The ecological niche: historical, modelling, and experimental approaches to one of ecology's central concepts

Michael Pedruski

Department of Biology

McGill University

Montréal, Québec

May 2015

Abstract

The ecological niche is key to our understanding of trophic interactions, species distributions, trait evolution, and competitive dynamics. The wide array of applications of the niche is matched by the diversity of its meanings, and it has been variously defined to be the ecological opportunities available in a community, the functional roles that species play in their community, the environmental conditions necessary for species persistence, the resource-use distribution of species, or combinations of these. Despite this heterogeneity all the niche definitions have assumed that species differ in their relation to the environment, and that understanding the ways in which these relations differ is essential for responding to questions in ecology and evolution.

My thesis uses historical, modelling, and experimental methods to explore how the niche has informed ecological thought, and how its current use can guide ecological and evolutionary research, especially as it regards competition. I used a citation network analysis to explore the structure of the niche literature from 1917-1999 and the pattern of its disciplinary spread from its origins among animal researchers. Surprisingly, this analysis revealed that while the niche had spread to a number of sub-disciplines by the close of the 20th century, integration between key sub-disciplines in the network was not strong, suggesting that a common niche literature had not yet emerged. Neutral theory has recently challenged

niche theory by suggesting that in some cases competitors may actually be equivalent, and thus that competition may be driven by stochastic processes and not inherent differences between competitors. I applied a modelling approach to assess the predictability of competitive outcome along gradients of fitness inequality (the difference in competitive ability between competitors) and demographic stochasticity, and found that both gradients interacted to affect competition. Outcomes not predicted by niche theory were common in some conditions, which suggests that competitive dynamics may be niche or neutrally structured dependent on how environmental conditions affect fitness inequality and stochasticity. Finally, I experimentally approached the question of how ecological niches might change in response to the imposition of environmental stressors, and found that while the niches of some populations were relatively unaffected by some forms of stress, other populations saw contraction in the size of their niches, and declines in their fitness within the niche after selection in some environments.

While my thesis demonstrates that the use and predictions of niche theory are context dependent, niche theory has productively inspired ecological thought in many areas, and is perennially changing in response to its own limitations. As the corner-stone of ecological thought for how organisms relate to their environments it will no doubt continue to be at the forefront of responses to emerging questions in ecology and evolution.

Abrégé

La niche écologique est au coeur de notre compréhension des interactions trophiques, la répartition des espèces, l'évolution des traits, et les dynamiques compétitives. La vaste gamme des applications de la niche est reflétée par la diversité de ses définitions, et elle a été définie comme les opportunités écologiques qui sont disponibles dans une communauté, les rôles fonctionnels que les espèces jouent dans leurs communautés, les conditions environnementales qui sont nécessaires pour la survie des espèces, la distribution de l'utilisation des ressources des espèces, ou des combinaisons de ces dernières. Malgré cette hétérogénéité, toutes les définitions de la niche ont assumé que les espèces diffèrent dans leurs relations avec l'environnement, et que la compréhension de ces différences est essentielle pour les questions dans l'écologie et l'évolution.

Ma thèse utilise des méthodes historiques, de modélisation, et expérimentales pour explorer la façon dont la niche a façonné la pensée écologique, et comment son utilisation peut guider des recherches écologiques et évolutives, particulièrement dans le cadre de la compétition. J'ai utilisé une analyse de réseau de citation pour explorer la structure de la littérature de la niche entre 1917 et 1999 et la mainère de sa propagation disciplinaire de ses origines chez les chercheurs zoologiques. Étonnamment, cette analyse a montré que, bien que la niche s'est propagée à plusieurs sous-disciplines par la fin du 20ième siècle, l'intégration

entre les sous-disciplines clé dans le réseau n'était pas forte, ce qui suggère qu'une littérature commune n'avait pas encore été matérialisée. La théorie neutre de l'écologie a récemment contesté la théorie de la niche en suggérant que dans quelques cas, les compétiteurs pourraient être équivalent, et donc la compétition pourrait être dirigée par des processus stochastiques, au lieu des différences entre des compétiteurs. J'ai utilisé une approche de modélisation pour évaluer la caractère prévisible des résultats de la compétition le long des gradients de l'inégalité de fitness (la différence entre compétiteurs dans la force compétitive) et de la stochasticité démographique, et j'ai trouvé que les deux gradients ont interagi pour affecter les résultats de la compétition. Des résultats qui n'avaient pas été prédits par la théorie de la niche étaient fréquents dans certaines conditions, ce qui suggère que les dynamiques compétitives peuvent être structurées dans une façon niche ou neutre, dépendamment des conditions environnementales affectant les inégalités de fitness et la stochasticité. Finalement, j'ai approché la question de l'effet des stress environnementaux sur l'évolution de la niche d'une façon expérimentale, et j'ai trouvé que bien que les niches de certaines populations n'aient pas été relativement fortement affectées par certaines formes de stress, d'autres populations ont connu des contractions de la taille de leur niche, et des baisses de fitness dans la niche après la sélection dans certains environnements.

Bien que ma thèse montre que l'utilisation et les prédictions de la théorie de la niche sont dépendantes du contexte, la théorie de la niche a utilement inspirée la pensée écologique dans plusieurs domaines, et est en constant changement en réponse à ses propres limitations. En tant que pierre angulaire de la pensée écologique sur la relation entre les organismes et l'environnement, la niche continuera à être à l'avant-garde des réponses aux questions émergentes dans l'écologie et l'évolution.

Acknowledgements

A thesis is a massive undertaking, and would be impossible were it not for the legions of colleagues and friends that have provided guidance and support throughout. During my degree I was lucky enough to have many opportunities to teach, and I thank Anne-Marie L'Heureux and Sonia Bujold, the two lab co-ordinators who oversaw most of my teaching endeavours for the wonderful support they provided along with the other teaching assistants I taught with, and the professors who oversaw the courses.

I'm indebted to many staff members in the Biology department at McGill, most obviously Susan Bocti and Ancil Gittens, the staff members responsible for graduate students during my time in the department, as well as Susan Gabe, Joseph Iantomasi, Anna McNicoll, Lucy Scigliano, and Carole Verdone-Smith. I thank Mark Romer and Claire Cooney of the McGill Phytotron for their years of technical assistance during my work with diatoms. Guillaume Larocque of the QCBS also provided essential assistance by helping me get started on citation network analysis.

During my PhD I was blessed to have wonderful and supportive colleagues, officemates, and lab-mates drawn from the Abouheif, Fussmann, and Gonzalez labs. There is not enough space here to document the ways in which each of these individuals have made an impact, but to Xoxo O'Farrill, Matthew Mitchell, Pradeep Pillai, Caolan Kovach-Orr, Felipe Dargent, Fe-

Preface

Thesis format and author contributions

This thesis is a manuscript based thesis composed of three articles written for submission to scientific journals preceded by a general introduction, followed by a general discussion, and separated by connecting statements. Chapter 2 has been accepted for publication at *Ecosphere*, Chapter 3 has been published in *Royal Society Open Science*, and Chapter 4 is in revision for the *Journal of Evolutionary Biology*, but the formatting of these chapters has been altered for consistency throughout this thesis.

I am the primary author of all the chapters of the thesis, and I took the lead in developing the questions examined in each, executing the studies, analysing the results, and composing the manuscripts. Gregor Fussmann and Andrew Gonzalez were my co-authors on each paper, and provided invaluable guidance in all of these aspects.

Novelty of thesis research

My thesis contains three original direct contributions to knowledge.

Chapter 2

Chapter 2 provides a unique quantitative investigation of the history and patterns of use of one of ecology's central concepts, the ecological niche. In line with its importance the niche has been heavily reviewed, but these reviews have largely focused on parsing the different definitions of the niche, and not on how ecologists have used them. Such a perspective provides unique insights not only on the niche, but also on the discipline of ecology itself.

Chapter 3

Chapter 3 contributes directly to ecology's current dialogue on synthesizing between the niche and neutral perspectives in competition theory. This chapter provides a much needed examination of how fitness inequality and demographic stochasticity interact to affect competitive outcome, and its conclusions are not only important contributions to the dialogue in theoretical ecology, but also suggest new directions for empirical ecological research.

Chapter 4

Chapter 4 examines how environmental conditions not only affect ecological dynamics, but may lead to changes in those dynamics through evolution of the ecological niche and fitness inequalities. As such it offers an important look at how ecological and evolutionary processes affect each other on short time scales, and in particular furnishes a rare look at how evolution may affect competition through changes to fitness inequality between ecologically similar species in a variety of stressful environments.

Contents

5 General conclusion   **195**

List of Figures

List of Tables

Chapter 1

General introduction

1.1 The ecological niche

The niche is a central concept in the fields of ecology and evolution. Since its introduction in the early 20th century the niche has been involved in explanations of biodiversity (Hutchinson 1961), trophic structure (Elton 1927; Thompson et al. 2012), community susceptibility to invasion (Tilman 2004), parasite and disease dynamics (Levine et al. 2007), and species distributions (Warren 2012), among others. While these applications have all been important, the niche's impact has arguably been the strongest on ecological thought about competition, a force that Darwin (1859) set very near the heart of the emerging sciences of ecology and evolutionary biology. Through this relationship to competition the niche has been used to predict which competitors are likely to dominate in specific conditions (Tilman 1982), and how competition might lead to changes in populations through evolutionary processes like trait adaptation (MacArthur and Levins 1967; Grant and Grant 2006). Consequently, the niche is a fundamental concept for understanding community composition, ecological dynamics, and how these may translate into evolutionary change (Figure 1.1).

The diversity of the niche's applications in ecology is mirrored by the complex history of the concept itself. Over the course of the 20th century the niche was defined a number of times, most notably by Joseph Grinnell and his colleagues (Grinnell and Swarth 1913; Chandler 1914; Grinnell 1914; Taylor 1916; Grinnell 1917, 1922; Grinnell and Storer 1924), Charles Elton (Elton 1924, 1927), and G. E. Hutchinson (Hutchinson 1944, 1957). While each definition was in some way unique, all of the definitions expressed the belief that not all species interact similarly with the environment, and that these organismal-environmental relationships can be formally categorized in a way that is productive for ecology.

Grinnell's niche represented the ecological opportunities provided by a community that

were broad enough for only one species to occupy (Grinnell and Swarth 1913). The emphasis on the opportunities provided by the community is important; Grinnell was interested in the distribution of species, and he effectively used the niche to identify the ways that species relied on each other (e.g. for shelter), and the ways that species impeded each other (e.g. by competing for the same niche).

Elton's niche (Elton 1927) was more focused on the functional role that a species played in its environment, and particularly on the trophic role that it played. Some authors have suggested that the difference in the definitions of Grinnell and Elton is slight (Schoener 1989), but there was a clear difference in the uses to which they put the niche (Griesemer 1992). As Grinnell's focus was on species distributions, and Grinnellian niches were defined by the opportunities offered by a given community, the spatial scale at which Grinnell compared niche use across communities tended to be modest. Furthermore, Grinnell's focus was on which species, of the ecologically similar species present in a region, occupied that niche. Conversely, Elton's niche found much broader application spatially and had less of a taxonomic focus. In his textbook Animal Ecology he offered examples of species occupying the same niche in widely separated communities that presumably had few species (if any) in common. Consequently, whereas Grinnell had focused on taxonomic differences in the composition of ecologically similar communities, Elton was much more focused on the similarities in functional composition of taxonomically different communities.

Hutchinson's niche represented an indisputable departure from the niches of Elton or Grinnell in that it was not a property of a community, but rather was the property of a population or species (Colwell 1992). Hutchinson's niche essentially served to relate population fitness to environmental conditions by defining in multi-dimensional environment-space the conditions in which a population could persist (Hutchinson 1957). Hutchinson's definition

was heavily influenced by the notion that species competing for common resources could not coexist in a given space, and he split his niche definition into fundamental and realized components, to include those conditions in which persistence was possible either before ecological interactions intervened, or after ecological interactions took place, respectively.

While these three definitions effectively set the stage for the use of the niche in ecology, syntheses between them have kept the landscape of niche theory dynamic. In particular Hutchinson's student Robert MacArthur was largely responsible for extending Elton and Hutchinson's definitions into a niche theory that was based on quantitative resource use (MacArthur and Levins 1967; MacArthur 1970, 1972), and contemporary approaches to the niche often seek to integrate a species' impacts on the environment and its requirements of it (Leibold 1995; Chesson 2000; Chase and Leibold 2003).

The notion that species differ from each other in some important aspect of ecology naturally predates 1913, and as such, the ecological niche is a relatively young development from hypotheses that pre-date ecology itself. An understanding that species differ in the environments that they require to flourish has existed at least since classical antiquity (Theophrastus and Hort 1916), and was common in the writings of the phytogeographers (e.g. Humboldt and Bonpland 1805; Candolle 1820) that were foundational for ecology (Clements 1905; Scheiner and Willig 2008). In many ways Grinnell's niche owed much to this phytogeography background: having been influenced by Humboldt's work via the work of C. Hart Merriam (Merriam 1890; Wake et al. 2009), Grinnell developed a hierarchical distributional framework that related species distributions to environmental gradients (as had the phytogeographers) and employed terminology and concepts from phytogeography to do so. The niche, however, was not simply a repackaged phytogeographical concept, and the feature that arguably distinguished it most from past research was the niche's strong emphasis on the

ecological opportunities and constraints that were an emergent property of community composition via interactions between species; Grinnell et al. were cognizant of the importance of environmental conditions, but by considering these in other sections of their framework they were free to devote the niche to representing the impact of community composition. Consequently the niche was capable of explaining the presence or absence of a given species in appropriate environmental conditions as a function of either the other species on which it relied (e.g. for habitat or food), or the presence of other species with which it would compete to the point of exclusion (i.e. species that shared the same niche). This emphasis on species interactions was perpetuated by Elton's niche definition (Elton 1927) which had a focus on functional roles that relied strongly on trophic interactions, and Hutchinson's niche, which included the availability of potentially living food resources, and accounted for the impacts of ecological interactions like competition and predation (Hutchinson 1957).

One of the major consequences of niche theory for ecology has thus been to emphasize the relationships that exist between the organisms that constitute a community. Such a multi-trophic perspective should presumably be valuable regardless of the trophic position of the organism considered, and yet niche theory originally developed among animal researchers, despite the fact that plant ecology was more developed in the early 20th century (Shelford 1913). A potential explanation for this progression is that early ecology was a strongly divided science (Egerton 1976; Jax and Schwarz 2011), and plant ecologists were developing their own species interaction frameworks at this time (Clements 1916; Gleason 1926). Consequently, it is possible that the niche originally developed primarily among animal ecologists because it was animal ecologists who had access to, or interest in, the literature that used the concept.

Despite this historical divide, and the moderate confusion that has developed from the

5

multiple niche definitions in circulation, the niche occupies an essential place in 21st century ecology, and is now regularly used by researchers working with animals (e.g. Nosil and Sandoval 2008), plants (e.g. Nagaraju et al. 2013), and microbial life (e.g. Suen et al. 2007; Mullins et al. 2013).

1.2 Competition and the ecological niche

While the niche has found widespread application across ecology it has particularly strong links to one of the key questions in community ecology - the maintenance of biodiversity. The concept that species with similar ecological niches would enter into strong competition with each other, and thus fail to coexist as the more fit species excluded the less fit species, was widespread in early ecology (Darwin 1859; Grinnell and Storer 1924), and eventually came to be known as the competitive exclusion principle (Hardin 1960). The competitive exclusion principle has accumulated theoretical (e.g. Volterra 1928; MacArthur and Levins 1964; Levin 1970) and empirical (e.g. Gause 1934; Tilman 1981) support, and has even been suggested as a potential ecological law (Weber 1999). Despite this strong support, in natural settings competitive biodiversity often appears to exceed the number of niches available for it (Hutchinson 1961; Clark et al. 2007), suggesting that approaches to competitive exclusion that focus solely on niche differences among competitors are not completely sufficient.

Ecology has produced a number of responses to this competitive biodiversity paradox. While some ecologists have questioned the extent of competition's impact on ecological communities (Andrewartha and Birch 1954; Wiens 1977; Connor and Simberloff 1986; but see Schoener 1983), more recent responses to the competitive biodiversity paradox have assumed that competition has a strong impact on communities, but have developed different

visions of how competition limits competitive biodiversity. Clark et al. (Clark et al. 2004, 2007; Clark 2008) have developed a framework that ultimately suggests ecologists have underestimated the number of niches available, and as such no competitive biodiversity paradox exists. Instead they contend that it is necessary to develop high-dimensional niche models to perceive the trade-offs that are maintaining biodiversity. Much of Clark's framework can be seen as existing in opposition to ecological neutral theory, another important response to the competitive biodiversity paradox which suggests that competitive communities may be formed by functionally equivalent species such that competitive exclusion takes the form of a long-term stochastic walk to extinction (Bell 2000; Hubbell 2001). Despite the existence of clear functional differences between many species, neutral theory has demonstrated that many basic patterns in ecological data can be explained without recourse to niches (Bell 2000; Hubbell 2001), and a large literature has developed attempting to reconcile the neutral and niche perspectives or discern between them (e.g. Chave et al. 2002; Holt 2006; Holyoak and Loreau 2006; Leibold and McPeek 2006; McGill et al. 2006; Doncaster 2009).

Contemporary approaches to competition based on Chesson's concepts of equalizing and stabilizing mechanisms (Chesson 2000; HilleRisLambers et al. 2012) offer a framework that simultaneously reconciles the neutral and niche perspectives while also testing their application. This framework suggests that stable competitive coexistence (defined as the ability of either competitor to recover from rarity) is the end product not only of stabilizing mechanisms that focus intraspecific competition relative to interspecific competition (i.e., niche differentiation, for example different resource requirements or different responses to spatial or temporal environmental heterogeneity), but also of equalizing mechanisms that reduce the fitness inequalities between competitors (Chesson 2000; Nelson et al. 2005; Adler et al. 2007; Cadotte 2007; Nelson et al. 2007; Adler et al. 2010). While stable co-existence is only

possible when niche differentiation is present, fitness inequalities play an important role in competition by determining the amount of differentiation necessary to maintain competitors (Nelson et al. 2005; Adler et al. 2007). Systems without niche differentiation should result in exclusion of the less fit competitor by the more fit competitor, and in cases where the competitors have no fitness inequality in the absence of niche differentiation the system effectively becomes a neutral community where dynamics are governed by stochasticity (Chesson 2000).

A great amount of research has sought to demonstrate that the outcomes of competition in ecologically simple situations is predictable (e.g. Birch 1953; Hansen and Hubbell 1980; Tilman 1981; Tilman et al. 1981; Austin 1982; Holt et al. 1994; Wilson et al. 2007), but the advent of ecological neutral theory has increased interest in how stochasticity may affect these predictions (Tilman 2004), and there is some indication that it may result in outcomes not expected from a deterministic perspective (Okuyama 2015). An additional complicating factor arises from the variation of organismal fitness along environmental gradients (Hansen and Hubbell 1980; Tilman et al. 1981), as the influence of stochasticity on competitive outcome is likely to vary with the fitness inequality between competitors. This suggests that the tendency for competitive systems to be governed by niche or neutral processes may be context dependent.

1.3 Evolution of ecological niches

Given the important ecological consequences of a population's niche, understanding the factors that affect the form of the niche is key to the ecological goal of understanding the relationship between organisms and their environments. The niche, via the many traits that

define it, is subject to evolutionary change through selection or stochastic changes in gene frequencies (Fisher 1930; Wright 1932, 1948) given sufficient genetic variation (Bradshaw 1991; Hoffmann et al. 2003), and questions about how the niche responds to new environments have particular urgency given current rates of anthropogenic environmental change (Lavergne et al. 2010).

It is relatively easy to translate questions about the niche into the evolutionary sphere by recognizing that the niche essentially serves to map fitness through environmental space, the fundamental niche including all environmental conditions that lead to an absolute fitness (defined as r) greater than 0 (Holt and Gomulkiewicz 2004), and the realized niche including the environmental conditions where relative fitness is greater than 1 (in a competitive context).

A number of studies have investigated the consequences of selection in novel environments, and have demonstrated that populations can adapt rapidly to changes in parasite/disease incidence (Zbinden et al. 2008), predation (Reznick et al. 1990; Yoshida et al. 2003), temperature (Barrett et al. 2011), salinity (Dhar et al. 2011), and antibiotic presence (Perron et al. 2007). Such adaptation may lead to expansions of the fundamental niche along specific dimensions if it permits growth in habitats where conditions had previously prevented growth (Rainey and Travisano 1998; Urban et al. 2007; Costantini et al. 2009; Michel et al. 2004; Holt et al. 2005; Bell and Gonzalez 2009), but it may also lead to contractions along other dimensions of the niche if adaptive responses to one selection pressure lead to pleiotropic antagonisms or mutational degradation that reduce fitness along another axis of the niche (Turner and Elena 2000; Cooper 2014; Leiby and Marx 2014; but see Ostrowski et al. 2007; Bataillon et al. 2011). Any change in fitness within the fundamental niche also has the potential to affect the fitness inequalities that structure the realized niche in simple compet-

itive settings, and selection frequently does lead to changes in relative fitness (Moore 1952; Mueller 1988; Bennett and Lenski 1993; Lenski and Travisano 1994; Zbinden et al. 2008).

While clear examples of niche expansion exist, and the potential for it is implied by rapid evolution, many empiricists have noted that niches can be surprisingly stable (Rickelfs and Latham 1992; Wiens et al. 2010; Wasof et al. 2015). A number of different explanations have been proposed to explain the inability of populations to adapt, including insufficient genetic variation (Bradshaw 1991), overly strong or insufficient genetic correlations between traits (Wagner and Altenberg 1996; Kirkpatrick 2009; Futuyma 2010), stabilizing selection (Haller and Hendry 2014), and gene flow (Futuyma 2010), all of which could potentially affect the adaptability of the niche. Furthermore, the emerging paradigm of evolutionary rescue (the phenomenon in which populations that would otherwise go extinct discover a sufficiently adapted phenotype to persist) has highlighted the demographic aspects of niche evolution. This work has shown that the ability of the niche to include new environments (either by niche expansion or niche displacement) is dependent on sufficient population size to allow for standing genetic variation or the generation of mutations beneficial in the new environment (Bell and Gonzalez 2009), the degree of maladaptation in the new environment (Holt and Gaines 1992; Osmond and de Mazancourt 2013), and the extent of spatial connection between environments (Holt and Gaines 1992; Holt 1996; Gomulkiewicz et al. 1999). Finally, interspecific interactions may constrain ecological niches by forcing populations to evolve to be more similar or dissimilar to their competitors (e.g. limiting similarity), depending on the distribution of other species' niches (Hutchinson 1959; MacArthur and Levins 1967; Abrams 1987; Tilman 2004; Schwilk and Ackerly 2005; Gravel et al. 2006; Herben and Goldberg 2014). Consequently, niche expansion is most likely to occur when populations have sufficient genetic variation, when the underlying traits that underpin niche expansion are

relatively few and not subject to trade-offs with each other, when environments outside the niche are not already occupied by other species, and when selection for niche expansion is present, but not so great that the population goes extinct.

Despite this extensive research examining the potential for adaptation, there are some important gaps in the research literature. While research often addresses the impacts of different stressors (Goho and Bell 2000), it is relatively rare for research to address the impacts of stressors in concert. Such a multiple stressor perspective is essential as populations often encounter stressors together in nature, and the presence of an additional stressor may lead to synergistic or antagonistic effects (Vinebrooke et al. 2004; Crain et al. 2008). Additionally, while there has been a great amount of research on the evolution of niche differentiation (MacArthur 1958; Hutchinson 1959; MacArthur and Levins 1967; Slatkin 1980; Abrams 1987; Doebeli 1996; Grant and Grant 2006; Lawrence et al. 2012; Bailey et al. 2013), relatively little research focuses on the evolution of fitness inequalities between competitors (Lankau 2011), despite the fact that fitness inequalities also play a role in determining competitive coexistence. Understanding whether environmental change is likely to result in competitive systems with larger or smaller fitness inequalities is key not only to understanding how the potential for competitive coexistence will change, but also to what extent a niche theoretic view of competition is likely to apply.

1.4   Thesis questions and chapter summaries

My thesis broadly seeks to understand how the ecological niche can guide thinking about ecological and evolutionary processes that affect community composition, and in particular competitive coexistence. To achieve this goal I pursue here a number of questions about

the ecological niche: how its history has shaped the discipline of ecology, how its predictions for competitive outcome are affected by incorporating variable fitness inequalities and stochasticity into competitive dynamics, and how environmental conditions might not only determine ecological dynamics, but also the ways in which those dynamics may change. All three of these questions address issues fundamental to the practice of ecology today.

1.4.1 Chapter 2

The importance of the ecological niche has been reflected in the number of reviews that have been written about it (e.g. Udvardy 1959; Whittaker et al. 1973; Hutchinson 1978; Colwell 1992; Griesemer 1992; Leibold 1995; Chase and Leibold 2003), yet these reviews have for the most part focused on parsing the different definitions of the niche, and not on tracking the way that different communities have used it. Citation analysis provides a powerful tool for exploring the history of concepts and their communication (Garfield et al. 1964; Mina et al. 2007), and for uncovering relationships between disciplines or authors (e.g. Lee 2015), and consequently I employ this technique to perform a unique quantitative analysis of the history of one of ecology's central concepts. In particular, I ask (1) what route the niche took in its spread from the animal researchers who defined it to its present use across ecology, (2) what role the different definitions of the niche have played in this spread, and (3) to what extent the conceptual unification that has resulted from adoption of the niche has also manifested in an integration of the niche literature.

