} \\ \text{for } j \text{ from 1 to } b-k}} + \overbrace{\sum_{j=1}^{b-k}\binom{r_\ell}{j}\binom{R_\ell-r_\ell}{b-k-j}}^{\substack{\text{Total \# of ways using } j \text{ local HR} \\ \text{and } b-k-j \text{ nonlocal LR} \\ \text{for } j \text{ from 1 to } b-k}} \right)}{C(b)}. \tag{2.55}$$

For each value of k, species i uses k nonlocal high-use resources. Because each nonlocal high-use resource is equally likely to be used, the probability of any high-use resource being used is $\frac{k}{R_h-r_h}$. Therefore, the functional redundancy of each nonlocal high-use resource is

$$\Omega_a^h = S \sum_{k=\max(1,b+r_h-R_h)}^{\min(b-1,r_h)} \frac{k}{R_h-r_h}\, p_{h_k}. \tag{2.56}$$

2.2.6 Functional redundancy of nonlocal low-use resources: Ω_a^ℓ

2.2.6.1 Case studies for $b=1$ and $b=2$

Resource breadth $b=1$

Again, I begin with the simplest scenarios where each species uses $b=1$ resource. Any species that lives in the local community must use either a local high-use or local low-use resource.

Because this is the only resource that the species can use, none of the species that persist in the local community can use a nonlocal resource. Therefore, when $b = 1$, the functional redundancy of nonlocal low-use resources is $\Omega_a^\ell = 0$.

Resource breadth $b = 2$

Next, I consider the scenario where each species uses exactly $b = 2$ resources. Using the same reasoning that I did in Equation (2.42), any local species i that uses a given nonlocal low-use resource, P_{ℓ_j}, must also use a local low-use or high-use resource. Therefore, the probability of species i using P_{ℓ_j} is

$$\frac{\binom{R_\ell - r_\ell}{1}\left(\binom{r_h}{1}\sigma + \binom{r_\ell}{1}\right)}{C(2)} = \frac{(R_\ell - r_\ell)(r_h\sigma + r_\ell)}{C(2)}. \tag{2.57}$$

Since there are $R_\ell - r_\ell$ nonlocal low-use resources, the functional redundancy of each is

$$\Omega_a^\ell = \frac{1}{R_\ell - r_\ell} \cdot \frac{(R_\ell - r_\ell)(r_h\sigma + r_\ell)}{C(2)}\, S = \frac{r_h\sigma + r_\ell}{C(2)}\, S. \tag{2.58}$$

2.2.6.2 Exact expression for functional redundancy of nonlocal low-use resources: Ω_a^ℓ

To derive a general formula for the functional redundancy of nonlocal low-use resources, I again let P_{ℓ_j} be a focal nonlocal low-use resource and i be a local species that uses P_{ℓ_j}. Of the b resources that species i uses, at least one and a maximum of $\min b - 1, R_\ell$ must be nonlocal and high-use. This results in a range of possible scenarios:

1. P_{ℓ_j} is the only nonlocal low-use resource used by species i. That is, the other $b - 1$ resources are either local low-use resources, or local or nonlocal high-use resources.

2. species i uses P_{ℓ_j} along with one additional nonlocal low-use resource; the remaining $b - 2$ resources are either local low-use resources or local or nonlocal high-use resources.

$$\vdots$$

k. species i uses P_{ℓ_j} along with $k - 1$ additional nonlocal low-use resources; the remaining $b - k$ resources are either local low-use resources or local or nonlocal high-use resources.

$$\vdots$$

$b-1$. all $b-1$ resources used by species i (i.e., every resource except the one require to persist in the local community) are nonlocal low-use resources.

Other than P_{ℓ_j}, each of the $b-1$ resources used by species i are either high-use or low-use. Of these, at least one must be a local resource in order for species i to persist in the local community. Denoting the local resource ρ_j, each of the remaining $b-2$ resources (excluding P_{ℓ_j} and ρ_j) can be either local or nonlocal and either high-use or low use. Let p_{ℓ_k} be the probability that species i uses exactly k nonlocal low-use resources. This probability that be expressed as

$$p_{\ell_k} = \frac{\binom{R_\ell - r_\ell}{k}\left(\sum_{j=1}^{b-k}\binom{r_\ell}{j}\binom{R_h}{b-k-j}\sigma^{b-k-j} + \sum_{j=1}^{b-k}\binom{r_h}{j}\binom{R_h - r_h}{b-k-j}\sigma^{b-k}\right)}{C(b)}. \tag{2.59}$$

For each such k, species i uses k nonlocal low-use resources. Because each nonlocal low-use resource is equally likely to be used, the probability that any given low-use resource is used is $\frac{k}{R_\ell - r_\ell}$. Therefore, the functional redundancy of each nonlocal low-use resource is

$$\Omega_a^\ell = S \sum_{k=\max(1,b+r_\ell-R_\ell)}^{\min(b-1,r_\ell)} \frac{k}{R_\ell - r_\ell} p_{\ell_k}. \tag{2.60}$$

2.3 Summary

In this Chapter, I developed models of functional redundancies by assuming that the community is driven by the environmental filtering community assembly. That is, a species can persist in the community if it can use at least one resource there. The resources were also assumed to be substitutable—all are from one source. I considered two types of resource use distribution. First, all resources were with equal probability to be used by a species, which called *equal resource use*. Then, I relaxed this assumption to consider that some resources are more likely to be used than others, I referred this case as *unequal resource use*. Under each case of resource use distribution, I first assumed that the resource breadth—number of resources, b, used by each species, has a delta distribution. That is, each species uses the same number of resources in the metacommunity. Then, to capture more realistic biological scenarios under the *equal resource use*, I considered two other distributions for b, uniform distribution and triangular distributions.

Under the *equal resource use* assumption, the relationship between the functional redundancies and the local resource complexity, r, were similar under different distributions of b (delta, uniform, triangular). For any given distribution of b, with pmf φ_b over a range of $(b_{\min}, b_{\max})$, the functional redundancy of local resources, Ω_p in Equation (2.19), is independent from the local resource complexity, r.

$$\Omega_p = \frac{S}{R}\sum_{b=b_{\min}}^{b_{\max}} b\varphi_b.$$

In contrast, the functional redundancy of nonlocal resources in Equation (2.19), Ω_a is monotonically increasing with the local resource complexity, r. More precisely, it saturates to Ω_p, when r is closer enough to R.

$$\Omega_a \approx \frac{S}{R}\sum_{b=b_{\min}}^{b_{\max}} b\left(1-\left(1-\frac{r}{R}\right)^{b-1}\right)\varphi_b.$$

The functional redundancy of overall resources, Ω_t, is also monotonically increasing against r, and saturates to Ω_p for higher values of r. The saturation point—value of r to reach the maximum Ω_p—is lower for Ω_t compares to the one of Ω_a. Specifically, Ω_t in Equation (2.20) is

$$\Omega_t \approx \frac{S}{R}\left[\sum_{b=b_{\min}}^{b_{\max}} b\varphi_b - \sum_{b=b_{\min}}^{b_{\max}} b\left(1-\left(1-\frac{r}{R}\right)^{b-1}\right)\varphi_b\right].$$

Next, I extended the EF model with the *unequal resource use* only under the delta distribution for the resource breadth, b. I developed the functional redundancies of two classes of resources: *high-use resources* (HR), and *low-use resources* (LR), separately. I used subscripts ℓ and h to refer any parameters in the low-use classes and in the high-use classes, respectively. The functional redundancies in both classes were similar by swapping the subscripts ℓ and h and scaling the high-use resources with a scaling factor σ. Different from the *equal resource use* case, the functional redundancy of local high-use resources (resp. low-use resources), Ω_p^h in Equation (2.45) (resp. Ω_p^l in Equation (2.53)), is more complicated. In the special case studies $b = 1$ and $b = 2$, I discovered that both Ω_p^h and Ω_p^ℓ were independent from the local high-use resource complexity, r_h, and local low-use resource complexity, r_ℓ, respectively. One might expect that the general Ω_p^h (resp. Ω_p^ℓ) would be constant against the local high-use resource complexity, r_h (resp. local low-use resource complexity, r_ℓ). However, that still needs further analyses since the analytic approximations of Ω_p^h and of Ω_p^ℓ

were not straightforward and were not covered in this thesis.

$$\Omega_p^h = S \sum_{k=\max(1,b+r_h-R_h)}^{\min(b,r_h)} \frac{k}{r_h} \cdot \frac{\binom{r_h}{k}\sigma^k \sum\limits_{j=0}^{b-k} \binom{R_h-r_h}{j}\binom{R_\ell}{b-k-j}\sigma^j}{\sum\limits_{k=0}^{b} \sigma^k \binom{R_h}{k}\binom{R_\ell}{b-k}}$$

$$\Omega_p^\ell = S \sum_{k=\max(1,b+r_\ell-R_\ell)}^{\max(b,r_\ell)} \frac{k}{r_\ell} \cdot \frac{\binom{r_\ell}{k}\sigma^{b-k} \sum\limits_{j=0}^{b-k} \binom{R_\ell-r_\ell}{j}\binom{R_h}{b-k-j}\sigma^{-j}}{\sum\limits_{k=0}^{b} \sigma^k \binom{R_h}{k}\binom{R_\ell}{b-k}}.$$

For the nonlocal functional redundancy, the special case $b = 2$ for high-use resources and low-use resources depended on both low-use resource complexity, r_ℓ, and high-use resource complexity, r_h. The general expression of Ω_a^h (Equation (2.56)) and Ω_a^ℓ (Equation (2.60)) were more complicated to approximate. Therefore, the relationship between Ω_a^h (resp. Ω_a^ℓ) and the local high-use resource complexity, r_h (resp. local low-use resource complexity, r_ℓ) still need more analyses.

$$\Omega_a^h = S \sum_{k=\max(1,b+r_h-R_h)}^{\min(b-1,r_h)} \frac{k}{R_h - r_h} \cdot \frac{\binom{R_h-r_h}{k}\sigma^k \left(\sum\limits_{j=1}^{b-k} \binom{r_h}{j}\sigma^j \binom{R_\ell}{b-k-j} + \sum\limits_{j=1}^{b-k} \binom{r_\ell}{j}\binom{R_\ell-r_\ell}{b-k-j} \right)}{\sum\limits_{k=0}^{b} \sigma^k \binom{R_h}{k}\binom{R_\ell}{b-k}}$$

$$\Omega_a^\ell = S \sum_{k=\max(1,b+r_\ell-R_\ell)}^{\min(b-1,r_\ell)} \frac{k}{R_\ell - r_\ell} \cdot \frac{\binom{R_\ell-r_\ell}{k} \left(\sum\limits_{j=1}^{b-k} \binom{r_\ell}{j}\binom{R_h}{b-k-j}\sigma^{b-k-j} + \sum\limits_{j=1}^{b-k} \binom{r_h}{j}\binom{R_h-r_h}{b-k-j}\sigma^{b-k} \right)}{\sum\limits_{k=0}^{b} \sigma^k \binom{R_h}{k}\binom{R_\ell}{b-k}}.$$

Figure 2.13 summarizes the responses of functional redundancy with local resource complexity based on the equal resource use distribution, various number of metacommunity resources, number of species, and resource breadth distributions. In general, with environmental filtering, the functional redundancy of local resources is constant against local resource complexity, while the nonlocal and the average functional redundancy have upward redundancy trends (Figure 2.13). Moreover, the nonlocal and the overall functional redundancy saturate to the local FR when the resource breadth b is higher than one. Lower local functional redundancy correlates with slower saturation when $\Omega_a \neq 0$. Considering a delta distribution for the resource breadth b with fixed number of metacommunity resources and the number of species, higher value of b results in lower number of local resources needed for the nonlocal and the overall functional redundancy to reach the local FR. Smaller value of b provides slower saturation with lower value of Ω_p (Figure 2.13 A). Moreover, increasing the number of metacommunity resources results in higher local functional redundancy but slower saturation for the nonlocal and the overall FR (Figure 2.13 B). Keeping everything fixed but increasing the number of species, the maximum value of Ω_a and Ω_t increase while the minimum number of resources for them to achieve Ω_p remains constant (Figure 2.13 C). Overall, the trend of the functional redundancy for most of the breadth distributions is similar to the one with a delta breadth distribution. Also, there is no significant different saturation points among most of the breadth distributions. Based on Figure 2.13 D, the local functional redundancy for uniform, center triangular and delta distribution of resource breadth are close to each other when the other parameters are fixed. The right triangular has the highest maximum functional redundancy and the left triangular has the lowest.

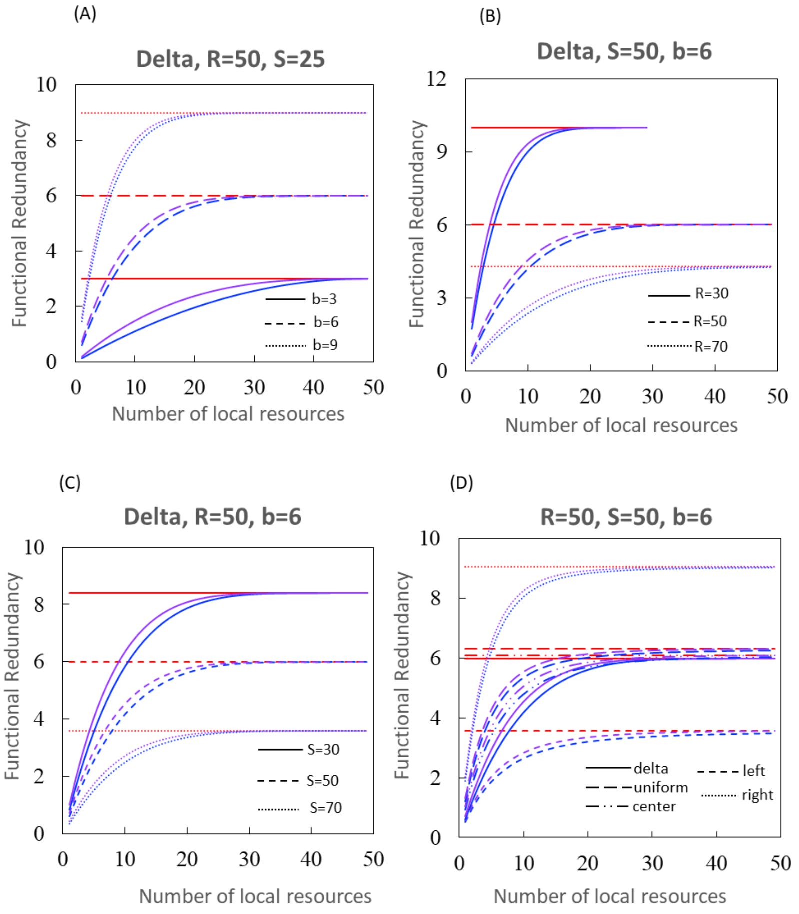

Figure 2.13: Functional redundancies with equal resource use: Ω_p (Red lines), Ω_a (blue lines), Ω_t (purple lines). (A-C): with delta breadth distribution. (A): the effect of the number of resources used by each species (b) with $R = 50, S = 50$; (B) the number of resources present in the metacommunity (R) with $S = 50$, $b = 6$; (C) the number of consumer species present in the metacommunity (S) with $R = 50$, $b = 6$; and (D) the shape of the resource breadth distribution (delta, uniform, left, center, right).

Chapter 3

Niche partitioning

3.1 Basic definitions and assumptions

In Chapter 2, my mathematical models were based on the community assembly theory of *environmental filtering* (EF), where the sole requirement for persistence in a local community is the presence of at least one usable resource. In other words, if a species can find at least one of its resources locally, it can persist. In this chapter, I will explore similar questions and analyses of ecological communities under the assumption of *niche partitioning* (NP). Recall from the Introduction (Chapter 1) that this is a community assembly theory based on competition. Thus, in order to persist, a species must not only find a resource that it can use, but also outcompete every other species for that resource. Admittedly, the EF and NP community assembly paradigms are idealistic, and there are almost certainly elements of both processes underlying the assembly of most ecological communities. However, depending on the specific community, either EF or NP may be the more important determinant of community structure. Thus, by considering models at both ends of the spectrum, I can infer whether and how these different community assembly paradigms impact functional redundancy. This is useful for identifying signals of EF versus NP in empirical communities. It is also the first step towards understanding functional redundancy in more realistic communities that lie intermediate between fully EF and fully NP models.

To build a model for functional redundancy under the niche partitioning paradigm, I assume that each of the R resources present in the metacommunity has a single species that outcompetes all other species for that resource. Different mechanisms could be involved, but a classic example is the ability of stronger competitors to survive at lower concentrations of a resource (R^* rule) [82]. When the strongest competitor for any given resource is present, it will outcompete all other species for that resource. This prevents other species from accessing and, as a consequence, persisting on resources that they could otherwise use. Thus, in the niche partitioning model, persistence in the local community requires not only finding a usable resource but also outcompeting all other species for that same resource. For the sake of consistency, I will additionally assume that all S species present in the metacommunity are able to outcompete other species for at least one metacommunity resource. Otherwise, the species would not be able to persist, even at the metacommunity scale. For this reason, $R \geq S$.

To aid in model development, I distinguish between the following two types of resources, which are defined in reference to each individual species and that species' set of usable resources:

1. *primary resources*: resources for which a species is the strongest competitor; a species can always persist on these resources, regardless of whether other species are present.
2. *secondary resources*: resources for which a species is *not* the strongest competitor; a species can only persist on these resources in absence of the stronger competitors.

As in the previous chapter, I will consider a focal local community with $r \leq R$ resources, where r is the *resource complexity* of the local community. I will then ask how many of the S species present in the metacommunity can persist in the local community (i.e., what is the *species richness* of the local community), and how this impacts functional redundancy (Ω_a, Ω_p and Ω_t).

Under the assumptions of the niche partitioning model, there can only be one strongest competitor for any given resource. However, it is possible that a single species may be the strongest competitor for multiple resources (i.e., a single species may have more than one primary resource). In fact, a single species could potentially be the strongest competitor for anywhere from one to $b_{\max}$ resources, where $b_{\max}$ is the maximum resource breadth of any species in the metacommunity. To characterize variation in primary resources per species, we define a *competitive breadth distribution.* Analogous to the *resource breadth distribution*, the *competitive breadth distribution* describes the number of species that have anywhere from one to $b_{\max}$ primary resources. Like the resource breadth distribution, the simplest competitive breadth distribution is a delta distribution, wherein each species is the strongest competitor for the same number of resources. I term this scenario *equal competition* and contrast it with *unequal competition* wherein different species are the strongest competitors for different number of resources.

Specifying niche partitioning models requires defining both a resource breadth distribution and a competitive breadth distribution. These two distributions are not, however, fully independent because a species' primary and secondary resources must sum up to the species' resource breadth. Thus, for example, if species i has three primary resources and a resource breadth of b_i, then it must have $b_i - 3$ secondary resources. As a consequence, the resource breadth distribution and the competitive breadth distribution must be compatible (i.e., it must be possible to satisfy the competitive breadth distribution given the resource breadth distribution, which is not always true). Because of the complicated relationship between the resource breadth distribution and the competitive breadth distribution, for niche partitioning models, I focus on how differences in the competitive breadth distribution impact functional redundancy, and only consider delta distributions for resource breadth.

3.2 Equal competition

In the most basic niche partitioning model, I assume equal competition (i.e., a delta distribution for the competitive breadth distribution). Because I only consider a delta distribution for the resource breadth distribution as well, all S species in the metacommunity have the same resource breadth, denoted b, and the same competitive breadth, denoted n. If I additionally assume that all resources are equally likely to be used, then $R = nS$. My first goal is to derive an expression for local species richness. As I did in the previous chapter, I will begin by considering several examples, and will then use these to arrive at an expression for the general case.

3.2.1 Case studies for $n = 1$ and $n = 2$

Competitive breadth $n = 1$

In the simplest case, there is a bijective correspondence between the R resources in the metacommunity and the $S = R$ species. More specifically, each species has exactly one primary resource, and each resource is the primary resource for exactly one species. Therefore, the number of species that persist in the local community is $s = r$. Let ρ_{p_j} be a particular local resource. There is one local species for which ρ_{p_j} is a primary resource, and $s - 1$ local species for which it is not. Each of the $s - 1$ local species that are not the strongest competitor for ρ_{p_j} will have to find a different primary resource in the local community in order to persist. Besides their single primary resource, all species in the local community will also have $b-1$ secondary resources. These secondary resources can be drawn from the remaining $R-1$ resources (i.e., excluding their primary resource) present in the metacommunity. Assuming that all resources are equally likely to be used, each of the $s-1$ local species that do not use ρ_{p_j} as their primary resource would use ρ_{p_j} as a secondary resource with probability $\frac{b-1}{R-1}$. The functional redundancy of local resources is thus the sum of the one species that uses ρ_{p_j} as a primary resource and the $(s-1)\frac{b-1}{R-1}$ species that use ρ_{p_j} as a secondary resource:

$$\Omega_p = 1 + (s-1)\frac{b-1}{R-1} = 1 + (r-1)\frac{b-1}{R-1}. \tag{3.1}$$

Equation (3.1) highlights a fundamental difference between EF and NP with respect to predictions about functional redundancy. In EF, Ω_p is constant with respect to r (see Equation (2.3)). By contrast, in NP, at least for the scenario with $n=1$, Ω_p increases linearly with r.

Next, I consider a nonlocal resource, ρ_{a_j}. The species that uses ρ_{a_j} as a primary resource cannot persist in the local community. The only local species that use ρ_{a_j} must us it as one of their $b-1$ secondary resources. Again, assuming that all resources are equally likely to be used, the number of local species that use ρ_{a_j} is $s\frac{b-1}{R-1}$. Therefore, the functional redundancy of nonlocal resources is

$$\Omega_a = s\frac{b-1}{R-1} = r\frac{b-1}{R-1}. \tag{3.2}$$

Similar to Ω_p, Ω_a scales linearly with r for $n=1$. Indeed, both functional redundancies have the same slope, and differ only in their intercepts. Finally, I consider Ω_t, the total functional redundancy. Since the metacommunity contains r local and $R-r$ nonlocal resources, the total functional redundancy of each resource in the metacommunity is

$$\begin{aligned}
\Omega_t &= \frac{r}{R}\Omega_p + \frac{R-r}{R}\Omega_a \\
&= \frac{r}{R}\Omega_p + \frac{R-r}{R}\left(\Omega_p + \frac{b-1}{R-1} - 1\right) \\
&= \Omega_p + \frac{(R-r)(b-1)}{R(R-1)} - \frac{R-r}{R} \\
&= 1 + \frac{(r-1)(b-1)}{R-1} + \frac{(R-r)(b-1)-(R-r)(R-1)}{R(R-1)} \\
&= \frac{R(R-1)+R(r-1)(b-1)+(R-r)(b-1)-(R-r)(R-1)}{R(R-1)} \\
&= \frac{(R-R+r)(R-1)+(R(r-1)+R-r)(b-1)}{R(R-1)} \\
&= \frac{r(R-1)+(Rr-r)(b-1)}{R(R-1)} \\
&= \frac{r(R-1)+r(R-1)(b-1)}{R(R-1)} \\
&= \frac{r(R-1)(1+b-1)}{R(R-1)} \\
&= \frac{r(R-1)b}{R(R-1)} \\
&= \frac{rb}{R}.
\end{aligned} \tag{3.3}$$

Recall that in the EF model, total functional redundancy also depended on r. More specifically, for EF and $b = 1$, $\Omega_t = \frac{rS}{R^2}$. By contrast, for NP and $b = 1$, $\Omega_t = \frac{r}{R}$. Thus, the EF model has an additional factor of $\frac{S}{R}$. This is a direct result of the fact that the number of species in the local community is limited by availability of species in the metacommunity under the EF model, whereas it is limited by the availability of resources in the local community under the NP model.