1.4.2 Chapter 3

The debate over the niche and neutral perspectives in competition theory has left community ecology in a position of uncertainty about whether these frameworks need be integrated, and if so, how this synthesis should play out. In chapter 3 I use a resource competition model that has played an essential role in the development of contemporary niche theory (Tilman 1982) to ask to what extent the characterization of competition as a neutral or niche driven process is dependent on environmental context. Specifically I ask (1) how competition along a gradient in fitness inequality affects competitive outcome, (2) how competition along a gradient in stochasticity affects competitive outcome, (3) and how these gradients interact.

1.4.3 Chapter 4

The relationship between an organism's fitness and its environment lies at the heart of ecology. It defines an organism's fundamental niche, and by dictating the relative abilities of competitors (Birch 1953; Tilman et al. 1981), the efficiencies of predators (Lankford et al. 2001), and susceptibility to pathogens (Antonovics 2009), it also defines an organism's realized niche. Experimental evolution has demonstrated that many populations respond rapidly to environmental pressures leading to altered competitive and trophic dynamics (Yoshida et al. 2003), and in an era of rapid anthropogenic change it is essential to understand how the niche, and the fitnesses that constitute it are likely to respond to environmental changes. In chapter 4 we examine how the fundamental niches of populations respond to different individual stressors as well as a multiple-stressor treatment. In particular I ask (1) whether selection in stressful environments leads to the expansion of the fundamental niche, and (2) how selection in stressful environments affects the fitness inequalities that structure the

realized niche in simple competitive systems. In doing so I take advantage of an emerging ecological model system, yeast (Replansky et al. 2008), to address a fundamental question that sits at the boundary of ecological and evolutionary dynamics.

Niche

Competition
Predation, Mutualism
Parasitism, etc.

Competition
Predation, Mutualism
Parasitism, etc.

Community composition
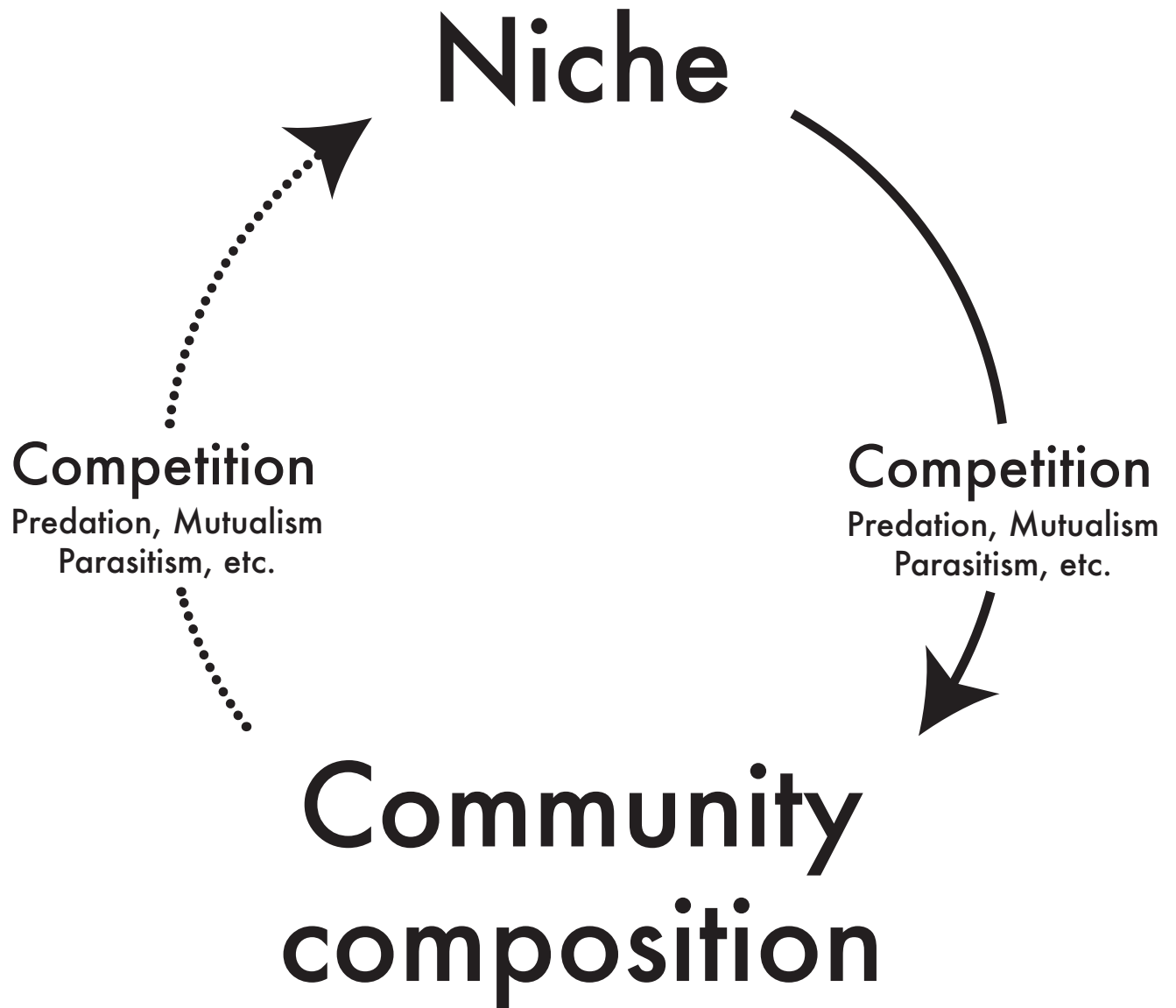
Figure 1.1. A set of ecological niches leads to effects on community composition through a variety of processes, though historically it has been most strongly associated with competition. Community composition in turn affects how ecological niches evolve through those same processes.

1.5   Literature Cited

Abrams, P. A. 1987. Alternative models of character displacement and niche shift. I. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. Evolution 41:651–661.

Adler, P. B., S. P. Ellner, and J. M. Levine. 2010. Coexistence of perennial plants: an embarrassment of niches. Ecology Letters 13:1019–1029.

Adler, P. B., J. HilleRisLambers, and J. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.

Antonovics, J. 2009. The effect of sterilizing diseases on host abundance and distribution along environmental gradients. Proceedings of the Royal Society B 276:1443–1448.

Austin, M. P. 1982. Use of a relative physiological performance value in the prediction of performance in multispecies mixtures from monoculture performance. Journal of Ecology 70:559–570.

Bailey, S. F., J. R. Dettman, P. B. Rainey, and R. Kassen. 2013. Competition both drives and impedes diversification in a model adaptive radiation. Proceedings of the Royal Society B 280:20131253.

Barrett, R. D. H., A. Paccard, T. H. Healy, S. Bergek, P. M. Schulte, and D. Schluter. 2011. Rapid evolution of cold tolerance in stickleback. Proceedings of the Royal Society B 278:233–238.

Bataillon, T., T. Zhang, and R. Kassen. 2011. Cost of adaptation and fitness effects of beneficial mutations in *Pseudomonas fluorescens.* Genetics 189:939–949.

Bell, G. 2000. The distribution of abundance in neutral communities. The American Naturalist 155:606–617.

Bell, G., and A. Gonzalez. 2009. Evolutionary rescue can prevent extinction following environmental change. Ecology Letters 12:942–948.

Bennett, A. F., and R. E. Lenski. 1993. Evolutionary adaptation to temperature II. Thermal niches of experimental lines of Escherichia coli. Evolution 47:1–12.

Birch, L. C. 1953. Experimental background to the study of the distribution and abundance of insects: III. The relation between innate capacity for increase and survival of different species of beetles living together on the same food. Evolution 7:136–144.

Bradshaw, A. D. 1991. Genostasis and the limits to evolution. Philosophical Transactions: Biological Sciences 333:289–305.

Cadotte, M. W. 2007. Concurrent niche and neutral processes in the competition-colonization model of species coexistence. Proceedings of the Royal Society of London. Series B. 274:2739–2744.

Candolle, A.-P. d. 1820. Essai élémentaire de géographie botanique. F.G. Levrault, Strasbourg.

Chandler, A. C. 1914. The effect of extent of distribution on speciation. The American Naturalist 48:129–160.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches linking classical and contemporary approaches. University of Chicago Press, Chicago.

Chave, J., H. C. Muller-Landau, and S. A. Levin. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. The American Naturalist 159:1–23.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Clark, J. S. 2008. Beyond neutral science. Trends in Ecology & Evolution 24:8–15.

Clark, J. S., M. Dietze, S. Chakraborty, P. K. Agarwal, I. Ibanez, S. LaDeau, and M. Wolosin. 2007. Resolving the biodiversity paradox. Ecology Letters 10:647–662.

Clark, J. S., S. LaDeau, and I. Ibanez. 2004. Fecundity of trees and the colonization-competition hypothesis. Ecological Monographs 74:415–442.

Clements, F. E. 1905. Research methods in ecology. The University Publishing Company, Lincoln.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Insitution of Washington, Washington.

Colwell, R. K. 1992. Niche: a bifurcation in the conceptual lineage of the term. Pages 241–248 *in* E. F. Keller and E. A. Lloyd, editors. Keywords in evolutionary biology. Harvard University Press, Cambridge.

Connor, E. F., and D. Simberloff. 1986. Competition, scientific method, and null models in ecology: because field experiments are difficult to perform, ecologists often rely on evidence that is nonexperimental and that therefore needs to be rigorously evaluated. American Scientist 74:155–162.

Cooper, V. S. 2014. The origins of specialization: insights from bacteria held 25 years in captivity. PLoS Biology 12:e1001790.

Costantini, C., D. Ayala, W. Guelbeogo, M. Pombi, C. Some, I. Bassole, K. Ose, J.-M. Fotsing, N. Sagnon, D. Fontenille, N. Besansky, and F. Simard. 2009. Living at the edge: biogeographic patterns of habitat segregation conform to speciation by niche expansion in *Anopheles gambiae*. BMC Ecol. 9:16.

Crain, C. M., K. Kroeker, and B. S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters 11:1304–1315.

Darwin, C. 1859. On the origin of species. John Murray, London.

Dhar, R., R. Sägesser, C. Weikert, J. Yuan, and A. Wagner. 2011. Adaptation of *Saccharomyces cerevisiae* to saline stress through laboratory evolution. Journal of Evolutionary Biology 24:1135–1153.

Doebeli, M. 1996. An explicit genetic model for ecological character displacement. Ecology 77:510–520.

Doncaster, C. P. 2009. Ecological equivalence: a realistic assumption for niche theory as a testable alternative to neutral theory. PLoS ONE 4:e7460.

Egerton, F. N. 1976. Ecological studies and observations before 1900. Pages 175–179 *in* B. J. Taylor and T. J. White, editors. Issues and ideas in America. University of Oklahoma Press, Norman.

Elton, C. S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. Journal of Experimental Biology 2:119–163.

Elton, C. S. 1927. Animal ecology. Macmillan Co., New York.

Fisher, R. A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford.

Futuyma, D. J. 2010. Evolutionary constraint and ecological consequences. Evolution 64:1865–1884.

Garfield, E., I. H. Sher, and R. J. Torpie. 1964. The use of citation data in writing the history of science. Institute for Scientific Information Inc., Philadelphia.

Gause, G. F. 1934. The struggle for existence. The Williams and Wilkins Company, Baltimore.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53:7–26.

Goho, S., and G. Bell. 2000. Mild environmental stress elicits mutations affecting fitness in *Chlamydomonas.* Proceedings of the Royal Society of London B 267:123–129.

Gomulkiewicz, R., R. D. Holt, and M. Barfield. 1999. The effects of density dependence and immigration on local adaptation and niche evolution in a black-hole sink environment. Theoretical Population Biology 55:283 – 296.

Grant, P. R., and B. R. Grant. 2006. Evolution of character displacement in Darwin's finches. Science 313:224–226.

Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters 9:399–409.

Griesemer, J. R. 1992. Niche: historical perspectives. Pages 231–240 *in* E. F. Keller and E. A. Lloyd, editors. Keywords in evolutionary biology. Harvard University Press, Cambridge.

Grinnell, J. 1914. An account of the mammals and birds of the lower Colorado Valley. University of California Press, Berkeley.

Grinnell, J. 1917. The niche relationships of the California Thrasher. Auk 34:427–433.

Grinnell, J. 1922. The trend of avian populations in California. Science 56:671–676.

Grinnell, J., and T. I. Storer. 1924. Animal life in the Yosemite; an account of the mammals, birds, reptiles, and amphilbians in a cross-section of the Sierra Nevada. University of California Press, Berkeley.

Grinnell, J., and H. S. Swarth. 1913. An account of the birds and mammals of the San Jacinto area of southern California: with remarks upon the behavior of goegraphic races on the margins of their habitats. University of California Press, Berkeley.

Haller, B. C., and A. P. Hendry. 2014. Solving the paradox of stasis: squashed stabilizing selection and the limits of detection. Evolution 68:483–500.

Hansen, S. R., and S. P. Hubbell. 1980. Single nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes. Science 207:1491–1493.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Herben, T., and D. E. Goldberg. 2014. Community assembly by limiting similarity vs. competitive hierarchies: testing the consequences of dispersion of individual traits. Journal of Ecology 102:156–166.

HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. Rethinking community assembly through the lens of coexistence theory. Annual Review oF Ecology, Evolution, and Systematics 43:227–248.

Hoffmann, A. A., R. J. Hallas, J. A. Dean, and M. Schiffer. 2003. Low potential for climatic stress adaptation in a rainforest *Drosophila* species. Science 301:100–102.

Holt, R., and M. Gaines. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. Evolutionary Ecology 6:433–447.

Holt, R. D. 1996. Demographic constraints in evolution: towards unifying the evolutionary theories of senescence and niche conservatism. Evolutionary Ecology 10:1–11.

Holt, R. D. 2006. Emergent neutrality. Trends in Ecology & Evolution 21:531–533.

Holt, R. D., M. Barfield, and R. Gomulkiewicz 2005. Theories of niche conservatism and evolution: could exotic species be potential tests? Pages 259–290 *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species invasions: insights into ecology, evolution, and biogeography. Sinauer associates, Sunderland.

Holt, R. D., and R. Gomulkiewicz 2004. Conservation implications of niche conservatism and

evolution in heterogeneous environments. Pages 244–264 *in* R. Ferrière, U. Dieckmann, and D. Couvet, editors. Evolutionary conservation biology. Cambridge University Press, Cambridge.

Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. The American Naturalist 144:741–771.

Holyoak, M., and M. Loreau. 2006. Reconciling empirical ecology with neutral community models. Ecology 87:1370–1377.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press., Princeton.

Humboldt, A. v., and A. Bonpland. 1805. Essai sur la géographie des plantes. Levrault, Schoell et compangie, Paris.

Hutchinson, G. E. 1944. Limnological studies in Conneticut. VII. A critical examination of the supposed relationship between phytoplankton periodicity and chemical changes in lake waters. Ecology 25:3–26.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415–427.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? The American Naturalist 93:145–159.

Hutchinson, G. E. 1961. The paradox of the plankton. The American Naturalist 95:137–145.

Hutchinson, G. E. 1978. An introduction to population ecology. Yale University Press, New Haven.

Jax, K., and A. Schwarz 2011. The fundamental subdivisions of ecology. Pages 175–179

in A. Schwarz and K. Jax, editors. Ecology revisited reflecting on concepts, advancing science. Springer, Dordrecht.

Kirkpatrick, M. 2009. Patterns of quantitative genetic variation in multiple dimensions. Genetica 136:271–284.

Lankau, R. A. 2011. Rapid evolutionary change and the coexistence of species. Annual Review of Ecology, Evolution, and Systematics 42:335–354.

Lankford, T. E., J. M. Billerbeck, and D. O. Conover. 2001. Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in *Menidia menidia*. Evolution 55:1873–1881.

Lavergne, S., N. Mouquet, W. Thuiller, and O. Ronce. 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. Annual Review of Ecology, Evolution, and Systematics 41:321–350.

Lawrence, D., F. Fiegna, V. Behrends, J. G. Bundy, A. B. Phillimore, T. Bell, and T. G. Barraclough. 2012. Species interactions alter evolutionary responses to a novel environment. PLoS Biology 10:e1001330.

Lee, H. 2015. Uncovering the multidisciplinary nature of technology management: journal citation network analysis. Scientometrics 102:51–75.

Leibold, M. 1995. The niche concept revisited: mechanistic models and community context. Ecology 76:1371–1382.

Leibold, M., and M. McPeek. 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87:1399–1410.

Leiby, N., and C. J. Marx. 2014. Metabolic erosion primarily through mutation accumulation, and not tradeoffs, drives limited evolution of substrate specificity in *Escherichia coli*. PLoS Biology 12:e1001789.

Lenski, R. E., and M. Travisano. 1994. Dynamics of adaptation and diversification: a 10,000-generation experiment with bacterial populations. Proceedings of the National Academy of Sciences USA 91:6808–6814.

Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. The American Naturalist 104:413–423.

Levine, R. S., A. Peterson, K. L. Yorita, D. Carroll, I. K. Damon, and M. G. Reynolds. 2007. Ecological Niche and Geographic Distribution of Human Monkeypox in Africa. PLoS ONE 2:e176.

MacArthur, R. 1970. Species packing and competitive equilibrium for many species. Theoretical Population Biology 1:1 – 11.

MacArthur, R. 1972. Geographical ecology: patterns in the distribution of species. Princeton University Press, Princeton.

MacArthur, R., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences USA 51:1207–1210.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377–385.

McGill, B. J., B. A. Maurer, and M. D. Weiser. 2006. Empirical evaluation of netural theory. Ecology 87:1411–1423.

Merriam, C. H. 1890. Results of a biological survey of the San Francisco mountain region and desert of the Little Colorado, Arizona. Government Printing Office, Washington.

Michel, A., R. S. Arias, B. E. Scheffler, S. O. Duke, M. Netherland, and F. E. Dayan. 2004.

Somatic mutation-mediated evolution of herbicide resistance in the nonindigenous invasive plant hydrilla (*Hydrilla verticillata*). Molecular Ecology 13:3229–3237.

Mina, A., R. Ramlogan, G. Tampubolon, and J. S. Metcalfe. 2007. Mapping evolutionary trajectories: applications to the growth and transformation of medical knowledge. Research Policy 36:789 – 806.

Moore, J. A. 1952. Competition between *Drosophila melanogaster* and *Drosophila simulans*: II. The improvement of competitive ability through selection. Proceedings of the National Academy of Sciences USA 38:813–817.

Mueller, L. D. 1988. Evolution of competitive ability in *Drosophila* by density-dependent natural selection. Proceedings of the National Academy of Sciences USA 85:4383–4386.

Mullins, J. C., G. Garofolo, M. Van Ert, A. Fasanella, L. Lukhnova, M. E. Hugh-Jones, and J. K. Blackburn. 2013. Ecological niche modeling of *Bacillus anthracis* on three continents: evidence for genetic-ecological divergence? PLoS ONE 8:e72451.

Nagaraju, S. K., R. Gudasalamani, N. Barve, J. Ghazoul, G. K. Narayanagowda, and U. S. Ramanan. 2013. Do ecological niche model predictions reflect the adaptive landscape of species?: a test using *Myristica malabarica* Lam., an endemic tree in the western Ghats, India. PLoS ONE 8:e82066.

Nelson, W., E. McCauley, and R. M. Nisbet. 2007. Stage-structured cycles generate strong fitness-equalizing mechanisms. Evolutionary Ecology 21:499–515.

Nelson, W. A., E. McCauley, and F. J. Wrona. 2005. Stage-structured cycles promote genetic diversity in a predator-prey system of *Daphnia* and algae. Nature 433:413–417.

Nosil, P., and C. P. Sandoval. 2008. Ecological niche dimensionality and the evolutionary diversification of stick insects. PLoS ONE 3:e1907.

Okuyama, T. 2015. Demographic stochasticity alters the outcome of exploitation competition. Journal of Theoretical Biology 365:347–351.

Osmond, M. M., and C. de Mazancourt. 2013. How competition affects evolutionary rescue. Philosophical Transactions of the Royal Society of London B: Biological Sciences 368:20120085.

Ostrowski, E. A., C. Ofria, and R. E. Lenski. 2007. Ecological specialization and adaptive decay in digital organisms. The American Naturalist 169:E1–E20.

Perron, G. G., A. Gonzalez, and A. Buckling. 2007. Source-sink dynamics shape the evolution of antibiotic resistance and its pleiotropic fitness cost. Proceedings of the Royal Society B 274:2351–2356.

Rainey, P. B., and M. Travisano. 1998. Adaptive radiation in a heterogeneous environment. Nature 394:69–72.

Replansky, T., V. Koufopanou, D. Greig, and G. Bell. 2008. *Saccharomyces sensu stricto* as a model system for evolution and ecology. Trends in Ecology & Evolution 23:494 – 501.

Reznick, D. A., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. Nature 346:357–359.

Rickelfs, R. E., and R. E. Latham. 1992. Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. The American Naturalist pages 1305–1321.

Scheiner, S. M., and M. R. Willig. 2008. A general theory of ecology. Theoretical Ecology 1:21–28.

Schoener, T. W. 1983. Field experiments on interspecific competition. The American Naturalist 122:240–285.

Schoener, T. W. 1989. The ecological niche. Pages 79–115 *in* Ecological concepts. Blackwell Scientific Publications, Oxford.

Schwilk, D. W., and D. D. Ackerly. 2005. Limiting similarity and functional diversity along environmental gradients. Ecology Letters 8:272–281.

Shelford, V. E. 1913. Animal communities in temperate America, as illustrated in the Chicago region; a study in animal ecology,. Pub. for the Geographic Society of Chicago by the University of Chicago Press, Chicago.

Slatkin, M. 1980. Ecological character displacement. Ecology 61:163–177.

Suen, G., B. S. Goldman, and R. D. Welch. 2007. Predicting prokaryotic ecological niches using genome sequence analysis. PLoS ONE 2:e743.

Taylor, W. P. 1916. The status of the beavers of western North America with a consideration of the factors in their speciation. University of California publications in zoology 12:413–495.

Theophrastus, and A. Hort. 1916. Enquiry into plants and minor works on odours and weather signs. G.P. Putnam's Sons, New York.

Thompson, R. M., U. Brose, J. A. Dunne, R. O. Hall, S. Hladyz, R. L. Kitching, N. D. Martinez, H. Rantala, T. N. Romanuk, D. B. Stouffer, and J. M. Tylianakis. 2012. Food webs: reconciling the structure and function of biodiversity. Trends in Ecology & Evolution 27:689–697.

Tilman, D. 1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology 62:802–815.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton.

Tilman, D. 2004. Niche trade-offs, neutrality, and community structure: a stochastic theory

of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences USA 101:10854–10861.

Tilman, D., M. Mattson, and S. Langer. 1981. Competition and nutrient kinetics along a temperature gradient: an experimental test of a mechanistic approach to niche theory. Limnology and Oceanography 26:1020–1033.

Turner, P. E., and S. F. Elena. 2000. Cost of host radiation in an RNA virus. Genetics 156:1465–1470.

Udvardy, M. F. D. 1959. Notes on the ecological concepts of habitat, biotope and niche. Ecology 40:725–728.

Urban, M. C., B. L. Phillips, D. K. Skelly, and R. Shine. 2007. The cane toad's (*Chaunus [Bufo] marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. Proceedings of the Royal Society B 274:1413–1419.

Vinebrooke, R. D., K. L. Cottingham, J. Norberg, Marten Scheffer, S. I. Dodson, S. C. Maberly, and U. Sommer. 2004. Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. Oikos 104:451–457.

Volterra, V. 1928. Variations and fluctuations of the number of individuals in animal species living together. Journal du Conseil International de l'Exploration de la Mer 3:3–51.

Wagner, G. P., and L. Altenberg. 1996. Perspective: complex adaptations and the evolution of evolvability. Evolution 50:967–976.

Wake, D. B., E. A. Hadly, and D. D. Ackerly. 2009. Biogeography, changing climates, and niche evolution. Proceedings of the National Academy of Sciences 106:19631–19636.

Warren, D. L. 2012. In defense of 'niche modeling'. Trends in Ecology & Evolution 27:497–500.

Wasof, S., J. Lenoir, P. A. Aarrestad, I. G. Alsos, W. S. Armbruster, G. Austrheim,

V. Bakkestuen, H. J. B. Birks, K. A. Bråthen, O. Broennimann, J. Brunet, H. H. Bruun, C. J. Dahlberg, M. Diekmann, S. Dullinger, M. Dynesius, R. Ejrnaes, J.-C. Gégout, B. J. Graae, J.-A. Grytnes, A. Guisan, K. Hylander, I. S. Jónsdóttir, J. Kapfer, K. Klanderud, M. Luoto, A. Milbau, M. Moora, B. Nygaard, A. Odland, H. Pauli, V. Ravolainen, S. Reinhardt, S. M. Sandvik, F. H. Schei, J. D. M. Speed, J.-C. Svenning, W. Thuiller, L. U. Tveraabak, V. Vandvik, L. G. Velle, R. Virtanen, P. Vittoz, W. Willner, T. Wohlgemuth, N. E. Zimmermann, M. Zobel, and G. Decocq. 2015. Disjunct populations of European vascular plant species keep the same climatic niches. Global Ecology and Biogeography 24:1401–1412.

Weber, M. 1999. The aim and structure of ecological theory. Philosophy of Science 66:71–93.

Whittaker, R. H., S. A. Levin, and R. B. Root. 1973. Niche, habitat, and ecotope. The American Naturalist 107:321–338.

Wiens, J. A. 1977. On competition and variable environments. American Scientist 65:590–597.

Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, T. Jonathan Davies, J.-A. Grytnes, S. P. Harrison, B. A. Hawkins, R. D. Holt, C. M. McCain, and P. R. Stephens. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13:1310–1324.

Wilson, J. B., E. Spijkerman, and J. Huisman. 2007. Is there really insufficient support for Tilman's R* concept? A comment on Miller et al. The American Naturalist 169:700–706.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Pages 356–366 *in* Proceedings of the sixth international congress of genetics.

Wright, S. 1948. On the roles of directed and random changes in the genetics of populations. Evolution 2:279–294.

Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, and N. G. Hairston. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. Nature 424:303–306.

Zbinden, M., C. R. Haag, and D. Ebert. 2008. Experimental evolution of field populations of *Daphnia magna* in response to parasite treatment. Journal of Evolutionary Biology 21:1068–1078.

Chapter 2

A network approach reveals surprises about the history of the niche

Michael T. Pedruski, Gregor F. Fussmann, and Andrew Gonzalez.

Department of Biology, McGill University, 1205 Dr. Penfield, Montréal QC, H3A 1B1

2.1 Abstract

The ecological niche is a prominent theoretical concept in many ecological fields, central to ecological understanding of species interactions and community structure. To better understand this important concept, and the impact it has had on ecology, we used a citation analysis to examine the history of the niche through the citation behaviours of the ecologists who used it during the 20th century. In particular we sought to document the spread of the niche across ecological sub-disciplines, to evaluate whether the existence of different niche definitions facilitated the spread of the niche, and to see whether the conceptual integration stemming from adoption of the niche has also yielded an integration of the niche literature across sub-disciplinary boundaries. We show that the ecological niche has been adopted by a number of sub-disciplines, but that this success does not appear to have relied strongly on the different niche definitions, nor has it led to general integration of the niche literature across sub-disciplinary boundaries. Our analysis thus not only examines the history of one of ecology's central concepts, it also suggests that despite the conceptual unification that resulted from the broad adoption of the niche, a unified niche literature had not emerged by the close of the 20th century.

2.2 Key words

Ecological niche; Citation network; History of ecology; Disciplinary integration

2.3 Introduction

The ecological niche is one of the key concepts in community ecology, central to our understanding of competitive exclusion (Grinnell and Storer 1924; Gause 1934; Hardin 1960), the trophic structure of communities (Elton 1927; Thompson et al. 2012), the relationship between organismal fitness and environmental conditions (Hutchinson 1957), and trait evolution (MacArthur and Levins 1967). Despite its fundamental status in ecology today, the niche didn't appear in ecological literature until well after the development of ecology as a discipline. The term is widely reported to have first appeared in the ecological literature with Johnson (1910), who uses the term just once without an explicit definition to refer to environmental spaces, each of which is expected to be occupied by a different species. The first major development of a niche definition quickly followed in 1913 by Joseph Grinnell and colleagues (e.g. Grinnell and Swarth 1913; Chandler 1914; Grinnell 1914; Taylor 1916; Grinnell 1917), who effectively defined the niche as an ecological opportunity in the community that was sufficient for just one species.

As ecology matured over the course of the 20th century a number of niche definitions joined that of Grinnell et al., notably those of Elton (1927), and Hutchinson (1957) (Box 1). Elton proposed a niche concept that was focused on demonstrating similarities in the structures of different communities in terms of the functional roles that the constituent species played. In contrast to the niches of Grinnell and Elton, Hutchinson's niche was less a property of the community than it was a property of a population (Colwell 1992; Griesemer 1992; Colwell and Rangel 2009), and it developed a formal relationship between an organism's fitness and environmental conditions.

Despite the apparent differences in the definitions of Grinnell, Elton, and Hutchinson,

contemporary ecologists often consider the niche to represent both a species' requirements of its environment and its impacts on the environment (Leibold 1995). This impact-requirement definition synthesizes Grinnell, Elton, and Hutchinson's niches, and has positioned the niche as a concept that could potentially summarize all of an organism's ecological interactions with implications for almost all ecological research.

Given the theoretical importance of the niche it might not seem surprising that the concept has been adopted by many branches of ecology. Yet during the initial period of the niche's development, ecology was a strongly divided science, and its different streams such as plant ecology, limnology, and animal ecology had developed relatively independently of one another (Egerton 1976), with authors tending to focus their research on either animals or plants, but rarely both (Jax and Schwarz 2011). Grinnell and his colleagues were zoologists, and Elton an animal ecologist, and as a consequence the ecological niche entered the world through the publications of animal researchers in an era when plant ecology was more developed (Shelford 1913). Contemporary ecology, on the other hand, has not only broadly adopted the niche, but also attempts to integrate understandings of community structure across more than one trophic level. Given the disciplinary history of the niche, and its central role in ecology today, we wanted to examine how the niche spread in ecology, and to investigate whether the conceptual integration that resulted from its broad adoption might be evident in the citation behaviour of ecologists. Consequently, we performed a citation network analysis with the following goals:

1. We wanted to quantify the spread of the niche in the ecological literature: How widely is the niche concept used, and can it legitimately be said to be used in a way that is consistent with its role as a unifying concept? If the niche concept has actually only been taken up by a small number of ecological sub-disciplines, or remains marginal

in those sub-disciplines, it may be that the niche has not led to as much conceptual unification as we believe.

2. We wanted to ask what role the different niche definitions have played in the spread of the niche concept: The niche has a notoriously polysemic history which has caused its share of confusion, but we suggest that the existence of many definitions may have been one of the keys to its success. If each author's definition attracted different audiences it is possible that the niche's spread has in fact relied on its many definitions.

3. We wanted to ask whether the development of the niche framework in ecology has led to an integrated body of literature: If the use of the niche among ecologists signals acceptance of a common theoretical framework, it follows that ecologists should be interested in other research using the niche. Consequently, we asked whether ecologists using the niche cited other publications using the niche regardless of the sub-discipline or taxonomic group in which either ecologist was working. If the niche literature proves to be integrated across sub-disciplines it suggests that not only the conceptual underpinnings, but also the research literature of ecology has become integrated across sub-disciplines. Conversely, if citations between ecological sub-disciplines are rare, it may be that assimilation of the niche concept has occurred but we are still awaiting an interdisciplinary use of the concept in ecology.

2.4 Methods

2.4.1 Citation network construction

To assess these questions we searched the Web of Science (Web of Science Core Collection) for papers with the topic search term "niche*" published between 1900 and 1999, with data collection running from June 18, 2013 to August 30, 2013. Web of science topic searches return results that include the search term in the title, abstract, keywords, or Keywords Plus fields, but do not perform full text searches, and as such should be regarded as a highly conservative estimate of the actual circulation of the niche in the ecological literature. As this search returned many results for the niche that used it in a non-ecological sense, we made the decision to exclude these, including or excluding references based on their titles, and when titles were ambiguous by using other available information, including the keywords, the abstract, and the source publication. None of the papers that played an important role in defining the niche were returned by our search: Grinnell (1917), and Elton's textbook (Elton 1927) were not found in the Web of Science core collection, and neither Elton (1927), nor Hutchinson (1957) used 'niche' in their title, nor did they provide an abstract or keywords. Consequently, to address our questions, we manually added these references to the search results (with data collection on February 24, 2014), and refer to them hereafter as 'key definitions'. We constructed a network based on the citations between these records, and used this network to evaluate our questions about the nature of the niche's spread, the importance of the three niche definitions, and the integrated nature of the ecological literature. Selection of relevant records was done in the Web of Science interface, and all subsequent manipulation, and analysis of records was done in R version 3.0.2 (R Core Team 2013) using the packages bibtex version 0.3-6 (Francois 2013), and igraph version 0.6.5-2 (Csardi and Nepusz 2006)

(detailed methods in Appendix 2.1).

2.4.2 Citation network analysis

To address our questions about the effects of the niche on the disciplinary structure of ecology it was necessary to assign a sub-discipline to each record in our network, which we did by defining the target audience of the record. For journal articles we did this based on the title of the journal, and, if necessary, by using descriptions of the journal. Records without an associated journal (e.g. proceedings papers) were classified on the associated book title, conference title, or publication series if appropriate. Records published in journals were classified based on title of the journal, and if necessary by using descriptions of the journal.

To assess the relationship between the different niche definitions and the uptake of the niche by sub-disciplines we compared the identities of the sub-disciplines citing each key definition, and also analyzed whether citation of a given definition was sub-discipline dependent for the eight sub-disciplines that cited all three definitions using a χ^2 test. We also examined the in-degree centrality of the different papers in our network, a measure of the importance of a paper determined by the number of citations it has received. To assess hypotheses about the integration of sub-disciplines we focused on the linkages between six sub-disciplines that played important roles in the formation of ecology (Egerton 1976): 'Animal research' (a combination of the animal ecology and animal science sub-disciplines), 'plant research' (a combination of the plant ecology and plant science sub-disciplines), limnology and oceanography, medicine, agronomy, and conservation. To assess questions about whether the general ecology literature was providing a vector for the communication of concepts between different sub-disciplines, we further refined our focus to the general ecology, animal research, and plant research sub-disciplines, which were the sub-disciplines with the most papers, and also

37

the sub-disciplines most relevant to ecology's history of separation.

We used randomization tests (Quinn and Keough 2002) to test hypotheses about the integration of different sub-disciplines, generally by retaining as much of the network structure as possible while randomizing either the origin or destination of citations. A detailed list of the null models and randomization methods used is available in Appendix 2.2.

2.5 Results

2.5.1 The disciplinary spread of the niche

Our final dataset included 3687 records, and demonstrated that the niche spread from early records in animal science and animal ecology into 41 sub-disciplines over the course of the 20th century (including 1 record for which the sub-discipline was classified as "Other") (Fig. 2.1). For some of our sub-disciplines the niche remained a marginal concept, only returning a few records, but for the majority of our sub-disciplines it has clearly found acceptance, with 31 of the sub-disciplines having more than 10 records, and 18 sub-disciplines having more than 50 (Table 2.1). The rate of disciplinary uptake was greatest in the 1970s-1980s (Fig. 2.1, Table 2.1), with 19 sub-disciplines added in the years 1970-1979. The decade 1970-1979 was also the period at which the network was at its most cohesive, with the fewest number of network sub-components scaled by the total number of vertices (Fig. 2.5 in Appendix 2.3), and half of the top 1% of papers in terms of citations received were published in the decade. In contrast to disciplinary uptake, the number of records on the niche, the number of citations from niche papers, and the number of publications invoking the niche all had their greatest rates of increase in the 1990s (Fig. 2.1). Interestingly, most disciplines appeared in the niche citation network without reference to other papers in the network: in only ten of our

forty-one sub-disciplines did a paper published in the sub-discipline's first year cite another paper in the network. This tendency for disciplines to enter the network independently of papers already in the network was broadly paralleled by the overall structure of the network, where citations between papers were relatively rare and concentrated, with an average of 1.22 intra-network citations per paper, and a median of 0 intra-network citations per paper.

2.5.2   The impact of multiple niche definitions

We found little evidence that the number of niche definitions was important to the disciplinary uptake by the niche. All three of the key definitions we included were within the top 1% of papers in terms of citations received, but Hutchinson (1957) received far more citations than the other two key definitions (Fig. 2.2) - indeed, Hutchinson (1957) was the most cited record in the entire network, surpassing its nearest competitor by 39 citations.

A core of eight sub-disciplines cited all three of our key definitions, and a number of disciplines cited two, one, or no definitions (Fig. 2.6 and Table 2.3 in Appendix 2.3), but, key to our question about the effect of multiple definitions, all sub-disciplines that cited a definition cited Hutchinson (1957), and none of the citations to Grinnell (1917) nor Elton (1927) in our network pre-date 1957. Furthermore, there was no significant relationship between the key definitions and the eight sub-disciplines that cited all three definitions in terms of citation patterns ($\chi^2 = 14.26$, df = 14, p = 0.43).

2.5.3   The integration of the niche within ecological literature

Our results suggest that while sub-disciplines in the niche network were well integrated with the general ecological literature, they were not generally strongly integrated with one

another. There was marked heterogeneity in the number and identity of sub-disciplines that each sub-discipline cited, and was cited by (Fig. 2.3). When we examined the number of citations in both directions between animal research, plant research, limnology and oceanography, medicine, agronomy, and conservation in the niche network we found that the majority of interconnections between these sub-disciplines were represented by significantly fewer citations than would be expected by chance (Table 2.2). For example, while the mean null expectation for connections between animal and plant research was roughly 153 citations, our network only had 11 (Fig. 2.7 in Appendix 2.3). The exceptions to this pattern of low interconnectivity were largely due to interconnections involving agronomy or conservation, where the number of citations was so low that the null expectation boundary for inter-disciplinary links included 0 citations in two of the five exceptions. Despite this under-connected network, there appeared to be a trend towards increasing citations between the animal and plant research sub-disciplines towards the end of the 20th century, so we evaluated the citation patterns of records published from 1990-1999, but found no change in the patterns of interconnections between sub-disciplines from the whole network results (Table 2.4 in Appendix 2.3). Whereas inter-connections between sub-disciplines revealed a trend towards less linkage than expected from a null model, citations within sub-disciplines were either within the null expectation, or were significantly greater than expected by chance (Table 2.2; Table 2.4 in Appendix 2.3).

In addition to potential direct integration between sub-disciplines, sub-disciplines might also be integrated if many link to a common body of research. The number of sub-disciplines that cited papers in general ecology was greater than expected given the number of citations that papers in general ecology had (31 sub-disciplines cited it, mean null expectation = 23.6 disciplines, n = 1000, p = 0.001), over half of the citations in our network pointed to papers

in the general ecology sub-discipline (which represented less than one fifth of the papers in the network), and of the 36 papers in the top 1% of papers (in terms of citations received) 25 were from general ecology (Fig. 2.8 in Appendix 2.3), demonstrating the central place of the general ecology sub-discipline in the niche network.

Interestingly, while the linkages from other sub-disciplines to general ecology in the niche network were strong, the opposite was not true: significantly fewer other sub-disciplines were cited by papers in general ecology than expected from the null model (18 disciplines were cited, mean null expectation = 37.1 disciplines, n = 1000, p = 0.001). Concordant with this, over half of the citations given by general ecology papers were to other papers in general ecology.

Despite the prominent position of the general ecology sub-discipline in the niche citation network, it does not appear that the general ecology literature was immediately integrating for the animal and plant research sub-disciplines. There were significantly fewer cases of a general ecology paper citing papers from both plant and animal research (which might have indicated a role for general ecology papers in integrating research from these sub-disciplines) than would be expected by chance (5 common citations observed, mean null expectation = 41.1, n=1000, p = 0.001), and there were significantly fewer cases of papers in animal and plant research citing the same general ecology paper (which might have indicated that general ecology papers were providing a common source of ideas for these sub-disciplines) than would be expected by chance given the number of citations general ecology papers received (24 co-citations observed, mean null expectation = 69.5, n = 1000, p = 0.001). We also looked to see if papers in animal and plant research were integrated by papers in general ecology at a distance of three or four citations (Fig. 2.4 in Appendix 2.2), and found that the number of general ecology papers that played this indirect role was within the expectations

of the null model (44 indirect link papers, mean null expectation = 50.3, n = 1000, p = 0.408). Thus, our analysis suggests that while many sub-disciplines in the niche network cite the general ecology sub-discipline, for the plant and animal research sub-disciplines this does not provide integration at the level of individual papers.

2.6   Discussion

The first goal of our paper was to document the spread of the ecological niche from animal researchers to other ecological sub-disciplines, and in particular to plant research. Perhaps not surprisingly, the first sub-disciplines to take up the niche in our network as it left animal research were the general ecology and general science sub-disciplines, in papers concerning the ecology of animals. Subsequent spread followed in a number of sub-disciplines that either had obvious associations with animal research (e.g. anthropology, medicine) or potentially broad taxonomic focus (e.g. limnology, evolutionary biology, theoretical ecology). The first plant research paper in our network appeared in 1974, but despite the relatively late adoption of the niche, combined plant research was the third sub-discipline in terms of records by the end of the 20th century, surpassing many sub-disciplines that had preceded it in the network. The niche has clearly become an important concept for ecological researchers working with a variety of taxonomic groups and in a variety of ecosystems.

Despite our expectation that the existence of multiple niche definitions would play a role in attracting sub-disciplines to the niche concept, this does not appear to have been the case: relative citation of the different niche definitions was not sub-discipline dependent for the sub-disciplines that cited all three definitions, and only Hutchinson's definition had sub-discipline citations unique to itself. Altogether these results suggest that only Hutchinson's

niche has been truly essential for the disciplinary success of the niche, potentially because his definition was the most general, and possibly also because his definition was, in some ways, the most accessible. Grinnell's niche, while typically understood today as representing the environmental necessities of a species, was actually embedded in a sophisticated system for categorizing the distributions of both species and species assemblages that owed much to C. Hart Merriam (Merriam 1890, 1899; Wake et al. 2009) and classification systems used then in botany (Grinnell and Swarth 1913), which may have proved to be a barrier to ecologists not fluent in this work. Elton's niche, on the other hand, was descriptively simple, but Elton's focus was strongly animal-centric which may have dissuaded researchers not interested in animals (Hutchinson 1978). Furthermore, both Grinnell (1917) and Elton (1927) were targeted at researchers who worked with animals. Hutchinson's niche on the other hand, while mathematically complex, was a stand-alone concept that was so general in its formulation that it could reasonably apply to any living organism. In addition, Hutchinson's niche was published in a venue that had no taxonomic focus, and over his career Hutchinson produced publications that bridged the traditional animal-plant and terrestrial-aquatic divides (Hutchinson 1951, 1959, 1961). Of course, while Hutchinson's definition was wildly successful in terms of citations received from both papers and disciplines, part of its success may also be attributed to the fact that the niche was already a well established concept by the time Hutchinson's definition was introduced.

It is worth briefly noting that none of our key definitions cited each other, and the influence of the niche definitions on each other has a bit of a notorious history: Elton (1927) both cited and praised Grinnell and Storer (1924), which dealt with the niche, but insisted that his niche was developed independently of Grinnell's (Elton and Miller 1954), and Hutchinson, while a great admirer of Grinnell (Hutchinson 1978), and aware of Elton (1927) (e.g. Hutchinson

1951), cited neither when crafting his own definition. While these omissions have attracted attention from reviewers of the niche (Colwell and Rangel 2009), they do fit into the trend where the vast majority of the papers (and some sub-disciplines) in our network did not cite a niche definition. The traditionally accepted initial use of the term by Johnson (1910) without an explicit definition suggests that the term would have been easily grasped by readers, and consequently it is possible that later authors also felt that the term was intuitive, rather than novel, or possibly in such broad circulation that it needed no definition or external reference (Hutchinson 1978). Warming (1909), for example, used the niche (in translation) in a hybrid sense, retaining its non-ecological meaning of a nook or cranny, but specifically referring to a cranny in the abstract space of nature.

We also showed that, at least for the niche, the years 1970-1979 formed a remarkable decade. During this period the rate of new sub-disciplines adopting the niche was greatest, the cohesiveness of the network was at its peak, and it also was when the majority of well cited papers in our network were published. This decade also coincided with a turning point with respect to attitudes about competition, generality, and theory in ecology (Kingsland 1985; Cooper 2003; Slack 2010), which may have heralded an end to the greatest success of broad conceptual devices like the niche, which was strongly linked to competition by both Grinnell (Grinnell and Storer 1924) and Hutchinson (1957), and to some extent by Elton (Elton 1946; Elton and Miller 1954) also. After this period, as ecology moved into a phase of increasing interest in historical contingency and skepticism about the role of competition (e.g. Connor and Simberloff 1986), the rate at which new sub-disciplines joined the network slowed down, and the network became more fragmented, despite the fact that the number of papers, journals, and citations in the network continued to grow exponentially.

Our analysis dealt with a network that was, by definition, conceptually integrated in

44

that all the records included had a strong emphasis on the ecological niche. Given this conceptual unity, it is surprising that our analysis revealed a network that shows relatively little integration among the different sub-disciplines that constitute it, specifically in terms of links between the animal research, agronomy, limnology and oceanography, medicine, plant research, and conservation sub-disciplines. While more sub-disciplines cited the general ecology sub-discipline than would be expected from a null model, the number of individual general ecology papers cited by papers in both the animal and plant research sub-disciplines was lower than expected, and so it does not seem that individual general ecology papers directly provided a common source of ideas to the two sub-disciplines. Similarly, the co-citation of animal and plant research by papers in the general ecology sub-discipline was less common than expected, suggesting that individual papers in the general ecological literature were not generally integrating research from the animal and plant research sub-disciplines either. Consequently, it appears that integration of different sub-disciplines by the general ecology sub-discipline exists at the level of the sub-discipline, and not at the level of individual papers.

Sub-disciplines tended to be internally integrated, suggesting that ideas may have been exchanged within disciplines relatively frequently, with connections to other sub-disciplines mediated through different papers. This strong internal integration is particularly the case for the general ecology sub-discipline, which may suggest that, while linkages to the animal and plant research sub-disciplines appeared to be mediated through different papers, there might still be common flows of information to them mediated by papers within the general ecology sub-discipline, though at the level of three and four link connections this only happened at a frequency commensurate with the null expectation.

As with any study that attempts to ask broad questions about the literature our analysis

comes with a set of provisos and caveats. Our original search did not return any of our key definitions, a symptom of the way in which our search returned only a limited fraction of the papers published that address the ecological niche. Instead, the results returned were restricted to those papers in the Web of Science core collection that focused sufficiently on niche research to have 'niche' in the title, keywords, Keywords Plus, or abstract. An obvious consequence of these limited results is that we've had to form conclusions based on a small subset of the total ecological literature invoking the niche, and as a result, there are potentially gaps in the network that obscured the transmission of the niche concept. On the other hand, by using only papers that were strongly focused on the niche, our dataset forms a more conservative estimate of conceptual unification, and thus our expectation of a unified literary network was strong.

A number of decisions were required in preparing the data set: we had to decide which records used the niche in an ecologic sense, and we had to estimate the target audience of different publications, all while assuming that the sub-discipline of the paper was the same as that of its publication. The selection of relevant papers was usually straightforward, and given the strength of our trends we doubt that any mistakes made are likely to have had strong effects on our results. The classification of sub-disciplines was more complex, but we feel confident with our assignments, especially given the tendency for strong intra-disciplinary citation. Of course, journals are unlikely to be exclusively read by, or publish exclusively on just one discipline's work, but authors do select publications for the audience they believe that the publication will reach, and publications select papers with the same consideration in mind. Consequently, we felt that classification based on publication source was a reasonably proxy for the sub-discipline of each of our records.

Our decision to limit our network to the 20th century has a number of consequences, in

particular that later papers in the network had less time to accumulate citations. While it is possible that this could account for the remarkable success of papers from the 1970s, we don't believe this to be an artifact. Citation and paper count per year increased through time, such that the number of citations issued by 1999 publications, and the number of publications from 1999, accounted for over 10% of the total citations and publications, respectively. Given these numbers, almost any of the 2930 papers from the 90s could have easily entered the top 1% of cited papers, but instead only two papers did. Indeed, when looking at how citations from papers published in 1999 were apportioned, while the majority went to papers from the 1990s, papers from the 1970s did better at attracting citations than those from the 1990s on a per paper basis. Our final caveat deals with the key definitions of the niche. While the Grinnellian, Eltonian, and Hutchinsonian niches were certainly the most important in terms of the development of the niche concept (Wake et al. 2009), choosing a publication to represent them was somewhat subjective. We chose the publications for which their definitions are best known, but in all three cases the authors had discussed niches in earlier publications (e.g. Grinnell and Swarth 1913; Elton 1924; Hutchinson 1944). These earlier publications were probably most problematic for Grinnell, who often discussed and employed the ecologic niche at greater length in lesser known publications than Grinnell (1917), especially Grinnell and Swarth (1913).