Competitive breadth $n = 2$

Next, I consider the scenario where each species has two primary resources, $n = 2$. This adds an additional requirement that the resource breadth be $b \geq 2$. Since each local species has to find at least one primary resource in the local community, there are two possibilities for the partitioning of primary resources between the local and metacommunities:

1. One primary resource is local, and the other is nonlocal.

2. Both primary resources are local.

I will compute the species richness (expected number of species) for both cases, denoted s_1 and s_2, respectively. The sum will of these two quantities will be the total species richness, $s = s_1 + s_2$.

In the first case, there are r choices for the local primary resource and $R - r$ choices for the nonlocal primary resource. Assuming that all resources are equally likely to be used (as either primary or secondary resources), the probability of a species having one local primary resource and one nonlocal primary resource is $\frac{\binom{r}{1}\binom{R-r}{1}}{\binom{R}{2}} = \frac{r(R-r)}{\binom{R}{2}}$. Hence, the expected number of species with one local primary resource and one nonlocal primary resource is:

$$s_1 = S \cdot \frac{r(R-r)}{\binom{R}{2}}. \tag{3.4}$$

In the second case, there are $\frac{\binom{r}{2}}{\binom{R}{2}}$ choices for the two primary local resources. Again, assuming that all resources are equally likely to be used, the expected number of species having two local primary resources is

$$s_2 = S \cdot \frac{\binom{r}{2}}{\binom{R}{2}}. \tag{3.5}$$

Adding Equations 3.4 and 3.5 gives the species richness of the local community,

$$s = s_1 + s_2 = \frac{S(r(R-r) + \binom{r}{2})}{\binom{R}{2}} = \frac{Sr(2R - r - 1)}{R(R-1)}. \tag{3.6}$$

Next, I use Equation (3.6) to derive expressions for functional redundancy. Consider a focal local resource, ρ_{p_j}. Exactly one of the s local species must use resource ρ_{p_j} as a primary resource. Each of the $s - 1$ other local species must use two other primary resources, leaving $b - 2$ secondary resources that could potentially be allocated to resource ρ_{p_j}. The probability that one of the $b - 2$ remaining resources is, in fact, allocated to ρ_{p_j} is $\frac{b-2}{R-2}$. Therefore, the functional redundancy of local resources is

$$\Omega_p = 1 + (s-1)\frac{b-2}{R-2} = 1 + \frac{Sr(b-2)(2R-r-1)}{R(R-1)(R-2)} = 1 + \frac{S(b-2)(2R-1)r - S(b-2)r^2}{R(R-1)(R-2)}. \tag{3.7}$$

It is again useful to compare the NP expression for Ω_p with the EF expression for Ω_p. Under the assumptions of NP, the functional redundancy of local resources is a quadratic function of r. By contrast, under the assumptions of EF, the functional redundancy is constant with respect to r (see

Equation (2.14)).

Next, I consider the functional redundancy of nonlocal resources, again assuming that each species has $n = 2$ primary resources, allowing for two possible ways of partitioning primary resources between the local and metacommunities (i.e., both primary resources are local or one primary resource is local and one nonlocal). For a local species with only one local primary resource, the probability that ρ_{a_j} is its second primary resource is $\frac{1}{R-r}$, while the probability that ρ_{a_j} is used as a secondary resource is $\frac{b-2}{R-2}$. For a local species with two local primary resources, ρ_{a_j} cannot be used as a primary resource. It can, however, be used as a secondary resource, and this will occur with probability $\frac{b-2}{R-2}$. Thus, the functional redundancy of nonlocal resources, (i.e., the expected number of local species that use a give nonlocal resource) is

$$\begin{aligned}
\Omega_a &= s_1 \frac{1}{R-r} + s_1 \frac{b-2}{R-2} + s_2 \frac{b-2}{R-2} \\
&= \frac{s_1}{R-r} + (s_1 + s_2) \frac{b-2}{R-2} \\
&= \frac{s_1}{R-r} + s \frac{b-2}{R-2} \\
&= \frac{s_1}{R-r} + \Omega_p - 1 + \frac{b-2}{R-2} \quad \text{(using Equation (3.7))} \\
&= \Omega_p - 1 + \frac{s_1(R-2) + (b-2)(R-r)}{(R-r)(R-2)} \\
&= \frac{Sr(b-2)(2R-r-1)}{R(R-1)(R-2)} + \frac{Sr(R-r)(R-2) + \binom{R}{2}(b-2)(R-r)}{\binom{R}{2}(R-r)(R-2)} \\
&= \frac{Sr(b-2)(2R-r-1)}{R(R-1)(R-2)} + \frac{2Sr(R-r)(R-2) + R(R-1)(b-2)(R-r)}{R(R-1)(R-r)(R-2)} \\
&= \frac{Sr(b-2)(2R-r-1)}{R(R-1)(R-2)} + \frac{2Sr(R-2) + R(R-1)(b-2)}{R(R-1)(R-2)} \\
&= \frac{R(R-1)(b-2) + S[b(2R-1) - 2(R+1)]r - S(b-2)r^2}{R(R-1)(R-2)}
\end{aligned} \tag{3.8}$$

Using Equation (3.7) and Equation (3.8), the total functional redundancy for this scenario is

$$\begin{aligned}
\Omega_t &= \frac{r}{R}\Omega_p + \frac{R-r}{R}\Omega_a \\
&= \frac{r}{R}\left(1 + \frac{S(b-2)(2R-1)r - S(b-2)r^2}{R(R-1)(R-2)}\right) + \frac{R-r}{R} \cdot \frac{R(R-1)(b-2) + S[b(2R-1) - 2(R+1)]r - S(b-2)r^2}{R(R-1)(R-2)} \\
&= \frac{S(b-2)(2R-1)r - S(b-2)r^2}{R(R-1)(R-2)} + \frac{r-2}{R-2} + \frac{R-r}{R}\left(\frac{b}{R-2} + \frac{2Sr}{R(R-1)}\right).
\end{aligned} \tag{3.9}$$

Similar to local functional redundancy, Ω_p, in Equation (3.7), both the nonlocal functional redundancy, Ω_a, and the overall Ω_t, has a quadratic relationship with environmental complexity, r, under niche partitioning. This is, again, in contrast to the EF model, where the relationships between nonlocal and overall functional redundancy against environmental complexity were linear.

3.2.2 Exact expressions for functional redundancy

I now derive general formulae for functional redundancy when each species has $n > 2$ primary resources (and thus $b - n \geq 0$ secondary resources). As in the two previous examples, each species that persists in the local community must have at least one and at most $\min(n, r)$ local primary resources. Consider a focal species i. If $n \leq r$ (which I generally expect to be the case), there are a range of possible scenarios for how species i's primary resources can be distributed between the local and metacommunities:

- one of species i's primary resources is local,
- two of species i's primary resources are local,

$$\vdots$$

- n of species i's primary resources are local.

As always, assuming that all resources are used equally (as primary or secondary resources), then the probability that species i will have exactly k local primary resources is $\frac{\binom{r}{k}\binom{R-r}{n-k}}{\binom{R}{n}}$. Summing over all possible values of k then gives probability that species i will have at least one local primary resource:

$$p = \sum_{k=\max(1,n+r-R)}^{r} \frac{\binom{r}{k}\binom{R-r}{n-k}}{\binom{R}{n}}. \tag{3.10}$$

If, on the other hand, $n > r$, then even if species i uses all r local resources as primary resource, it must still have an additional $n - r$ primary resources in the metacommunity. In this case, the above sum must be terminated at $r < n$. In other words, the probability that species i will use at least one local primary resource, is

$$p = \sum_{k=\max(1,n+r-R)}^{\min(n,r)} \frac{\binom{r}{k}\binom{R-r}{n-k}}{\binom{R}{n}}. \tag{3.11}$$

3.2.2.1 Species richness

Regardless of n, species richness, s, in the niche partitioning model is the product of the total number of species in the metacommunity, S, multiplied by the probability, p, that any given species i will have at least one local primary resource. For $n = 1$ this was trivially $s = r$, and for $n = 2$, I computed s explicitly in Equation 3.6. For general n, species richness, s, is the product of the number of species in the metacommunity, S, multiplied by p as given in Equation 3.11, which simplifies to

$$s = Sp = S\left(1 - \frac{(R-n)\Gamma(R-n)\Gamma(R-r+1)}{\Gamma(R-r-n+1)\Gamma(R+1)}\right). \tag{3.12}$$

Following the same arguments as in Section 2.1.1.3, Equation (3.12) can be simplified with some biologically reasonable assumptions. Specifically, I assume that $R \gg r$, which means that $(R-r-1)! \approx R!$ and $(R-r-n)! \approx (R-n)!$. Additionally, I can approximate $(R-r-1)\cdots(R-r-(n-1)) \approx (R-r)^{n-1}$ when $R - r \gg n-1$. Similarly, I can approximate $R(R-1)\cdots(R-n) \approx R^{n+1}$ when $R \gg n$. Therefore, when $R \gg n$ and $R - r \gg n - 1$ ($R \gg r + n - 1$), we have the following relationships:

$$\begin{aligned}\frac{(R-n)\Gamma(R-n)}{\Gamma(R+1)} &= \frac{(R-n)!}{R!}\\ &\approx \frac{1}{R\cdots(R-(n-1))}\\ &\approx R^n,\end{aligned}$$

and

$$\begin{aligned}\frac{\Gamma(R-r+1)}{\Gamma(R-r-n+1)} &= \frac{(R-r)!}{(R-r-n)!}\\ &\approx (R-r)\cdots(R-r-(n-1))\\ &\approx (R-r)^n.\end{aligned}$$

Thus, the expression for species richness, s, simplifies to

$$s \approx S\left(1 - \frac{(R-r)^n}{R^n}\right) = S\left(1 - \left(1 - \frac{r}{R}\right)^n\right).$$

Similar to local species richness in the EF model, local species richness in the NP model increases monotonically with increasing environmental complexity, r. The only difference is that resource breadth, b, in the EF model is now replaced with competitive breadth, n. This is perhaps not surprising, because the criterion for persistence in the EF model is finding a usable resource, which depends on resource breadth, b. By contrast, the criterion for persistence in the NP model is finding a primary resource, which depends on competitive, n.

3.2.2.2 Functional redundancies

Local functional redundancy: Ω_p

To find the functional redundancy of local resources, I follow the same arguments outlined in Section 3.2.1, for the case of $n = 2$. Let ρ_{p_j} be a focal local resource. Exactly one local species should use ρ_{p_j}. Each of the other $s - 1$ local species have n primary resources, and $b - n$ secondary resources, allocated from the remaining $R - n$ resources. Therefore, each of these species will use ρ_{p_j} as a secondary resource with probability $\frac{b-n}{R-n}$, making the functional redundancy of local resources is

$$\Omega_p = 1 + (s-1)\frac{b-n}{R-n} \approx 1 + \left[S\left(1 - \left(1 - \frac{r}{R}\right)^n\right) - 1\right]\frac{b-n}{R-n}. \tag{3.13}$$

nonlocal functional redundancy: Ω_a

Next, I derive an expression for the functional redundancy of nonlocal resources. Let ρ_{a_j} be a focal nonlocal resource and let s_k be the number of local species that have exactly k local primary resources. There are s_0 species with $k = 0$. These species cannot persist in the local community because they do not have a primary resource in the local community. Likewise, there are s_n species with $k = n$ local primary resources. These species have no primary resources outside the local community, and thus can only use ρ_{a_j} as a secondary resource. Finally, there are an additional $s_1 + s_2 + \cdots + s_{n-1}$ species that have at least one local and at least one nonlocal resource. These species can potentially use ρ_{a_j} as either a primary or a secondary resource.

If a species has exactly $k \leq n$ local primary resources, then it has an additional $n-k$ nonlocal primary resources. Assuming that all resources are used equally, the probability of ρ_{a_j} being used as a primary nonlocal resource is $\frac{n-k}{R-r}$. The $b - n$ secondary resources are chosen uniformly from the remaining $R - n$ resources, and so a species would use ρ_{a_j} as a secondary resource with probability

$\frac{b-n}{R-n}$. Therefore, the functional redundancy of nonlocal resources is

$$\begin{aligned}\Omega_a &= \sum_{k=\max(1,n+r-R)}^{\min(n,r)} s_k \left(\frac{n-k}{R-r} + \frac{b-n}{R-n} \right) \\ &= \sum_{k=\max(1,n+r-R)}^{\min(n,r)} S \frac{\binom{r}{k}\binom{R-r}{n-k}}{\binom{R}{n}} \left(\frac{n-k}{R-r} + \frac{b-n}{R-n} \right) \\ &= \sum_{k=\max(1,n+r-R)}^{\min(n,r)} S \frac{\binom{r}{k}\binom{R-r}{n-k}}{\binom{R}{n}} \cdot \frac{n-k}{R-r} \quad + \sum_{k=\max(1,n+r-R)}^{\min(n,r)} S \frac{\binom{r}{k}\binom{R-r}{n-k}}{\binom{R}{n}} \cdot \frac{b-n}{R-n} \\ &= \sum_{k=\max(1,n+r-R)}^{\min(n,r)} S \frac{\binom{r}{k}\binom{R-r}{n-k}}{\binom{R}{n}} \cdot \frac{n-k}{R-r} \quad + \quad s \cdot \frac{b-n}{R-n}. \end{aligned} \tag{3.14}$$

As in Equation 2.18, the summation term can be both simplified and approximated. Specifically, when $R \gg r$, $(R-r-1)! \approx R!$ and $(R-r-n)! \approx (R-n)!$. Additionally, when when $R-r \gg n-1$, $(R-r-1)\cdots(R-r-(n-1)) \approx (R-r)^{n-1}$ and when $R \gg n$, $R(R-1)\cdots(R-n) \approx R^{n+1}$. Therefore, when $R \gg n$ and $R-r \gg n-1$ ($R \gg r+n-1$), Equation (3.14) becomes

$$\begin{aligned}\sum_{k=\max(1,n+r-R)}^{\min(n,r)} S \frac{\binom{r}{k}\binom{R-r}{n-k}}{\binom{R}{n}} \cdot \frac{n-k}{R-r} &= \frac{Sn}{R} - \frac{(R-n)nS\Gamma(R-r)\Gamma(R-n)}{\Gamma(R-r+1-n)\Gamma(R+1)} \\ &\approx \frac{Sn}{R}\left(1-\left(1-\frac{r}{R}\right)^{n-1}\right). \end{aligned} \tag{3.15}$$

Combining the approximate local species richness, s, in Equation 3.12 with the approximation in Equation 3.15 gives the approximate functional redundancy of nonlocal resources, Ω_a, as

$$\begin{aligned}\Omega_a &\approx \frac{Sn}{R}\left(1-\left(1-\frac{r}{R}\right)^{n-1}\right) + S\left(1-\left(1-\frac{r}{R}\right)^{n}\right)\frac{b-n}{R-n} \\ &= S\left[\frac{n}{R}\left(1-\left(1-\frac{r}{R}\right)^{n-1}\right) + \frac{b-n}{R-n}\left(1-\left(1-\frac{r}{R}\right)^{n}\right)\right]. \end{aligned} \tag{3.16}$$

Using Equation (3.13) and Equation (3.14), the overall functional redundancy in this scenario is

$$\begin{aligned}\Omega_t &\approx \frac{r}{R}\left(1+\left[S\left(1-\left(1-\frac{r}{R}\right)^{n}\right)-1\right]\frac{b-n}{R-n}\right) + \frac{R-r}{R}S\left[\frac{n}{R}\left(1-\left(1-\frac{r}{R}\right)^{n-1}\right) + \frac{b-n}{R-n}\left(1-\left(1-\frac{r}{R}\right)^{n}\right)\right] \\ &\approx S\left(1-\left(1-\frac{r}{R}\right)^{n}\right)\frac{b-n}{R-n} + \frac{r}{R}\left(1-\frac{b-n}{R-n}\right) + \frac{R-r}{R}S\frac{n}{R}\left(1-\left(1-\frac{r}{R}\right)^{n-1}\right) \\ &\approx \left[S\left(1-\left(1-\frac{r}{R}\right)^{n}\right)-\frac{r}{R}\right]\frac{b-n}{R-n} + \frac{r}{R} + \frac{R-r}{R}S\frac{n}{R}\left(1-\left(1-\frac{r}{R}\right)^{n-1}\right). \end{aligned} \tag{3.17}$$

Recall that, in Chapter 2, under EF assumptions, the functional redundancy of nonlocal resources, Ω_a, and the overall resources, Ω_t, depended on resource complexity, r, but the functional redundancy of local resources, Ω_p, did not. By contrast, under NP assumptions, Ω_p, Ω_a, and Ω_t depend on r.

3.3 Unequal competition

Previously in this chapter, I assumed that all species have the same resource breadth $b \geq 1$, and the same competitive breadth $n \leq b$ (i.e., they outcompete other species for the same number of resources/they have the same number of primary resources). In this section, I will continue to assume that all species have the same resource breadth. However, I will consider scenarios where n varies across species. To simplify my model, I will only consider scenarios where each species has either $n = 1$ or $n = b$ primary resources. Biologically, species that can outcompete other species for a disproportionate number of resources might be problematic invasive species, although this may not always be the case. More generally, our goal is not to model specific biological examples, but rather to examine how variation competitive breadth across a community impacts functional redundancy. As in my previous models for equal competition, I will assume that no resource is a primary resource for more than one species.

As in my previous EF and NP models, I will assume that every resource is a primary resource for some species. This, along with the aforementioned assumptions, forces there to be exactly $R = S + b - 1$ available resources in the metacommunity. Figure 3.1 shows an example of how S species might use various resources in the metacommunity. For each species i, R_{ij} denoted its j^{th} resource. The circled resources are primary, and are all distinct. The non-circled resources are secondary for that particular species, but they are primary for some other species.

3.3.1 Species richness

I begin by deriving an expression for the species richness of the local community under the assumptions of my unequal competition model. There are two types of species: a single species that has b primary resources (hereafter referred to as the *alpha species*), and the remaining $S - 1$ species that have only one primary resource (hereafter referred to as *beta species*).

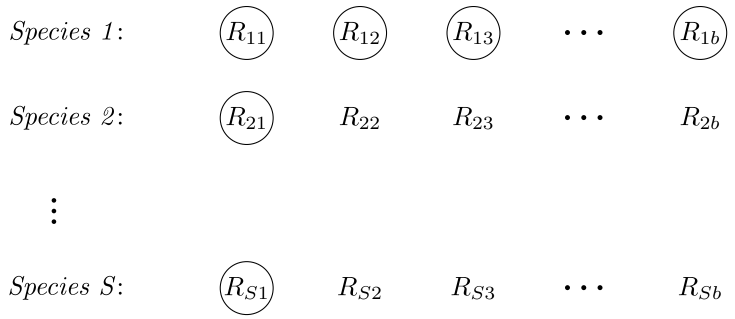

Figure 3.1: In the unequal competition model in this section, one species from the metacommunity will outcompete all others for each of its b resources, whereas the other $S-1$ species all only outcompete a single resource. R_{ij} denoted the j^{th} resource of each i species. Primary resources are circled, and by assumption, no resource is primary for more than one species. Secondary resources are non-circled but are primary for other species.

Beta species A species that outcompetes other species for exactly one resource will persist in the local community if and only if its primary resource is local. Assuming that all resources are equally likely to be found in the local community, this occurs with probability $p_\beta = \frac{r}{R}$.

Alpha species A species that outcompetes other species for every resource that it uses will persist in the local community if and only if at least one of its b primary resources is local. The analysis is similar to persistence in Chapter 2. Assuming that all resources are equally likely to be found in the local community, the probability that at least one of the b resources used by an alpha species uses will be found in the local community is identical to the expressions derived in Equation 2.11 and Equation 2.12:

$$p_\alpha = \sum_{k=\max(1,b+r-R)}^{\min(b,r)} \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}.$$

Let ρ_j be a focal resource in the metacommunity. Assuming that all resources are equally likely to be the primary resource of a beta species, ρ_j will be one of the b primary resources of the alpha species with probability $\frac{b}{R}$. Otherwise, it will be the primary resource for one of the $S-1$ beta species, and this happens with probability $\frac{S-1}{R}$. Note that these two probabilities sum to 1 because $R = S + b - 1$. Therefore, assuming that all resources in the metacommunity are equally likely to be in the local community, the probability that ρ_j is in the local community is

$$p = \frac{S-1}{R} \cdot \frac{r}{R} + \frac{b}{R} \sum_{k=\max(1,b+r-R)}^{\min(b,r)} \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}. \tag{3.18}$$

The local species richness is then given by $s = Sp$.

3.3.2 Functional redundancy of local resources: Ω_p

I now derive an expression for local functional redundancy. Let ρ_{p_j} be a focal local resource. ρ_{p_j} could be a primary resource for the alpha species, or for any one of the beta species. I will consider these two cases separately.

- **Case α:** ρ_{p_j} *is a primary resource of the alpha species.* In this scenario, none of the $s-1$ beta species in the local community can use ρ_{p_j} as their primary resource. However, a beta species might use ρ_{p_j} as one of its $b-1$ secondary resources. Indeed, any given beta species will do so with probability $\frac{b-1}{R-1}$. Therefore, the expected number of local species that use ρ_{p_j} is

$$\Omega_{p_\alpha} = 1 + (s-1)\frac{b-1}{R-1}. \tag{3.19}$$

- **Case β:** ρ_{p_j} *is a primary resource for one of the beta species.* Of the s local species, exactly $s-2$ are beta species that do not use ρ_{p_j} as a primary resource (there are $s-1$ beta species and one of them uses ρ_{p_j}). Assuming that these species are equally likely to use any resource in the metacommunity, then each beta species will use ρ_{p_j} with probability $\frac{b-1}{R-1}$. The alpha species cannot use ρ_{p_j} as a secondary resource because it has no secondary resources. Thus, similar to the equal competition case in Section 3.2.2.2, the expected number of local species that use ρ_{p_j} is

$$\Omega_{p_\beta} = 1 + (s-2)\frac{b-1}{R-1}. \tag{3.20}$$

Assuming that resources are equally likely to be primary for the alpha species or a beta species, the focal local resource, ρ_{p_j} should be the primary resource of a beta species with probability $\frac{S-1}{R}$, and is a primary resource of the alpha species with probability $\frac{b}{R} = 1 - \frac{S-1}{R}$. Therefore, the functional redundancy of each local resource is the weighted average given by

$$\Omega_p = \frac{b}{R}\,\Omega_{p_\alpha} + \frac{S-1}{R}\,\Omega_{p_\beta} = \frac{b}{R}\left(1+(s-1)\frac{b-1}{R-1}\right) + \frac{S-1}{R}\left(1+(s-2)\frac{b-1}{R-1}\right). \qquad (3.21)$$

3.3.3 Functional redundancy of nonlocal resources: Ω_a

Next, I derive an expression for nonlocal functional redundancy. Let ρ_{a_j} be a focal nonlocal resource. ρ_{a_j} could be a primary resource for the alpha species, or for any one of the beta species. Again, I will consider these two cases separately.