A number of questions about the niche's role in structuring ecology remain. While we have documented the spread of the niche, how the word was chosen by a number of prominent ecologists to represent a central concept in their discipline remains unclear. Cox (1980) has shown that the word was being used to refer to animal living spaces in English as early as the 18th century, and indeed the word has Latin roots that indicate a space for life. Still, a number of obvious competitors exist, for example *la station*, as used by Candolle

47

(1820). How the niche, a concept pioneered in animal ecology during a time of dominance by plant ecologists, came to dominance remains to be addressed, though Kingsland (1985) has noted that the transfer of concepts from animal to plant research in the 1960s played an important role in stimulating the latter. Our analysis also revealed a number of records using 'niche' in a non-ecological context that none the less retained an implicit emphasis on competition, and an in depth semantic study of the word would no doubt be fascinating. We limited our analysis of the niche network to papers from the 20th century to highlight the era in which the niche was emerging, and to restrict the data to manageable amount, but given the trend towards more citation between animal and plant research at the end of our data set it would be interesting to see whether current niche literature is more integrated. The timespan of our network also omits a number of subsequent developments in niche theory, such as Chesson (2000), and Hubbell (2001), and the question of how developments in theory after 1999 will affect the integration of niche literature remains unanswered. The question also remains of what factors maintained the lack of integration we observed in the 20th century literature despite conceptual unification. It is possible that, despite a common conceptual background, practical differences caused by taxonomy were sufficient to maintain the separation (e.g. Daubenmire 1968), or it could be that the niche was actually used in subtly different fashions in different sub-disciplines, or indeed that adherence to the concept was only marginal in some sub-disciplines.

Ultimately, our research suggests that while ecology experienced increasing conceptual unification during the 20th century as many sub-disciplines adopted the niche, the niche literature remained fragmented. Even from its earliest stages ecology has struggled with the extent to which it represented one or many disciplines (Kingsland 2005), and our analysis suggests that the emergence of a truly integrated discipline may be yet to come. Still, the

niche has undeniably furnished a concept around which many of ecology's central questions have been organized, and despite skepticism from some reviewers, the use of the niche continued to expand exponentially into the 21st century. Whether the niche has entered a codified space, as might be suggested by the centrality of papers from the 1970s in our network, or whether new innovations and definitions are still to come remains to be seen.

2.7 Acknowledgements

2.8 Box 1: The niche definitions of Grinnell, Elton, and Hutchinson

Over the course of its history a number of different definitions of the niche have been proposed. Here we summarize the definitions of Joseph Grinnell, Charles Elton and G.E. Hutchinson.

Grinnell's niche: At its core the Grinnellian niche describes an ecological opportunity of sufficient breadth to support one, and only one, species (Grinnell and Swarth 1913; Grinnell 1914). Grinnell spent much of his professional life attached to the museum of Vertebrate Zoology at Berkeley (Hutchinson 1978), and his publications were often focused on species distributions and community composition. Many of Grinnell's observations about niches

49

dealt with ecologically similar species that were not found in sympatry, or noted that no two-species with identical niches could be established together (e.g. Grinnell 1914, 1917), which Grinnell occasionally explicitly attributed to competitive exclusion (e.g. Grinnell and Storer 1924). While Grinnell invoked the niche to explain differences in community biodiversity and population abundance (Grinnell 1922), the Grinnellian niche primarily served to mark the taxonomic differences of ecologically similar associations by tracking the different species that occupied each opportunity-space in each community.

Elton's niche: If Grinnell's niche was defined by the opportunities furnished by the environment, Elton's niche was more focused on the role of a species in its environment. Indeed, Elton (1927) went so far as to explicitly invoke socio-economic parallels to the niche, famously suggesting that one should think of a badger as having a role in its community just as vicars have a role in human communities. While Elton's original uses of the niche were strongly focused on the trophic roles of species, and less explicitly focused on competition than Grinnell had been, Elton and Miller (1954) noted that the niche inherently served as the expected boundaries for competition. In contrast to Grinnell's focus on taxonomic differences between communities, Elton's niche lent itself more to demonstrating the functional similarity of taxonomically different communities.

Hutchinson's niche: Hutchinson's niche existed in two forms: the fundamental niche, which represented the (multidimensional) environmental conditions in which a population could exist in the absence of ecological interactions, and the realized niche, which represented the conditions in which a population could exist in the presence of ecological interactions (Hutchinson 1957). As such, Hutchinson's niche was fundamentally focused on the relationship between the environment and a population's fitness, and, unlike the niches of Grinnell or Elton, was quantifiable. A number of reviewers have noted that Hutchinson's niche in

50

many ways echoed the Grinnellian niche's emphasis on habitat requirements (Leibold 1995), or that the two differed in that Hutchinson's niche was unambiguously a property of the organism, and not the community (Colwell 1992), but it is also worth pointing out that while Grinnell envisioned niches that had definite existence in the world, Hutchinson's niche existed in abstract environmental space that might, or might not, be represented in the actual environment (Godsoe 2010; Holt 2009).

2.9   Literature Cited

Candolle, A.-P. d. 1820. Essai élémentaire de géographie botanique. F.G. Levrault, Strasbourg.

Chandler, A. C. 1914. The effect of extent of distribution on speciation. The American Naturalist 48:129–160.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Colwell, R. K. 1992. Niche: a bifurcation in the conceptual lineage of the term. Pages 241–248 *in* E. F. Keller and E. A. Lloyd, editors. Keywords in evolutionary biology. Harvard University Press, Cambridge.

Colwell, R. K., and T. F. Rangel. 2009. Hutchinson's duality: The once and future niche. Proceedings of the National Academy of Sciences 106:19651–19658.

Connor, E. F., and D. Simberloff. 1986. Competition, scientific method, and null models in ecology: because field experiments are difficult to perform, ecologists often rely on evidence that is nonexperimental and that therefore needs to be rigorously evaluated. American Scientist 74:155–162.

Cooper, G. J. 2003. The science of the struggle for existence. Cambridge University Press, Cambridge.

Cox, D. L. 1980. A note on the queer history of "Niche". Bulletin of the Ecological Society of America 61:201–202.

Csardi, G., and T. Nepusz. 2006. The igraph software package for complex network research. InterJournal Complex Systems 1695.

Daubenmire, R. 1968. Plant communities: a text book of plant synecology. Harper and Row, New York.

Egerton, F. N. 1976. Ecological studies and observations before 1900. Pages 175–179 *in* B. J. Taylor and T. J. White, editors. Issues and ideas in America. University of Oklahoma Press, Norman.

Elton, C. 1946. Competition and the structure of ecological communities. Journal of Animal Ecology 15:54–68.

Elton, C. S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. Journal of Experimental Biology 2:119–163.

Elton, C. S. 1927. Animal ecology. Macmillan Co., New York.

Elton, C. S., and R. S. Miller. 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. Journal of Ecology 42:460–496.

Francois, R. 2013. bibtex: bibtex parser. R package version 0.3-6.

Gause, G. F. 1934. The struggle for existence. The Williams and Wilkins Company, Baltimore.

Godsoe, W. 2010. I can't define the niche but I know it when I see it: a formal link between statistical theory and the ecological niche. Oikos 199:53–60.

Griesemer, J. R. 1992. Niche: historical perspectives. Pages 231–240 *in* E. F. Keller and E. A. Lloyd, editors. Keywords in evolutionary biology. Harvard University Press, Cambridge.

Grinnell, J. 1914. An account of the mammals and birds of the lower Colorado Valley. University of California Press, Berkeley.

Grinnell, J. 1917. The niche relationships of the California Thrasher. Auk 34:427–433.

Grinnell, J. 1922. The trend of avian populations in California. Science 56:671–676.

Grinnell, J., and T. I. Storer. 1924. Animal life in the Yosemite; an account of the mammals, birds, reptiles, and amphilbians in a cross-section of the Sierra Nevada. University of California Press, Berkeley.

Grinnell, J., and H. S. Swarth. 1913. An account of the birds and mammals of the San Jacinto area of southern California: with remarks upon the behavior of goegraphic races on the margins of their habitats. University of California Press, Berkeley.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65–70.

Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences USA 106:19659–19665.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press., Princeton.

Hutchinson, G. E. 1944. Limnological studies in Conneticut. VII. A critical examination of the supposed relationship between phytoplankton periodicity and chemical changes in lake waters. Ecology 25:3–26.

Hutchinson, G. E. 1951. Copepodology for the ornithologist. Ecology 32:571–577.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415–427.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? The American Naturalist 93:145–159.

Hutchinson, G. E. 1961. The paradox of the plankton. The American Naturalist 95:137–145.

Hutchinson, G. E. 1978. An introduction to population ecology. Yale University Press, New Haven.

Jax, K., and A. Schwarz 2011. The fundamental subdivisions of ecology. Pages 175–179 *in* A. Schwarz and K. Jax, editors. Ecology revisited reflecting on concepts, advancing science. Springer, Dordrecht.

Johnson, R. H. 1910. Determinate evolution in the color-pattern of the Lady-Beetes. Carnegie Insitution of Washington, Washington.

Kingsland, S. E. 1985. Modeling nature: episodes in the history of population ecology. University of Chicago Press, Chicago.

Kingsland, S. E. 2005. The evolution of american ecology: 1890-2000. Johns Hopkins University Press, Baltimore.

Leibold, M. 1995. The niche concept revisited: mechanistic models and community context. Ecology 76:1371–1382.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377–385.

Merriam, C. H. 1890. Results of a biological survey of the San Francisco mountain region and desert of the Little Colorado, Arizona. Government Printing Office, Washington.

Merriam, C. H. 1899. Results of a biological survey of Mount Shasta California. Government Printing Office, Washington.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Shelford, V. E. 1913. Animal communities in temperate America, as illustrated in the Chicago region; a study in animal ecology,. Pub. for the Geographic Society of Chicago by the University of Chicago Press, Chicago.

Slack, N. G. 2010. G. Evelyn Hutchinson and the invention of modern ecology. Yale University Press, New Haven.

Taylor, W. P. 1916. The status of the beavers of western North America with a consideration of the factors in their speciation. University of California publications in zoology 12:413–495.

Thompson, R. M., U. Brose, J. A. Dunne, R. O. Hall, S. Hladyz, R. L. Kitching, N. D. Martinez, H. Rantala, T. N. Romanuk, D. B. Stouffer, and J. M. Tylianakis. 2012. Food webs: reconciling the structure and function of biodiversity. Trends in Ecology & Evolution 27:689–697.

Wake, D. B., E. A. Hadly, and D. D. Ackerly. 2009. Biogeography, changing climates, and niche evolution. Proceedings of the National Academy of Sciences 106:19631–19636.

Warming, E. 1909. Oecology of plants: an introduction to the study of plant-communities. Oxford University Press, Oxford.

Table 2.1. The number of papers and year of network entry for each sub-discipline in the network.

Sub-discipline	Paper count	Entry year	Sub-discipline	Paper count	Entry year
General ecology	639	1944	Geology	40	1979
Animal science	551	1917	Plant ecology	38	1977
Limnology and Oceanography	321	1961	Behavioural ecology	37	1977
Plant science	306	1974	Forestry	34	1988
Medicine	164	1970	Engineering	26	1979
Microbiology	149	1977	Biogeography	25	1984
Evolutionary biology	138	1957	Microbial ecology	20	1985
Entomology	135	1975	Biotechnology	17	1992
General biology	131	1970	Human ecology	14	1975
Conservation	109	1969	Veterinary science	14	1981
Agronomy	108	1975	Scientific philosophy	9	1980
General science	103	1946	Education	7	1979
Theoretical biology	89	1957	Climate change	7	1996
Paleobiology	70	1978	Interdisciplinary	6	1989
Terrestrial ecosystems	62	1979	Landscape ecology	6	1989
Animal ecology	55	1927	Computer science	6	1991
Parasitology	54	1983	Geography	5	1978
Cell biology	52	1977	Law	2	1997
Anthropology	47	1972	Economics	1	1991
Environmental science	47	1977	Other	1	1991
Primatology	42	1974			

Table 2.2. Comparison of realized and expected citations between the animal research, agronomy, limnology and oceanography (L& O), medicine, plant research, and conservation sub-disciplines. +: The observed citations were significantly higher than the null expectation; o: the observed citations are were not significantly different from the null expectation; -: the realized citations were significantly less than the null expectation. Significance was determined after Holm correction for all tests in the table (Holm 1979), n=1000 randomizations for each cell.

	Animal research	Agronomy	L& O	Medicine	Plant research	Conservation
Animal research	o					
Agronomy	-	o				
L& O	-	o	+			
Medicine	-	o	-	o		
Plant research	-	-	-	-	+	
Conservation	o	o	-	o	-	+
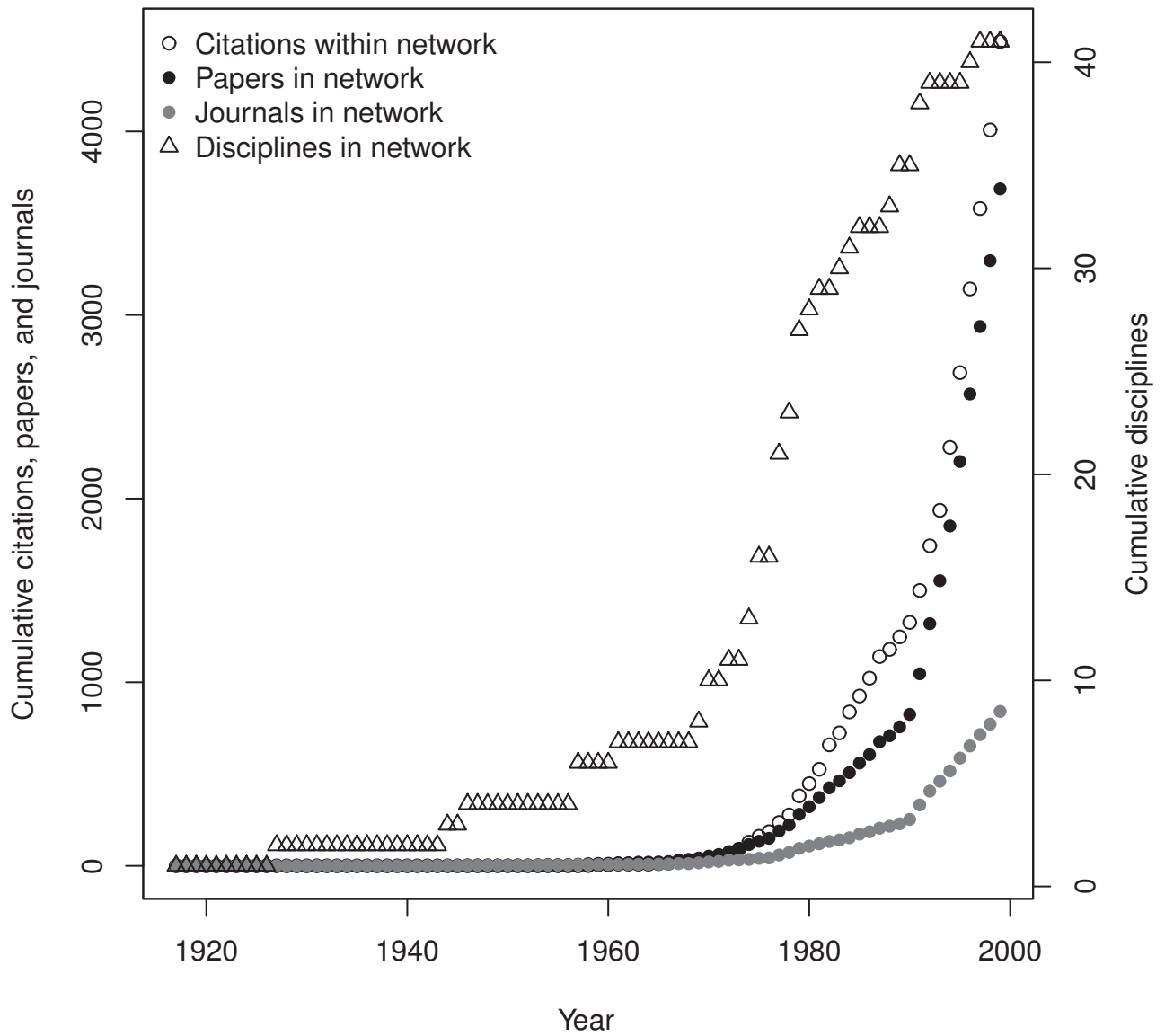
Fig. 2.1. Cumulative counts of citations, records, journals, and disciplines within the network from 1917-1999.
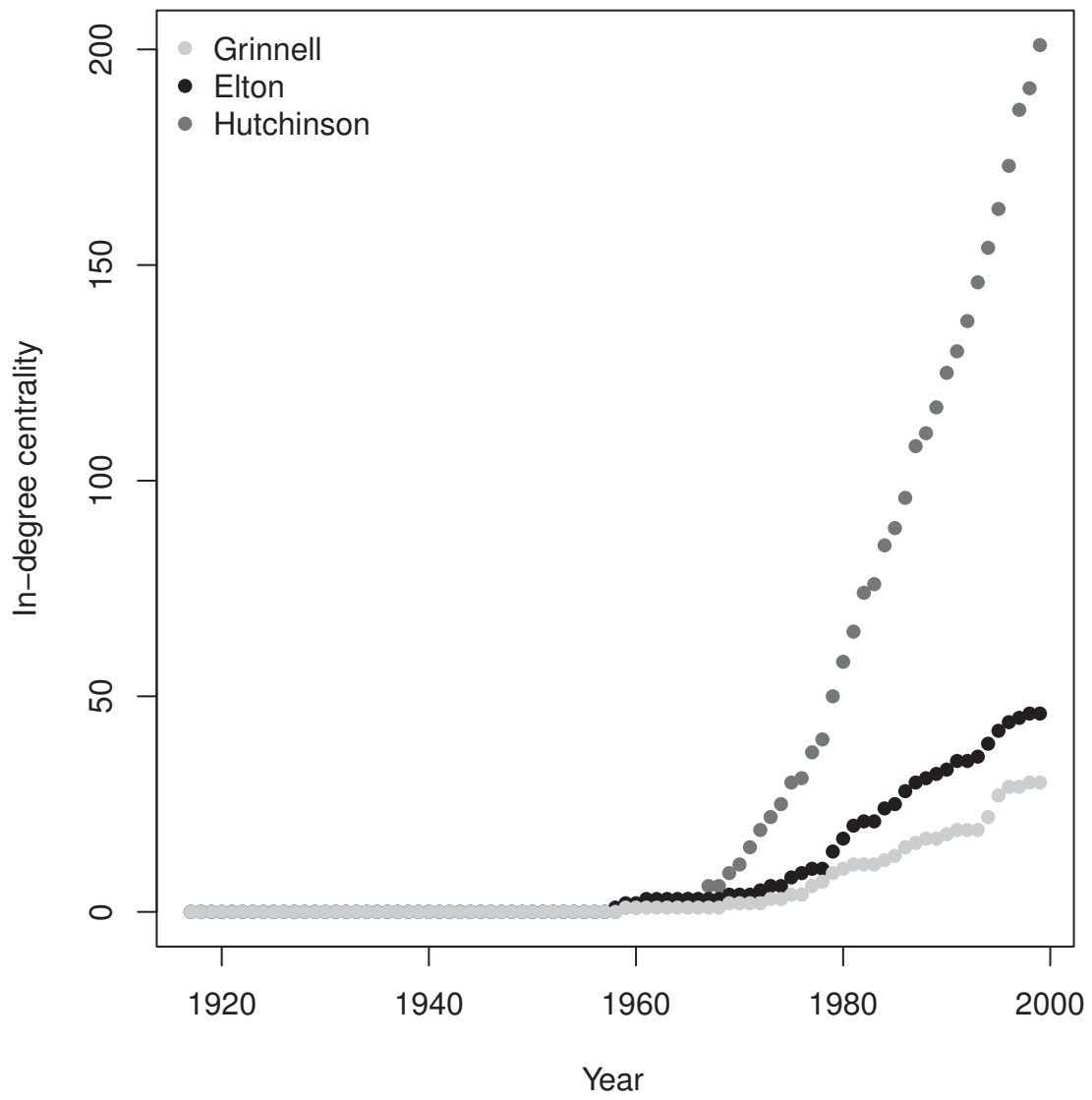
Fig. 2.2. The in-degree centrality of each key definition through time from 1917-1999.
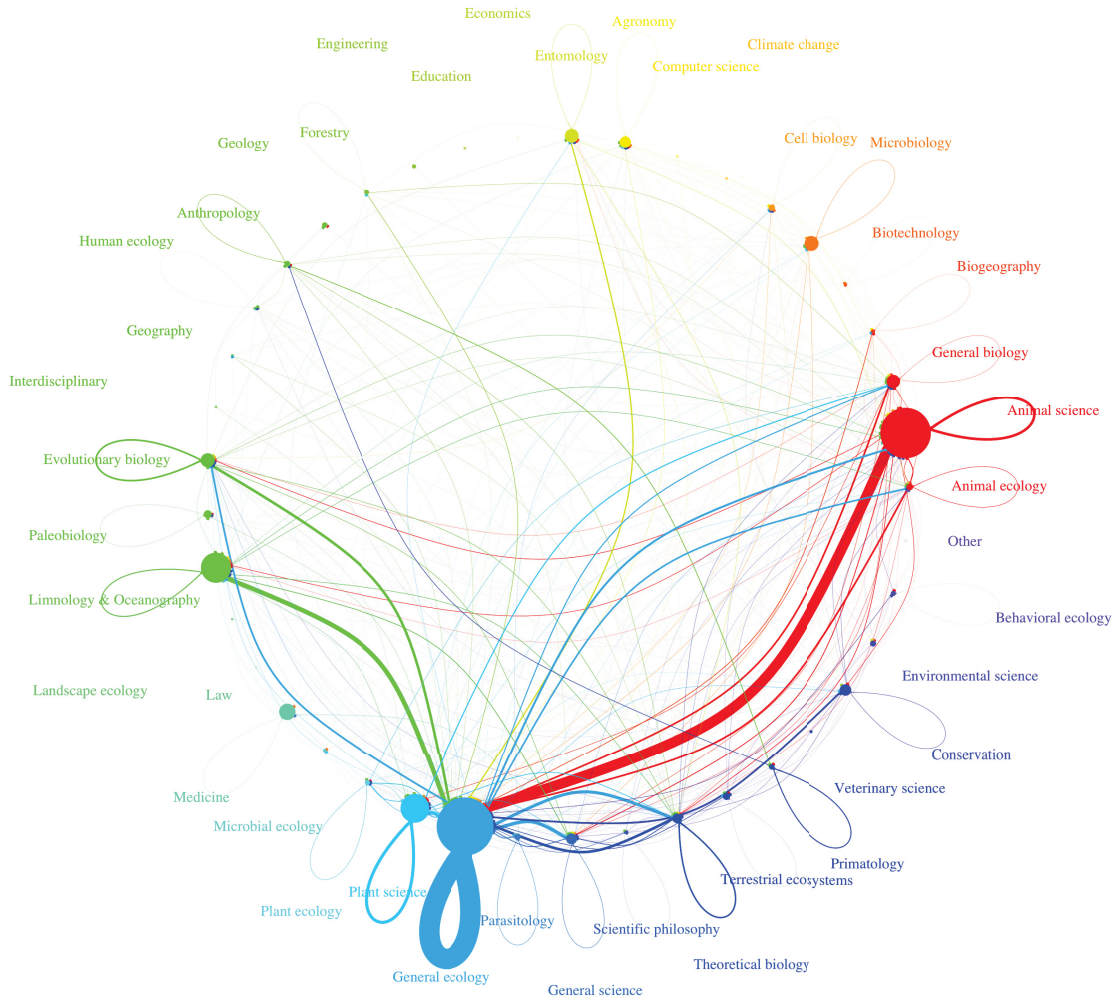
Fig. 2.3. Citations within our niche network figured across the 41 sub-disciplines in our network. The sizes of vertices are scaled to the number of papers in each sub-discipline, and the width of the connecting lines is scaled to the number of citations between disciplines. The vertices are colour coded by their sub-discipline, and the links between them are colour coded by the citing sub-discipline.

Appendices to Chapter 2

Appendix 2.1: Detailed methods of network construction from Pedruski et al. *A network approach reveals surprises about the history of the niche*

Papers without DOI values (1466 papers + the three key definitions) were assigned a dummy DOI for the purposes of assaying connections between papers. We then searched all the citations given by papers in the network for the name of the first author and year of papers without DOIs to identify potential instances of these papers without DOIs being cited by other papers in the network. Potential matches were identified, and in case of a confirmed match the dummy DOI was added to the citation before the network was constructed. While this method relied on the author name and year being correctly entered into the cited references of other papers for identification of potential citations (or at least that if the year or name was entered incorrectly another paper cited would have the correct name and year), given the relative rarity of matches with the correct year and name we expect that the number of any undetected matches would be relatively small. There are only two 'near-miss' cases we know of: papers that cited Hutchinson (1957) as Hutchinson (1958), and papers that cited Grinnell (1917) as Grinnell (1991).

After these modifications the network was constructed by searching for matches to a paper's DOI in the cited references of every other paper included in the network.

When calculating the number of journals present in our data set we collapsed journals 202 and 203, and 765,766 as being unambiguous duplicates.

Appendix 2.2: Null hypotheses and statistical methods from Pedruski et al. *A network approach reveals surprises about the history of the niche*

- **Relationship between the different niche definitions and sub-disciplinary spread of the niche concept**

  H_o: There is no relationship between sub-discipline identity and citation of the three key niche definitions among those sub-disciplines in which all three definitions have been cited.