- **Case** α: ρ_{a_j} *is a primary resource for the alpha species.* Similar to the arguments laid out in Section 3.2.2.2, I assume that the alpha species wins $\max(1, b+r-R) \le k \le \min(b, r)$ local resources, with probability $\frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}$. This leaves $b-k$ nonlocal primary resources that it will use with probability $\frac{b-k}{R-r}$. Therefore, the probability of a local alpha species using a given nonlocal resource is
$$\sum_{k=\max(1,b+r-R)}^{\min(b,r)} \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} \cdot \frac{b-k}{R-r}.$$
- **Case** β: ρ_{a_j} *is a primary resource for one of the beta species.* Let i be a focal local beta species. If species i lives in the local community, its sole primary resource must be local, which will occur with probability $\frac{r}{R}$. nonlocal resources cannot be primary, but they can be among the $b-1$ secondary resources used by species i. Assuming that all of the $R-1$ non-primary resources are equally likely to be used, the probability that species i uses any focal resource is $\frac{b-1}{R-1}$. Therefore, the probability of a local beta species using a focal nonlocal resource is
$$\frac{r}{R} \cdot \frac{b-1}{R-1}.$$

The nonlocal functional redundancy, Ω_a, of local species can then be expressed as the weighted average of the number of alpha and beta species that use a given nonlocal resource. Specifically, this is the product

$$\Omega_a = S\left(\frac{S-1}{R} \cdot \frac{r}{R} \cdot \frac{b-1}{R-1} + \frac{b}{R} \sum_{k=\max(1,b+r-R)}^{\min(b,r)} \frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} \cdot \frac{b-k}{R-r}\right). \qquad (3.22)$$

3.3.4 Approximations

Similar to EF models (Chapter 2) and equal competition NP models (Chapter 3.2), the formulas that I derived for unequal competition NP models are generally too complicated to have simple and intuitive closed forms. However, they can be approximated given certain reasonable assumptions on the parameters. To approximate the probability of any given species being able to persist in the local community, p (see Equation 3.18), I again make the biologically reasonable assumption that $R \gg r$, which means that $(R-r-1)! \approx R!$ and $(R-r-b)! \approx (R-b)!$. Additionally, when $R-r \gg b-1$, $(R-r-1)\cdots(R-r-(b-1)) \approx (R-r)^{b-1}$ and when $R \gg b$ and $R-r \gg b-1$ $R(R-1)\cdots(R-b) \approx R^{b+1}$. Using these approximations, the probability, p, of any given species being able to persist in the local community simplifies to

$$p \approx \frac{b}{R}\left(1-\left(1-\frac{r}{R}\right)^{b}\right)+\frac{S-1}{R}\cdot\frac{r}{R}. \tag{3.23}$$

Extending this approximation to local functional redundancy, Ω_p, Equation 3.21 simplifies to

$$\begin{aligned}
\Omega_p \approx\ & \frac{b}{R}\left[1+\left(S\left[\frac{b}{R}\left(1-\left(1-\frac{r}{R}\right)^{b}\right)+\frac{S-1}{R}\cdot\frac{r}{R}\right]-1\right)\frac{b-1}{R-1}\right] \\
&+\frac{S-1}{R}\left[1+\left(S\left[\frac{b}{R}\left(1-\left(1-\frac{r}{R}\right)^{b}\right)+\frac{S-1}{R}\cdot\frac{r}{R}\right]-2\right)\frac{b-1}{R-1}\right] \\
=\ & \frac{b}{R}\left[1+\left(\frac{Sb}{R}\left[1-\left(1-\frac{r}{R}\right)^{b}\right]+\frac{S-1}{R}\cdot\frac{Sr}{R}-1\right)\frac{b-1}{R-1}\right] \\
&+\frac{S-1}{R}\left[1+\left(\frac{Sb}{R}\left[1-\left(1-\frac{r}{R}\right)^{b}\right]+\frac{S-1}{R}\cdot\frac{Sr}{R}-2\right)\frac{b-1}{R-1}\right] \\
=\ & 1+\left(\frac{Sb}{R}\left[1-\left(1-\frac{r}{R}\right)^{b}\right]+\frac{S-1}{R}\cdot\frac{Sr}{R}-1-\frac{S-1}{R}\right)\frac{b-1}{R-1} \\
=\ & 1+\left(\frac{Sb}{R}\left[1-\left(1-\frac{r}{R}\right)^{b}\right]+\frac{S-1}{R}\left[\frac{Sr}{R}-1\right]-1\right)\frac{b-1}{R-1}.
\end{aligned} \tag{3.24}$$

Even using the approximations outlined above, the formula for nonlocal functional redundancy, Ω_a, is more complicated due to the summation term that contains the EF functional redundancy originally derived in Equation (2.16). However, as in EF models (see Equation 2.18), I can approximate the functional redundancy of nonlocal resources, under the same assumptions that $R-r \gg b-1$,

$R - r \gg b - 1$, $R \gg b$, and $R - r \gg b - 1$. This gives:

$$\begin{aligned}\sum_{k=\max(1,b+r-R)}^{\min(b,r)} S\frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} \cdot \frac{b-k}{R-r} &= \frac{Sb}{R} - \frac{(R-b)bS\Gamma(R-r)\Gamma(R-b)}{\Gamma(R-r+1-b)\Gamma(R+1)} \\ &\approx \frac{Sb}{R} \cdot \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right).\end{aligned} \tag{3.25}$$

Using the same approximation methods in Equation (2.18), the functional redundancy, Ω_a, of the niche partitioning with unequal competition model simplifies to

$$\Omega_a \approx S\left[\frac{S-1}{R} \cdot \frac{r}{R} \cdot \frac{b-1}{R-1} + \frac{b}{R} \cdot \frac{b}{R}\left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right)\right]. \tag{3.26}$$

3.4 Summary

In this Chapter, I developed models for functional redundancy under the niche partitioning paradigm of community assembly. That is, a species can persist in a local community if it can both find *and* outcompete all other species for at least one local resource. As in Chapter 2 for EF models, I assumed that the resources were substitutable. Thus, a species can use any one of its usable resources to fulfill requirements for survival, reproduction, etc. For NP models, I only considered scenarios where all species use the same number of resources. This implies a delta distribution for the resource breadth, b. Within this subset of scenarios, I began by considering a delta distribution for competitive breadth (*equal competition*), such that all species have use the same number of primary resources, n (and thus the same number of secondary resources as well, $b - n$). I then extended my models to consider scenarios with alternate competitive breadth distributions (*unequal competition*). In particular, I considered scenarios where one species has b primary resources (and thus no secondary resources), while all other species have one primary resource (and thus $b - 1$ secondary resources). Regardless of the competitive breadth distribution (e.g., equal vs. unequal competition), the NP functional redundancies Ω_p and Ω_a both increase logarithmically with $1 - \frac{r}{R}$ (see Equation (3.13), Equation (3.17), Equation (3.24), Equation (3.26)). More specifically, the local and nonlocal functional redundancies under the niche partitioning are

- **Equal competition:**

$$
\begin{aligned}
\Omega_p &= 1 + \left[S\left(1 - \left(1 - \frac{r}{R}\right)^n\right) - 1\right]\frac{b-n}{R-n}\\
\Omega_a &= S\left[\frac{n}{R}\left(1 - \left(1 - \frac{r}{R}\right)^{n-1}\right) + \frac{b-n}{R-n}\left(1 - \left(1 - \frac{r}{R}\right)^n\right)\right].
\end{aligned}
$$

- **Unequal competition:**

$$
\begin{aligned}
\Omega_p &= 1 + \left(\frac{Sb}{R}\left[1 - \left(1 - \frac{r}{R}\right)^b\right] + \frac{S-1}{R}\left[\frac{Sr}{R} - 1\right] - 1\right)\frac{b-1}{R-1}\\
\Omega_a &= S\left[\frac{S-1}{R}\cdot\frac{r}{R}\cdot\frac{b-1}{R-1} + \frac{b}{R}\cdot\frac{b}{R}\left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right)\right].
\end{aligned}
$$

While total functional redundancy is:

$$\Omega_t = \frac{r}{R}\Omega_p + \frac{R-r}{R}\Omega_a.$$

Thus, the functional redundancies of the various NP scenarios have the same qualitative behaviors. That is, in general, niche partitioning assembly results in monotonically increasing functional redundancy with local resource complexity. This is in stark contrast with EF models, where local functional redundancy was independent of resource complexity. Thus, the relationship between functional redundancy and local resource complexity is different between these two community assembly models, regardless of whether competition is equal or not. This is interesting because it suggests that local functional redundancy might provide a signal of the mode of community assembly. In particular, given enough data, it should be possible to plot functional redundancy against resource complexity and then use this to infer which community assembly model is most important to structuring any given community. If local functional redundancy is constant with respect to environmental complexity, the community is likely assembled according to EF. By contrast, if local functional redundancy increases with environmental complexity, the community is likely structured by NP (i.e., competition is important).

Figure 3.2 shows that all functional redundancies for niche partitioning with equal competition are positively correlated to the environmental complexity with an increasing curvilinear trend and same absolute maximum values. The maximum value of the functional redundancy for niche partitioning is the local FR from the basic environmental filtering model. The saturation points of the functional redundancy in this case are high local resource complexities. Therefore, the saturation speed is slower than the one with environmental filtering. Higher number of resource breadth, b, results in higher maximum value. Hence, lower b decreases the slope of the functional redundancy in this scenario. In other words, lower b slows the saturation speed (Figure 3.2 A). Increasing the number of metacommunity resources means either increasing the number of species or the number of primary resources or both. Higher number of primary resources results in increasing slopes of the functional redundancy but constant saturation speed (Figure 3.2 B). Increasing the number of species, the functional redundancy slopes increase and the saturation speed decelerates. Similar to environmental filtering, increasing the number of species while fixing the other parameters increases the maximum value of the functional redundancy (Figure 3.2 C). Considering all the parameters of interest (R, S, b, n) the same, all different distributions explored (right triangular, uniform, center triangular, delta, left triangular, logseries, lognormal, exponential and negative binomial) result in reasonably same functional redundancy trends (Figure 3.2 D). This is different from what I found in the environmental filtering case.

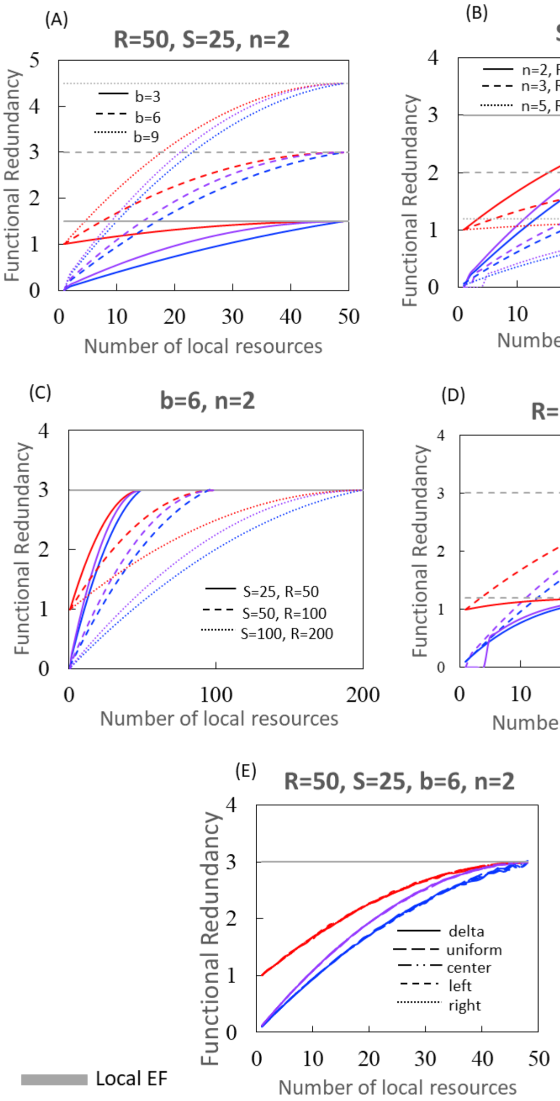

Figure 3.2: Functional redundancies with equal resource use, and a delta competition breadth: Ω_p (Red lines), Ω_a (blue lines), Ω_t (purple lines). (A-D): with delta breadth distribution. (A): the effect of the number of resources used by each species (b) with $R = 50, S = 25, n = 2$; (B) the number of resources present in the metacommunity (R) or the competition breadth (n), with $S = 25, b = 6$; (C) the number of consumer species present in the metacommunity (S) or the number of resources present in the metacommunity (R), with $b = 6$, $n = 2$; (D) the number of consumer species present in the metacommunity (S) or the competition breadth (n) with $b = 6$, $R = 50$; (E) the shape of the resource breadth distribution (delta, uniform, left, center, right).

Referring to Figure 3.3, with the unequal competition niche partitioning, all functional redundancies are positively correlated to environmental complexity and tend to a more linear trend for lower values of resource breadth. The maximum value for the functional redundancy in this scenario is the local functional redundancy of the basic environmental filtering. The saturation point of the functional redundancy is the total number of resources, R. That is, the saturation speed is really slow compared to the environmental filtering and the niche partitioning with equal competition. Higher number of resource breadth results in higher maximum value (Figure 3.3 A). Since the saturation point is the number of metacommunity resources, lower breadth resources decreases the slope of the functional redundancy but has a rapid saturation speed compare to higher ones (Figure 3.3 A). In contrast with the basic niche partitioning, the nonlocal functional redundancy does not saturate to the maximum value when the distribution of winning is not even among the species. With the unequal niche partitioning, increasing the number of species rises the total number of metacommunity resources when keeping the resource breadth fixed. Therefore, similar to the environmental filtering, the maximum value of the functional redundancy increases with the number of species in the unequal competition case (Figure 3.3 B). As the total number of metacommunity resources increases, the saturation speed is getting slower (Figure 3.3 B–C). In Figure 3.3 C, due to the relation $R = S + w(b-1)$, increasing the number of species, w, that outcompete other species for all of its b resources, rises the total number of metacommunity resources when keeping the number of species and b fixed. Nevertheless, the maximum value of the functional redundancy decreases when there are more strong competitors (species outcompete others for their entire b resources), and the trend tends to be more curvilinear. Therefore, increase in the number of strong competitors results in lower slopes of the functional redundancies and slower speed of reaching its maximum value (Figure 3.3 C). Considering other distributions of the breadth resources, the trend of the functional redundancy stays the same for each of the breadth distributions (Figure 3.3 D). Since the uniform breadth distribution has the highest value of $b = 15$ compared to the other models, it has the highest slope of the functional redundancy as well. The delta breadth distribution has higher functional redundancy slope than the triangular distributions. The maximum values of the functional redundancy for the distributions other than the delta are smaller than the Ω_p from the environmental filtering model.

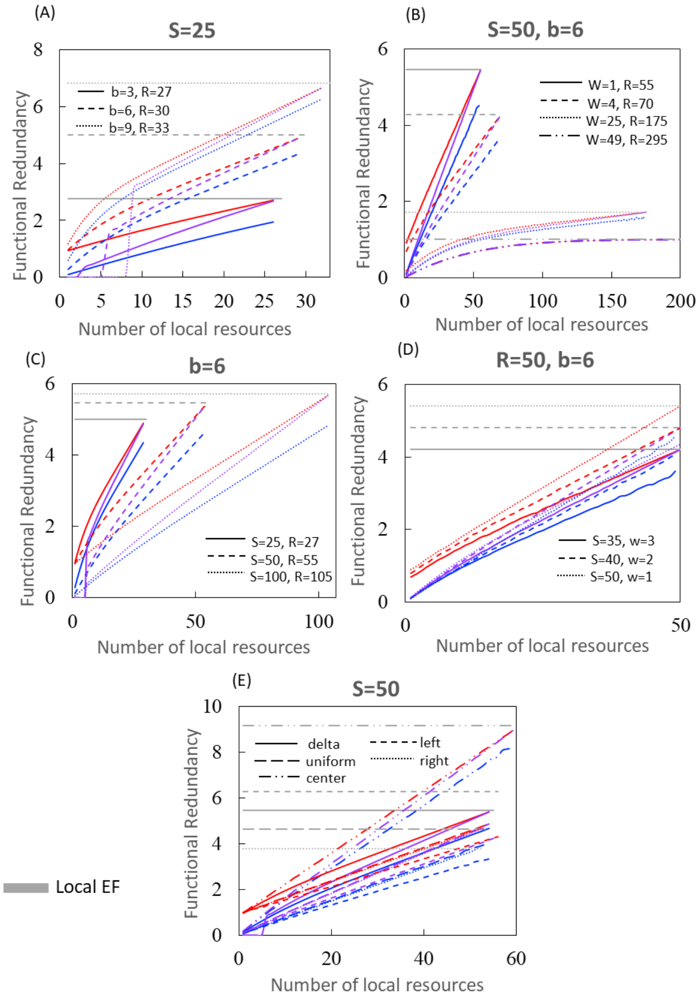

Figure 3.3: Functional redundancies with equal resource use with uneven distribution of competition breadth ($S - w$ species win only one resource while the other w win all of their resources): Ω_p (Red lines), Ω_a (blue lines), Ω_t (purple lines). (A-D): with delta breadth distribution. (A): the effect of the number of resources used by each species $S = 25, w = 1$; (B) the number of resources present in the metacommunity (R) or the unevenness of competition breadth (w); (C) the number of consumer species (S) or the resources present in the metacommunity with breadth $b = 6$, $w = 1$; (D) the number of consumer species (S) or the competition breadth (w) with $R = 50, b = 6$; (E) the shape of the resource breadth distribution (delta, uniform, left, center, right).

Chapter 4

Non-substitutable resources

In the models proposed in Chapter 2 and Chapter 3, all resources were *substitutable*. Thus, for Chapter 2, a species could persist (in the local community or metacommunity) if it could find any one of its usable resources. In Chapter 3, I imposed restrictions involving competition, but resources remained substitutable. Thus, a species could persist if it could find *and* outcompete other species for any one of its usable resources. In this chapter, I extend my models to consider nonsubstitutable resources. These are resources that satisfy different requirements for reproduction, survival, etc. As a motivating example, microbes must be able to find both a carbon source and a nitrogen source in order to survive. Typically, the chemicals that a microbial taxon can use as a carbon source are distinct from the chemicals that it can use as a nitrogen source.

For fully nonsubstitutable resources (i.e., those where having more of one type of resource does not compensate for having less of another), each category of resource can be treated independently from the others. To understand how the presence of multiple nonsubstitutable resource categories impact functional redundancy, I will look at each resource category individually. In general, there could be many different resource categories (different categories of micronutrients, different categories of macronutrients, shelter, breeding sites, etc.) and I can index these different categories as $U = \{1, \ldots, u\}$. For my thesis, I will only consider $u = 2$ (i.e., two categories, for example carbon sources and nitrogen sources).

To differentiate between resource categories, I use subscripts on the same notation described in Chapter 1. For instance, for resource category q (e.g., carbon sources), I can define the following:

- R_q: the number of resources of category q in the metacommunity,
- r_q: the number of resources of category q in the local community,
- b_q: the resource breadth of a given species specifically for resource category q. That is, each species is capable of using b_q resources from resource category q,
- p_q: the probability that a species can use at least one resource from category q that is present in the local community.
- Ω_{p_q}: the functional redundancy of each local category q resource,
- Ω_{a_q}: the functional redundancy of each nonlocal category q resource.

As before, let $R = \sum_{q \in U} R_q > 2$ be the total number of resources in the metacommunity, $r = \sum_{q \in U} r_q > 2$ the number of resources in the local community, and $b = \sum_{q \in U} b_q > 2$ the resource breadth of the species. The analysis in this chapter will be conducted with $u = 2$, that is only two different sources will be considered. Such a scenario is said to be *two-dimensional*, and the aforementioned definitions are illustrated by an example in Figure 4.1. In Section 4.1, I will look at the functional redundancy of individual resources from each source, against the environmental complexity, with only environmental filtering as the community assembly. Section 4.2 will consider only the niche partitioning as the community assembly. Finally, in Section 4.2.3, a mixture of environmental filtering and niche partitioning will be examined.

4.1 Environmental filtering

In this Section, I consider two resource categories that both follow the EF model of community assembly. Thus, each species needs to find at least one usable resource from each resource category in order to persist in the local community. Throughout this section, I assume that b follows a delta distribution, and then I consider different values of b. Using the notation indexed by resource categories, each source q has a resource breadth b_q. That is, a species should be capable of using b_q resources from category q. As mentioned, I assume a two-dimensional scenario, such that there are two resource categories, denoted C_1 and C_2. Because $b = b_1 + b_2$, where $b_q \in \mathbb{N} \backslash \{0\}$, $b \geq 2$ for two different resource categories.

4.1.1 Case studies for $b = 2$ and $b = 3$

Resource breadth $b = 2$

This scenario is similar to Section 2.1.1.1 of Chapter 2, but with different *persistence criteria*. In this case, every species must find at least one usable resource from *each* resource category to persist in the local community. As a consequence, the resource breadth for each resource category must be $b_1 = b_2 = 1$, such that $b = b_1 + b_2 = 2$. The probability that a randomly selected species from the metacommunity uses at least one local resource from any single resource category was derived in Equation (2.1) of Chapter 2. The probability that a randomly selected species from the metacommunity uses at least one local resource for *two* resource categories is then the product of the probability for each individual resource category:

$$p = \prod_{q \in U} p_q = \prod_{q \in U} \frac{r_q}{R_q} = \frac{r_1 r_2}{R_1 R_2}. \tag{4.1}$$

Multiplying Equation (4.1) by the number of species in the metacommunity, S, gives the expected number of species that can live in the local community, s. For each local resource from each resource category q, the number of local species that can use it is then given by:

$$\Omega_p^q = \frac{s}{r_q} = S \frac{\prod\limits_{j \in U} \frac{r_j}{R_j}}{r_q} = S \frac{\prod\limits_{j \in U \setminus \{q\}} r_j}{\prod\limits_{j \in U} R_j}. \tag{4.2}$$

That is, $\Omega_p^1 = S \frac{r_2}{R_1 R_2}$ and $\Omega_p^2 = S \frac{r_1}{R_1 R_2}$. Thus, local functional redundancy depends on resource complexity. However, this dependence is on the complexity of the *alternate* resource. Thus, for instance, increasing the diversity of nitrogen sources should increase carbon source functional redundancy, while increasing the diversity of carbon sources should increase nitrogen source functional redundancy. Similar to one-dimensional models, the complexity of the focal resource category remains independent of the resource complexity of that resource category.

In the case that $b = 2$, there can be no species that use nonlocal resources from either resource category q. Thus, $\Omega_a^q = 0$.

Resource breadth $b = 3$ In this scenario, b can be partitioned between the two resource categories in two ways, either $(b_1 = 1, b_2 = 2)$ or $(b_1 = 2, b_2 = 1)$. I will only treat the case $b_1 = 1$ and $b_2 = 2$; the other case is symmetric. The probability, p_1, of a species being able to use at least one local resource from the first resource category, C_1, can be derived using a similar argument as in Equation (2.1). Meanwhile, the probability, p_2 of a species being able to use at least one local resource from the second resource category, C_2 is given by an expression similar to Equation (2.5). The probability of a species being able to find at least one local resource from *both* resource categories is then the joint probability:

$$p = p_1 p_2 = \frac{r_1}{R_1} \frac{2r_2R_2 - r_2^2 - r_2}{R_2\,(R_2 - 1)}. \tag{4.3}$$

Multiplying Equation (4.3) by the number of species, S, in the metacommunity gives the expected number of species that can live in the local community as $s = Sp$. For any given focal local species, there are two possible resource distributions based on the values of r_1 and r_2.

- One local resource from C_1, one local resource from C_2 and one nonlocal resource from C_2, or
- One local resource from C_1 and two local resources from C_2 (assuming $r_2 \geq 2$).