  H_a: There is a relationship between sub-discipline identity and citation of the three key niche definitions among those sub-disciplines in which all three definitions have been cited.

  Evaluation: 3 x 8 χ^2 table of citation counts from each discipline to each key definition.

- **Evaluating linkages between the animal research, agronomy, limnology and oceanography, medicine, plant research, and conservation sub-disciplines.**

  H_o: The number of citations between a pair of sub-disciplines does not differ from the pattern that would be produced by randomly reassigning the endpoint of citations from a given record to any record it could potentially have cited.

  H_a: The number of citations between a pair of sub-disciplines does differ from the pattern that would be produced by randomly by randomly reassigning the endpoint of citations from a given record to any record it could potentially have cited.

  Evaluation: For each paper we repeatedly randomly reassigned the endpoint of each of

the citations it gave to the set of papers as old as, or older than, it without replacement, and counted the number of citations that passed between the two focal disciplines. We then calculated the statistical expectation of the number of citations between each pair, and calculated the deviation from this expectation for both the simulated and observed results. Our p-value was calculated as the proportion of results (either theoretical or observed) that had a deviation from the statistical expectation as great as, or greater than, that of the observed value. Given the application of multiple tests to the same hypothesis we applied a Holm-Bonferroni correction (Holm 1979) to determine significance.

- **Evaluating linkages between the animal research, agronomy, limnology and oceanography, medicine, plant research, and conservation sub-disciplines 1990-1999.**

  H_o: The number of citations between a pair of sub-disciplines does not differ from the pattern that would be produced by randomly reassigning the endpoint of citations from a given record published in, or after 1990, to any record it could potentially have cited.

  H_a: The number of citations between a pair of sub-disciplines does differ from the pattern that would be produced by randomly reassigning the endpoint of citations from a given record published in, or after 1990, to any record it could potentially have cited.

  Evaluation: For each paper published in, or after, 1990 we repeatedly randomly reassigned the endpoint of each of the citations it gave to the set of papers as old, or older than, it without replacement, and counted the number of citations that passed

between the two focal disciplines. We then calculated the statistical expectation of the number of citations between each pair, and calculated the deviation from this expectation for both the simulated and observed results. Our p-value was calculated as the proportion of results (either randomized or observed) that had a deviation from the statistical expectation as great as, or greater than, that of the observed value. Given the application of multiple tests to the same hypothesis we applied a Holm-Bonferroni correction (Holm 1979) to determine significance.

- **Evaluating sub-disciplinary citation of the general ecology sub-discipline.**

  H_o: The number of sub-disciplines that cite papers from the general ecology sub-discipline does not differ from the number that would be produced by randomly reassigning the origin of citations that each general ecology paper received to any paper in the network as old as, or younger than, it.

  H_a: The number of sub-disciplines that cite papers from the general ecology sub-discipline does differ from the number that would be produced by randomly reassigning the origin of citations that each general ecology paper received to any paper in the network as old as, or younger than, it.

  Evaluation: For every record in the general-ecology sub-discipline we repeatedly randomly reassigned the origin of all the citations it received to the set of papers as old as, or younger than, it without replacement. Given the complexity of calculating the statistical expectation, we calculated the deviation of randomized and observed results from the mean of the randomized results, and our p-value was calculated as the proportion of results (either randomized or observed) that had a deviation from this mean as great as, or greater than, the observed value.

- **Evaluating sub-disciplinary citation by the general ecology sub-discipline.**

  H_o: The number of sub-disciplines cited by the general ecology sub-discipline does not differ from the number that would be produced by randomly reassigning the endpoint of citations from each general ecology paper to any paper in the network as old as, or older than, it.

  H_a: The number of sub-disciplines cited by the general ecology sub-discipline does differ from the number that would be produced by randomly reassigning the endpoint of citations from each general ecology paper to any paper in the network as old as, or older than, it.

  Evaluation: For every record in the general-ecology sub-discipline we repeatedly randomly reassigned the endpoint of all the citations it issued to the set of papers as old as, or older than, it without replacement. Given the complexity of calculating the statistical expectation, we calculated the deviation of randomized and observed results from the mean of the randomized results, and our p-value was calculated as the proportion of results (either randomized or observed) that had a deviation from this mean as great as, or greater than, the observed value.

- **Evaluating direct integration of animal and plant research by papers in the general ecology sub-discipline.**

  H_o: The number of papers in the general ecology sub-discipline that cite papers in both animal and plant research is not different from the number that would be expected by randomly reassigning the endpoint of citations from each general ecology paper to any paper in the network as old as, or older than, it.

  H_a: The number of papers in the general ecology sub-discipline that cite papers in

both animal and plant research is different from the number that would be expected by randomly reassigning the endpoint of citations from each general ecology paper to any paper in the network as old as, or older than, it.

Evaluation: For every paper in the general-ecology sub-discipline we randomly reassigned the endpoint of all the citations it issued to the set of papers as old as, or older than, it without replacement. We then calculated the statistical expectation of the number of general ecology papers that would cite papers in both animal and plant research, and calculated the deviation from this expectation for both the simulated and observed results. Our p-value was calculated as the proportion of results (either randomized or observed) that had a deviation from the statistical expectation as great as, or greater than, that of the observed value.

- **Evaluating direct sourcing of ideas to animal and plant research by papers in the general ecology sub-discipline.**

  H_o: The number of papers in the general ecology sub-discipline co-cited by papers in animal and plant research is not different from the number that would be expected by randomly reassigning the origin of citations to each general ecology paper from any paper in the network as old as, or younger than, it.

  H_a: The number of papers in the general ecology sub-discipline co-cited by papers in animal and plant research is different from the number that would be expected by randomly reassigning the origin of citations to each general ecology paper from any paper in the network as old as, or younger than, it.

  Evaluation: For every record in the general-ecology sub-discipline we randomly reassigned the origin of all the citations it received to the set of papers as old as, or younger

67

than, it without replacement. Given the complexity of calculating the statistical expectation, we calculated the deviation of randomized and observed results from the mean of the randomized results, and our p-value was calculated as the proportion of results (either randomized or observed) that had a deviation from this mean as great as, or greater than, the observed value

- **Evaluating indirect sourcing of ideas to animal and plant research by papers in the general ecology sub-discipline.**

  H_o*:* The number of papers in the general ecology sub-discipline that furnish liasons between animal and plant research at a remove of three or four citations (Figure 2.4), with intervening papers also being in the general ecology sub-discipline, is not different from what would be expected by randomly reassigning citations from all papers to papers as old as, or older than, them.

  H_a*:* The number of papers in the general ecology sub-discipline that furnish liasons between animal and plant research at a remove of three or four citations, with intervening papers also being in the general ecology sub-discipline, is different from what would be expected by randomly reassigning citations from all papers to papers as old as, or older than, them.

  Evaluation: For every paper in the general-ecology, animal research, and plant research sub-disciplines we randomly reassigned the endpoint of all citations issued to the set of papers as old as, or older than, them without replacement. We calculated the number of papers in the general ecology sub-discipline that were necessary to link plant and animal research papers through a chain of one or two intervening general ecology papers. Given the complexity of calculating the statistical expectation, we calculated

the deviation of randomized and observed results from the mean of the randomized results, and our p-value was calculated as the proportion of results (either randomized or observed) that had a deviation from this mean as great as, or greater than, the observed value.

Patterns constituting an indirect link
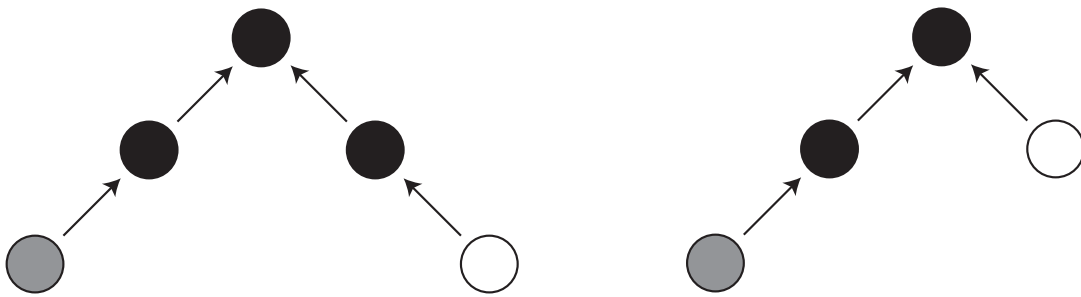
Patterns not constituting an indirect link
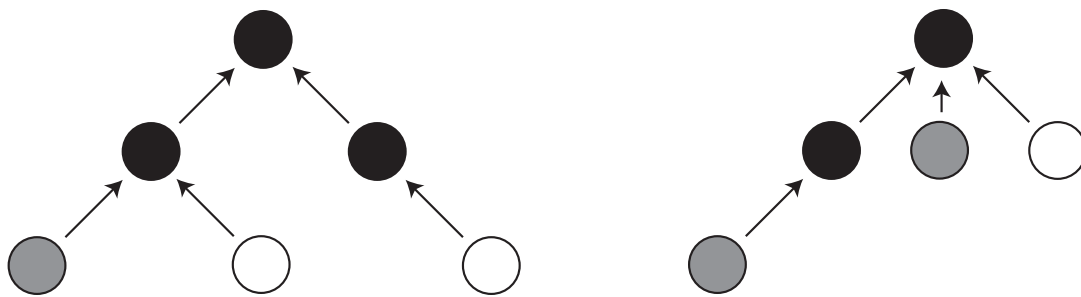
Fig. 2.4. Examples of citation patterns considered to be valid or invalid direct links between the general ecological literature (black) and animal and plant research papers (white and grey).

Appendix 2.3: Supplementary Figures and Tables from Pedruski et al. *A network approach reveals surprises about the history of the niche*

Table 2.3. The sub-disciplines that collectively cite all three, two, one, or none of the key definitions.

All three definitions	Grinnell and Hutchinson	Elton and Hutchinson	Hutchinson only	No definition
Animal science	Animal ecology	Entomology	Agronomy	Biotechnology
Anthropology	Human ecology	Evolutionary biology	Behavioural ecology	Cell biology
Conservation		Forestry	Biogeography	Climate change
General ecology		General biology	Environmental Science	Computer science
General science		Geography	Interdisciplinary	Economics
Limnology and Oceanography		Plant science	Landscape ecology	Education
Scientific philosophy			Paleobiology	Engineering
Theoretical biology			Parasitology	Geology
			Plant ecology	Law
				Medicine
				Microbial ecology
				Microbiology
				Other
				Terrestrial ecosystems
				Veterinary science

Table 2.4. Comparison of realized and null model prediction for citations between the animal research, agronomy, limnology and oceanography (L& O), medicine, plant research, and conservation sub-disciplines for papers published after 1989. +: The observed citations were significantly higher than the null expectation; o: the observed citations are were not significantly different from the null expectation; -: the realized citations were significantly less than the null expectation. Significance was determined after Holm correction for all tests in the table (Holm 1979), n=1000 randomizations for each cell.

	Animal research	Agronomy	L& O	Medicine	Plant research	Conservation
Animal research	+					
Agronomy	-	o				
L& O	-	o	+			
Medicine	-	o	-	o		
Plant research	-	-	-	-	+	
Conservation	o	o	-	o	-	+
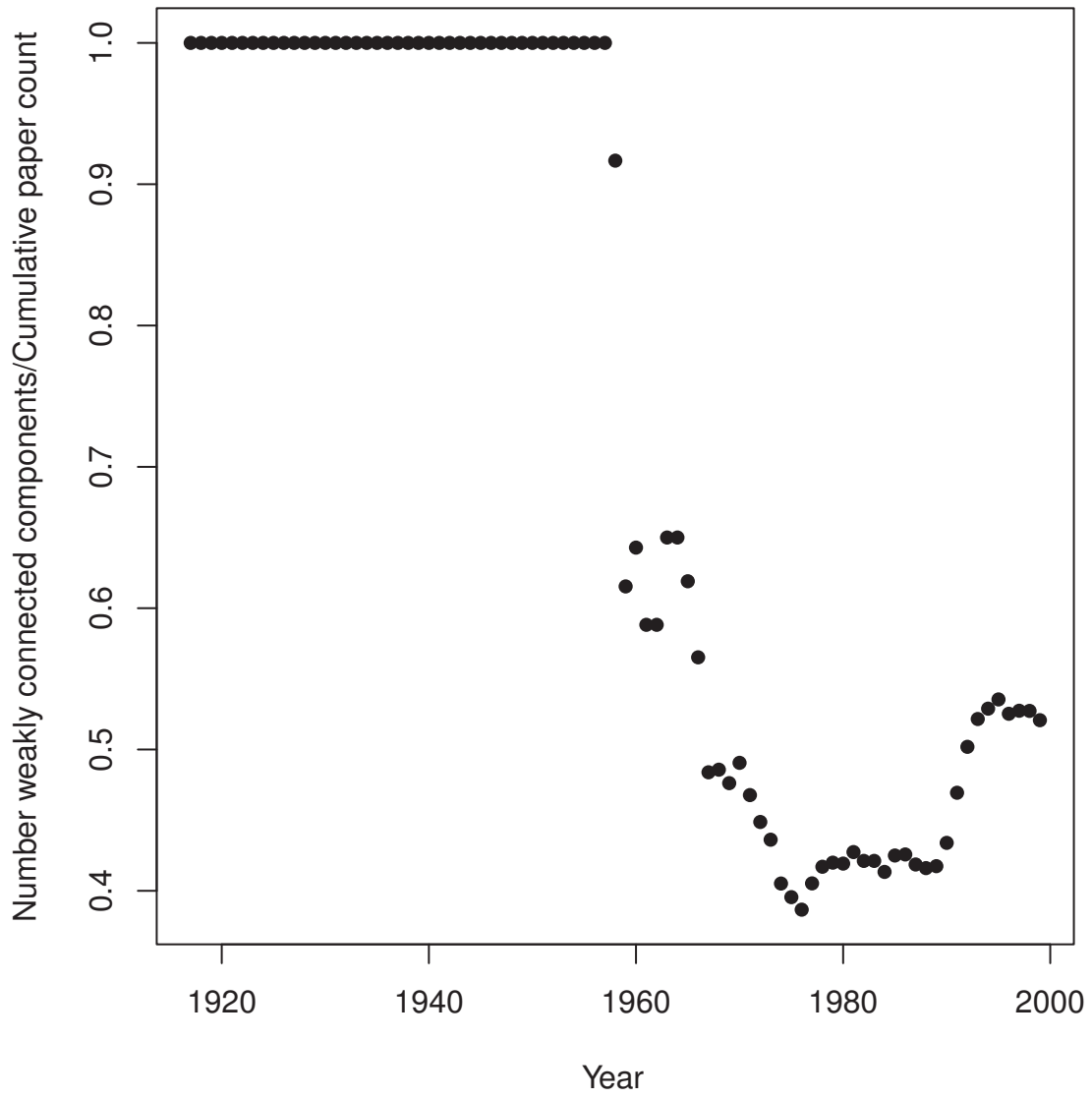
Fig. 2.5. The number of weakly connected components (groups of papers linked by citations) in the network scaled by the total number of records in the network from 1917-1999.
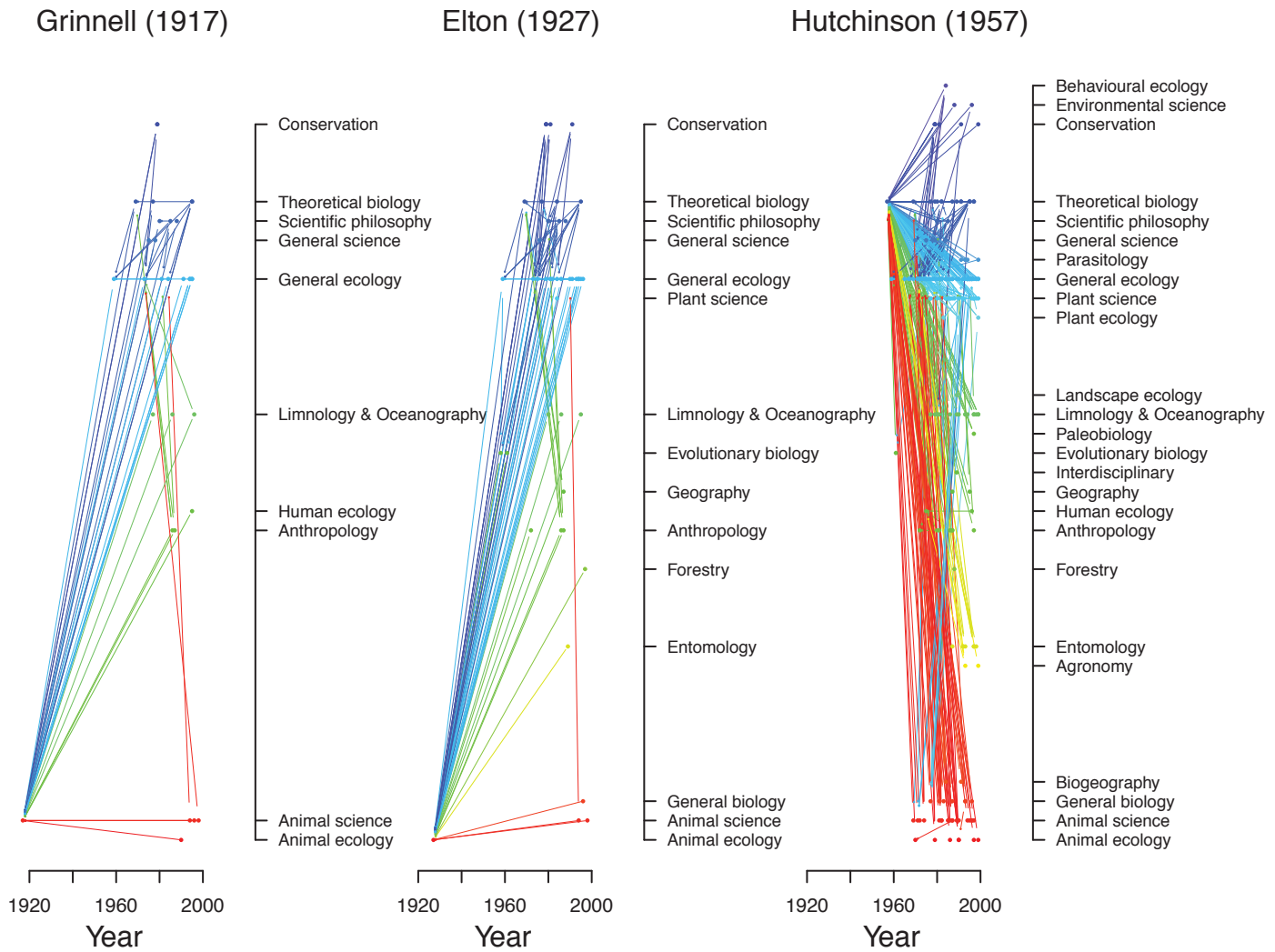
Fig. 2.6. The networks of papers that cited the three key definitions from 1917-1999. Papers are colour coded by their sub-discipline, and citations between papers are colour coded by the sub-discipline of the citing paper.
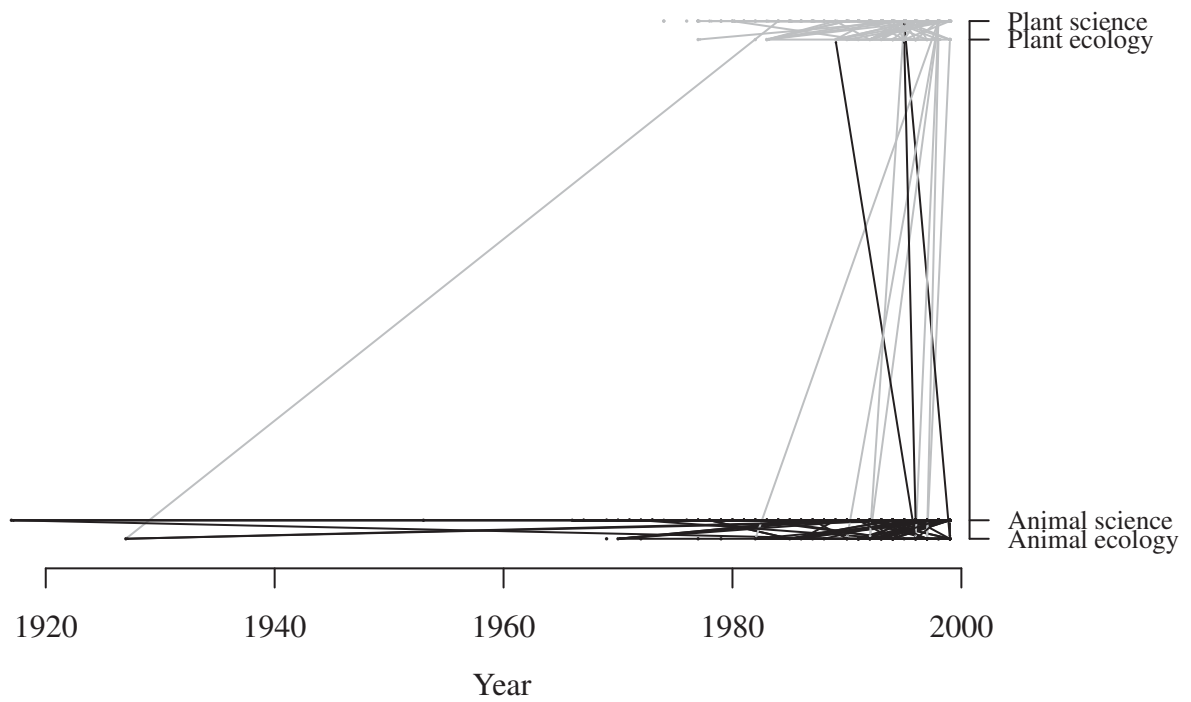
Fig. 2.7. The network of animal research (animal ecology and animal science) and plant research (plant ecology and plant science) papers from 1917-1999.
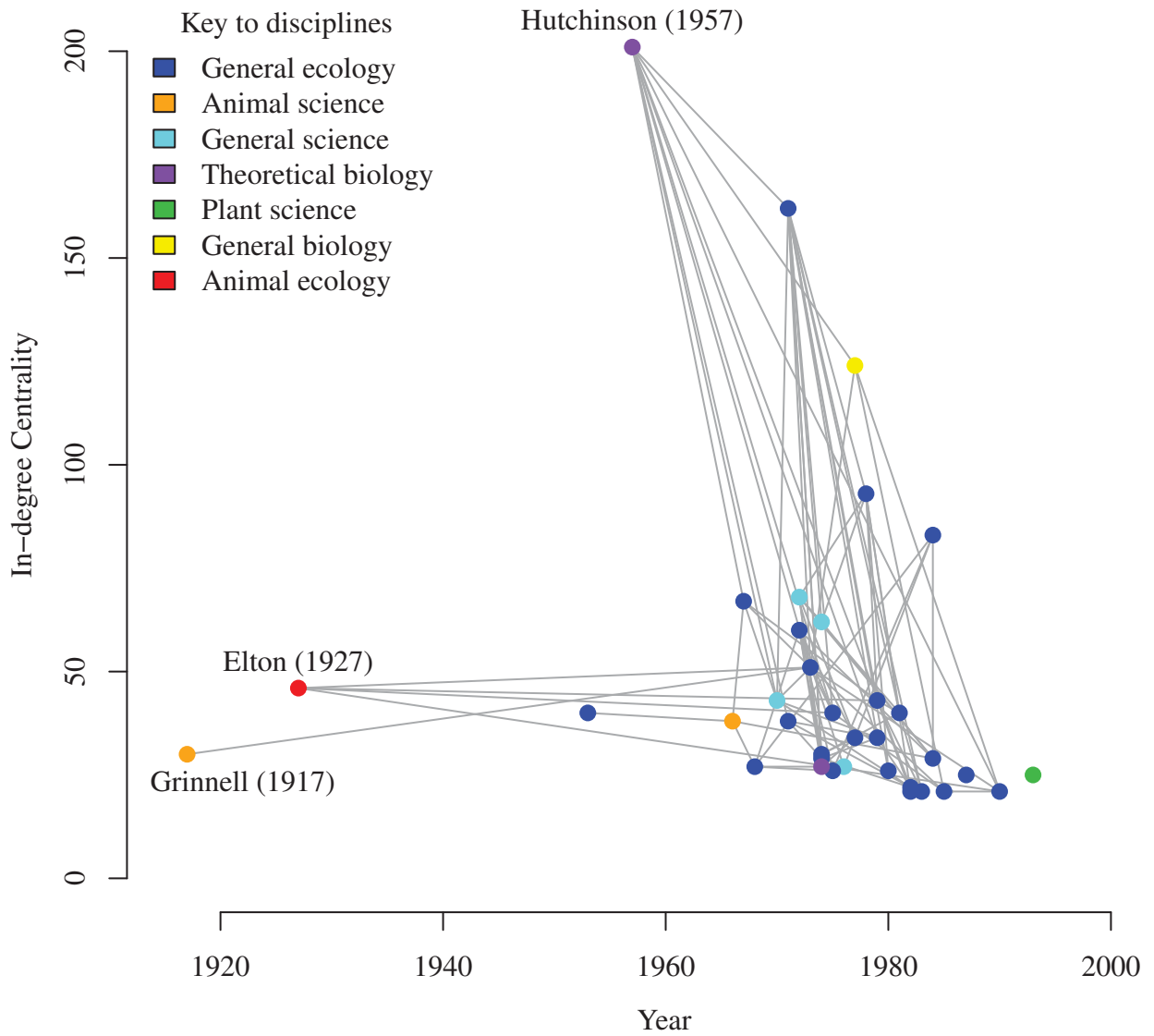
Fig. 2.8. The network of the 36 papers in our network that received more than 20 citations (i.e. the top 1% of papers in terms of citations received) plotted against in-degree centrality, sub-discipline, and year.