First, I consider the functional redundancy of local resources. Again, I treat the functional redundancy of resources from each different resource category independently. Following the reasoning in 4.1.1 and accounting for the two possible resource distributions outlined above, the probability of any focal local species using any focal local resource from resource category C_1 is $\frac{1}{r_1}\frac{r_1 r_2(R_2 - r_2)}{R_1\binom{R_2}{2}} + \frac{1}{r_1}\frac{r_1\binom{r_2}{2}}{R_1\binom{R_2}{2}}$. Likewise, the probability of any focal local species using any focal local resource from resource category C_2 is $\frac{1}{r_2}\frac{r_1 r_2(R_2 - r_2)}{R_1\binom{R_2}{2}} + \frac{2}{r_2}\frac{r_1\binom{r_2}{2}}{R_1\binom{R_2}{2}}$. Therefore, the functional redundancies of local resources from resource categories C_1 and C_2 are:

$$\begin{aligned} \Omega_p^1 = S\left(\frac{1}{r_1}\frac{r_1 r_2(R_2 - r_2)}{R_1\binom{R_2}{2}} + \frac{1}{r_1}\frac{r_1\binom{r_2}{2}}{R_1\binom{R_2}{2}}\right) &= S\left(\frac{2r_2(R_2 - r_2)}{R_1R_2(R_2 - 1)} + \frac{r_2(r_2 - 1)}{R_1R_2(R_2 - 1)}\right) \\ &= S\frac{2r_2(R_2 - 1) - r_2^2}{R_1R_2(R_2 - 1)}, \end{aligned} \tag{4.4}$$

$$\begin{aligned} \Omega_p^2 = S\left(\frac{1}{r_2}\frac{r_1 r_2(R_2 - r_2)}{R_1\binom{R_2}{2}} + \frac{2}{r_2}\frac{r_1\binom{r_2}{2}}{R_1\binom{R_2}{2}}\right) &= S\left(\frac{2r_1(R_2 - r_2)}{R_1R_2(R_2 - 1)} + \frac{2r_1(r_2 - 1)}{R_1R_2(R_2 - 1)}\right) \\ &= S\frac{2r_1(R_2 - 1)}{R_1R_2(R_2 - 1)} = \frac{2Sr_1}{R_1R_2}, \end{aligned} \tag{4.5}$$

respectively. As was the case for $b = 2$, both Ω_p^1 and Ω_p^2 are independent from their respective environmental complexity, r_1 and r_2. This is consistent with my findings for local functional redundancy in Section 2.1 on EF in one dimension (i.e., a single substitutable resource). Interestingly, however, analysing the local functional redundancy of each resource category against environmental complexity of the other resource category, Ω_p^1 exhibits a quadratic dependence on r_2, while Ω_p^2 exhibits a quadratic dependence on r_1. This is in keeping with findings for $b = 2$, where the functional redundancy of one resource category was dependent on the environmental complexity of the other resource category.

Next, I consider the functional redundancy of nonlocal resources. Because $b_1 = 1$, no local species can use a nonlocal resource from resource category C_1. Therefore, $\Omega_a^1 = 0$. For resource category C_2, a local species can use either one local and one nonlocal resource or two local resources. This gives the functional redundancy of any given nonlocal resource from C_2 as

$$\Omega_a^2 = S\frac{1}{R_2 - r_2}\frac{2r_1r_2}{R_1R_2}. \tag{4.6}$$

Hence, when species can only use one resource from a particular resource category, C_i, (i.e. $b_i = 1$), the nonlocal functional redundancy of any resource within the category is constant (and equal to zero) with respect to its own resource complexity, r_i, as well as the resource complexities of other resource categories. However, when species can use more than one resource from a particular resource category (i.e., $b_i = 2$), the nonlocal functional redundancy of any resource within the category, Ω_a^i, increases linearly with respect to the resource complexity of resources from other resource categories, and exhibits a nonlinear dependence on the resource complexity of its own resource category.

4.1.2 General expressions for functional redundancy

For general b, a given species uses at least one local resource from resource category C_i with probability p_i, derived in Equation (2.11). Therefore, the likelihood of using at least one local resource from each resource category is the product of the p_i's

$$p = \prod_{i\in U} p_i = \prod_{i\in U} \sum_{k=\max(1,b_i+r_i-R_i)}^{\min(b_i,r_i)} \frac{\binom{r_i}{k}\binom{R_i-r_i}{b_i-k}}{\binom{R_i}{b_i}}. \tag{4.7}$$

Multiplying the probability, p, in Equation (4.7) by the number of species in the metacommunity,

S, gives the expected number of species that can persist in the local community, $s = Sp$.

For each resource category C_i, the probability of any given local resource being used by a particular local species that uses $k-1$ additional local resources and $b_i - k$ nonlocal resources from the same resource category is given by $\frac{k}{r_i}\frac{\binom{r_i}{k}\binom{R_i-r_i}{b_i-k}}{\binom{R_i}{b_i}}\prod_{j\in U\backslash\{i\}} p_j$, where $U\backslash\{i\}$ is the set of resource categories other than resources category C_i.

Therefore, the number of species that use each local resource from resource category C_i is

$$\Omega_p^i = S \sum_{k=\max(1,b_i+r_i-R_i)}^{\min(b_i,r_i)} \frac{k}{r_i}\frac{\binom{r_i}{k}\binom{R_i-r_i}{b_i-k}}{\binom{R_i}{b_i}} \prod_{j\in U\backslash\{i\}} p_j, \tag{4.8}$$

where $p_j = \sum_{k=\max(1,b_j+r_j-R_j)}^{\min(b_j,r_j)} \frac{\binom{r_j}{k}\binom{R_j-r_j}{b_j-k}}{\binom{R_j}{b_j}}$.

Following the approximation outlined in Section 2.1.1, $\sum_{k=\max(1,b_i+r_i-R_i)}^{\min(b_i,r_i)} \frac{k}{r_i}\frac{\binom{r_i}{k}\binom{R_i-r_i}{b_i-k}}{\binom{R_i}{b_i}} \approx \frac{b_i}{R_i}$, and $p_j \approx \left(1-\left(1-\frac{r_j}{R_j}\right)^{b_j}\right)$. Therefore, the functional redundancy of local resources for each resource category C_i can be simplified to

$$\Omega_p^i \approx \frac{b_i S}{R_i} \prod_{j\in U\backslash\{i\}} \left(1-\left(1-\frac{r_j}{R_j}\right)^{b_j}\right). \tag{4.9}$$

Thus, similar to the individual case studies, the local functional redundancy for any particular resource category C_i only depends on the environmental complexity of the other resources categories. That is, for the EF model, local functional redundancy of resources in resource category C_i is independent of the resource complexity of resource category C_i, but is an increasing function of the resource complexity of all other resource categories C_j, $j \neq i$. Figure 4.1 shows an illustrated example of EF predictions for functional redundancy for the two-dimensional case (i.e., two nonsubstitutable resource categories).

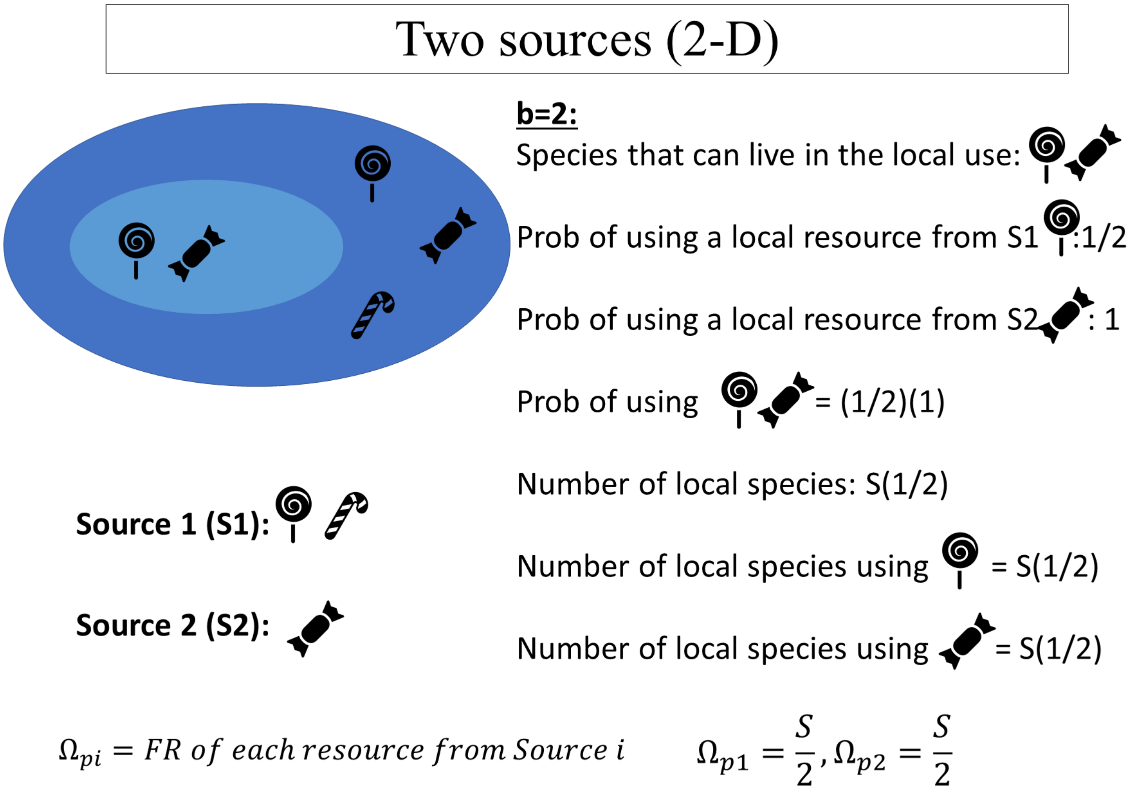

Figure 4.1: Example of a two-dimensional scenario.

To derive an expression for nonlocal functional redundancy, I consider a nonlocal resource from resource category C_i used by a local species that also uses $b_i - (k-1)$ additional nonlocal resources and k additional local resources from the same resource category. Based on arguments presented in Chapter 2, the number of local species that will use this nonlocal resource is given by Equation (2.16). Using the probability given in Equation (4.7), the functional redundancy of each nonlocal resource from resource category C_i is

$$\Omega_a^i = S \sum_{k=\max(1,b_i+r_i-R_i)}^{\min(b_i,r_i)} \frac{b_i - k}{R_i - r_i} \frac{\binom{r_i}{k}\binom{R_i-r_i}{b_i-k}}{\binom{R_i}{b_i}} \prod_{j \in U \setminus \{i\}} p_j. \tag{4.10}$$

Using a similar approximation to that outlined in Section 2.1.1.3, p_j simplifies to

$$\sum_{k=\max(1,b_i+r_i-R_i)}^{\min(b_i,r_i)} \frac{b_i-k}{R_i-r_i}\frac{\binom{r_i}{k}\binom{R_i-r_i}{b_i-k}}{\binom{R_i}{b_i}} \approx \frac{b_i}{R_i}\left(1-\left(1-\frac{r_i}{R_i}\right)^{(b_i-1)}\right).$$

Therefore, Equation (4.10) can be approximated as

$$\Omega_a^i \approx \frac{b_i S}{R_i}\left(1-\left(1-\frac{r_i}{R_i}\right)^{(b_i-1)}\right)\prod_{j\in U\setminus\{i\}}\left(1-\left(1-\frac{r_j}{R_j}\right)^{b_j}\right). \tag{4.11}$$

Notably, the functional redundancy of nonlocal resources from a given resource category depends on the resource complexity of each resource category, including its own. Thus, once again, my findings in higher dimensional (nonsubstitutable resources) EF systems are in line with my findings for a single substitutable resource.

4.2 Niche partitioning

In this section, I once again consider different categories of nonsubstitutable resources. However, this time, I assume that community assembly occurs according to niche partitioning (NP) for all dimensions. For the one-dimensional NP scenario outlined in Chapter 3, a species can persist in the local community if it can find at least one primary resource. For the multi-dimensional nonsubstitutable resource scenario, the analogous requirement is that a species can persist in the local community if it can find at least one primary resource from each resource category. Similar to Chapter 3, I consider equal competition and unequal competition niche partitioning for the nonsubstitutable resources case. The notations of Chapter 3 are adopted in this section by using subscripts of each source.

4.2.1 Equal competition

For the equal competition scenario, each species has the same number $n_i > 0$ of primary resources from resource category C_i. Therefore, I have $R_i = n_i S$ for all resource categories, C_i, where $n = \sum_{i\in U} n_i$. As usual, I will look at several case studies based on specific values of n before moving on to the derivation of general expressions for functional redundancy. Similar to Section 4.1, $n = 1$ is not possible for nonsubstitutable resources.

4.2.1.1 Case studies for $n = 2$ and $n = 3$

Primary resources $n = 2$

For this scenario, each species has exactly one primary resource from resource category C_1 and one primary resource from resource category C_2. That is, $n_1 = 1$ and $n_2 = 1$. A given species will have one local primary resource from C_1 with probability $p_1 = \frac{r_1}{R_1}$ and one local primary resource from C_2 with probability $p_2 = \frac{r_2}{R_2}$. Therefore, the probability, p, of a species persisting in the local community is exactly the same as Equation (4.1). Hence, the number of local species, s, is also the same as of Section 4.1.1.

For a given local resource A from resource category C_i, it is a primary resource for one of the s local species. The remaining $s - 1$ local species can use A as their secondary resource with probability of $\frac{b_i - n_i}{R_i - n_i} = \frac{b_i - 1}{R_i - 1}$. Therefore, the functional redundancy of a local resource from resource category C_i is

$$\Omega_p^i = 1 + (s-1)\frac{b_i - 1}{R_i - 1} = 1 + \left(S\frac{r_1 r_2}{R_1 R_2} - 1\right)\frac{b_i - 1}{R_i - 1}. \tag{4.12}$$

The functional redundancy of local resources from each resource category depends linearly on the resource complexity of each source. This is in contrast with the environmental filtering case of Section 4.1.1, where I found Ω_p^i is constant against the resource complexity of resource category C_i, but is linearly increasing against the resource complexity of the other resource category C_j, $j \neq i$.

A given local species X can use b_i resources from resource category C_i where one of them is in the local and a primary resource of X. The remaining $b_i - 1$ resources can only be used by X as a secondary resource. Therefore, a given nonlocal resource is a used by X as its secondary resource with probability $\frac{b_i - 1}{R_i - 1}$. Hence, the functional redundancy of nonlocal resources from resource category C_i is

$$\Omega_a^i = s\frac{b_i - 1}{R_i - 1} = S\frac{r_1 r_2}{R_1 R_2}\frac{b_i - 1}{R_i - 1}. \tag{4.13}$$

Thus, Ω_a^i depends on the resource complexity of each resource category. This is different from my findings in Section 4.1.1, where Ω_a^i is independent against the resource complexity of the resource category C_i.

Primary resources $n = 3$

Similar to Section 4.1.1, I will only look at the case $(n_1 = 1, n_2 = 2)$, as the other case $(n_1 = 2, n_2 = 1)$ can be treated symmetrically. That is, I will treat the case where species has one primary resource from resource category C_1 and two primary resources from resource category C_2. The probability of a given species to live in the local community is the probability of the given species to has at least one of its primary resources from each resource category C_1 and C_2 in the local community. The probability, p_1, for a species to has at least one of its primary resources from resource category C_1 in the local community is $\frac{r_1}{R_1}$. As for the resource category C_2, since $n_2 = 2$, the probability of a species to have at least one of its primary resources from resource category C_2 in the local community is similar to the one described in Equation (3.6), $\frac{r_2(r_2-1)}{R_2(R_2-1)} + \frac{2r_2(R_2-r_2)}{R_2(R_2-1)}$. Therefore, the probability of a species to be a local species is the joint distribution:

$$p = p_1 p_2 = \frac{r_1}{R_1} \frac{r_2(r_2-1) + 2r_2(R_2-r_2)}{R_2(R_2-1)} = \frac{r_1}{R_1} \frac{r_2(2R_2-1) - r_2^2}{R_2(R_2-1)}. \tag{4.14}$$

Therefore, the expected number of local species is $s = Sp$.

Functional redundancy of local resources for each resource category: For a given local resource from resource category C_1, it is a primary resource for one of the s local species. The remaining $s-1$ local species can use the given resource as a secondary resource, with probability $\frac{b_1-1}{R_1-1}$. For a given local resource from resource category C_2, it is a primary resource for one of the s local species. The remaining $s-1$ can use it as a secondary resource with probability $\frac{b_2-2}{R_2-2}$, since $n_2 = 2$. Therefore, the functional redundancy of local resources from resource category C_1 and C_2 are

$$\Omega_p^1 = 1 + (s-1)\frac{b_1-1}{R_1-1} = 1 + \left(S \frac{r_1}{R_1} \frac{(r_2(2R_2-1) - r_2^2)}{R_2(R_2-1)} - 1 \right) \frac{b_1-1}{R_1-1}. \tag{4.15}$$

$$\Omega_p^2 = 1 + (s-1)\frac{b_2-2}{R_2-2} = 1 + \left(S \frac{r_1}{R_1} \frac{(r_2(2R_2-1) - r_2^2)}{R_2(R_2-1)} - 1 \right) \frac{b_2-2}{R_2-2}. \tag{4.16}$$

Based on equations of the functional redundancy of local resources from each resource category, I can conclude that both of them is an order n_i polynomial on the resource complexity r_i when the other resource complexity r_j, $j \neq i$ are kept fixed. In this case, it is linear $(n_1 = 1)$ against r_1 when r_2 is fixed, and quadratic $(n_2 = 2)$ against r_2 when r_1 is kept constant. The scale of the slopes of the trends against r_1 is the only difference between the Ω_p^1 and Ω_p^2. I will find out in Section 4.2.1.2

if these claims stay the same when I treat the general case of n.

Functional redundancy of nonlocal resources for each resource category: A given nonlocal resource from resource category C_1 is used as a secondary resource by a given local species with probability $\frac{b_1-1}{R_1-1}$, since ($n_1 = 1$). For a given nonlocal resource from resource category C_2, a local species can either have it as a primary resource, with probability $\frac{n_2-1}{R_2-r_2}$, if the local species has only one of its primary resources in the local community; or the local species can only use it as a secondary resource, with probability $\frac{b_2-2}{R_2-2}$, if the local species has both of its primary resources in the local community. Therefore, the functional redundancy of nonlocal resources from resource category C_1 and from C_2 are

$$\Omega_a^1 = s\frac{b_1-1}{R_1-1} = S\frac{r_1}{R_1}\frac{(r_2(2R_2-1)-r_2^2)}{R_2(R_2-1)}\frac{b_1-1}{R_1-1} \tag{4.17}$$

$$\Omega_a^2 = s\left(\frac{n_2-1}{R_2-r_2}+\frac{b_2-2}{R_2-2}\right) = S\frac{r_1}{R_1}\frac{(r_2(2R_2-1)-r_2^2)}{R_2(R_2-1)}\left(\frac{n_2-1}{R_2-r_2}+\frac{b_2-2}{R_2-2}\right). \tag{4.18}$$

The functional redundancy of nonlocal resources from resource category C_1 has the same trend as Ω_p^1 against both resource complexity r_1 and r_2. The one from resource category C_2 still has a linear trend against r_1 when r_2 is held constant, while it is a rational function on r_2. I have Section 4.2.1.2 to get a general sense of the general functional redundancies for the nonsubstitutable case with equal competition niche partitioning assembly.

4.2.1.2 General expressions for functional redundancies

Recall that, $n = \sum_{i\in U} n_i, n_i > 0$, where n_i is the number of primary resources of each species from resource category C_i. As mentioned, I can treat each resource category C_i independently. A species can have k local primary resources from a given resource category C_i and $n_i - k$ nonlocal primary resources from the same given resource category, where $\max(1, n_i + r_i - R_i) \leq k \leq \min(n_i, r_i)$, with probability $\frac{\binom{r_i}{k}\binom{R_i-r_i}{n_i-k}}{\binom{R_i}{n_i}}$. Therefore, the probability of having at least one primary resource from resource category C_i in the local community, p_i, is similar to Equation (3.11). The expected number of local species is

$$s = S\prod_{i\in U}\sum_{k=\max(1,n_i+r_i-R_i)}^{\min(n_i,r_i)}\frac{\binom{r_i}{k}\binom{R_i-r_i}{n_i-k}}{\binom{R_i}{n_i}}. \tag{4.19}$$

Functional redundancy of local resources for each resource category C_i: For a given local resource A from resource category C_i, it is a primary resource of one local species. The remaining local species, $s-1$ (where s is given in Equation (4.19)) can use the given local resource as a secondary resource with probability $\frac{b_i-n_i}{R_i-n_i}$. The functional redundancy of local resources from resource category C_i is

$$\Omega_p^i = 1+\frac{(s-1)(b_i-n_i)}{R_i-n_i} = 1+\frac{\left(S\prod_{i\in U}\sum_{k=\max(1,n_i+r_i-R_i)}^{\min(n_i,r_i)}\frac{\binom{r_i}{k}\binom{R_i-r_i}{n_i-k}}{\binom{R_i}{n_i}}-1\right)(b_i-n_i)}{R_i-n_i}. \tag{4.20}$$

Functional redundancy of nonlocal redundancy for each resource category C_i: Let M be a local species that has k number of local resources from resource category C_i where $\max(1,n_i+r_i-R_i)\le k\le\min(n_i,r_i)$. For a given nonlocal resource from resource category C_i, M can either have it as a primary resource or as a secondary resource. The probability of M having the given nonlocal resource as a primary resource is $\frac{n_i-k}{R_i-r_i}$. The probability of M using the given nonlocal resource as a secondary resource is $\frac{b_i-n_i}{R_i-n_i}$. Since M is a local species, the probability p_j of it outcompeting other species for at least one local resource from the other resource category C_j, $j\neq i$, is similar to Equation (3.11)). Therefore, the functional redundancy of a nonlocal resource from resource category C_i is

$$\Omega_a^i = S\prod_{j\in U\setminus\{i\}}p_j\sum_{k=\max(1,n_i+r_i-R_i)}^{\min(n_i,r_i)}\frac{\binom{r_i}{k}\binom{R_i-r_i}{n_i-k}}{\binom{R_i}{n_i}}\left(\frac{n_i-k}{R_i-r_i}+\frac{b_i-n_i}{R_i-n_i}\right). \tag{4.21}$$

4.2.1.3 Approximation of the general expressions of s, Ω_p^i, and Ω_a^i

Using the approximation methods in Section 3.2.2.1, the expected number of local species, s, simplifies to

$$s\approx S\prod_{i\in U}\left(1-\left(1-\frac{r_i}{R_i}\right)^{n_i}\right). \tag{4.22}$$

From Equation (4.22), I get the approximation of Ω_p^i as

$$\Omega_p^i\approx 1+\left(S\prod_{i\in U}\left(1-\left(1-\frac{r_i}{R_i}\right)^{n_i}\right)-1\right)\frac{b_i-n_i}{R_i-n_i}. \tag{4.23}$$

Similarly, using Equation (4.22) and the approximation of Ω_a in Equation (3.17), Ω_a^i simplifies to

$$\Omega_a^i \approx S\left[\frac{n_i}{R_i}\left(1-\left(1-\frac{r_i}{R_i}\right)^{n_i-1}\right)+\left(1-\left(1-\frac{r_i}{R_i}\right)^{n_i}\right)\frac{b_i-n_i}{R_i-n_i}\right]\prod_{j\in U\backslash\{i\}}\left(1-\left(1-\frac{r_j}{R_j}\right)^{n_j}\right). \tag{4.24}$$

Therefore, both functional redundancy of local resources and nonlocal resources from a given resource category C_i have an order n_i polynomial on r_i when keeping the other r_j, $j \neq i$ fixed.

4.2.2 Unequal competition

For this case, I consider two categories of outcompeting, there is one species that has all of its required resources to be primary, and the remaining species have exactly one primary resources. Therefore, the relation $R_i = S + b_i - 1$ holds for each resource category C_i. Denote α_i and β_i the class of species that has b_i primary resources and exactly one primary resource from a given resource category C_i, respectively. To build a model for the functional redundancy with unequal competition niche partitioning, I will look at specific scenarios based on the values of $b = \sum_{i\in U} b_i, b_i > 0$ and on the notations adopted in this chapter. As in Section 4.1, the scenario $b = 1$ is not part of the two-dimensional case.

4.2.2.1 Case studies $b = 2$ and $b = 3$

Resource breadth $b = 2$

In this case, I have $b_1 = b_2 = 1$. That is, species from β_1 has exactly one primary resource from resource category C_1 and species from α_1 also has one primary resource from C_1. Similarly, species from β_2 has exactly one primary resource from resource category C_2 and species from α_2 also has one primary resource from C_2. Since all species of this scenario has exactly one primary resource from each resource category, local species must have their primary resource in the local community. That is, the probability of a given species to be a local is $\frac{r_1 r_2}{R_1 R_2}$. This scenario can be treated exactly the same as the scenario $n = 2$ in Section 4.2.1.1. Hence,

$$\Omega_p^i = 1 + \left(S\frac{r_1 r_2}{R_1 R_2} - 1\right)\frac{b_i - 1}{R_i - 1}$$
$$\Omega_a^i = S\frac{r_1 r_2}{R_1 R_2}\frac{b_i - 1}{R_i - 1}.$$

Resource breadth $b = 3$

Similar to Section 4.1.1, I will treat the case $(b_1 = 1, b_2 = 2)$ since the other case is symmetrical. A given species persists in the local community if at least one of its primary resource from each resource category C_1 and C_2 are in the local community. All species has exactly one primary resource from resource category C_1. Therefore, same as in 4.2.2.1, the probability of a primary resource from resource category C_1 being in the local community is $\frac{r_1}{R_1}$. For the resource category C_2, species from β_2 has exactly one primary resource from resource category C_2, while the species from α_2 has $b_2 = 2$ primary resources from C_2. If a species is from α_2, the probability of at least one of its two primary resources from C_2 being in the local community is $\frac{\binom{r_2}{2}+r_2(R_2-r_2)}{\binom{R_2}{2}}$. If a species is from β_2, the probability of its one primary resource being in the local community is $\frac{r_2}{R_2}$. Therefore, the expected number of species in the local community is:

$$s = S\left(\frac{1}{R_1}\frac{r_1}{R_1} + \frac{S-1}{R_1}\frac{r_1}{R_1}\right)\left(\frac{2}{R_2}\frac{2r_2R_2 - r_2^2 - r_2}{R_2(R_2-1)} + \frac{S-1}{R_2}\frac{r_2}{R_2}\right). \tag{4.25}$$

Similar reasoning I used in Equation (3.21), Equation (3.22), with the species richness of Equation (4.25) and Equation (2.10), the functional redundancies for each given resource category C_i are

$$\Omega_p^i = \frac{b_i}{R_i}\left(1 + (s-1)\frac{b_i - 1}{R_i - 1}\right) + \frac{S-1}{R_i}\left(1 + (s-2)\frac{b_i - 1}{R_i - 1}\right).$$
$$\Omega_a^i = S\left(\frac{S-1}{R_i}\cdot\frac{r_i}{R_i}\cdot\frac{b_i-1}{R_i-1} + \frac{b_i}{R_i}\cdot\frac{2r_2S}{R_2(R_2-1)}\right).$$

4.2.2.2 General expressions for functional redundancies

More generally, consider a resource category C_i, the probability, $p_i = \sum_{k=\max(1,b_i+r_i-R_i)}^{\min(b_i,r_i)} \frac{\binom{r_i}{k}\binom{R_i-r_i}{b_i-k}}{\binom{R_i}{b_i}}$, of at least one of the b_i primary resources of a species from α_i being in the local community is similar to Equation (2.11) from Chapter 2. For a species from β_i, the probability of the primary resource being in the local community is $\frac{r_i}{R_i}$. Therefore, the expected number of species that can persist in the local community is

$$s = S\prod_{i\in U}\left(\frac{b_i}{R_i}p_i + \frac{S-1}{R_i}\frac{r_i}{R_i}\right). \tag{4.26}$$

To develop the local and nonlocal functional redundancy in this scenario, I use the species richness in Equation (4.26). For a given resource A from resource category C_i, one local species either from α_i class or β_i class has A as its primary resource. When A is a primary resource of a local species form β_i, the remaining local species $s-2$ from β_i can use A as a secondary resource, since the local species from α_i do not have a secondary resource. If A is a primary resource of a species from α_i, all $s-1$ local species from β_i can use A as a secondary resource. Therefore, the functional redundancy of local resources of resource category C_i is

$$\begin{aligned}\Omega_p^i &= \frac{b_i}{R_i}\left(1+\frac{(s-1)(b_i-1)}{R_i-1}\right)+\frac{S-1}{R_i}\left(1+\frac{(s-2)(b_i-1)}{R_i-1}\right)\\ &= 1+(s-1)\frac{b_i-1}{R_i-1}-\frac{S-1}{R_i}\cdot\frac{b_i-1}{R_i-1}\\ &= 1+\left(s-1-\frac{S-1}{R_i}\right)\frac{b_i-1}{R_i-1}.\end{aligned} \tag{4.27}$$

For the nonlocal functional redundancy, the probability of a local species from α_i having k primary local resources from resource category C_i, and has a given nonlocal resource from resource category C_i as a primary resource, is $\frac{b_i-k}{R_i-r_i}$. It use a given nonlocal resource from resource category C_i as a secondary resource with probability 0. Conversely, local species from β_i has a given nonlocal primary resource from resource category C_i with 0 probability, and use a given nonlocal resource from resource category C_i as a secondary resource with probability $\frac{b_i-1}{R_i-1}$. Therefore, the functional redundancy of a given nonlocal resource from source i is

$$\Omega_a^i = S\prod_{j\in U\setminus\{i\}}\left(\frac{b_j}{R_j}p_j+\frac{S-1}{R_j}\frac{r_j}{R_j}\right)\left(\frac{b_i}{R_i}\sum_{k=\max(1,b_i+r_i-R_i)}^{\min(b_i-1,r_i)}\frac{\binom{r_i}{k}\binom{R_i-r_i}{b_i-k}}{\binom{R_i}{b_i}}\frac{b_i-k}{R_i-r_i}+\frac{S-1}{R_i}\frac{r_i}{R_i}\frac{b_i-1}{R_i-1}\right) \tag{4.28}$$

4.2.3 Environmental filtering with niche partitioning

In this section, I have R_E number of resources that are from an environmental filtering pool, and R_N resources from a niche partitioning pool in the metacommunity. A species can persist in the local community if it uses at least one resource from the environmental filtering pool and has at least one primary resource from the niche partitioning pool in the local community. Similar to Section 4.1 and Section 4.2, I can consider the two pool of resources independently.

First, I consider the niche partitioning resources with equal competition case, then I will consider them with unequal competition.

4.2.3.1 Equal competition

As seen previously, I have $R_N = nS$ for the niche partitioning equal competition case. That means, every species has the same number n of primary resources from the niche partitioning pool. The probability of using at least one local resource from the environmental filtering pool, p_E, is similar to Equation (2.11). Same reasoning, Equation (3.11) gives the probability, p_N, of having at least one local primary resource from the niche partitioning pool. Therefore, the expected number of species that can live in the local community is

$$\begin{aligned} s = Sp_Ep_N &= S \sum_{k=\max(1,b_E+r_E-R_E)}^{\min(b_E,r_E)} \frac{\binom{r_E}{k}\binom{R_E-r_E}{b_E-k}}{\binom{R_E}{b_E}} \sum_{k=\max(1,n+r_N-R_N)}^{\min(n,r_N)} \frac{\binom{r_N}{k}\binom{R_N-r_N}{n-k}}{\binom{R_N}{n}}. \\ &\approx S\left(1-\left(1-\frac{r_E}{R_E}\right)^{b_E}\right)\left(1-\left(1-\frac{r_N}{R_N}\right)^{n}\right). \end{aligned} \tag{4.29}$$

If there are no niche partitioning resources, the number of local species that use each local environmental filtering resource, denoted by Ω_p, is given in Equation (2.14) of Chapter 2. Whereas, with niche partitioning resources, the functional redundancy of each local environmental filtering resources in the community is

$$\begin{aligned} \Omega_p^E &= p_N\Omega_p = p_N\frac{b_ES}{R_E}. \\ &\approx \left(1-\left(1-\frac{r_N}{R_N}\right)^{n}\right)\frac{b_ES}{R_E}. \end{aligned} \tag{4.30}$$

Similar reasoning, the functional redundancy of nonlocal resources from the environmental filtering pool is given by Equation (4.31), where Ω_a, given by Equation (2.16) is the number of local species that use each nonlocal resource when only environmental filtering pool is available in the community.

$$\begin{aligned} \Omega_a^E &= p_N\Omega_a. \\ &\approx \left(1-\left(1-\frac{r_N}{R_N}\right)^{n}\right)\left(1-\left(1-\frac{r_E}{R_E}\right)^{b_E-1}\right)\frac{b_ES}{R_E}. \end{aligned} \tag{4.31}$$

For each local resource from niche partitioning pool, the expected number of local species that use it is given by Equation (4.32), derived similarly as the Equation (3.13).

$$\Omega_p^N = 1 + \frac{(p_E p_N S - 1)(b_N - n)}{R_N - n}. \tag{4.32}$$

Following the steps I did to get Equation (3.14), the functional redundancy of nonlocal resources from the niche partitioning pool is

$$\begin{aligned}\Omega_a^N &= p_E \Omega_{a_{eq}} \\ &\approx \left(1 - \left(1 - \frac{r_E}{R_E}\right)^{b_E}\right) S \left(\frac{n}{R_N}\left(1 - \left(1 - \frac{r_N}{R_N}\right)^{n-1}\right) + \frac{b_N - n}{R_N - n}\left(1 - \left(1 - \frac{r_N}{R_N}\right)^{n}\right)\right),\end{aligned} \tag{4.33}$$

where $\Omega_{a_{eq}}$ is the functional redundancy of nonlocal resources from the equal competition niche partitioning pool when I consider zero environmental filtering resources, which is given by Equation (3.14).

4.2.3.2 Unequal competition

To recall, unequal competition means there is one species that has all of its resources as primary resources where the remaining $S-1$ has exactly one primary resource from their resources. That is, the relation $R_N = S + b_N - 1$ holds. The probability of having at least one primary local resource from the niche partitioning pool, p_N, is derived similarly as Equation (3.18). The functional redundancy of the resources from the environmental filtering pool in this case is similar to Equation (4.30) but the probability, p_N, of having at least one primary local resource from the niche partitioning pool is the same as Equation (3.23). Therefore, the functional redundancy of each local and nonlocal environmental filtering resources in the community are

$$\begin{aligned}\Omega_p^E &= p_N \Omega_p \\ &\approx \left(\frac{S-1}{R_N} \cdot \frac{r_N}{R_N} + \frac{b_N}{R_N}\left(1 - \left(1 - \frac{r_N}{R_N}\right)^{b_N}\right)\right) \frac{b_E S}{R_E}. \\ \Omega_a^E &= p_N \Omega_a \\ &\approx \left(\frac{S-1}{R_N} \cdot \frac{r_N}{R_N} + \frac{b_N}{R_N}\left(1 - \left(1 - \frac{r_N}{R_N}\right)^{b_N}\right)\right)\left(1 - \left(1 - \frac{r_E}{R_E}\right)^{b_E - 1}\right) \frac{b_E S}{R_E}.\end{aligned} \tag{4.34}$$

For each local resource from the niche partitioning pool, the functional redundancy is given by Ω_p^N, derived similarly to Equation (3.21) with $s = p_E p_N S$, which gives

$$\Omega_p^N \approx 1 + \left(\left[\left(1 - \left(1 - \frac{r_E}{R_E} \right)^{b_E} \right) \left[\frac{b_N}{R_N} \left(1 - \left(1 - \frac{r_N}{R_N} \right)^{b_N} \right) + \frac{S-1}{R_N} \cdot \frac{r_N}{R_N} \right] S \right] - \frac{S-1}{R_N} - 1 \right) \frac{b_N - 1}{R_N - 1}. \tag{4.35}$$

For each nonlocal resource from the niche partitioning pool, Equation (4.36), where $\Omega_{a_{uneq}}$ is similar to Equation (3.22), the functional redundancy of nonlocal resources from niche partitioning pool with unequal competition case and without environmental filtering resources.

$$\begin{aligned} \Omega_a^N &= p_E \Omega_{a_{uneq}} \\ &\approx \left(1 - \left(1 - \frac{r_E}{R_E} \right)^{b_E} \right) S \left(\frac{S-1}{R_N} \cdot \frac{r_N}{R_N} \cdot \frac{b_N - 1}{R_N - 1} + \frac{b_N}{R_N} \left(1 - \left(1 - \frac{r_N}{R_N} \right)^{b_N} \right) \frac{b_N S}{R_N} \right). \end{aligned} \tag{4.36}$$

4.3 Summary

In summary, this chapter assumed that resources are from two sources which are nonsubstitutable. That is, each species needs to use (for EF) or outcompete (for NP) at least one resource from each source to survive. The assumptions on equal resource and delta breadth distribution described in the previous chapters were also carried out in this chapter. I looked at three cases based on the community assembly of the community and developed the functional redundancies of each source separately.

Case EF: Resources from both sources follow the environmental filtering criteria. That is, a species persists if it uses at least one resource from each source. for each resource category C_i, the local functional redundancy, Ω_p^i only depends on the local resource complexity of the other source (Equation (4.9)). That is, it is only limited by the number of local resources from the other source than source i. More precisely, Ω_p^i is constant against, the r_i local resource complexity of source i, but monotonically increasing with the local resource complexity of the other sources. In contrast, the nonlocal functional redundancy, Ω_a^i in Equation (4.11), depends on the local resource complexity, r_i of source i and on each local resource complexity of other sources. In other words, it is limited by all the number of local resources from each source. More precisely, Ω_a^i is monotonically increasing with each local resource complexity of all sources. The models of functional redundancies for each resource category C_i are:

$$\begin{aligned}
\Omega_p^i &\approx \frac{b_i S}{R_i}\prod_{j\in U\setminus\{i\}}\left(1-\left(1-\frac{r_j}{R_j}\right)^{b_j}\right)\\
\Omega_a^i &\approx \frac{b_i S}{R_i}\left(1-\left(1-\frac{r_i}{R_i}\right)^{(b_i-1)}\right)\prod_{j\in U\setminus\{i\}}\left(1-\left(1-\frac{r_j}{R_j}\right)^{b_j}\right).
\end{aligned}$$

Case NP: Resources from both sources follow the niche partitioning criteria. That is, a species persists if it outcompete others for at least one resource from each source. First, I assumed the equal competition case. That is, for each resource category C_i, all species have the same n_i number of primary resources. In contrast to the Case EF, both local and nonlocal functional redundancy, Ω_p^i and Ω_a^i, in this case depend on all the local resource complexity of each source. More precisely, they are monotonically increasing with each local resource complexity of all sources (Equation (4.23) and Equation (4.24)). That is, they are limited by the number of local resources from all sources. for each resource category C_i, the functional redundancies under the equal competition are:

$$\begin{aligned}
\Omega_p^i &\approx 1+\left(\left[S\prod_{i\in U}\left(1-\left(1-\frac{r_i}{R_i}\right)^{n_i}\right)\right]-1\right)\frac{b_i-n_i}{R_i-n_i}\\
\Omega_a^i &\approx S\left[\frac{n_i}{R_i}\left(1-\left(1-\frac{r_i}{R_i}\right)^{n_i-1}\right)+\left(1-\left(1-\frac{r_i}{R_i}\right)^{n_i}\right)\frac{b_i-n_i}{R_i-n_i}\right]\prod_{j\in U\setminus\{i\}}\left(1-\left(1-\frac{r_j}{R_j}\right)^{n_j}\right).
\end{aligned}$$

Next, I treated the case under unequal competition. That is, for each resource category C_i, among the total S species, there is one strong competitor with b_i primary resources for source i, and $S-1$ competitors with exactly one primary resource from source i. Similar to the equal competition, both local and nonlocal functional redundancy, Ω_p^i and Ω_a^i, depend on all the local resource complexity of each source. More precisely, they are monotonically increasing with each local resource complexity of all sources (Equation (4.27) and Equation (4.28)). That is, they are limited by the number of local resources from all sources. for each resource category C_i, the functional redundancies under the unequal competition are:

$$\begin{aligned}
\Omega_p^i &\approx 1+\left(\left[S\prod_{i\in U}\left(\frac{b_i}{R_i}\left(1-\left(1-\frac{r_i}{R_i}\right)^{b_i}\right)+\frac{S-1}{R_i}\frac{r_i}{R_i}\right)\right]-1-\frac{S-1}{R_i}\right)\frac{b_i-1}{R_i-1}\\
\Omega_a^i &\approx S\left[\frac{b_i}{R_i}\left(1-\left(1-\frac{r_i}{R_i}\right)^{b_i-1}\right)+\frac{S-1}{R_i}\frac{r_i}{R_i}\frac{b_i-1}{R_i-1}\right]\prod_{j\in U\setminus\{i\}}\left[\frac{b_j}{R_j}\left(1-\left(1-\frac{r_j}{R_j}\right)^{b_j}\right)+\frac{S-1}{R_j}\frac{r_j}{R_j}\right].
\end{aligned}$$

Case EF and NP: Resources from one source (called EF source) follow the environmental filtering criteria, whereas, resources from the other source (called NP source) are under the niche partitioning criteria. That is, a species persists if it uses at least one resource from the EF source, and has at least one primary resource from the NP source. In this case, the number of resources form the NP source (resp. EF source) is b_N (resp. b_E). I assumed the source NP with equal competition case and with unequal competition case separately. For both cases, similar to the Case EF, the local functional redundancy of EF resources, Ω_p^E, only depends on the r_N local resource complexity of NP source (Equation (4.30)). More precisely, it is constant against the r_E local resource complexity of EF source, but monotonically increasing against r_N. The nonlocal functional redundancy of NP resources, Ω_a^E, is monotonically increasing against both r_E and r_N (Equation (4.31)). That is, for source EF, the local functional redundancy is limited by only the number of local resources from source NP, whereas, its nonlocal functional redundancy is limited by only the number of local resources from source NP. For the equal competition case for the NP source with n same number of primary resources across species. Similar to the Case NP, the functional redundancies of source NP are monotonically increasing with r_E and r_N (Equation (4.32) and Equation (4.33)). More precisely, they are limited by both local resource complexity of EF source and NP source. The functional redundancies under the equal competition are:

$$
\begin{aligned}
\Omega_p^E &\approx \left(1-\left(1-\frac{r_N}{R_N}\right)^n\right)\frac{b_E S}{R_E}\\
\Omega_a^E &\approx \left(1-\left(1-\frac{r_N}{R_N}\right)^n\right)\frac{b_E S}{R_E}\left(1-\left(1-\frac{r_E}{R_E}\right)^{(b_E-1)}\right)\\
\Omega_p^N &\approx 1+\frac{\left(\left[\left(1-\left(1-\frac{r_E}{R_E}\right)^{b_E}\right)\left(1-\left(1-\frac{r_N}{R_N}\right)^n\right)S\right]-1\right)(b_N-n)}{R_N-n}\\
\Omega_a^N &\approx \left(1-\left(1-\frac{r_E}{R_E}\right)^{b_E}\right)S\left[\frac{n}{R_N}\left(1-\left(1-\frac{r_N}{R_N}\right)^{n-1}\right)+\frac{b_N-n}{R_N-n}\left(1-\left(1-\frac{r_N}{R_N}\right)^n\right)\right].
\end{aligned}
$$

Under the unequal competition case for the NP source, that is, there is one strongly competitor outcompeting other species for b_N resources, and $S-1$ competitors with only one primary resource. Similar to the Case NP, the functional redundancies of source NP are monotonically increasing with r_E and r_N (Equation (4.32) and Equation (4.33)). More precisely, they are limited by both local resource complexity of EF source and NP source. The functional redundancies under the unequal competition are:

$$\Omega_p^E \approx \left[\frac{b_N}{R_N}\left(1-\left(1-\frac{r_N}{R_N}\right)^{b_N}\right)+\frac{S-1}{R_N}\cdot\frac{r_N}{R_N}\right]\frac{b_E S}{R_E}$$

$$\Omega_a^E \approx \left[\frac{b_N}{R_N}\left(1-\left(1-\frac{r_N}{R_N}\right)^{b_N}\right)+\frac{S-1}{R_N}\cdot\frac{r_N}{R_N}\right]\frac{b_E S}{R_E}\left(1-\left(1-\frac{r_E}{R_E}\right)^{(b_E-1)}\right)$$

$$\Omega_p^N \approx 1+\left(\left[\left(1-\left(1-\frac{r_E}{R_E}\right)^{b_E}\right)\left[\frac{b_N}{R_N}\left(1-\left(1-\frac{r_N}{R_N}\right)^{b_N}\right)+\frac{S-1}{R_N}\cdot\frac{r_N}{R_N}\right]S\right]-\frac{S-1}{R_N}-1\right)\frac{b_N-1}{R_N-1}$$

$$\Omega_a^N \approx \left(1-\left(1-\frac{r_E}{R_E}\right)^{b_E}\right)S\left[\frac{S-1}{R_N}\cdot\frac{r_N}{R_N}\cdot\frac{b_N-1}{R_N-1}+\frac{b_N}{R_N}\cdot\frac{b_N}{R_N}\left(1-\left(1-\frac{r_N}{R_N}\right)^{b_N-1}\right)\right].$$

Therefore, for nonsubstitutable resources, I can still distinguish the driver community assembly of a community by looking at individual functional redundancy of each source. for each resource category C_i, fix the r_j's local resource complexity of the other sources and assess the local functional redundancy of source i against its respective r_i to infer the community assembly. If all trends of each source are horizontal lines, the community is based on environmental filtering, and if at least one source has an upward trend of local functional redundancy against its respective local resource complexity, the community involves competitions.

Figure 4.2 shows a summary of 2D case results. The functional redundancy of local resources from axis 1 is constant against the number of local resources from axis 1, while it has an increasing redundancy trend against the number of resources from axis 2. In contrast, the nonlocal and the overall functional redundancy have an upward redundancy trend against both resource axes (Figure 4.2 A). For the 2D niche partitioning with equal winning distribution, the functional redundancy of resources from axis 1 tends toward a linear trend against axis 2 and to an upward redundancy trend against axis 1 (Figure 4.2 B–C). The nonlocal and overall functional redundancy have the same trends as the local one but with higher slopes (Figure 4.2 B–C). Figure 4.2 D–E displays the 2D case with environmental filtering and niche partitioning resource pool with equal resource use and equal winning distribution. The local functional redundancy of resources from the environmental filtering resource pool is constant against the environmental filtering axis and an increasing curvilinearly against the niche partitioning axis. For resources from the niche partitioning pool, the local functional redundancy has an increasing redundancy trend against the environmental filtering axis and a curvilinear upward trend against the niche partitioning axis. Similar results are true for nonlocal and overall functional redundancy but with higher slopes than the local (Figure 4.2 D–E).