Connecting statement 1

In Chapter 2 I examined the development of the niche concept, and the patterns of its use with a citation network analysis. I found that while the niche literature was not strongly integrated, the ecological niche, and Hutchinson's definition of the niche in particular, have been successful in ecology and the niche is now used in a number of different ecological sub-disciplines. In Chapter 3 I turn from this historical survey of the niche's use to a question that has perhaps the strongest historical associations with the niche - that of competitive coexistence. I adopt a modelling approach to determine to what extent the niche theory prediction of competitive exclusion of the less fit competitor by the more fit competitor is dependent on (1) the strength of the fitness inequality between competitors, (2) the strength of demographic stochasticity in the population, and (3) any interaction between these.

Chapter 3

Predicting the outcome of competition when fitness inequality is variable

Michael T. Pedruski, Gregor F. Fussmann, and Andrew Gonzalez.

Department of Biology, McGill University, 1205 Dr. Penfield, Montréal QC, H3A 1B1

3.1 Abstract

Contemporary approaches to understanding the coexistence of competitors have emphasized the importance of both niche differentiation and fitness inequality. While these factors are theoretically capable of predicting coexistence or exclusion in a deterministic context, they may not be sufficient predictors in stochastic communities. We use numerical simulations to investigate the outcome of two-species resource competition along gradients of fitness inequalities and initial population sizes in the presence of demographic stochasticity. We found that the deterministic prediction of more fit competitors excluding less fit competitors was often unobserved when fitness inequalities were low or stochasticity was particularly strong. Under these conditions dominance by the less fit competitor, long-term co-persistence of both competitors, or the extinction of both competitors could be common. Our results show that the result of competition does not depend solely on the magnitude of the fitness inequality between two species, but also on how fitness inequalities interact with stochastic processes.

3.2 Keywords

Competitive exclusion; Fitness inequality; Demographic stochasticity; Resource competition

3.3 Introduction

The competitive exclusion principle, which holds that only one species can persist per limiting resource or niche (Hardin 1960), is a long standing tenet of community ecology with both theoretical (Volterra 1928; MacArthur and Levins 1964; Levin 1970; Chesson 2000) and

empirical support (Gause 1934; MacArthur 1958; Tilman 1981). It positions competition as a major force in community dynamics with direct consequences for community composition, and consequently for biodiversity and ecosystem function.

Community ecology has traditionally explained competitive exclusion as the deterministic result of different competitive abilities among competitors, with the understanding that the most fit competitor should exclude other competitors unless differences exist between competitors that focus intraspecific competition relative to interspecific competition (i.e. niche differentiation) (Chesson 2000). Recently, neutral theory (Bell 2000; Hubbell 2001) has challenged community ecologists to demonstrate that extinctions in competitive systems are indeed the result of competitive inequalities between species (e.g. Tilman et al. 1982), and not simply the product of stochastic processes (Hubbell 2001; Lande et al. 2003).

Universal neutrality in competitive communities is unlikely, but the question of how frequently competitive interactions are settled by fitness inequalities, as opposed to stochastic extinctions, remains open. Population geneticists have extensively examined how drift and selection affect allele frequencies depending on the strength of selection and the effective population size (Merrell 1953; Otto and Whitlock 1997; Ohta 2002), and the same principles should presumably hold for species-level competitive dynamics: in situations where fitness inequalities are strong, competitive outcomes are likely to follow deterministic predictions, but where inequalities are weaker the importance of stochasticity will likely be greater.

Fitness inequality, the relative competitive abilities of competitors in a given niche (Adler et al. 2007), defines the deterministic prediction for the outcome of competition in that niche. Resource competition theory (Tilman 1982) offers a useful framework with which to address fitness inequality. The theoretical simplicity of the resource competition framework is captured in a single value per resource, R*, which reflects the resource concentration

at which a consumer-resource system will equilibrate when that resource is limiting, and constitutes a measure of fitness in equilibrium (Chesson 2000) which predicts dominance by the competitor with the lowest R* value. While resource competition theory has typically been investigated in a deterministic context (e.g. Tilman 1977; Sommer 1983), stochastic extensions have been studied (e.g. Tilman 2004; Gonzalez and De Feo 2007; Okuyama 2015), but a full investigation of how initial population size and fitness inequality interact to affect competitive dynamics remains to be done.

Stochasticity, which represents the influence of random or unconsidered forces on population dynamics, can manifest as unpredictable variation in the fertility and mortality of individuals (demographic stochasticity), or as the effects of unpredictable environmental variation on all the individuals in a population (environmental stochasticity) (Lande et al. 2003). While stochasticity can provide a basis for mechanisms of coexistence (Abrams 1984; Chesson 2000; Okuyama 2015), it can also reduce diversity when it causes rare types to disappear from a community.

Both fitness inequality and demographic stochasticity affect the predictability of resource competition outcomes, and it is often unclear whether specific extinctions are due to deterministic or stochastic processes, or the combination of both. In conditions where one competitor is markedly more fit outcomes are likely to be much more predictable than in cases where competitors are more evenly matched. While demographic stochasticity by definition strikes independently of fitness, large disparities in fitness are likely to quickly translate into large disparities in abundances, leaving the less fit competitor more exposed to both deterministic and stochastic extinction. Conversely, when fitnesses are relatively evenly matched, the community moves towards deterministic extinction more slowly, and both populations remain more or less equally vulnerable to demographic extinction for some

82

time. Consequently, both fitness inequality and demographic stochasticity will affect how often the deterministic prediction of dominance by the more fit competitor is realized.

Here we model two-species competition for a single resource using a classical resource competition framework (Tilman 1981) to investigate the effects of varying fitness inequality and stochasticity on the outcome of competition across a range of population sizes and growth rates. We use R* as our metric of fitness and predict that under certain conditions the general deterministic prediction of complete dominance by the most fit competitor will often be violated:

1. As fitness inequality weakens and initial growth rates are reduced we expect the timescale of persistence for both competitors will lengthen, potentially leading to co-persistence of both competitors. Both of these factors are likely to influence the amount of time needed for a consumer-resource system to achieve an equilibrium, and while resource competition theory suggests that competitive exclusion is inevitable in all but the most unrealistic of cases (i.e. a deterministic system with absolutely no fitness inequality), the magnitude of fitness inequality still plays an important role by determining the duration of co-persistence.

2. As initial population sizes become smaller and initial growth rates become lower we expect that demographic stochasticity will become an increasingly prominent factor in determining the outcome of competition, increasing the probability that either one, or both species, will go extinct, even if not resource limited.

3. As the strength of fitness inequality weakens or the strength of demographic stochasticity increases there will be increasing uncertainty in the identity of the species that dominates, with increased potential for the more fit species to go extinct stochastically

and cede the habitat to dominance by the less fit species.

Recent work on the factors governing competitive outcomes have focused on the roles of fitness inequality and niche differentiation (Aarssen 1984; Chesson 2000; Adler et al. 2007, 2010) as two independent factors affecting the possibility for competitive coexistence. For the sake of simplicity we have restricted our attention to systems solely governed by fitness inequality, but we demonstrate that when the strength of stochasticity is great, or when population dynamics are slow, knowledge of fitness inequalities may not be enough to predict competitive outcomes.

3.4   Methods

3.4.1   The model

We used a discretized version of a classical resource competition framework (Tilman 1981) based on Michaelis-Menten (Monod) dynamics to simulate resource competition between two species for a single mineral resource in an open system:

$$N_i(t+1) = N_i(t) + \frac{\mu_i N_i(t) R(t)}{K_i + R(t)} - D N_i(t), \tag{3.1}$$

$$R(t+1) = R(t) + D(I - R(t)) - \sum_i \frac{Q_i \mu_i N_i(t) R(t)}{K_i + R(t)}, \tag{3.2}$$

84

which yields $R_i^* = \dfrac{DK_i}{(\mu_i - D)}$, $\hspace{6cm}$ (3.3)

where $N_i(t) =$ the density of species i at time t,

$\quad R(t) =$ the concentration of the resource at time t,

$\quad \mu_i =$ the maximum growth rate of species i,

$\quad K_i =$ the half-saturation constant of species i,

$\quad D =$ the dilution rate,

$\quad I =$ the concentration at which new resources inflow,

$\quad Q_i =$ the amount of resource taken up by new individuals of species i, and

$\quad R_i^* =$ the equilibrial resource concentration of a system dominated by species i.

To investigate the effects of fitness inequality on resource competition we imposed different responses of our competing species to variation along an environmental gradient (e.g. temperature). These different responses to the environment were achieved by varying μ_i along the 35 levels of the gradient. We varied μ_i such that each species' R^* value increased linearly from one extreme of the environmental gradient to the other, with the same slope, but in opposite directions (Fig. 3.3 in Appendix 3.1). Both species' R^* curves crossed at the centre of the gradient, where fitness inequality was 0. We defined relative fitness as the R^* value of one competitor divided by the R^* of the other for any given point on the gradient, and we defined fitness inequality as the absolute difference in the relative fitnesses of the two competitors at a given point on the environmental gradient (Fig. 3.3 in Appendix 3.1).

While we ultimately see our model as offering a general demonstration of the consequences of fitness inequality and demographic stochasticity, we chose parameter values within the

range of a realistic phytoplankton system (Table 3.1), and describe the model here using the units relevant to such a system. To investigate how our model would perform under relatively low and high growth rates we let μ vary over two different ranges of values. In the low growth rate case μ had a median value of $0.105 \cdot \text{day}^{-1}$ (barely greater than the dilution rate), whereas in the high growth rate case μ had a median value of $0.4 \cdot \text{day}^{-1}$. One of the consequences of modelling two ranges of μ with preset R^* values is that to investigate these two ranges, while retaining the same R^* values, required that the value of K that we used change, and in the same direction as μ. Consequently, in our low growth model K was constant at $0.072 \, \mu\text{mol} \cdot \text{L}^{-1}$, and in the high growth model K was constant at $4.32 \, \mu\text{mol} \cdot \text{L}^{-1}$. As a result, one set of models had both high μ values and a high value for K, and the other set had low μ values and a low value for K. Per capita growth rates, $\mu_i R(\text{t})/(K_i+R(\text{t}))$, are more sensitive to changes in μ when resources are abundant (i.e. early in our simulations), and consequently initial growth will be relatively rapid when μ and K take on high values, and slower when both μ and K take on lower values, even though both combinations were constrained to give the same equilibrial fitness. For simplicity, we term the models looking at the two ranges in μ 'low-growth', and 'high-growth' for the duration of the paper, though it is worth remembering that when resources are low the relative growth rates of our models reverse (Fig. 3.4 in Appendix 3.1). Dilution of the system (D), which represents the rate of inflow and outflow of materials (i.e. resources and consumers), was held constant at $0.1 \cdot \text{day}^{-1}$, though to assess the robustness of our findings we also ran simulations for another set of dilution rates (see below). We arbitrarily parameterized Q to have a value of $1 \cdot 10^{-6}$ $\mu\text{mol} \cdot \text{individual}^{-1}$ for both competitors, and resource inflow at $10 \, \mu\text{mol} \cdot \text{L}^{-1}$, which was also chosen as the resource concentration at the beginning of the simulations.

To introduce the effects of stochasticity to the traditional resource competition framework

of equations 1 and 2 we allowed the population size in the next time step to be the sum of the population size in the previous time step, a Poisson draw for growth, and a modified Poisson draw for death (modified to prevent stochastic mortality from surpassing current population size), with the expectations of the Poisson draws being the deterministic predictions for these two terms (Adler and Drake 2008; Loreau and Mazancourt 2008) based on values at time t, or more formally:

$$N_i(t+1) = N_i(t) + pois(G) - minimum(pois(M), N_i(t)) \tag{3.4}$$

$$\text{where } G = \frac{\mu_i N_i(t) R(t)}{K_i + R(t)}, \tag{3.5}$$

$$\text{and } M = N_i(t)D. \tag{3.6}$$

No stochasticity was applied directly to the resource equation, though the resource concentration experienced indirect stochasticity as we forced resource uptake by the consumer to be equal to the actual growth that each competitor achieved, while verifying that the required resource uptake did not exceed the available resources.

Cases where both competitors had gone extinct by the end of simulations were termed dual extinctions. Cases where neither competitor had gone extinct by the end of the simulations were termed co-persistence, and the cases where only one competitor had gone extinct were

termed less fit dominant, more fit dominant, or dominance by any species at fitness equality, depending on the fitness inequality that characterized the simulated competition.

Populations were seeded with equal numbers of both competitors at one of 10 levels of initial population size (1, 2, 4, 8, 16, 32, 64, 128, 256, or 512 individuals). These initial population sizes formed the stochasticity treatment for our stochastic model, as the form of stochasticity was held constant (i.e. a Poisson distribution). Each population x environment treatment was replicated 100 times, and simulations were run for 20000 time steps. All simulations were conducted in Python 3.3.3 using the numpy package version 1.8.0, and exported to R for analysis using the rpy2 package version 2.3.8. Analyses of resulting data were done in R version 3.0.2 (R Core Team 2013). Contour plots were made using the filled.contour3 and filled legend functions (`https://r-forge.r-project.org/scm/viewvc.php/pkg/R/filled.contour3.R?view=log&root=detsel`, `http://wiki.cbr.washington.edu/qerm/sites/qerm/images/2/25/Filled.legend.R`).

3.4.2 Assessing generality

To assess the generality of our model we ran a number of additional simulations (Table 3.2 in Appendix 3.1) which are briefly described below, and the results of which are found in the Appendix 3.1. To compare our stochastic results to a deterministic baseline we executed a model with a deterministic framework based solely on equations 1 and 2. Whereas N_i was a discrete variable in our stochastic framework (with extinction defined as $N_i=0$), in the deterministic case population size was continuous (with an extinction threshold at $N_i < 1$) as simulations with small initial population sizes yielded population growth rates too low for any growth when population sizes were conservatively constrained to integer values. To assess the generality of our findings we also investigated deterministic and stochastic frameworks

that varied K with R^* instead of μ (while holding μ constant at the median values it took in the main models). We also ran our model with alternative dilution rates of 0.01·day^{-1}, and 0.05·day^{-1} (while varying either μ or K). We parameterized the alternative dilution rate models by retaining the R^* values, along with the constant parameter (either μ or K) from the model where dilution was set at 0.1·day^{-1} (i.e. 0.105·day^{-1} or 0.4·day^{-1} in the case of μ; 0.072 µmol·L^{-1} or 4.32 µmol·L^{-1} in the case of K), and recalculated the varying parameter using these constants and the appropriate dilution rate (Fig. 3.5 in Appendix 3.1).

3.5   Results

Our simulations showed that while the predictions of resource competition theory were often borne out in stochastic systems, certain conditions defined by fitness inequality, initial population size, and growth rate resulted in different outcomes. While these factors clearly interact, it is still possible to analyze their effects individually, and we describe these effects while highlighting interesting interactions.

3.5.1   Effects of fitness inequality

The outcome of resource competition varied widely across the fitness inequality gradient (Fig. 3.1). As the two competitors experienced increasing fitness inequality there was a marked trend towards greater dominance of the more fit competitor especially for larger initial population sizes and in the model with high growth rates. In the model with high growth rates the transition from equality (and thus either co-persistence, dominance by one competitor at equality, or dual extinction) to complete dominance by the more fit competitor was rapid (Fig. 3.1 row 1 - column 2), effectively taking place as soon as the environment left

89

fitness equality (i.e. 0.056 fitness inequality). Conversely, in the low growth rate model the transition to complete dominance by the more fit competitor was not complete until fitness inequalities were 0.450 fitness inequality (Fig. 3.1 row 1 - column 1). There was also a trend towards greater dominance of the less fit competitor as fitness inequality weakened, though in general dominance by the less fit competitor was less common (ranging from 0-34% of simulations, depending on the treatment), and thus the trend was less pronounced (Fig. 3.6 in Appendix 3.1).

The co-persistence of both competitors until the end of the simulations was highly contingent on the relative fitness of the competitors, with the frequency of co-persistence decreasing as the fitness inequality grew (Fig. 3.1 row 3). While this effect was observed in both low and high growth models, the extent to which it was realized was clearly dependent on growth rates, co-persistence being found as far as 0.393 fitness inequality in the low growth model, but was only found at equality in the high growth case. In contrast, dual extinction of competitors was largely unaffected by fitness inequality (Fig. 3.1 row 4).

3.5.2 Effects of initial population size

Initial population size affected the probability of observing all of the potential competitive outcomes. In general, dominance by the more fit competitor and co-persistence increased as the initial population size increased (Fig. 3.1, rows 1,3), while cases of dual extinction decreased as initial population size increased (Fig. 3.1, row 4). The frequency of dominance of the less fit competitor (Fig. 3.1 row 2), and the dominance of either competitor at fitness equality (Fig. 3.2) were also affected by initial population size, but the relationship between population size and frequency was dependent on growth rates: in the low growth model both had unimodal relationships to initial population size with maxima at intermediate population

sizes, whereas at high growth rates the frequency of both declined as initial population size increased.

3.5.3 Variation in growth rates

There were clear effects of growth rates on the outcome of resource competition (Fig. 3.1). In the high growth rate model the more fit competitor more often came to dominance, effectively dominating all communities where initial population sizes were sufficient to prevent stochastic extinction (Fig. 3.1 row 1), whereas in the slower growth model universal dominance by the more fit competitor was confined to higher fitness inequalities and initial population sizes (e.g. in the low growth rate model complete dominance by the more fit competitor was only reliably achieved at the three highest initial population sizes when fitness inequalities were maximal; conversely, in the high growth rate model dominance was reliably achieved at all but the three lowest initial population sizes). Higher growth rates also effectively prevented stochastic extinction at smaller population sizes than in slow growth models (Fig. 3.1 row 4), and reduced the frequency with which the less fit competitor dominated (Fig. 3.1 row 2; Fig. 3.6 in Appendix 3.1). Dominance by one competitor when fitness was equal was also affected, with the high growth rate model achieving maximum dominance at lower population sizes than the low growth rate model (Fig. 3.1). The effects of initial growth rates on co-persistence were more subtle, as higher growth rates led to an increase in the proportion of simulations yielding co-persistence near fitness-equality (i.e. co-persistence remained common even at lower initial population sizes), but a reduction in the proportion of simulations yielding co-persistence when fitness inequalities were greater (Fig. 3.1 row 3).

3.6 Discussion

Recent debate has focused on whether natural communities are niche structured or neutral (Hubbell 2001; Leibold and McPeek 2006; Adler et al. 2007; Clark et al. 2007), and by extension, whether the outcomes of competition in nature are predicted by fitness differences. Our results demonstrate that, even when assuming a resource competition framework, the predictability of competitive outcomes depended on all three of the factors we varied: the magnitude of fitness inequality, the strength of demographic stochasticity, and the magnitude of growth rates that competitors experience. We show that the prediction from niche-theory of dominance by the most fit competitor is most often realized when fitness inequalities are great, initial population sizes are high (and thus demographic stochasticity is weak), and growth rates are high. When any one of these conditions are not met it becomes increasingly likely that an outcome not predicted by resource competition theory will be realized: dominance of the less fit competitor, extinctions of both competitors, or the persistence of both competitors. Our model thus suggests that to answer questions about how ecological communities are structured ecologists will need to understand: 1) the magnitudes of fitness inequalities between competitors in the relevant environment, 2) how prevalent stochasticity is in that community, and 3) at what pace ecological interactions take place. We find the first question particularly interesting, as empirical evidence shows fitnesses vary along environmental gradients and suggests that regions of effective equivalence may exist (Birch 1953; Tilman et al. 1981; Chave 2004). Consequently, competitive systems may simultaneously behave in niche or neutral structured fashions depending on where a community finds itself along an environmental gradient, and how stochasticity and dynamics play out in that community. Ultimately, our results suggest that the question of whether commu-

nities are likely to be niche or neutrally structured may be extremely locally contingent, and while approaches that discuss fitness inequality offer unique insights to this problem, fitness inequality *per se* is not sufficient to make completely reliable predictions about how communities will be structured (Adler et al. 2007).

Our model makes several assumptions that affect the extent to which our findings are likely to be realized in empirical systems. The resource competition model we used has been well tested in both lab and field (Tilman 1981; Sommer 1986; Makulla and Sommer 1993), and makes clear predictions about competitive outcomes at equilibrium when competition is for a single limiting resource. The competitors in our simulations competed for a single limiting resource, but our use of a stochastic model, and our choice to model in discrete time with a limited number of time steps, does mean that our co-persistence results may include simulations where the expected outcome will eventually manifest, but has not done so by the end of our simulations (indeed, our deterministic simulations frequently resulted in the co-persistence of competitors (Fig. 3.7 in Appendix 3.1)). Still, the fitness inequality defined by the competitors' R* values was an excellent predictor of competitive outcome in conditions where stochasticity was minimal and the pace of competition was quick. Where these conditions were not met we found exceptions to the predictions of R* theory, such as regions of competitive co-persistence around fitness inequality, and the dominance of the less fit competitor. Furthermore, we assumed a non-spatial model of competition, and it is possible that spatial systems might experience either reduced departures from the deterministic prediction due to mitigating immigration or exacerbated departures from the deterministic prediction due to priority effects (Tilman 2004).

The relevance of our quantitative results to natural communities will depend on how closely our parameter values and implementation of stochasticity reflect those found in these

communities. With this obvious cautionary note in mind, we chose parameter values that could be realistic for some organisms and resources at a given timescale (e.g. phytoplankton on a daily time scale), and the consistency of the qualitative patterns in our results across a variety of parameter values suggests that the patterns we describe are likely to occur in natural systems. We also assumed that demographic stochasticity can be described by Poisson variance in both birth and death processes, a common assumption in ecology and population genetics (Kimura and Crow 1963; Adler and Drake 2008; Loreau and Mazancourt 2008).

The key qualitative patterns of our model are reasonably robust to variations in the parameters used to model growth, and the parameter by which R* was varied. Variation in the dilution rate, did in some cases lead to results that were different from our main model, but that do not challenge our conclusions (Fig. 3.7,3.8,3.9,3.10 in Appendix 3.1). Obviously, though we feel the assumptions of our model are justifiable, they are also simplistic. While some natural systems may be perennially limited by the same resource, others likely deal with a variety of challenges such as predation, disease, or new resources becoming limiting. Here we wished to investigate the effects of fitness inequality in a situation where it could be relatively easily quantified, but natural competitive systems may be more complicated.

A number of questions present themselves for future research. Our model implements only demographic stochasticity, and not environmental stochasticity. The effects of demographic stochasticity are strongest at small population sizes, whereas the effects of environmental stochasticity are largely independent of population size (Lande et al. 2003), and thus it is likely that introducing environmental stochasticity will increase the risk of extinction even in well established populations (Petchey et al. 1997; Gonzalez and De Feo 2007). Consequently, the combination of demographic and environmental stochasticity might further confound the

influice of fitness inequality on the outcome of competition (Adler and Drake 2008). Alternatively, environmental stochasticity might reinforce the effects of fitness inequality if less fit competitors are also more strongly affected by environmental stochasticity. Empirically, our model begs the question about how competitive fitness varies along environmental gradients in space and time, and how these environment-fitness gradients map onto real world settings (Holt 2009). Should regions of relative equality prove to be common in natural communities, particularly those in which competition occurs slowly or in which stochasticity is strong, it may well be that the predictability of competitive interactions cannot be taken for granted. Our results predict that co-persistence of competitors, or dominance by less fit competitors may be surprisingly common, and it would be exciting to see if this prediction holds in the field.

3.7 Conclusions

The ability to predict outcomes is a virtue for any scientific theory, and niche theory in particular makes strong predictions about when species should dominate ecological communities. Recent debate about the extent to which competitive outcomes can be successfully predicted has sparked questions about the suitability of specific competitive frameworks (Miller et al. 2005, 2007; Wilson et al. 2007), yet our results demonstrate that even within a single niche framework there can be considerable uncertainty in competitive outcomes if fitness inequalities are modest, growth rates are slow, or demographic stochasticity is strong. When any of these conditions are met unexpected outcomes, such as co-persistence, or dominance by the less fit competitor may emerge. Thus the extent to which competitive outcomes will be predictable in natural communities will depend on the environmental conditions present,

and how these relate to the competitors' experience of differences in fitness and stochasticity in their environment.

3.8   Acknowledgements

3.9   Funding

3.10   Literature Cited

Aarssen, L. W. 1984. On the distinction between niche and competitive ability: Implications for coexistence theory. Acta Biotheoretica 33:67–83.