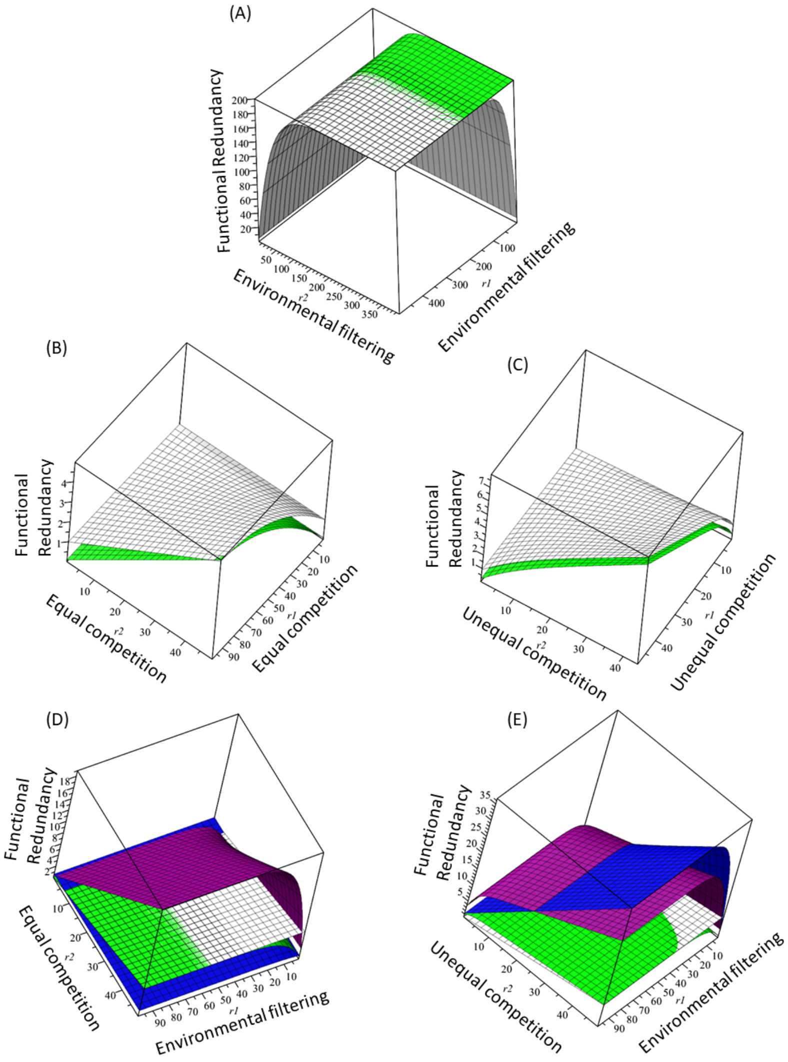

Figure 4.2: Nonsubstitutable resources with two sources of resources: $r1$ denotes the number of local resources from source 1, $r2$ the number of local resources from source 2. White represents Ω_{p1}, green –Ω_{a1} of source 1; blue–Ω_{p1} of NP and purple–Ω_{a1} of NP. A: Basic environmental filtering with $R1 = 100$, $R2 = 50$, $S = 50$, $b1 = 10$ and $b2 = 20$. B–C: Niche partitioning; B with equal competition: $R1 = 100$, $R2 = 50$, $S = 50$, $n1 = 2$, $n2 = 1$, $b1 = 10$ and $b2 = 20$; C with unequal competition: $R = 45$, $S = 41$ and $b = 5$. D–E: Basic environmental filtering, $r1$ axis represents the number of local resources from EF resource pool and $r2$ for number of resources from NP resource pool in the local community. D: EF with $R = 50$, $S = 25$ and $b = 20$ combined with NP equal competition: $R = 50, n = 2, b = 6$; E: EF with $R = 45$, $S = 41$ and $b = 5$ combined with NP unequal competition: $R = 45, b = 5$.

Chapter 5

Empirical Data

From previous chapters, I quantified the functional redundancies of a community by building mathematical models. I discovered that we can infer whether a community is driven by environmental filtering or niche partitioning community assembly, by assessing the trends of the functional redundancy of its resources against its local resource complexity. In this chapter, I will look at existing empirical ecological data as an application for my developed mathematical models. The data I will use is any type of ecological network along any gradients' variation, such as, elevation, land use, etc. The different variations are considered to describe the local communities. Some data record different specific species of the community, while others have higher level of taxonomy, like genus. The highest taxonomy level I will consider is genus. Collecting ecological data is known to be expensive, it is worth noting that the ideal data I want to use in this thesis is very scarce. Therefore, the quality of the metadata I collected is not statistically ideal as they have only a few number of distinct sites. For my meta-analysis, I will analyse some existing datasets with more than five datapoints. My primary goal is to assess the trend of the relationship between the local functional redundancy and the local resource complexity from the metadata collected. This is to assess whether our developed mathematical signals conforms with existing empirical observations of community assembly. For the analysis, I will perform a linear regression to assess the slope of a best fitted line between the functional redundancy and the local resource complexity. I will look at some examples of how we can estimate the parameters of the developed models in this thesis using empirical data.

5.1 Plant-pollinator interactions along an elevational gradient on Mt. Kilimanjaro.

I will start by describing the methods in the paper I extracted the dataset. The paper wanted to study patterns and drivers of specialization and robustness of the plant-pollinator network along a $3.4km$ elevational gradient of Mt. Kilimanjaro (Tanzania, East Africa). It records 67 quantitative plant–pollinator networks consisting of 268 observational hours and $4,380$ plant–pollinator interactions, with $3,757$ bee, 196 wasp, and 427 hoverfly interactions. There are 19 study sites ($100 \times 100m$) on the southern slopes of Mt. Kilimanjaro, spanning an elevational gradient from $993m$ above sea level ($ma.s.l.$) up to $4,390ma.s.l$, they were categorized as follows:

- Colline savanna and maize fields ($990 - 1,020ma.s.l.$): cover the major natural and anthropogenic habitat types of Mt. Kilimanjaro.
- Lower montane forest, agroforestry systems (Chagga home gardens), grasslands, coffee plantations ($1,260 - 1,920ma.s.l.$).
- Montane undisturbed and disturbed by former logging Ocotea forest ($2,120 - 2,470ma.s.l.$).
- Upper montane undisturbed and fire-disturbed Podocarpus forest ($2,850 - 2,990ma.s.l.$).
- Subalpine Erica forest (3,880 m a.s.l.).
- Alpine Helichrysum vegetation ($3,880 - 4,390ma.s.l.$).

This dataset is appropriate for applying our model because the average distance between study sites was $22.6 \pm SD13.1km$ where only two sites were nearer than $2km(1,920m)$, which is still above the average foraging ranges of most pollinators, assuring dispersion for metacommunity framework. Covering different seasons of the year for two years long $(2011, 2012)$, the authors conducted $320hrs$ of transect walks across the selected sites. Due to logistic constraints and unsuitable climatic conditions (rainy, mist, heavy wind, dense fog) at high elevations, the networks from each transect walk as sampling unit within a mixed-effects model framework were used to ensure that all species contributing to one network co-occurred in space and time and to reduce the susceptibility of network metrics errors in species identification, where species separated only within but not across networks. Each recorded interaction was where pollinator touched reproductive parts of herbaceous plant species or bushes during each transect walk. They counted pollinators visited different flowers of the same plant as a single interaction. In this paper, flower visitors were considered as pollinators even though the pollination success in unknown. They identified pollinator species of most considered interactions in the field or caught them with sweep to be identified by experienced taxonomists. They recorded and separated the escaped pollinators from the remaining considered interactions with a conservative approach within single networks. They collected or photographed the plant species including herbs and shrubs, and identified by the botanist on species level following the $1952 - 2012$ Flora of Tropical East Africa nomenclature.

5.1.1 Species from the paper

First this section summarize the pollinators appeared in the paper. It included all Hymenoptera (bees and wasps) and Syrphid Diptera (flower flies with two wings) pollinators. It excluded Butterflies due to relatively few observesd interactions, and nonsyrphid Diptera because its species are not reliable to distinguish morphologically. The networks in the paper were also restricted with those with a minimum five interactions. This excluded the study site Ocotea forest. The authors identified 187 pollinators species.

5.1.2 Resources from the paper

Next, this section gives a summary of the resources (plants or flowers) used in the paper. There were 141 plant species recorded. Total flower abundance and flower richness were recorded after each transect walk within 10 plots of $4 \times 5m$ rectangles. In the same years when transect walks conducted, they installed pan traps as a replicated sampling to estimate network-independent species richness of pollinator species on each site. They reported that species richness of pollinators with both pan trap sampling and net sampling were correlated using Pearson correlation, with coefficient $r = .7$ and p-value $p < .001$. Based on this, they calculated the *visitation rates* by

$$\frac{\text{Number of observed interaction per transect}}{\text{Flower abundance}} = \frac{\text{Measure of insect activity}}{\text{Flower abundance}}.$$

To account for the different *land use intensity* (LUI) of the study sites, the paper used an existing composite index of human land use developed in earlier studies as follows:

- averaged standardized estimates of annual plant biomass removal;

- averaged standardized estimates of agricultural inputs (irrigation, fertilization, insecticides, fungicide, herbicides);
- quantified differences of the vegetation structure to the natural vegetation in terms of canopy closure, canopy height, vegetation heterogeneity;
- quantified landscape composition $1.5km$ around each site.

5.1.3 Functional redundancy analysis

I analysed the dataset to find the functional redundancies of each of the 141 plants or resources for each of the 18 different elevations or local communities. First, since the original data did not record the network matrix, I need to form it. I considered pollinators as rows and plants as columns, with entry 1 when interactions were identified and 0 otherwise. Then, I calculated the resource complexity or the number of plants of each local community. Next, for each local community (different site), I formed a submatrix of the network matrix, which I called local submatrix, using their list of plants. Given a local community, I listed the pollinators of each plant using its local submatrix. These pollinators are the local species in which I used to calculate the functional redundancies for this particular site. Summing the rows of the formed local submatrix gave the local functional redundancy of the given site. For the nonlocal functional redundancy of the site, I formed the nonlocal submatrix using the list of plants outside the given site (local community) and the local species of the site. Then, summing the rows gave the functional redundancy of each plant outside the local community (the given site). Similarly, using the list of all plants and the local species, I formed the total submatrix to calculate the total functional redundancy by summing the rows of the submatrix. Each functional redundancy was recorded as a vector form with each site as the index. Then, I plot each recorded functional redundancy against the resource complexity. Next, I performed an ordinary linear regression for each functional redundancy, to assess whether the best linear fit has a nonzero slope or not. For this data, the best linear fit of the local functional redundancy is $\Omega_p = 6.15r - 16.33$ with a significant p-value 1.66×10^{-7}. Therefore, it is possible that the pollinators community of Mt. Kilimanjaro is driven more by niche partitioning than solely by environmental filtering. Figure 5.1 shows the linear fits of all three redundancies.

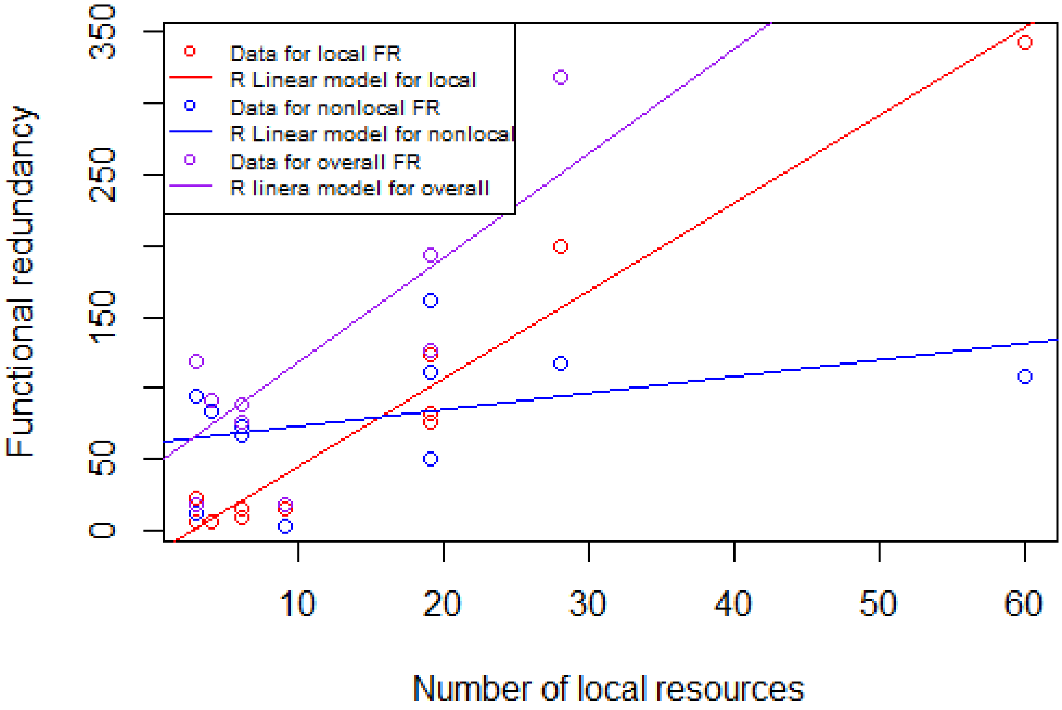

Figure 5.1: Linear regressions of the functional redundancies using the data from the plant-pollinator interactions along an elevational gradient on Mt. Kilimanjaro paper.

From the linear method, I concluded that the community assembly of the pollinators in Mt. Kilimanjaro includes niche partitioning. I first assume that the niche partitioning is with equal competition. To use the developed functional redundancy models, I need to estimate the parameters b of the breadth resources and n of the number of resource won using the *nls()* (nonlinear least squares) function in R. First, using the environmental filtering model of the Ω_p, the estimation of b was 36, with $R^2 = 111884$. Plugging this estimate into the NP with equal competition model of Ω_p, the estimation of n was 8 with $R^2 = 104428$. This is just an example of how we can fit our model to a data. The estimates the developed models need to be improved to get a better fit. Figure 5.2 shows the NP model with equal competition and the linear model for each functional redundancy.

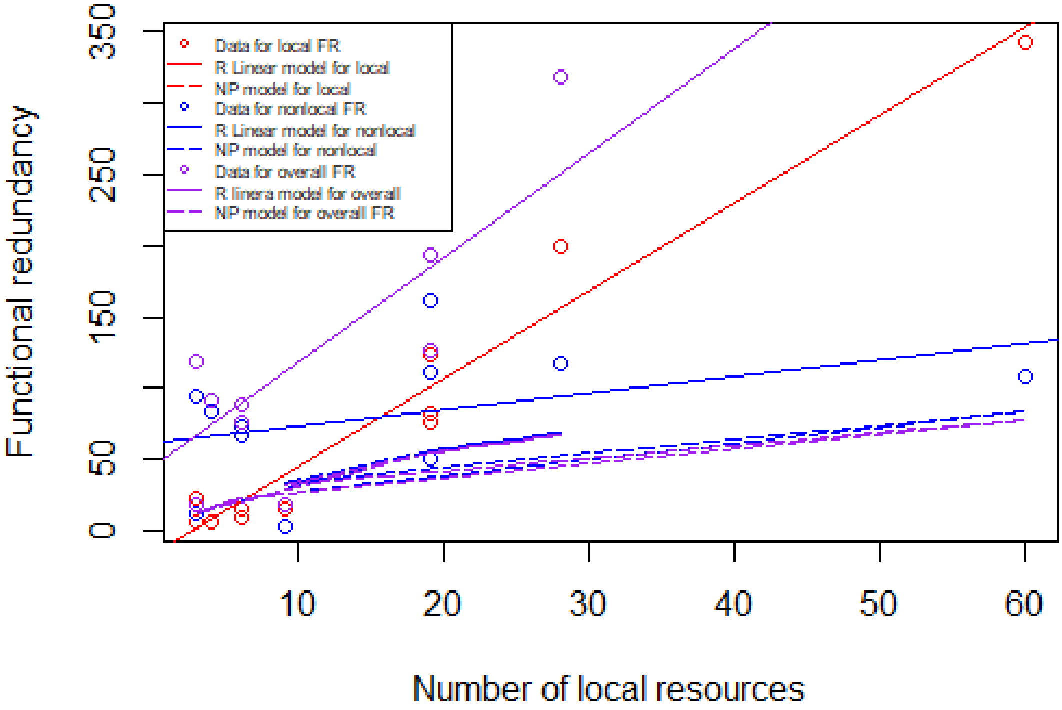

Figure 5.2: Linear regressions with the equal competition NP model of the functional redundancies using the data from the plant-pollinator interactions along an elevational gradient on Mt. Kilimanjaro paper.

5.2 Plant–herbivore interaction networks varies along elevational gradients in the European Alps.

I will start by describing the methods in the paper I extracted the dataset. The paper aimed to study specialization and robustness of plant-herbivore interaction networks vary along elevational gradients using bioinformatic on molecular. The method was a two-step DNA amplification PCR-based approach (DNA metabarcoding) to Orthopteran faeces. That is, the interaction was identified by a trace of plant marker in the insect faeces. They documented 48 networks of species interactions across 48 study sites along six elevational gradients in the Swiss Alps. There were $10,615$ interactions recorded of $28,127$ possible links. Each of the 48 sites differed in local climate and bedrock, and sampled from the following six gradients: areas of Bex, Calanda, Faido, Grindelwald, Martigny, and Salgesch. Each gradient was divided into 8 open grassland sites, spanned from 578 to $2,417 m.a.s.l.$, located on average $240m$ elevation apart from each other. And one network per site was quantified. Each site had a $10 \times 10m$ homogeneous composition of the surrounding vegetation survey plot. From this, in their data, the author recorded 49 sites with two from different gradient (Bex and Faido) but at the same elevation.

5.2.1 Species from the paper

This section summarize the herbivores described in the paper. The paper identified 45 Orthoptera species including 29 Caelifera and 16 Ensifera that feed on living plants. The authors conducted the surveys of the Orthopteran under sunny day during the summer at insect peak activity times. There were on average 10 individuals per species which identified by visual inspection. The authors identified 45 Orthopteran species.

5.2.2 Resources from the paper

This section summarize the resources (plants) used in the paper. The authors measured some plant functional traits by sampling well-developed, healthy leaves at minimum of three replicates across elevation range. From their conducted vegetation surveys, the authors identified 496 plant species from 265 genera and 63 families trophic level. Incorporating the DNA barcoding method, the total plant species recorded in the data is 597.

5.2.3 Functional redundancy analysis

I analysed the dataset to find the functional redundancies of each of the 597 plants or resources for each of the 49 different sites or local communities. The dataset from the paper recorded the network in terms of the intensity values of interactions not with a network matrix. Therefore, I need to transform the data structure of the recorded network into a matrix. I considered herbivores as rows and plants as columns, with entry 1 when interactions were identified (i.e. the intensity value is greater than 0) and 0 otherwise. Then, I calculated the resource complexity or the number of plants of each local community. Next, for each local community (different site), I formed a submatrix of the network matrix, using their list of plants. Given a local community, I listed the herbivores of each plant using its submatrix. These herbivore species I used to calculate the functional redundancies for a particular site. Summing the rows of the formed submatrix gave the local functional redundancy of the given local community. For the nonlocal functional redundancy, I formed the nonlocal submatrix using the list of plants outside the given site (local community) and its local species. Then, summing the rows gave the functional redundancy of each plant outside the given local community. Similarly, using the list of all plants and the local species, I formed the total submatrix to calculate the total functional redundancy by summing its rows. Each functional redundancy was recorded as a vector form with each site as the index. Then, I plot each recorded functional redundancy against the resource complexity. Next, I performed an ordinary linear regression (OLS) for each functional redundancy, to assess whether the best linear fit has a nonzero slope or not. For this data, the best linear fit of the local functional redundancy is $\Omega_p = 0.045r + 1.96$ with a 0.0216 significant p-value. Therefore, it is possible that the orthopetra community of Swiss Alps is driven more by niche partitioning than by environmental filtering. Next, non-local functional redundancy Ω_a has a significant p-value of 0.0294 and a line equation $\Omega_a = 0.015r + 0.813$. Finally, the total functional redundancy has a best fit line of $\Omega_t = 0.023r + 0.61$ with 0.00449 significant p-value. Figure 5.3 shows the linear fits of all three redundancies.

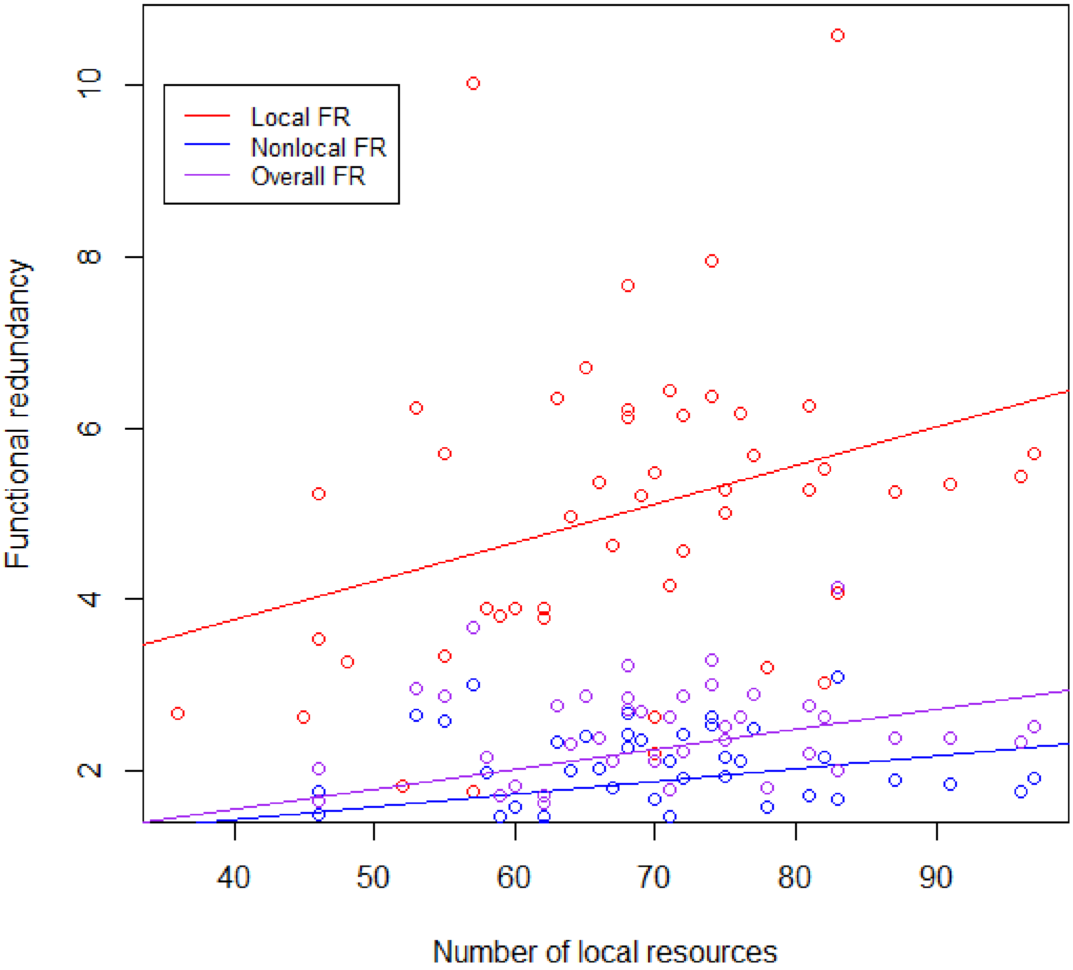

Figure 5.3: Linear regressions of the functional redundancies using the data from the plant–herbivore interaction networks varies along elevational gradients in the European Alps paper.