Abrams, P. 1984. Variability in resource consumption rates and the coexistence of competing species. Theoretical Population Biology 25:106 – 124.

Adler, P. B., and J. A. Drake. 2008. Environmental variation, stochastic extinction, and competitive coexistence. The American Naturalist 172:E186–E195.

Adler, P. B., S. P. Ellner, and J. M. Levine. 2010. Coexistence of perennial plants: an embarrassment of niches. Ecology Letters 13:1019–1029.

Adler, P. B., J. HilleRisLambers, and J. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Bell, G. 2000. The distribution of abundance in neutral communities. The American Naturalist 155:606–617.

Birch, L. C. 1953. Experimental background to the study of the distribution and abundance of insects: III. The relation between innate capacity for increase and survival of different species of beetles living together on the same food. Evolution 7:136–144.

Chave, J. 2004. Neutral theory and community ecology. Ecology Letters 7:241–253.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Clark, J. S., M. Dietze, S. Chakraborty, P. K. Agarwal, I. Ibanez, S. LaDeau, and M. Wolosin. 2007. Resolving the biodiversity paradox. Ecology Letters 10:647–662.

Gause, G. F. 1934. The struggle for existence. The Williams and Wilkins Company, Baltimore.

Gonzalez, A., and O. De Feo 2007. Environmental variability modulates the insurance effects of diversity in non-equilibirum communities. Pages pp. 159–177 *in* D. A. Vasseur and K. S. McCann, editors. The impact of environmental variability on environmental systems. Springer, Dordrecht.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences USA 106:19659–19665.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press., Princeton.

Kilham, S. S. 1975. Kinetics of silicon-limited growth in the freshwater diatom *Asterionella formosa*. Journal of Phycology 11:396–399.

Kimura, M., and J. F. Crow. 1963. The measurement of effective population number. Evolution 17:279–288.

Lande, R., S. Engen, and B.-E. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press., Oxford.

Leibold, M., and M. McPeek. 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87:1399–1410.

Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. The American Naturalist 104:413–423.

Loreau, M., and C. d. Mazancourt. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. The American Naturalist 172:E48–E66.

MacArthur, R., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences USA 51:1207–1210.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

Makulla, A., and U. Sommer. 1993. Relationships between resource ratios and phytoplankton species composition during spring in five north German lakes. Limnology and Oceanography 38:846–856.

Merrell, D. J. 1953. Gene frequency changes in small laboratory populations of *Drosophila melanogaster*. Evolution 7:95–101.

Miller, T. E., J. H. Burns, P. Munguia, E. L. Walters, J. M. Kneitel, P. M. Richards, N. Mouquet, and H. L. Buckley. 2005. A critical review of twenty years' use of the resource-ratio theory. The American Naturalist 165:439–448.

Miller, T. E., J. H. Burns, P. Munguia, E. L. Walters, J. M. Kneitel, P. M. Richards, N. Mouquet, and H. L. Buckley. 2007. Evaluating support for the resource-ratio hypothesis: a reply to Wilson et al. The American Naturalist 169:707–708.

Ohta, T. 2002. Near-neutrality in evolution of genes and gene regulation. Proceedings of the National Academy of Sciences USA 99:16134–16137.

Okuyama, T. 2015. Demographic stochasticity alters the outcome of exploitation competition. Journal of Theoretical Biology 365:347–351.

Otto, S. P., and M. C. Whitlock. 1997. The probability of fixation in populations of changing size. Genetics 146:723–733.

Petchey, O. L., A. Gonzalez, and H. B. Wilson. 1997. Effects on population persistence: the interaction between environmental noise colour, intraspecific competition and space. Proceedings of the Royal Society of London B 264:1841–1847.

R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Sommer, U. 1983. Nutrient competition between phytoplankton species in multispecies chemostat experiments. Archiv für Hydrobiologie 96:399–416.

Sommer, U. 1986. Phytoplankton competition along a gradient of dilution rates. Oecologia 68:503–506.

Sommer, U. 1993. Phytoplankton competition in Plußsee: a field test of the resource-ratio hypothesis. Limnology and Oceanography 38:838–845.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58:338–348.

Tilman, D. 1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology 62:802–815.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton.

Tilman, D. 2004. Niche trade-offs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences USA 101:10854–10861.

Tilman, D., S. S. Kilham, and P. Kilham. 1982. Phytoplankton community ecology: the role of limiting nutrients. Annual Review of Ecology and Systematics 13:349–372.

Tilman, D., M. Mattson, and S. Langer. 1981. Competition and nutrient kinetics along a temperature gradient: an experimental test of a mechanistic approach to niche theory. Limnology and Oceanography 26:1020–1033.

Volterra, V. 1928. Variations and fluctuations of the number of individuals in animal species living together. Journal du Conseil International de l'Exploration de la Mer 3:3–51.

Wilson, J. B., E. Spijkerman, and J. Huisman. 2007. Is there really insufficient support for Tilman's R* concept? A comment on Miller et al. The American Naturalist 169:700–706.

Table 3.1. The parameters and variables in the model, the parameterizations we chose, examples of units for which these parameterizations could be realistic for a phytoplankton system, and supporting references to empirical work (either experimental or field research) for these parameterizations.

Parameter or variable name	Nature	Units for which our model could realistically model a phytoplankton system	Range or value of parameter	Supporting reference for our parameterizations
N	Population size	Individuals·L^{-1}		
R	Concentration	µmol·L^{-1}		
μ	Rate	Day^{-1}	0.104 - 0.107 (Low growth); 0.343 - 0.493 (High growth)	Kilham (1975); Tilman et al. (1981, 1982); Tilman (1982)
K	Concentration	µmol·L^{-1}	0.072 (Low growth); 4.32 (High growth)	Tilman (1981)
D	Rate	Day^{-1}	0.1	Tilman et al. (1981)
I	Concentration	µmol·L^{-1}	10	Sommer (1993)
Q	Concentration· Individual^{-1}	µmol·Individual^{-1}	$1\cdot10^{-6}$	Tilman (1981)
R^*	Concentration	µmol·L^{-1}	1.10 - 1.78	Tilman (1981)
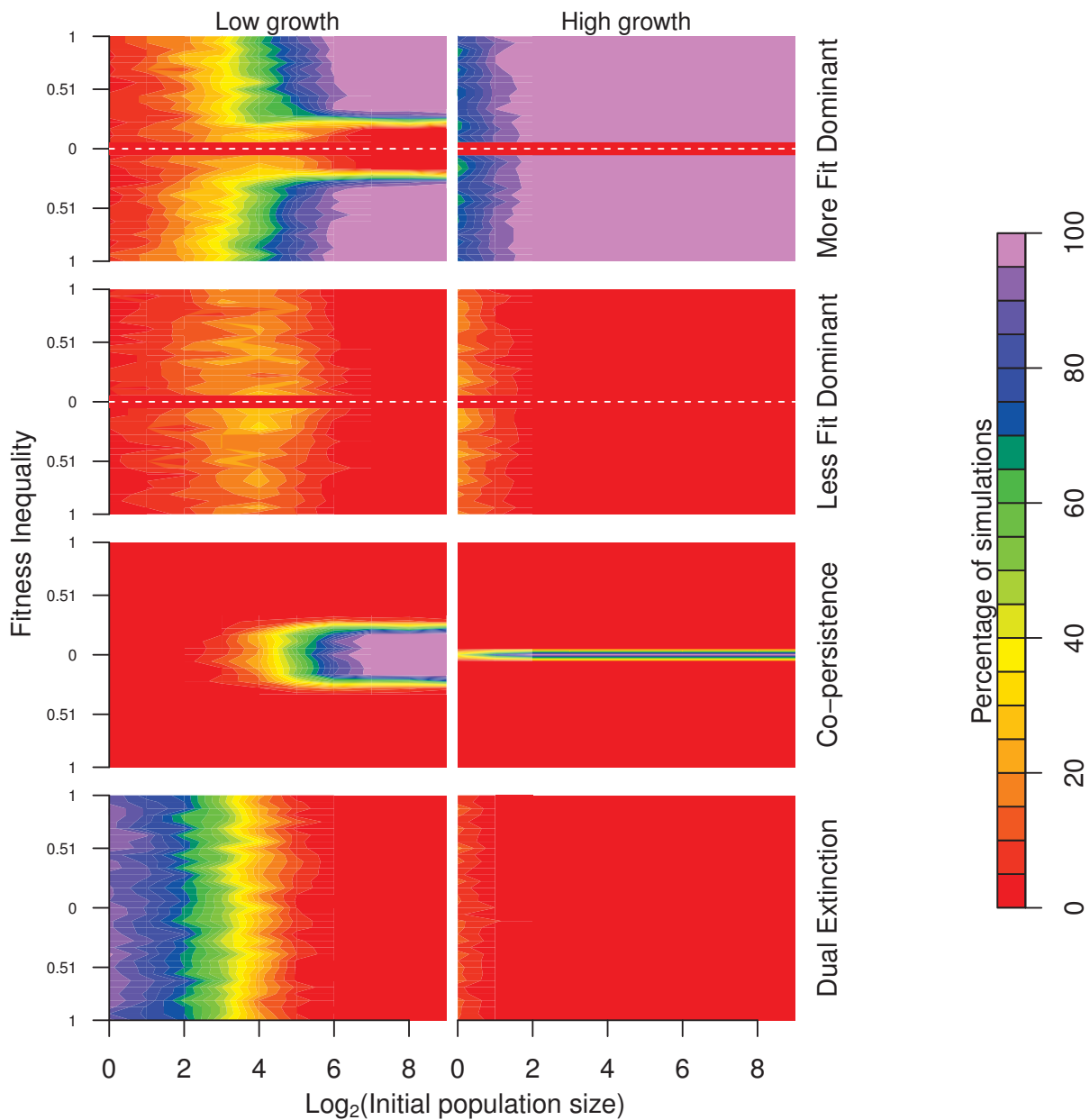
Fig. 3.1. The percentage of simulations yielding four of five possible outcomes as a function of initial population size, fitness inequality (along the 35 points on the environmental gradient), and growth rate. Results from the low growth model are in the left column, and results from the high growth model are in the right column. Each row represents a different potential result outcome: the first row shows simulations in which the more fit competitor has dominated, the second row shows simulations in which the less fit competitor has dominated, the third row gives the percentage of simulations in which both competitors have persisted to the end of simulations, and the fourth row shows simulations in which neither competitor has persisted to the end of simulations. Note that by definition the first and second rows have values of 0 when competitors have equal fitness.
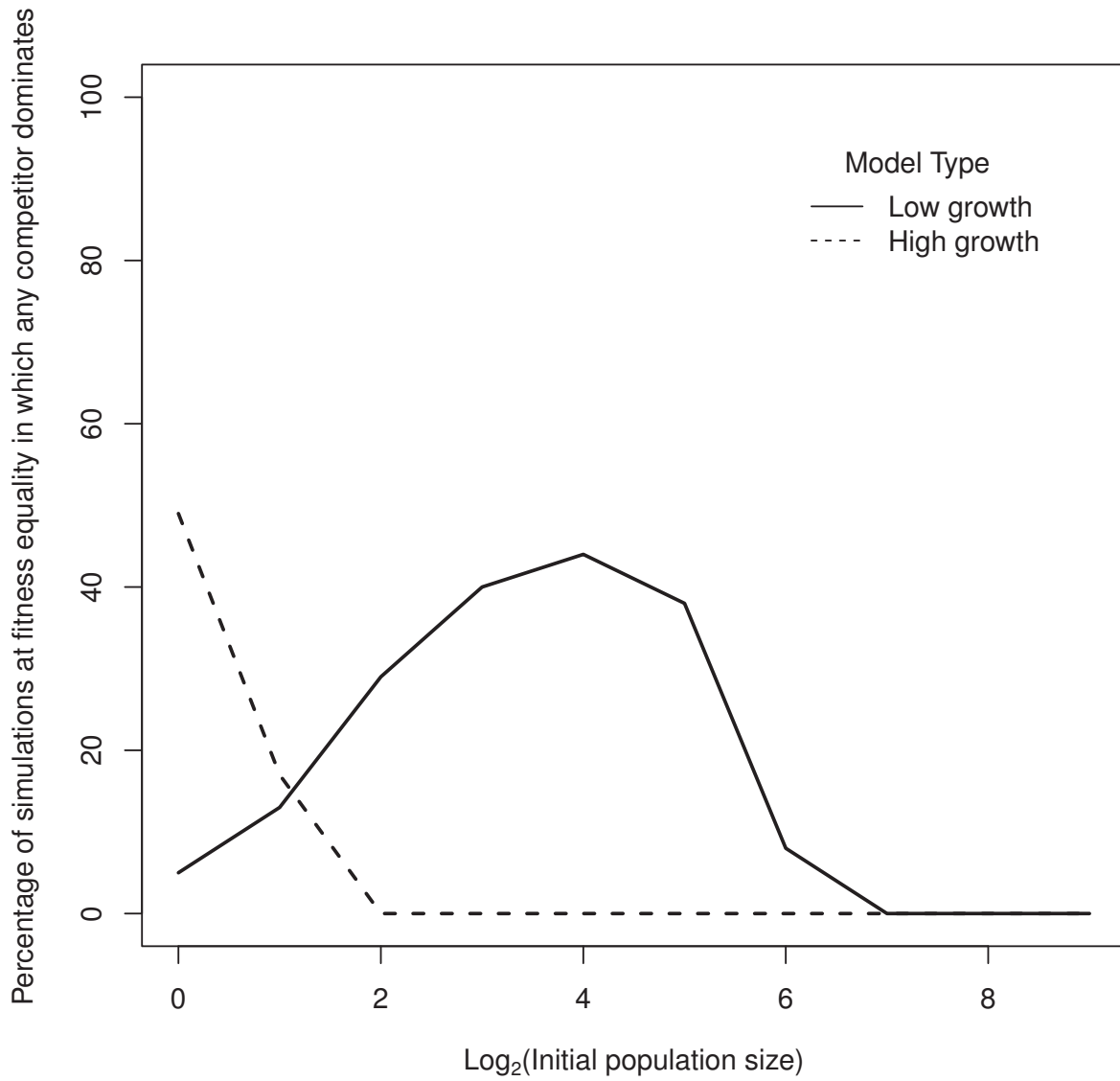
Fig. 3.2. The percentage of simulations at fitness equality that yield the dominance of any competitor as a function of initial population size and growth rate.

Appendix to Chapter 3

Appendix 3.1: Assessment of generality

Please refer to Table 3.1 for relevant units for all parameters and variables.

Results of models assessing generality

Effect of stochasticity

Competitive outcome was strongly affected by fitness inequality and growth rate in the deterministic version of our model, but was not affected by initial population size (Fig. 3.7). As with the stochastic model, dominance by the more fit competitor was restricted to simulations with some amount of fitness inequality, and co-persistence was restricted to simulations with relatively little fitness inequality between the competitors, though the fitness inequalities that resulted in co-persistence were more constrained to fitness equality in the deterministic model in the low growth conditions (similarly, the fitness inequalities resulting in dominance by the more fit competitor were more constrained in the deterministic low growth model). The deterministic model resulted in no dominance by the less fit competitor, dominance by any competitor at fitness equality, nor any dual extinction.

Effect of varying dilutions

Within both our deterministic and stochastic model frameworks there was a clear effect of varying the dilution rate on the outcome of competition realized at 20000 time steps, with increasing dominance by the more fit competitor as dilution increased, and decreasing co-persistence (Fig. 3.7, 3.8). In the stochastic model, where other results were possible, dilution had no discernible effect on the amount of dominance by any competitor at fitness equality, and any effects on the amount of dominance by the less fit competitor, or the amount of

dual extinction, were relatively weak. Generally, varying dilution rate had a greater effect on competitive outcome in low growth models than in the high growth models. The relationship between fitness inequality and the different potential outcomes of competition noted in the main (stochastic) model held except in the case of the lowest dilution rate in the low growth model where there was no obvious relationship between fitness inequality and dominance by either competitor, co-persistence, or dual extinction. In this case we expect the slow growth rate combined with the low dilution rate limited dynamics to such an extent that only demographic stochasticity had time to cause extinctions by the end of the simulations.

Effect of varying K (as opposed to μ)

The results of models varying K (Fig. 3.9, 3.10) were in many cases quite similar to the models where μ was varied (Fig. 3.7, 3.8), though there were a number of obvious differences. Whereas the μ-varying model returned no clear relationship between fitness inequality and co-persistence at the lowest dilution rate, all the models that varied K showed that co-persistence was found only in conditions of relatively minimal fitness inequality. Dual extinction was somewhat less common in K varying models than μ varying models where dilution rates were low. Finally, the relationships between dilution rate and the frequency of competitive outcomes differed in some ways from the relationships with μ varying models: in the low growth models there were clear effects of dilution rate on dominance by any competitor at fitness equality when K was varied (Fig. 3.11), and the monotonic relationships between dilution rate and both dominance by the more fit competitor and co-persistence were not held by the low growth deterministic model that varied K - in this case the fitness inequality conditions that resulted in co-persistence were most restricted at intermediate dilution rates.