From the linear method, I concluded that the community assembly of the orthoptera in Swiss Alps includes niche partitioning. I first assume that the niche partitioning is with equal competition. To attempt fitting the functional redundancy of equal niche partitioning models developed in this thesis. I need to estimate the parameters b of the breadth resources and n of the number of resource won using the *nls()* (nonlinear least squares) function in R. First, using the environmental filtering model of the Ω_p, the estimation of b was 67, with $R^2 = 161.2$. Plugging this estimate into the NP with equal competition model of Ω_p, the estimation of n was 16 with $R^2 = 179.5$. This is just an example of how we can fit our model to a data. The estimates of the developed models need to be improved to get a better fit. Figure 5.4 shows the NP model with equal competition and the linear model for each functional redundancy.

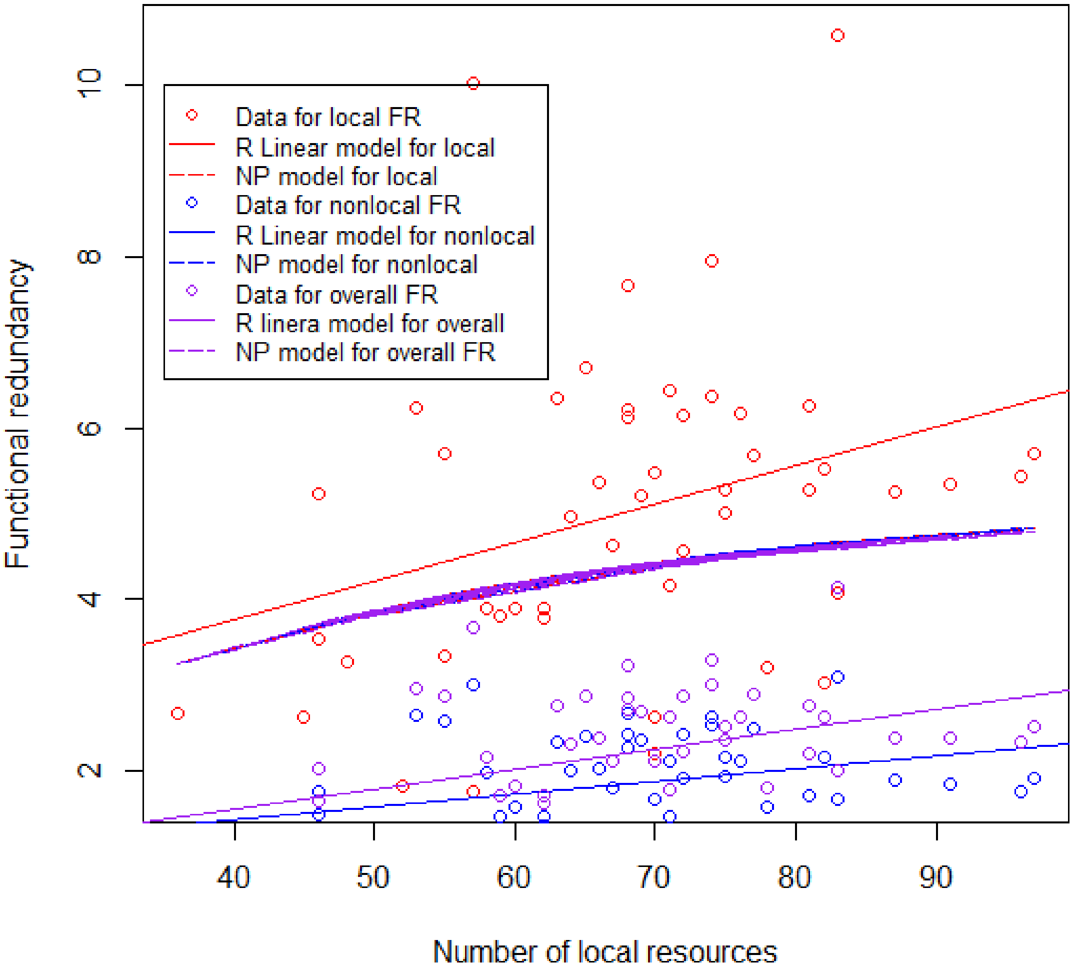

Figure 5.4: Linear regressions with the equal competition NP model of the functional redundancies using the data from the plant–herbivore interaction networks varies along elevational gradients in the European Alps paper.

Chapter 6

Conclusion and Discussion

In conclusion, I developed models of functional redundancy of ecological communities using metacommunity framework, based on community assembly and resource complexity. To determine how functional redundancy scales with ecosystem complexity, I compare the developed models to each other, and applied them to some empirical systems. First, I considered substitutable resources. I then extend the analysis to nonsubstitutable resources. My findings provide insight into the relationships between functional redundancy and resource complexity and how these vary based on assumptions about how ecological communities are structured or assembled (i.e., environmental filtering versus niche partitioning). This dissertation has five chapters excluding this current one. In Chapter 1, I covered ecological background and some terminology, and introduced the mathematical notations and methodology. In Chapter 2, I developed the environmental filtering models for substitutable resources. In Chapter 3, I developed the niche partitioning models for substitutable resources. In Chapter 4, I extended both environmental filtering and niche partitioning models to consider nonsubstitutable resources. Finally, in Chapter 5, I presented some applications on empirical data. I will summarize each one of them and will present the conclusions of my dissertation in this chapter.

6.1 Summary of ecological background

In Chapter 1, I introduced some ecological terms used in this thesis, the overview of the topic, and the biological motivations of the study. The overall goal of the project is to assess the impacts of environmental complexity on functional redundancy. After acknowledging the challenges on defining the term ”functional redundancy“, I used the definition from [54], that is the number of different species that perform similar roles in an ecological community. This was followed by some empirical evidences on the prevalent of functional redundancy in both macro and microorganism communities, and some examples of communities with less apparent functional redundancy. Since I developed resource-consumer models, with the consumers were the species, I considered the environmental complexity of a community as its resource complexity which is its number of resources available. Several studies investigated the impacts of resource complexity on ecological patterns like ecosystem function, resilience and diversity, but not on functional redundancy. Unfortunately, human activities (e.g. fishing, deforestation, etc.) tend to decrease the complexity of the environment, so it is imperial for me to understand how this destruction impacts functional redundancy which is critical for ecosystem stability and resilience. I considered both types of resources (substitutable and nonsubstitutable) separately for my models because complexity of both have the potential to impact community and ecosystem characteristics, including functional redundancy in a positive manner. For the structure of a community, I considered the two ends of the community assembly framework: niche theory and neutral theory, though acknowledged that true communities likely emerge as various forces.

6.2 Summary of models

6.2.1 Substitutable resources

I developed the models with substitutable resources assumption in Chapter 2 and Chapter 3. Chapter 2 covered the models of environmental filtering with equal resource use and several distributions of resource breadth, b (delta, uniform, triangular); with unequal resource use and delta resource breadth. Chapter 3 covered the models of niche partitioning with equal resource use and equal competition; and unequal competition.

Under the *equal resource use* assumption, the relationship between the functional redundancies and the local resource complexity, r, were similar under different distributions of b (delta, uniform, triangular). For any given distribution of b, with pmf φ_b over a range of $[b_{\min}, b_{\max}]$, the functional redundancies, Ω_p, Ω_a, Ω_t, in Equation (2.19), are

$$\begin{aligned}
\Omega_p &= \frac{S}{R} \sum_{b=b_{\min}}^{b_{\max}} b\varphi_b. \\
\Omega_a &= \frac{S}{R} \sum_{b=b_{\min}}^{b_{\max}} b \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \varphi_b. \\
\Omega_t &= \frac{S}{R} \left[\sum_{b=b_{\min}}^{b_{\max}} b\varphi_b - \sum_{b=b_{\min}}^{b_{\max}} b \left(1 - \left(1 - \frac{r}{R}\right)^{b-1}\right) \varphi_b \right].
\end{aligned}$$

With the *unequal resource use* and a delta distribution resource breadth, b, I developed the functional redundancies of two classes of resources separately: *high-use resources* (HR), and *low-use resources* (LR). I used subscripts l and h to refer any parameters in the low-use classes and in the high-use, respectively. The functional redundancies in both classes were similar by swapping the subscripts and scaling the high-use resources with a scaling factor σ. Different from the *equal resource use* case, the functional redundancy of local high-use resources (resp. low-use resources), Ω_p^h in Equation (2.45) (resp. Ω_p^l in Equation (2.53)), is more complicated. The functional redundancies in each resource class are

$$\begin{aligned}
\Omega_p^h &= S \sum_{k=\max(1,b+r_h-R_h)}^{\min(b,r_h)} \frac{k}{r_h} \cdot \frac{\binom{r_h}{k}\sigma^k \sum_{j=0}^{b-k} \binom{R_h-r_h}{j}\binom{R_\ell}{b-k-j}\sigma^j}{\sum_{k=0}^{b} \sigma^k \binom{R_h}{k}\binom{R_\ell}{b-k}} \\
\Omega_p^\ell &= S \sum_{k=\max(1,b+r_\ell-R_\ell)}^{\max(b,r_\ell)} \frac{k}{r_\ell} \cdot \frac{\binom{r_\ell}{k}\sigma^{b-k} \sum_{j=0}^{b-k} \binom{R_\ell-r_\ell}{j}\binom{R_h}{b-k-j}\sigma^{-j}}{\sum_{k=0}^{b} \sigma^k \binom{R_h}{k}\binom{R_\ell}{b-k}} \\
\Omega_a^h &= S \sum_{k=\max(1,b+r_h-R_h)}^{\min(b-1,r_h)} \frac{k}{R_h - r_h} \cdot \frac{\binom{R_h-r_h}{k}\sigma^k \left(\sum_{j=1}^{b-k} \binom{r_h}{j}\sigma^j\binom{R_\ell}{b-k-j} + \sum_{j=1}^{b-k} \binom{r_\ell}{j}\binom{R_\ell-r_\ell}{b-k-j} \right)}{\sum_{k=0}^{b} \sigma^k \binom{R_h}{k}\binom{R_\ell}{b-k}} \\
\Omega_a^\ell &= S \sum_{k=\max(1,b+r_\ell-R_\ell)}^{\min(b-1,r_\ell)} \frac{k}{R_\ell - r_\ell} \cdot \frac{\binom{R_\ell-r_\ell}{k} \left(\sum_{j=1}^{b-k} \binom{r_\ell}{j}\binom{R_h}{b-k-j}\sigma^{b-k-j} + \sum_{j=1}^{b-k} \binom{r_h}{j}\binom{R_h-r_h}{b-k-j}\sigma^{b-k} \right)}{\sum_{k=0}^{b} \sigma^k \binom{R_h}{k}\binom{R_\ell}{b-k}}.
\end{aligned}$$

Regardless of the competitive breadth distribution (e.g., equal vs. unequal competition), the NP functional redundancies Ω_p and Ω_a increase logarithmically with $1 - \frac{r}{R}$ (see Equation (3.13), Equation (3.17), Equation (3.24), Equation (3.26)). More specifically, the local and nonlocal functional redundancies under the niche partitioning are

- **Equal competition:**

$$\begin{aligned}\Omega_p &= 1 + \left[S\left(1-\left(1-\frac{r}{R}\right)^n\right)-1\right]\frac{b-n}{R-n}\\ \Omega_a &= S\left[\frac{n}{R}\left(1-\left(1-\frac{r}{R}\right)^{n-1}\right)+\frac{b-n}{R-n}\left(1-\left(1-\frac{r}{R}\right)^n\right)\right].\end{aligned}$$

- **Unequal competition:**

$$\begin{aligned}\Omega_p &= 1 + \left(\frac{Sb}{R}\left[1-\left(1-\frac{r}{R}\right)^b\right]+\frac{S-1}{R}\left[\frac{Sr}{R}-1\right]-1\right)\frac{b-1}{R-1}\\ \Omega_a &= S\left[\frac{S-1}{R}\cdot\frac{r}{R}\cdot\frac{b-1}{R-1}+\frac{b}{R}\cdot\frac{b}{R}\left(1-\left(1-\frac{r}{R}\right)^{b-1}\right)\right].\end{aligned}$$

6.2.2 Nonsubstitutable resources

I extended the substitutable models to nonsubstitutable with two sources (2D) in Chapter 4. I looked at three cases based on the community assembly and developed the functional redundancies of each source separately.

Case EF: Resources from both sources follow the environmental filtering criteria. That is, a species persists if it uses at least one resource from each source. For each source i, the local functional redundancy, Ω_p^i, only depends on the local resource complexity of the other source (Equation (4.9)). In contrast, the nonlocal functional redundancy, Ω_a^i in Equation (4.11), was monotonically increased with local resource complexity, r_i of source i and on each local resource complexity of other sources. The models of functional redundancies for each source i are:

$$\begin{aligned}\Omega_p^i &\approx \frac{b_i S}{R_i}\prod_{j\in U\setminus\{i\}}\left(1-\left(1-\frac{r_j}{R_j}\right)^{b_j}\right)\\ \Omega_a^i &\approx \frac{b_i S}{R_i}\left(1-\left(1-\frac{r_i}{R_i}\right)^{(b_i-1)}\right)\prod_{j\in U\setminus\{i\}}\left(1-\left(1-\frac{r_j}{R_j}\right)^{b_j}\right).\end{aligned}$$

Case NP: Resources from both sources follow the niche partitioning criteria, where equal and unequal competition case were treated separately. In contrast to the Case EF, both local and nonlocal functional redundancy, Ω_p^i and Ω_a^i, were monotonically increasing with all the local resource complexity of each source. For each source i, the functional redundancies under the equal competition are (Equation (4.23) and Equation (4.24)):

$$\Omega_p^i \approx 1 + \left(\left[S \prod_{i \in U} \left(1 - \left(1 - \frac{r_i}{R_i} \right)^{n_i} \right) \right] - 1 \right) \frac{b_i - n_i}{R_i - n_i}$$

$$\Omega_a^i \approx S \left[\frac{n_i}{R_i} \left(1 - \left(1 - \frac{r_i}{R_i} \right)^{n_i - 1} \right) + \left(1 - \left(1 - \frac{r_i}{R_i} \right)^{n_i} \right) \frac{b_i - n_i}{R_i - n_i} \right] \prod_{j \in U \setminus \{i\}} \left(1 - \left(1 - \frac{r_j}{R_j} \right)^{n_j} \right).$$

For each source i, the functional redundancies under the unequal competition are (Equation (4.27) and Equation (4.28)):

$$\Omega_p^i \approx 1 + \left(\left[S \prod_{i \in U} \left(\frac{b_i}{R_i} \left(1 - \left(1 - \frac{r_i}{R_i} \right)^{b_i} \right) + \frac{S-1}{R_i} \frac{r_i}{R_i} \right) \right] - 1 - \frac{S-1}{R_i} \right) \frac{b_i - 1}{R_i - 1}$$

$$\Omega_a^i \approx S \left[\frac{b_i}{R_i} \left(1 - \left(1 - \frac{r_i}{R_i} \right)^{b_i - 1} \right) + \frac{S-1}{R_i} \frac{r_i}{R_i} \frac{b_i - 1}{R_i - 1} \right] \prod_{j \in U \setminus \{i\}} \left[\frac{b_j}{R_j} \left(1 - \left(1 - \frac{r_j}{R_j} \right)^{b_j} \right) + \frac{S-1}{R_j} \frac{r_j}{R_j} \right].$$

Case EF and NP: Resources from one source (called EF source) follow the environmental filtering criteria, whereas, resources from the other source (called NP source) are under the niche partitioning criteria. I assumed the source NP with equal competition case and with unequal competition case separately. For both cases, similar to the Case EF, the local functional redundancy of EF resources, Ω_p^E, only depends on the r_N local resource complexity of NP source (Equation (4.30)). The nonlocal functional redundancy of NP resources, Ω_a^E, is monotonically increasing against both r_E and r_N (Equation (4.31)). For the equal competition case of the NP source with n same number of primary resources across species, similar to the Case NP, the functional redundancies of source NP were monotonically increasing with r_E and r_N (Equation (4.32) and Equation (4.33)). The functional redundancies under the equal competition are:

$$\Omega_p^E \approx \left(1 - \left(1 - \frac{r_N}{R_N} \right)^n \right) \frac{b_E S}{R_E}$$

$$\Omega_a^E \approx \left(1 - \left(1 - \frac{r_N}{R_N} \right)^n \right) \frac{b_E S}{R_E} \left(1 - \left(1 - \frac{r_E}{R_E} \right)^{(b_E - 1)} \right)$$

$$\Omega_p^N \approx 1 + \frac{\left(\left[\left(1 - \left(1 - \frac{r_E}{R_E} \right)^{b_E} \right) \left(1 - \left(1 - \frac{r_N}{R_N} \right)^n \right) S \right] - 1 \right) (b_N - n)}{R_N - n}$$

$$\Omega_a^N \approx \left(1 - \left(1 - \frac{r_E}{R_E} \right)^{b_E} \right) S \left[\frac{n}{R_N} \left(1 - \left(1 - \frac{r_N}{R_N} \right)^{n-1} \right) + \frac{b_N - n}{R_N - n} \left(1 - \left(1 - \frac{r_N}{R_N} \right)^n \right) \right].$$

The functional redundancies under the unequal competition are (Equation (4.32) and Equation (4.33)):

$$\Omega_p^E \approx \left[\frac{b_N}{R_N}\left(1-\left(1-\frac{r_N}{R_N}\right)^{b_N}\right)+\frac{S-1}{R_N}\cdot\frac{r_N}{R_N}\right]\frac{b_E S}{R_E}$$

$$\Omega_a^E \approx \left[\frac{b_N}{R_N}\left(1-\left(1-\frac{r_N}{R_N}\right)^{b_N}\right)+\frac{S-1}{R_N}\cdot\frac{r_N}{R_N}\right]\frac{b_E S}{R_E}\left(1-\left(1-\frac{r_E}{R_E}\right)^{(b_E-1)}\right)$$

$$\Omega_p^N \approx 1+\left(\left[\left(1-\left(1-\frac{r_E}{R_E}\right)^{b_E}\right)\left[\frac{b_N}{R_N}\left(1-\left(1-\frac{r_N}{R_N}\right)^{b_N}\right)+\frac{S-1}{R_N}\cdot\frac{r_N}{R_N}\right]S\right]-\frac{S-1}{R_N}-1\right)\frac{b_N-1}{R_N-1}$$

$$\Omega_a^N \approx \left(1-\left(1-\frac{r_E}{R_E}\right)^{b_E}\right)S\left[\frac{S-1}{R_N}\cdot\frac{r_N}{R_N}\cdot\frac{b_N-1}{R_N-1}+\frac{b_N}{R_N}\cdot\frac{b_N}{R_N}\left(1-\left(1-\frac{r_N}{R_N}\right)^{b_N-1}\right)\right].$$

6.3 Summary of findings

I found fundamental differences in functional redundancy depending on the community assembly and the resource types. For the environmental filtering model, the local functional redundancy was constant as a function of resource complexity. Both nonlocal and overall functional redundancy, however, were increasing monotonically. By contrast, for the niche partitioning model, local, nonlocal and overall functional redundancy increased monotonically with resource complexity. The results I found for substitutable resources provide a key foundation to how functional redundancy respond to nonsubstitutable resources. In fact, I found that local resource complexity of each nonsubstitutable resource axis distinctively affects functional redundancy. The findings from the basic environmental filtering (with delta resource breadth distribution) and the basic niche partitioning (with delta resource breadth and number of primary resources distribution) remain unchanged with different distributions for resource use, for resource breadth, and number of primary resources. Similarly, varying the values of the different parameters of the developed models provide similar results on the trends of functional redundancy against local resource complexity. In what follows, I will summarize our findings based on different resource types, community assembly, distributions and parameter values.

6.3.1 Substitutable resources

My results in this resource type drive fundamental theories for the higher dimension of resource axes. Regardless of the resource use distribution, resource complexity does not affect the functional redundancy of local resources for environmental filtering. In contrast, with equal resource use distribution but any distribution of number of primary resources, the local functional redundancy for niche partitioning increases with the local resource complexity. Both community assembly result in increasing trend for nonlocal and overall functional redundancy with local resource complexity. These results were qualitatively unchanged when the distribution of resource breadth or the distribution of resource use varies. However, different distributions of resource breadth result in different maximum values of functional redundancy, as well as the minimum number of resources for maintaining a constant functional redundancy for environmental filtering. As for niche partitioning, all distributions of the resource breadth have the same maximum functional redundancy and the minimum number of resources to achieve it. The average functional redundancy of the basic environmental filtering model saturates faster than of niche partitioning models.

6.3.1.1 Environmental filtering

Equal resource use The functional redundancy of local resources had a simplified expression for the environmental filtering with equal resource use (Equation (2.15)). This simple expression gives us biological insight on the trend of functional redundancy with environmental complexity. Under certain conditions (when the number of resources in the metacommunity is relatively high compare to the one in the local), the functional redundancy of the nonlocal and the overall resources could be approximated to simpler expressions (Equation (2.18)). In general, with environmental filtering, the functional redundancy of local resources is constant against local resource complexity, while the nonlocal and the average functional redundancy have upward redundancy trends and saturate to the local when the resource breadth b is higher than one. For a delta distribution for the resource breadth b with fixed number of metacommunity resources and the number of species, higher value of b results in lower number of local resources needed for the nonlocal and the overall functional redundancy to reach the local. Increasing the number of metacommunity resources results in higher local functional redundancy but slower saturation for the nonlocal and the overall. Keeping everything fixed but increasing the number of species, the maximum value of Ω_a and Ω_t increase while the minimum number of resources for them to achieve Ω_p remains constant. Overall, most of the distributions do not change the trend of the functional redundancy with delta breadth distribution.

Unequal resource use The approximation of the functional redundancy for the environmental filtering with unequal resource use is not straightforward.the special case $b = 2$ for high-use resources and low-use resources depended on both low-use resource complexity, r_l, and high-use resource complexity, r_h. The general expression of Ω_a^h (Equation (2.56)) and Ω_a^l (Equation (2.60)) were more complicated to approximate. Therefore, the relationship between Ω_a^h (resp. Ω_a^l) and the local high-use resource complexity, r_h (resp. local low-Use resource complexity, r_l) still need more analyses.

6.3.1.2 Niche partitioning

Equal competition For the basic niche partitioning case—with equal competition, the expression of the local and nonlocal functional redundancy can be approximated to a simpler expressions (Equation (3.13), Equation (3.17)).

All functional redundancies for niche partitioning with equal competition are positively correlated to the environmental complexity with an increasing curvilinear trend and same absolute maximum values. The maximum value of the functional redundancy for niche partitioning is the local one from the basic environmental filtering model. Higher number of resource breadth, b, results in higher maximum value, that is, slows the saturation speed. Higher number of primary resources results in increasing slopes of the functional redundancy but constant saturation speed. Increasing the number of species, the functional redundancy slopes increases and the saturation speed decelerates. Similar to environmental filtering, increasing the number of species while fixing the other parameters increases the maximum value of the functional redundancy. Considering all the parameters of interest (R, S, b, n) the same, all different distributions result in reasonably same functional redundancy behaviors. This is different from what I found in the environmental filtering case.

Unequal competition Similar to the equal competition, the local functional redundancy, Ω_p in this scenario can be simplified to a simpler expression (Equation (3.24)). The nonlocal functional redundancy can be approximated to a simpler expression but not straightforward (Equation (3.26)).

Similar to the equal competition NP case, all functional redundancies in this scenario are positively correlated to environmental complexity but tend to a more linear trend for lower values of resource breadth. The maximum value for the functional redundancy in this scenario is the local functional redundancy of the basic environmental filtering. The saturation speed is really slow compared to the environmental filtering and the niche partitioning with equal competition because the saturation point of the functional redundancy is the total number of resources, R. Higher number of resource breadth results in higher maximum value. Lower breadth resources decreases the slope of the functional redundancy but has a rapid saturation speed compare to higher ones. In contrast with the basic niche partitioning, the nonlocal functional redundancy does not saturate to the maximum value when the distribution of winning is not even among the species. With the unequal niche partitioning, increasing the number of species rises the total number of metacommunity resources when keeping the resource breadth fixed. Therefore, similar to the environmental filtering, the maximum value of the functional redundancy increases with the number of species in the unequal competition case. As the total number of metacommunity resources increases, the saturation speed is getting slower. The trend of the functional redundancy for other distributions of the breadth resources is similar to the delta breadth distribution.

6.3.2 Nonsubstitutable resources

For nonsubstitutable 2D case of environmental filtering, the functional redundancy of local resources from resource axis 1 is constant against the number of local resources from the same axis. It has an increasing redundancy trend against the number of resources from axis 2. In contrast, the nonlocal and the overall functional redundancy have an upward redundancy trend against both resource axes. For the 2D niche partitioning with equal competition, the functional redundancy of resources from axis 1 tends toward a linear trend against axis 2 and to an upward redundancy trend against axis 1. The nonlocal and overall functional redundancy have the same trends as the local one but with higher slopes. For the 2D case with environmental filtering and niche partitioning resource pool with equal resource use and equal competition, the local functional redundancy of resources from the environmental filtering resource pool is constant against the environmental filtering axis and an increasing curvilinearly against the niche partitioning axis. For resources from the niche partitioning pool, the local functional redundancy has an increasing redundancy trend against the environmental filtering axis and a curvilinear upward trend against the niche partitioning axis. Similar results are true for nonlocal and overall functional redundancy but with higher slopes than the local.

6.4 Discussions

This study provides a new quantification of functional redundancy which can serves as a trade-offs of community assembly in ecological systems. Understanding the trend of functional redundancy in a community can offer a valuable insight on a comprehensive analysis of species selection and resource competition, shedding light on the importance of resource diversity, and the stability of ecological processes under varying conditions. These findings contribute to our understanding of the intricate interactions and community assembly in ecological systems. This can serve as an evidence of competition between species which can shed light on the controversial topic "ghost of competition past" by [14]. This study serves as a foundation for future studies in the field of ecology on competition evidences, community assembly, functional redundancy and species coexistence. Most importantly, this theory can be used to validate experimental study on community assembly and functional redundancy.

Among the four proposed paradigm for metacommunities (patch dynamics, mass effects, species-sorting and neutral) [48], I considered neutral theory for my models. That is assumed all species to have similar rates of birth, death and dispersal [34]; also did not account for movement between communities like immigration, colonization, or extinction. Neutral theory has used to understanding several ecological processes (e.g.: species abundances and biodiversity) even though it has lack of experimental supports [65]. This is because it holds its own value and capacity on testing hypotheses in ecology [65, 51, 7, 20]. Similar to the belief on pluralistic approach for the biodiversity patterns, I also adopt this belief that functional redundancy patterns would be driven by a combination of the four basic ecological processes (selection, drift, speciation and dispersal) [83]. That is why I framed our models using metacommunity framework to account for processes on a local and a regional scale. At geographic scales of regions or continents is tremendously challenging due to the need of incorporating evolutionary processes with little opportunity of experimental works, which requires a further analysis using advanced tools in molecular biology, phylogenetics, or paleontology. Our models provide us null models, which give a fundamental framework for assessing relationships between functional redundancy and environmental complexity. That is, this study described community assembly without specifying the colonization process [26]. Species in the metacommunity are assumed to already satisfy the persistence conditions, that is, our metacommunity is already in equilibrium. Therefore, species are assumed to coexist in the global community. That is, species in our metacommunity that use the same resources tended to differ by a constant size ratio [37] or using the concept of limiting similarity [62], and species extinction and resource limitation were omitted.

Niche difference in this study only accounts for difference in resource use, which is often allowed by differences in species morphological adaptations (e.g. beak size for birds). Assuming niche based on only resource axes is more empirically practical than focusing on an undefined number of niche dimensions, "n-dimensional niche" by Hutchinson [3]. Other processes like cross-feeding were omitted for our heuristic models. Considering cross-feeding will add additional conditions for species to live in a community, as well as the consideration of species extinction. Predators of the consumer species were not present in our models, that is, I only analysed two levels of food chain at a time. Increasing the depth of food chains in our model would lead to species extinction as well as incorporating extra parameters, that is, it needs more complicated mathematical models and/or computational efforts. Nevertheless, our models provide a wealth of future work on more complex ecological networks like food-webs related to functional redundancy.

Both competition mechanisms described in [12] do not entirely fit in our models as both involves species exclusion. The competition mechanism I adopt in this study is a type of both contest competition and resource competition, which is more on resource dominance. Based on Case (2000), contest competition occurs when one species interfere other species access to a resource [12]. In this definition, the type of interference was not explicitly delineated. For our models, interference only means the interfering species (or the "winner") uses the resource best (e.g. with small energy), without excluding the interfered species (or the "weaker"). That is, the interfered species can still use the resource with limited competency on its usage, which may impact its fitness in a local community. Since the competition in our models involves resource acquisition, it may also consider as a resource competition mechanism without species exclusion.

Multi-dimensional of our models refers to multiple resource axes that cannot be substituted. In this study, I only considered the two dimensional case. Nevertheless, the outcomes of the multi-dimensional case is believed to be the same as the ones from the two dimensional case with extended number of resource axes only. The substitutable resources case in our models was considered without distinguishing the resource uptake effort of each. Resource selection by the consumers contributes to the distribution of resources. Therefore, resource uptake effort and prey or habitat selection in predator-prey interaction can be covered by considering various resource distributions, as in our models of high and low resources.

I found that the functional redundancy of local resources increases with local resource complexity depending on the underlying mechanism. Increasing local resources richness without species competition has a constant effect on local functional redundancy, whereas it increases the local functional redundancy with presence of competition in the community. Functional redundancy promotes ecosystem resilience and stability [8], therefore my results indicate that competitive local communities are more vulnerable to resilience and stability, in the absence of other ecological forces. Existing studies mainly used diversity to infer stability in competitive communities [19, 10, 87, 47], whereas functional redundancy is more direct driver of stability and resilience than diversity [8].

Our results also demonstrate that higher number of resources used by each species increases the local functional redundancy. A species is considered as a generalist when it uses many resources in the community. Therefore, this result indicates that a community with more generalist species is more stable and resilient. This theory supports several experimental works in both micro- and macro-communities. Microbial communities are more stable and resilient when they contain more generalist species [80]. For instance, [52] highlights the stability and resilience of bacteria communities due to rapid shift from specialists to generalists. For macro-organism communities, [70] points out that plant-frugivores network with generalist birds like toucans and cracids is more stable and resilient.

Caveat

The major sources of ecological systems complexity include the large number of diverse components, nonlinear interactions, scale multiplicity, and spatial heterogeneity, with increase of complexity scale when incorporating human actions like disturbances, management or conservation interventions. By no means I can completely “reduce” the complexity of ecological systems, but our models give valuable insights which serve as grounded theories on what happens in systems closer to reality. No ecological dynamics either among athletes or between species and environments were incorporated in the built models. Other processes like energy flow and chemical reactions were not considered in the study. Incorporating such complex concepts requires much more research with ample of time and powerful tools and techniques for modeling. Throughout the study, species behaviors were not included in the assumptions for the models. For instance, foraging behavior might would change our model since it dictates the use of resources in the community. This caveat could be enlighten by discovering the right distribution of resource use with species behavior incorporated. In our models, I assumed deterministic survival condition. Since species behaviors help organism's fitness and survival in a community, incorporating this dynamic into the stochastic of the species persistence. This would lead to accounting for abundances, thinking about death-birth dynamics of species, as our model is a presence-absence model only. Phylogenetic conservation and morphological characteristics were not considered in our model, though I am aware that they play an important role to resource use structure. This study considered mechanistic competitions which can be served as null models for the more realistic one. The two dimensional case I explored in this study can serve as a framework even though I have not fully looked at high dimension of resources.

Appendices

Appendix A Approximations and Asymptotics

A.0.1 Stirling's approximation of the $(b-1)^{th}$ term of Ω_a

The probability of a given non-local resource used with exactly $b-2$ resources outside the local community and one local resource is

$$\frac{b-1}{R-r} \cdot \frac{\binom{r}{1}\binom{R-r}{b-1}}{\binom{R}{b}} = \frac{b(b-1)(R-b)!}{R!} \cdot \frac{r(R-r-1)!}{(R-r-b+1)!}.$$

Using *Stirling's approximation*, $n! \approx \sqrt{2\pi n}\left(\frac{n}{e}\right)^n$, [60], we have

$$\begin{aligned}
\frac{b-1}{R-r} \cdot \frac{\binom{r}{1}\binom{R-r}{b-1}}{\binom{R}{b}} &= \frac{b(b-1)(R-b)!}{R!} \cdot \frac{r(R-r-1)!}{(R-r-b+1)!} \\
&\approx \frac{b(b-1)\sqrt{2\pi(R-b)}\left(\frac{R-b}{e}\right)^{R-b}}{\sqrt{2\pi R}\left(\frac{R}{e}\right)^{R}} \cdot \frac{r\sqrt{2\pi(R-r-1)}\left(\frac{R-r-1}{e}\right)^{R-r-1}}{\sqrt{2\pi(R-r-b+1)}\left(\frac{R-r-b+1}{e}\right)^{R-r-b+1}} \\
&\approx \frac{b(b-1)\sqrt{R-b}\,(R-b)^{R-b}\left(\frac{1}{e}\right)^{R-b}}{\sqrt{R}R^{R}\left(\frac{1}{e}\right)^{R}} \cdot \frac{r\sqrt{R-r-1}\,(R-r-1)^{R-r-1}\left(\frac{1}{e}\right)^{R-r-1}}{\sqrt{R-r-b+1}\,(R-r-b+1)^{R-r-b+1}\left(\frac{1}{e}\right)^{R-r-b+1}} \\
&\approx \frac{b(b-1)\sqrt{R-b}\,(R-b)^{R-b}}{\sqrt{R}R^{R}} \cdot \frac{r\sqrt{R-r-1}\,(R-r-1)^{R-r-1}\left(\frac{1}{e}\right)^{2R-r-b-1}}{\sqrt{R-r-b+1}\,(R-r-b+1)^{R-r-b+1}\left(\frac{1}{e}\right)^{2R-r-b+1}} \\
&\approx \frac{e^2 b(b-1)\sqrt{R-b}\,(R-b)^{R-b}}{\sqrt{R}R^{R}} \cdot \frac{r\sqrt{R-r-1}\,(R-r-1)^{R-r-1}}{\sqrt{R-r-b+1}\,(R-r-b+1)^{R-r-b+1}}.
\end{aligned}$$

A.0.2 Stirling's approximation of the $(b-2)^{th}$ term of Ω_a

The probability of a given non-local resource used with exactly $b-3$ resources outside the local community and two local resources is

$$\frac{b-2}{R-r} \cdot \frac{\binom{r}{2}\binom{R-r}{b-2}}{\binom{R}{b}} = \frac{b-2}{R-r} \cdot \frac{r!(R-r)!b!(R-b)!}{2!(r-2)!(b-2)!(R-r-(b-2))!R!} = \frac{r(r-1)(R-r-1)!b(b-1)(b-2)(R-b)!}{2!(R-r-(b-2))!R!}.$$

Using *Stirling's approximation*, $n! \approx \sqrt{2\pi n}\left(\frac{n}{e}\right)^n$, [60], we have

$$\begin{aligned}
\frac{b-2}{R-r}\frac{\binom{r}{2}\binom{R-r}{b-2}}{\binom{R}{b}} &= \frac{b-2}{R-r}\frac{r!(R-r)!b!(R-b)!}{2!(r-2)!(b-2)!(R-r-(b-2))!R!} \\
&= \frac{r(r-1)b(b-1)(b-2)(R-r-1)!(R-b)!}{2(R-r-(b-2))!R!} \\
&\approx \frac{r(r-1)b(b-1)(b-2)\sqrt{2\pi(R-r-1)}\left(\frac{R-r-1}{e}\right)^{R-r-1}}{2\sqrt{2\pi R}\left(\frac{R}{e}\right)^{R}} \\
&\quad \frac{\sqrt{2\pi(R-b)}\left(\frac{R-b}{e}\right)^{R-b}}{\sqrt{2\pi(R-r-(b-2))}\left(\frac{R-r-(b-2)}{e}\right)^{R-r-(b-2)}} \\
&= \frac{r(r-1)b(b-1)(b-2)e^{3}\sqrt{R-r-1}(R-r-1)^{R-r-1}\sqrt{R-b}(R-b)^{R-b}}{2\sqrt{R}R^{R}\sqrt{R-r-(b-2)}(R-r-(b-2))^{R-r-(b-2)}} \\
&= \frac{e^{3}r(r-1)b(b-1)(b-2)\sqrt{R-r-1}(R-r-1)^{R-r-1}}{2\sqrt{R}R^{R}} \\
&\quad \times \frac{\sqrt{R-b}(R-b)^{R-b}}{\sqrt{R-r-(b-2)}(R-r-(b-2))^{R-r-(b-2)}}.
\end{aligned}$$

A.0.3 Stirling's approximation of the k^{th} term of Ω_a

The probability of a given non-local resource used with exactly $b-k$ resources outside the local community and k local resources is

$$\begin{aligned}
\frac{b-k}{R-r}\frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} &= \frac{b-k}{R-r}\frac{r!(R-r)!b!(R-b)!}{k!(r-k)!(b-k)!(R-r-(b-k))!R!} \\
&= \frac{r(r-1)\cdots(r-(k+1))(R-r-1)!b(b-1)\cdots(b-(k+1))(R-b)!}{k!(R-r-(b-k))!R!}.
\end{aligned}$$

Using *Stirling's approximation*, $n! \approx \sqrt{2\pi n}\left(\frac{n}{e}\right)^{n}$, [60], we have

$$\begin{aligned}
\frac{b-k}{R-r}\frac{\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}} &= \frac{r(r-1)\cdots(r-(k+1))(R-r-1)!b(b-1)\cdots(b-(k+1))(R-b)!}{k!(R-r-(b-k))!R!} \\
&\approx \frac{\prod\limits_{i=0}^{k+1}(r-i)\sqrt{2\pi(R-r-1)}\left(\frac{R-r-1}{e}\right)^{R-r-1}\prod\limits_{j=0}^{k+1}(b-j)\sqrt{2\pi(R-b)}\left(\frac{R-b}{e}\right)^{R-b}}{k!\sqrt{2\pi(R-r-(b-k))}\left(\frac{R-r-(b-k)}{e}\right)^{R-r-(b-k)}\sqrt{2\pi R}\left(\frac{R}{e}\right)^{R}} \\
&= \frac{\prod\limits_{i=0}^{k+1}(r-i)(b-i)\sqrt{(R-r-1)}(R-r-1)^{R-r-1}\sqrt{(R-b)}(R-b)^{R-b}e^{k+1}}{k!\sqrt{(R-r-(b-k))}(R-r-(b-k))^{R-r-(b-k)}\sqrt{R}R^{R}} \\
&= \frac{e^{k+1}\prod\limits_{i=0}^{k+1}(r-i)(b-i)\sqrt{(R-r-1)}(R-r-1)^{R-r-1}}{k!\sqrt{R}R^{R}} \\
&\quad \times \frac{\sqrt{(R-b)}(R-b)^{R-b}}{\sqrt{(R-r-(b-k))}(R-r-(b-k))^{R-r-(b-k)}}.
\end{aligned}$$

A.0.4 Difference between $\left(1-\frac{\binom{R-r}{b}}{\binom{R}{b}}\right)\frac{r\binom{R-r}{b-1}}{\binom{R}{b}}$ and $\frac{b-1}{R-r}\frac{r\binom{R-r}{b-1}}{\binom{R}{b}}$

- $\left(1-\frac{\binom{R-r}{b}}{\binom{R}{b}}\right)\frac{b-1}{R-r}$ is the probability of using at least one resource in the local community and exactly $b-1$ resources are outside.
- $\frac{b-1}{R-r}\frac{r\binom{R-r}{b-1}}{\binom{R}{b}}$ is the probability of a given absent resource used with $b-2$ other non-local resources and exactly one local resource.

Approximate expression for nonlocal functional redundancy Ω_a using Stirling's approximation and a Taylor series expansion

As suggested, each local species can use a maximum of $b-1$ nonlocal resources. The contribution to nonlocal functional redundancy for species that use exactly $b-1$ nonlocal resources, $\Omega_{a_{b-1}}$, is

$$\Omega_a \approx \left(1-\frac{\begin{pmatrix}R-r\\ b\end{pmatrix}}{\begin{pmatrix}R\\ b\end{pmatrix}}\right)\frac{S\,(b-1)}{R-r}, \tag{1}$$

$$\Omega_{a_{b-1}} = \frac{b-1}{R-r} \cdot \frac{S\binom{r}{1}\binom{R-r}{b-1}}{\binom{R}{b}}, \tag{2}$$

where $\frac{b-1}{R-r}$ is the probability of choosing any given nonlocal resource from among the $b-1$ nonlocal resources used and $\frac{S\binom{r}{1}\binom{R-r}{b-1}}{\binom{R}{b}}$ is the number of species that use exactly $b-1$ nonlocal resources.

Biologically, it is often reasonable to assume that $r \ll R$ and $b \ll R$ in which case I can use *Stirling's approximation* [60] to simplify $\Omega_{a_{b-1}}$ as follows

$$\approx S \cdot \tfrac{e^2 rb(b-1)(R-b)^{R-b+1/2}(R-r-1)^{R-r-1/2}}{R^{R+1/2}(R-r-b+1)^{R-r-b+3/2}}$$

$$\approx S \cdot \tfrac{e^2 rb(b-1)(R-b)^{R-b+1/2} R^R}{R^{R+1/2}(R-b)^{R-b}}$$

$$= Se^2 rb(b-1)\sqrt{\tfrac{R-b}{R}} = Se^2 rb(b-1)\left(1 - \tfrac{b}{R}\right)^{1/2}.$$

Further applying a *first order Taylor expansion* around

$$\Omega_{a_{b-1}} \approx Se^2 rb(b-1) \cdot \frac{b}{2R} = \frac{e^2 b(b-1)}{2} \cdot \Omega_p. \tag{3}$$

Using similar arguments, the contribution to nonlocal functional redundancy by species that use exactly $b-2$ nonlocal resources, $\Omega_{a_{b-2}}$ is

$$\Omega_{a_{b-2}} = \frac{b-2}{R-r} \cdot \frac{S\binom{r}{2}\binom{R-r}{b-2}}{\binom{R}{b}}, \tag{4}$$

where, $\frac{b-2}{R-r}$ is the probability of choosing any given nonlocal resource from among the $b-2$ used and $\frac{S\binom{r}{2}\binom{R-r}{b-2}}{\binom{R}{b}}$ is the number of species that use exactly $b-2$ nonlocal resources (and 2 local resources). Similar to the $b-1$ case, applying Stirling's approximation gives

$$\begin{aligned}
\Omega_a &\approx S(2e)^{-1}b(b-1)(b-2)r(r-1)\sqrt{\frac{(R-r-1)(R-b)}{(R-r-(b-2))R}}\cdot\frac{(R-r-1)^{R-r-1}(R-b)^{R-b}}{(R-r-(b-2))^{R-r-(b-2)}R^R}\\
&\approx S(2e)^{-1}b(b-1)(b-2)r(r-1)\cdot\frac{(R-r-1)^{R-r-1/2}(R-b)^{R-b+1/2}}{(R-r-(b-2))^{R-r-(b-2)+1/2}R^{R+1/2}}\\
&\approx S(2e)^{-1}b(b-1)(b-2)r(r-1)\cdot\frac{R^R(R-b)^{R-b+1/2}}{(R-b)^{R-b}R^{R+1/2}}\quad\text{(if } R\gg r\text{, then } R-r-(b-2)+\tfrac{1}{2}\approx R-b)\\
&= S(2e)^{-1}b(b-1)(b-2)r(r-1)\left(\frac{R-b}{R}\right)^{1/2}\\
&= S(2e)^{-1}b(b-1)(b-2)r(r-1)\left(1-\frac{b}{R}\right)^{1/2}.
\end{aligned}$$

Further applying a *first order Taylor expansion* around $\frac{b}{R}\ll 1$, gives

$$\Omega_{a_{b-2}}\approx S(2e)^{-1}b(b-1)(b-2)r(r-1)\cdot\frac{b}{2R}=\frac{b(b-1)(b-2)r(r-1)}{4e}\cdot\Omega_p. \tag{5}$$

More generally, considering the contribution to nonlocal functional redundancy by species that use exactly $b-k$ nonlocal resources (and hence k local resources), $\Omega_{a_{b-k}}$, is

$$\Omega_a=\frac{b-k}{R-r}\cdot\frac{S\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}, \tag{6}$$

where $\dfrac{b-k}{R-r}$ is the probability of choosing any given nonlocal resource from among the $b-k$ used and $\dfrac{S\binom{r}{k}\binom{R-r}{b-k}}{\binom{R}{b}}$ is the expected number of local species using exactly $b-k$ nonlocal resources and k local resources. As before, following the approximation methods above gives

$$\begin{aligned}
\Omega_{a_{b-k}} &\approx S\cdot\frac{e^{k+1}\prod_{i=0}^{k+1}(r-i)(b-i)\sqrt{(R-r-1)}(R-r-1)^{R-r-1}}{k!\sqrt{R}R^R}\cdot\frac{\sqrt{(R-b)}(R-b)^{R-b}}{\sqrt{(R-r-(b-k))}(R-r-(b-k))^{R-r-(b-k)}}\\
&= S\cdot\frac{e^{k+1}\prod_{i=0}^{k+1}(r-i)(b-i)(R-r-1)^{R-r-1/2}(R-b)^{R-b+1/2}}{k!R^{R+1/2}(R-r-(b-k))^{R-r-(b-k)+1/2}}\\
&\approx S\cdot\frac{e^{k+1}\prod_{i=0}^{k+1}(r-i)(b-i)R^R(R-b)^{R-b+1/2}}{k!R^{R+1/2}(R-r-(b-k))^{R-b}}\qquad\text{(if } R\gg r\text{, then } R-r-(b-k)+\tfrac{1}{2}\approx R-b)\\
&= S\cdot\frac{e^{k+1}\prod_{i=0}^{k+1}(r-i)(b-i)}{k!}\left(\frac{R-b}{R}\right)^{1/2}=S\cdot\frac{e^{k+1}\prod_{i=0}^{k+1}(r-i)(b-i)}{k!}\left(1-\frac{b}{R}\right)^{1/2}.
\end{aligned}$$

Again applying a *first order Taylor expansion* around $\frac{b}{R} \ll 1$ gives

$$\Omega_{a_{b-k}} \approx \frac{Se^{k+1}\prod_{i=0}^{k+1}(r-i)(b-i)}{k!} \cdot \frac{b}{2R} = \frac{e^{k+1}\prod_{i=0}^{k+1}(r-i)(b-i)}{2k!}\,\Omega_p. \tag{7}$$

Summing the contributions to nonlocal functional redundancy across all possible values of k then gives an approximation for the total nonlocal functional redundancy as

$$\Omega_a \approx \sum_{k=\max(1,b+r-R)}^{\min(b-1,r)} \frac{e^{k+1}\prod_{i=0}^{k+1}(r-i)(b-i)}{2k!}\,\Omega_p. \tag{8}$$

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