106

Discussion of models assessing generality

Though some of the patterns observed in our focal model (stochastic, varying μ, $D{=}0.1$) were not represented in all of the models we deployed to assess generality we feel that none of these deviations challenge our conclusions. Many of these differences are trivial (e.g. the lack of any effect of varying initial population size in the deterministic model), and others most likely reflect different timescales of competition as opposed to any fundamental violation of our understanding of the focal model. For example, the broad co-persistence in the low growth models varying μ and having a dilution of 0.01 is likely due to a combination of low stochastic mortality and growth rates that do not vary strongly at low resource concentrations (the difference in net growth rate between highly fit and unfit individuals narrows in the μ-varying model as resource concentrations decline).
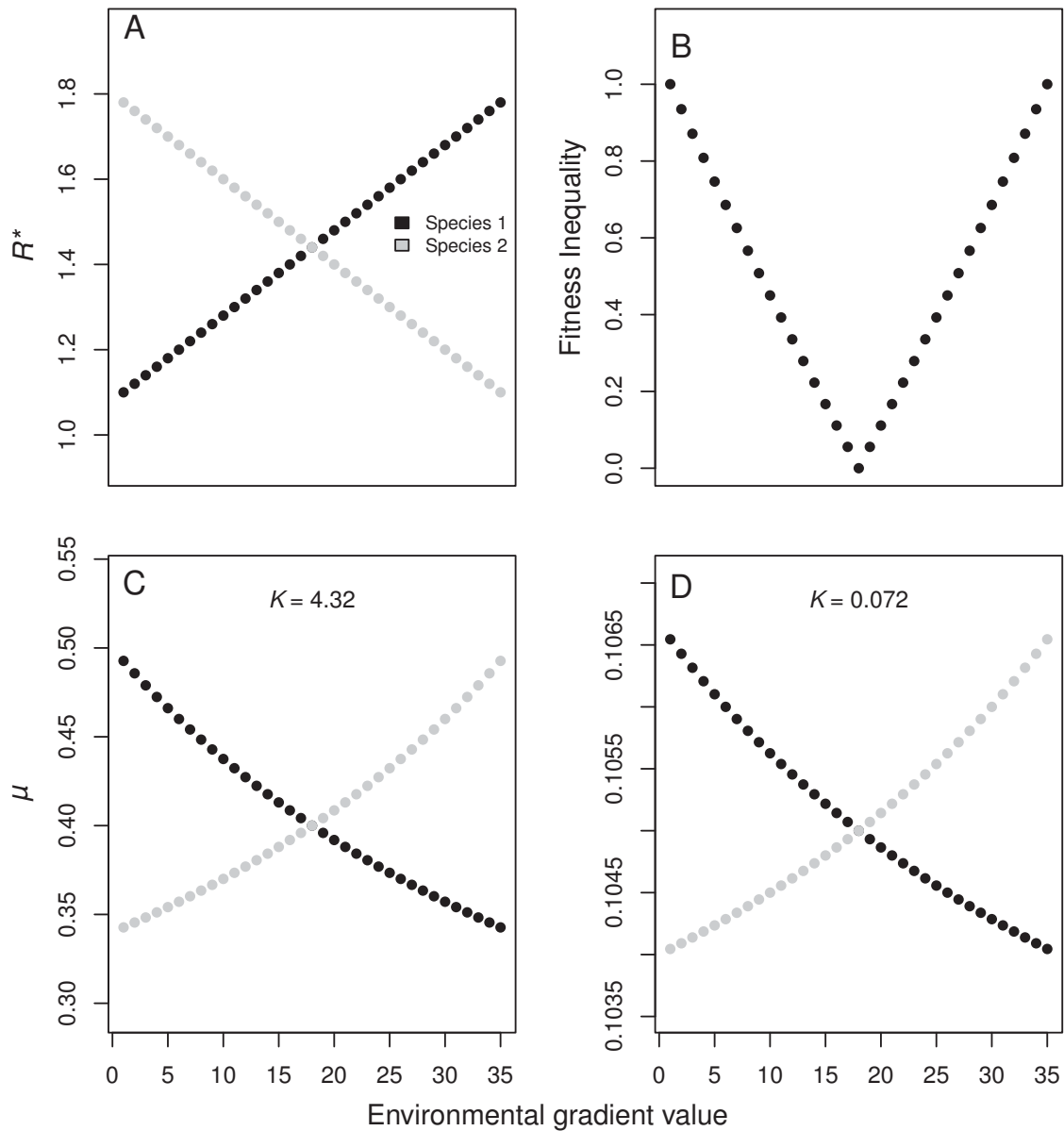
Fig. 3.3. R^* values for both species in our focal model (stochastic, varying μ, D=0.1) over the environmental gradient (A), the fitness inequality between the competitors over the gradient (B), and the μ values and K constants used to parameterize the low growth rate (C), and high growth rate models (D).
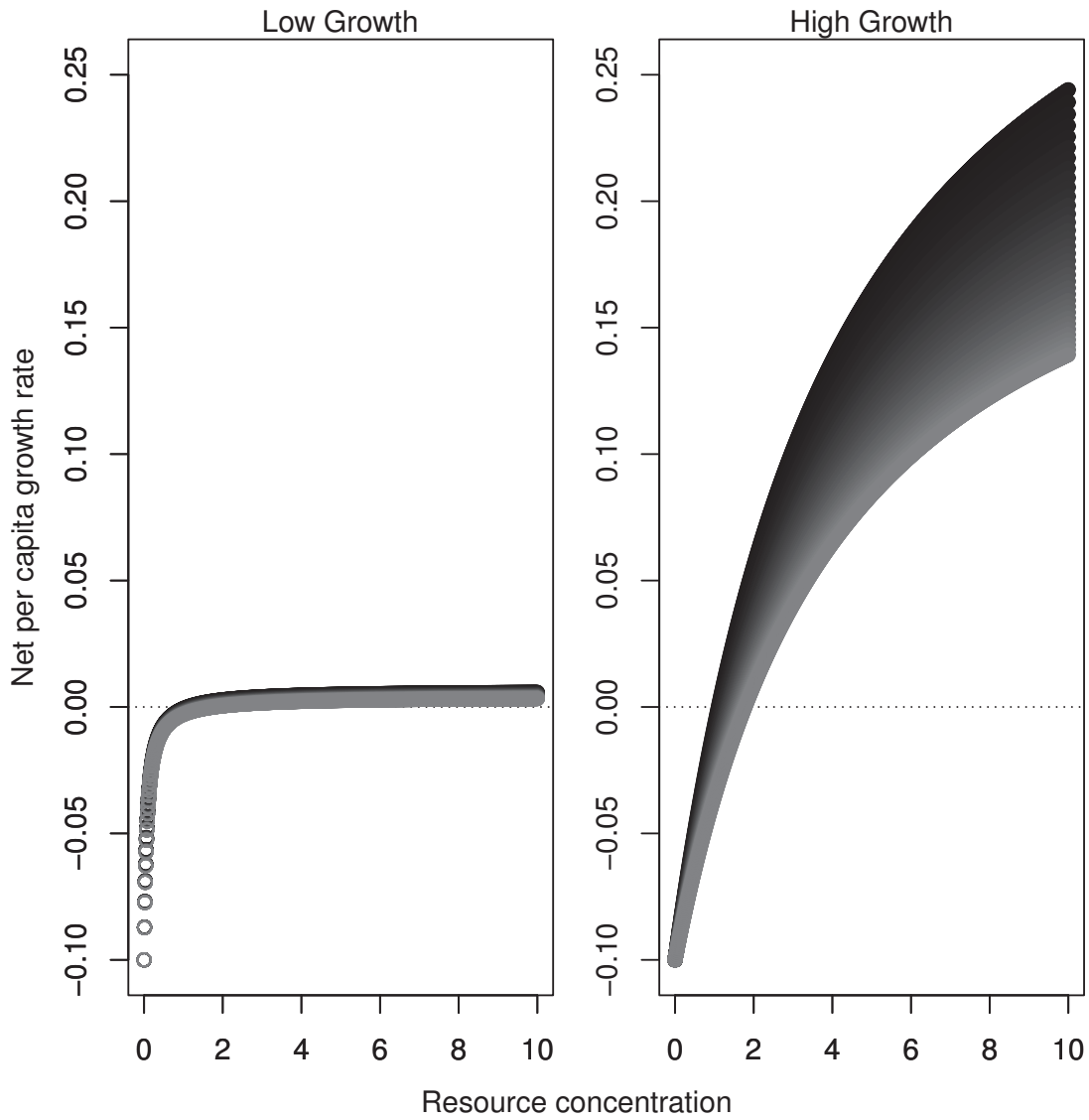
Fig. 3.4. Deterministic net per captia growth rates as a function of resource concentration and the environmental gradient (darker greys represent environmental gradient values that give a fitness advantage) in the focal model. Dotted line indicates 0 growth, and therefore R^*.
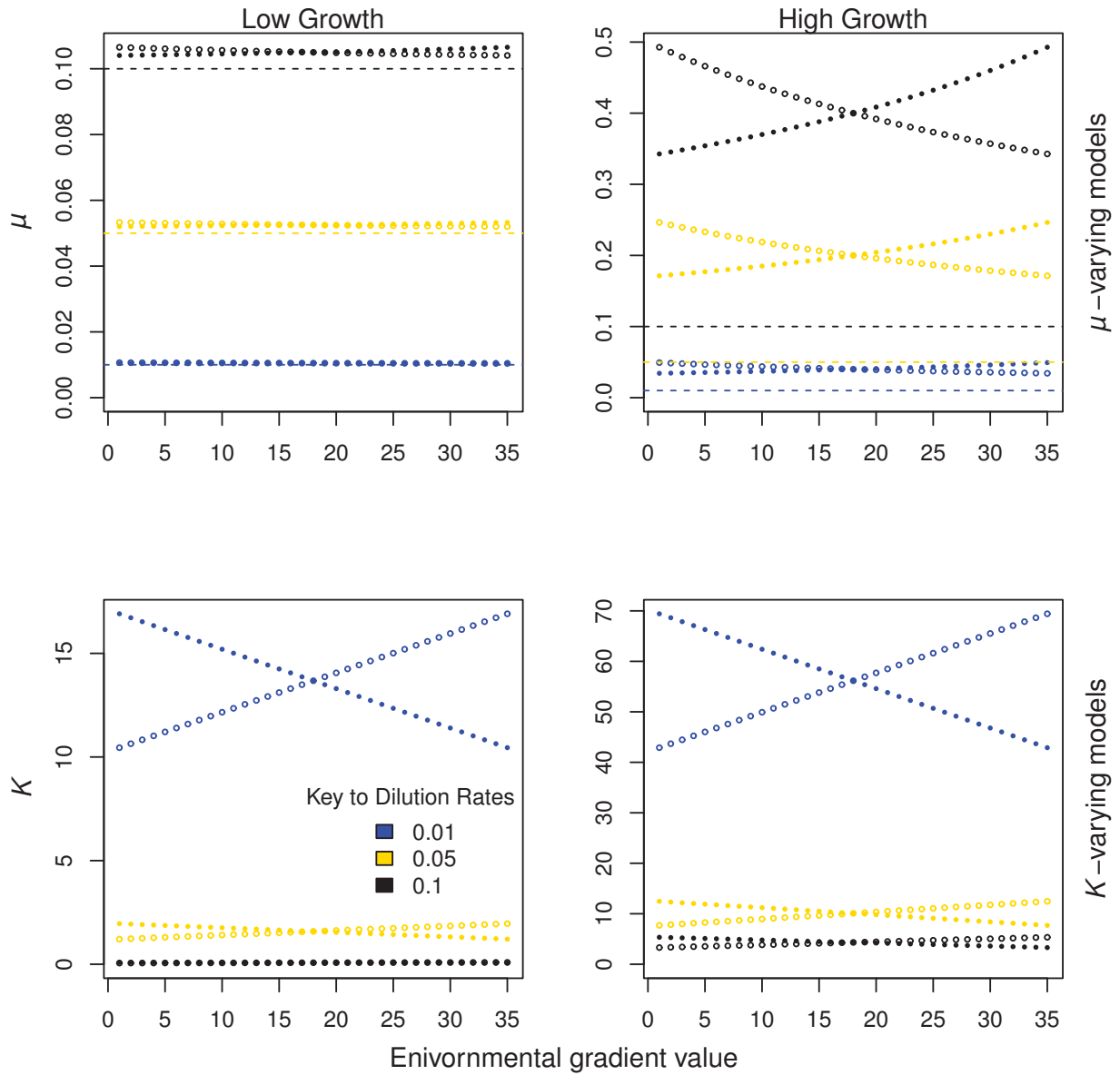
Fig. 3.5. μ and K parameters used in simulations that varied dilution rate. Note that in the cases where μ varied (top row) K was either fixed at 0.072 (low growth) or 4.32 (high growth), and in the cases where K varied (bottom row) μ was either fixed at 0.105 (low growth) or 0.4 (high-growth). Species 1 values in filled points, species 2 values in open points, and dilution rates figured as dashed lines in μ-varying plots.
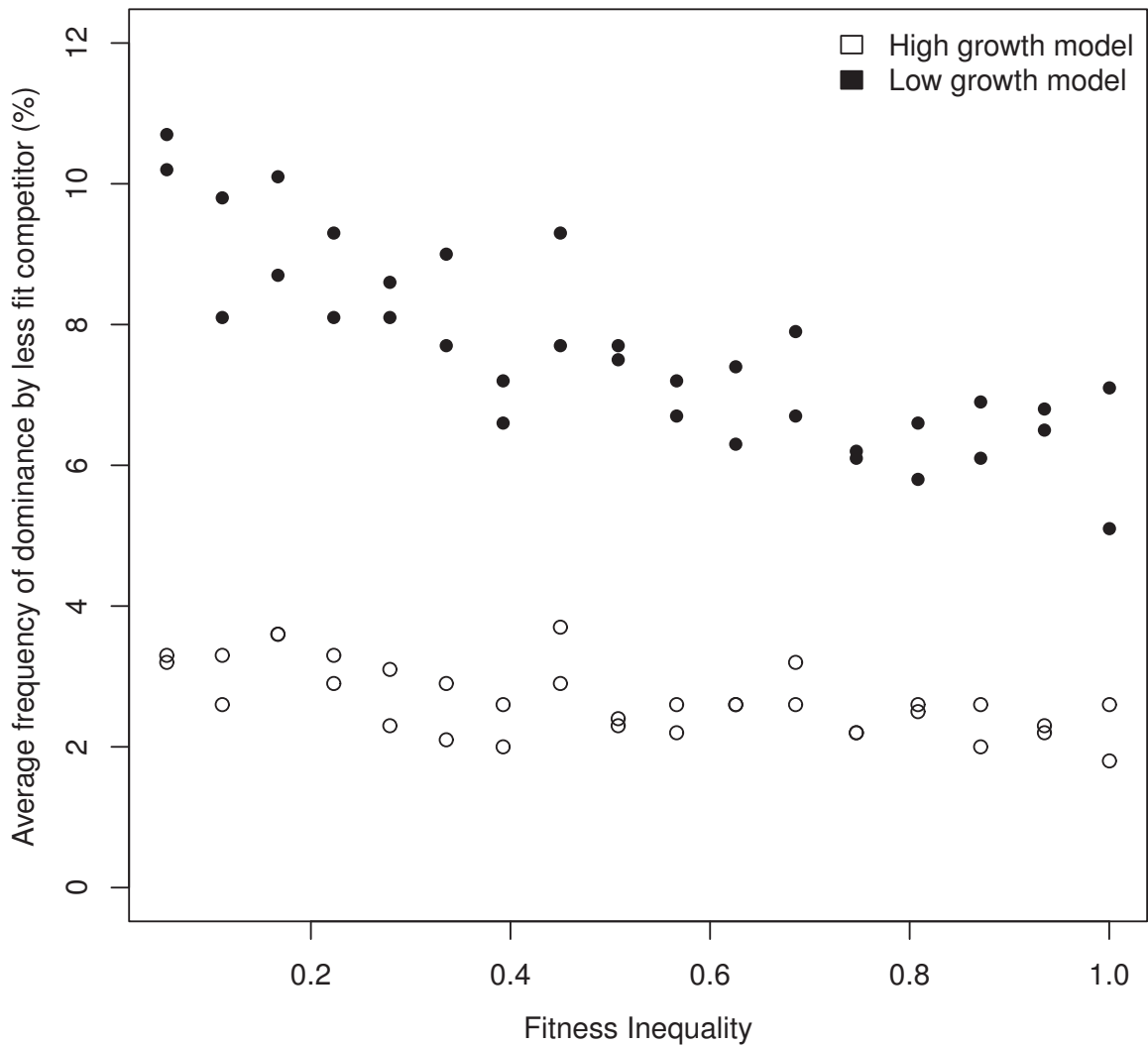
Fig. 3.6. The percentage of simulations resulting in the dominance of the less fit competitor averaged across all initial population sizes as a function of fitness inequality and the relative growth rate in our focal model (stochastic, varying μ, D=0.1). The two results for each fitness inequality value (except 0 fitness inequality, where by definition dominance of the less fit competitor was impossible) reflect the use of the absolute difference in calculating fitness inequality across the 35 points in the environmental gradient.

Fig. 3.7. The percentage of simulations yielding four of five possible outcomes as a function of initial population size, fitness inequality (along the 35 points on the environmental gradient), and growth rate when μ is varied in the deterministic framework at three different dilution rates. Each column represents simulations from a combination of dilution and growth rates, and each row represents a different potential result outcome: the first row shows simulations in which the more fit competitor has dominated, the second row shows simulations in which the less fit competitor has dominated, the third row gives the percentage of simulations in which both competitors have persisted to the end of simulations, and the fourth row shows simulations in which neither competitor has persisted to the end of simulations. Note that by definition the first and second rows have values of 0 when competitors have equal fitness.

Fig. 3.8. The percentage of simulations yielding four of five possible outcomes as a function of initial population size, fitness inequality (along the 35 points on the environmental gradient), and growth rate when μ is varied in the stochastic framework at three different dilution rates. Each column represents simulations from a combination of dilution and growth rates, and each row represents a different potential result outcome: the first row shows simulations in which the more fit competitor has dominated, the second row shows simulations in which the less fit competitor has dominated, the third row gives the percentage of simulations in which both competitors have persisted to the end of simulations, and the fourth row shows simulations in which neither competitor has persisted to the end of simulations. Note that by definition the first and second rows have values of 0 when competitors have equal fitness.

Fig. 3.9. The percentage of simulations yielding four of five possible outcomes as a function of initial population size, fitness inequality (along the 35 points on the environmental gradient), and growth rate when K is varied in the deterministic framework at three different dilution rates. Each column represents simulations from a combination of dilution and growth rates, and each row represents a different potential result outcome: the first row shows simulations in which the more fit competitor has dominated, the second row shows simulations in which the less fit competitor has dominated, the third row gives the percentage of simulations in which both competitors have persisted to the end of simulations, and the fourth row shows simulations in which neither competitor has persisted to the end of simulations. Note that by definition the first and second rows have values of 0 when competitors have equal fitness.

Fig. 3.10. The percentage of simulations yielding four of five possible outcomes as a function of initial population size, fitness inequality (along the 35 points on the environmental gradient), and growth rate when K is varied in the stochastic framework at three different dilution rates. Each column represents simulations from a combination of dilution and growth rates, and each row represents a different potential result outcome: the first row shows simulations in which the more fit competitor has dominated, the second row shows simulations in which the less fit competitor has dominated, the third row gives the percentage of simulations in which both competitors have persisted to the end of simulations, and the fourth row shows simulations in which neither competitor has persisted to the end of simulations. Note that by definition the first and second rows have values of 0 when competitors have equal fitness.

Fig. 3.11. The percentage of simulations resulting in dominance by one competitor at fitness equality as a function of initial population size when either μ or K is varied in the stochastic framework at three different dilution rates.

Table 3.2. Listing of all the different models we examined to assess the generality of the results.

Dilution rate	Parameter varied	Growth rate	Deterministic/Stochastic framework
0.01	μ	Low	Stochastic
0.05	μ	Low	Stochastic
0.10	μ	Low	Stochastic
0.01	μ	High	Stochastic
0.05	μ	High	Stochastic
0.10	μ	High	Stochastic
0.01	K	Low	Stochastic
0.05	K	Low	Stochastic
0.10	K	Low	Stochastic
0.01	K	High	Stochastic
0.05	K	High	Stochastic
0.10	K	High	Stochastic
0.01	μ	Low	Deterministic
0.05	μ	Low	Deterministic
0.10	μ	Low	Deterministic
0.01	μ	High	Deterministic
0.05	μ	High	Deterministic
0.10	μ	High	Deterministic
0.01	K	Low	Deterministic
0.05	K	Low	Deterministic
0.10	K	Low	Deterministic
0.01	K	High	Deterministic
0.05	K	High	Deterministic
0.10	K	High	Deterministic

Connecting statement 2

In Chapter 3 I examined the relationship between the niche and ecological dynamics by modelling competition along gradients of inequality and demographic stochasticity. I found that the tendency for competition to result in the prediction of exclusion of the less fit competitor by the more fit competitor was dependent both on the strength of stochasticity and the strength of fitness inequality. Given the importance of fitness inequality for competitive dynamics in the absence of niche differentiation, in Chapter 4 I investigate the evolution of the fundamental niche and fitness inequality of two species of yeast in a number of different selective environments that differ in the number and kind of stressors they pose. In particular I ask (1) whether selection in stressful environments leads to an expansion of the fundamental niche, and (2) how selection in stressful environments affects the fitness inequalities that structure the realized niche in simple competitive systems.

Chapter 4

Selection in stressful environments leads to niche contraction in an evolutionary model system

Michael T. Pedruski, Gregor F. Fussmann, and Andrew Gonzalez.

Department of Biology, McGill University, 1205 Dr. Penfield, Montréal QC, H3A 1B1

4.1 Abstract

A population's niche plays a fundamental role in determining ecological dynamics. Consequently, understanding the factors that structure the niche and environment-fitness relationships is of central importance to ecology. Here we examine experimentally how selection in different environmental conditions affects the niche, absolute fitness, and fitness inequalities in populations of two species of yeast. We show that, contrary to our expectation of niche expansion after selection in stressful environments, some of our populations experienced dramatic contraction of the niche, and severe reductions in fitness in the environments that remained within the niche. While ecologists have long understood that the outcome of ecological interactions is dependent on environmental conditions, our results demonstrate that some populations bear a burden of 'environments-past' that may affect the outcome of interactions as much as the current conditions in which they find themselves. Ultimately, our results demonstrate that on short time scales environmental conditions act on biotic populations not only by defining their fitness, but also by determining how their fitness changes.

4.1.1 Key words

Ecological niche; Fitness inequality; Multiple stressors; Yeast

4.2 Introduction

At its core ecology is concerned with an organism's relationship to its environment, both abiotic and biotic. Hutchinson's fundamental and realized niches (Hutchinson 1957) have proven to be invaluable concepts for describing the relationship between a population's en-

vironment and its ability to persist. The fundamental niche describes the suite of environmental conditions in which a population could persist in the absence of biotic interactions (e.g. competition, predation, parasitism, mutualism), while the realized niche describes the environmental conditions under which it is capable of persisting in the presence of biotic interactions. Consequently, an understanding of a population's niche is central to understanding that population's distribution and abundance, and great amounts of effort have been invested in uncovering these relationships through theory and experiments (Holt 2009).

Both the fundamental niche and the realized niche define the link between a population's fitness and its environment. While spatial processes have the potential to complicate this relationship (Pulliam 2000), the fundamental niche by definition represents the environmental space where absolute fitness (defined as r) is greater than 0 (Holt and Gomulkiewicz 2004), and the realized niche represents the environmental space where relative fitness is greater than 1, at least in the context of competitive interactions for a shared niche. Recent ecological research on competition and species distributions has increasingly turned from approaches that simply identify the boundaries of a population's niche to approaches that integrate fitness over a range of environmental conditions (Adler et al. 2007; Kearney and Porter 2009; Holt 2014). Where data are available these more detailed approaches have clear advantages as fitness is sure to vary along environmental gradients (Hooper et al. 2008), and fitness inequalities, the relative competitive abilities of species within a niche, play a crucial role in competitive dynamics (Adler et al. 2007).

Given that the niche, and the fitness variation that structures it, are key to understanding the distribution of species and the composition of ecological communities, it is important to understand the factors that structure them. Processes such as natural selection and genetic drift (Fisher 1930; Wright 1932, 1948) affect the niche when they act on variation that

underpins the relationship between phenotype and fitness in a given environment. Evolutionary ecology has demonstrated the potential for expansion of the fundamental niche as new ecological conditions become available (Rainey and Travisano 1998; Urban et al. 2007; Costantini et al. 2009), or as adaptation permits growth in conditions that had previously impeded it (Michel et al. 2004; Holt et al. 2005; Bell and Gonzalez 2009). There may, however, be significant impediments to adaptation, if, for example, poor environmental conditions result in heightened genetic drift and reduced mutational input (Bridle and Vines 2007). Furthermore, trade-offs or mutations may cause reduced fitness along niche dimensions not actively under selection (Turner and Elena 2000; Cooper 2014; Leiby and Marx 2014), though some evidence suggests that niche expansion along one axis need not necessarily result in niche contraction along others (Ostrowski et al. 2007; Bataillon et al. 2011). The adaptation of the niche also has demographic constraints, as closed populations outside of their fundamental niche will go extinct unless adapted phenotypes are discovered (a phenomenon known as evolutionary rescue). Experimental and theoretical work on evolutionary rescue has demonstrated that niches are most likely to adapt when population sizes are high (Bell and Gonzalez 2009), or when the population is not severely maladapted in the new environment (Osmond and de Mazancourt 2013). Finally, in addition to modifying the fundamental niche, as evolution modifies the fitness of populations in an environment it may also alter the fitness inequalities that structure the relationship between the fundamental and realized niches. For example, if adaptation alters the relative fitness of competitors (Moore 1952; Mueller 1988; Lenski and Travisano 1994) it may alter the realized niche without affecting the boundaries of the fundamental niche.

Here we examine how selection in four different environments affects the fundamental niche of populations of two closely related species of yeast, *Saccharomyces cerevisiae* and *S.*

paradoxus. We expected three of the environments to be stressful due to dextrose limitation, salt stress, or a combination of these two, and we expected one environment to be benign. Before and after selection we assayed the fitness of populations along 2 dimensions of their niche (dextrose and salt concentration), and examined how selection altered fitness inequalities between the two species. We expected that populations selected in the two environments with only one stressor (i.e. dextrose limitation or salt stress) would adapt to these conditions and other similar environments while retaining the ability to grow in benign conditions, leading to niche expansion if environments not initially included in the niche were brought within it by this adaptation. For the populations selected in the environment with two stressors our predictions about adaptation were complicated by the knowledge that stressors experienced in concert may have additive, synergistic, or antagonistic effects (Crain et al. 2008), and that trade-offs between traits can limit the potential for adaptation (Futuyma 2010), but we still expected to see adaptation, and potentially niche expansion, in this environment, especially given shared stress responses to starvation and osmotic stress in yeast (Gasch 2003). Despite our expectation that niche size would increase for these populations, we had also expected to see mixed responses of fitness across environmental conditions, with positive changes in the stressful environments that populations had been selected in (and in similar environments), but potentially negative changes in fitness for dissimilar environments (e.g. benign conditions) due to fitness trade-offs. Both of the yeast species we worked with had previously demonstrated an ability to adapt to glucose limitation (Paquin and Adams 1983; Ferea et al. 1999; Goddard and Bradford 2003) and salt stress (Dhar et al. 2011; Gonzalez and Bell 2013), though *S. paradoxus* is known to be more sensitive to salt and less likely to adapt to salt stress at the salt concentration we used for our salt stress treatment, and consequently we expected *S. cerevisiae* to have greater evolutionary advantage in these en-

vironments. Consequently, while we expected fitness inequality to be relatively low in some of the assay environments (i.e. those with very low salt or dextrose concentrations, or with very high salt concentrations), we expected it to be relatively high in environments with moderate salt concentrations and moderate to high dextrose. Furthermore, we expected the fitness inequality between the two species to widen the most in these moderate salt concentrations. Ultimately, our two species experimental approach provides a look at how repeatable niche evolution is when different species face the same selective environments, how selection in specific environments affects fitness in other environments, and how fitness inequalities between species can change as a result of selection.

4.3 Materials and Methods

4.3.1 Experimental overview

Our experimental system consisted of the yeast strains *S. cerevisiae* BY4741 (haploid) and *S. paradoxus* CBS 432 (diploid). For each species we founded six experimental lines, with each line derived from a single colony. Each colony was grown in 1 mL yeast prosteose dextrose (YPD: 10 g/L yeast extract, 20 g/L peptone, 20 g/L dextrose) for 1 day before being introduced into four different selection conditions (Table 4.1) on Day 0 of the experiment. One of our selection conditions was YPD, and the other three were modifications of YPD to reduce the concentration of dextrose (LD: 1.6 g/L dextrose), increase the concentration of salt (HS: 80 g/L NaCl), or both (LD + HS: 1.6 g/L dextrose, 80 g/L NaCl).

We expected that the LD, HS, and LD + HS environments would be stressful for our populations, either because of the relatively low levels of dextrose, yeast's preferred carbohydrate (Feldmann et al. 2012), or because of high osmotic pressure (Hohmann 2002). During

the selection phase of the experiment each line was incubated in 1 mL of the appropriate medium in 48 well plates (Greiner Bio-One) on a shaker (at 80 rotations per minute). Every three days 100 µL of culture medium was transferred to 900 µL of fresh medium, until the twelfth day when the selection phase ended ($\sim$ 13 generations in ideal conditions, 4 transfers each of $\log_2(10)$ generations). All cultures were maintained in the same incubator at 28°C.

On day 0 and after selection had run for 12 days we measured the ability of each population to grow in fifty different environments along crossed salt and dextrose concentration gradients (ten levels of [Dextrose]: 0 g/L, 0.1 g/L, 0.2 g/L, 0.4 g/L, 0.8 g/L, 1.6 g/L, 3.2 g/L, 6.4 g/L, 12.8 g/L and 20 g/L; five levels of [NaCl]: 0 g/L, 20 g/L, 40 g/L, 60 g/L, and 80 g/L). Populations were incubated in YPD for 24 h before these fitesss assays to give each line a common physiological state before we measured their performance in assay environments (Goho and Bell 2000b). While this means that performance in the assay environments may involve an element of physiological transition from YPD to the assay environment, we wanted to avoid potential differences in performance that would emerge from immediate physiological differences between the populations (e.g. populations that performed poorly because they had just been transferred from a stressful environment). For the day 0 fitness assay we sampled the cultures that acted as the source for the selection lines (ancestral condition), and for the day 12 assay we sampled 100 µL from each selection line on day 12 and cultured it in 900 µL YPD for a day before assaying fitness. All fitness assays consisted of introducing 5 µL of culture into 245 µL of assay medium in 96 well plates (Corning Inc.) and then measuring optical density (OD) of the assay populations at 600 nm over a series of 10 time points in a plate reader (Synergy HT, BioTek, Winooski VT). The 10 time points in the Day 0 assay took place over $\sim$28 hours, but due to the greater number of assay cultures on day 12 it was necessary to spread these reads over a longer period ($\sim$50 hours). To

confirm that the longer time period of the day 12 assay didn't unduly skew our results we also plotted our results omitting the last measurement for the day 12 assay and found only minor differences from the analysis presented here (Appendix 4.1). Unlike selection plates, assay plates were not maintained on a shaker. While the location of dextrose concentrations was randomized on assay plates, to minimize potential for inoculation error all the replicates for a given selection background and salt assay combination were assayed on the same assay plate. To limit the potential for effects due to plate placement, plate location in incubators changed after every assay read. Finally, to estimate the yield of each population in the environment of selection we took OD readings of 100 µL of each selection population at every transfer point (Days 3, 6, 9, 12).

4.3.2 Analysis

We estimated the growth rate (r) of cultures in each assay condition by non-linear regression of the sequential OD readings to the logistic model (Winsor 1932) using a Levenberg-Marquardt algorithm with initial conditions of r=0.2, K=1.0, and initial density=OD at first measurement. The corresponding average blank OD for each assay medium at each time point was subtracted from the OD of assay wells before analysis. In order to balance the goal of assessing growth rate in stressful conditions with the goal of achieving reliable parameter estimates we only attempted to fit OD data to the logistic model for cultures that both achieved a final OD greater than 0.08 (roughly equivalent to the average blank value in a YPD well) and doubled their initial OD. Both thresholds were assessed after blank values had been subtracted from OD, and the cultures that did not meet both thresholds were assigned a value of r=0.

We calculated the change in niche size by examining the difference in the number of

environmental conditions that each line was capable of growing in before and after selection (Bataillon et al. 2011), defined as those environmental conditions where $r > 0$ (Holt and Gomulkiewicz 2004). We also used r as our measure of fitness, which while just one measure of fitness, is likely to be important in sequential batch culture in its role as a determinant of both population size (and thus probability of being transferred, particularly in stressed populations which grew more slowly), and the ability to claim resources after transfer.

While we exposed mixed cultures to our selection conditions along with the two mono-cultures, practical constraints prevented us from analyzing the mixed cultures beyond yield in the environments of selection, and consequently we do not present any mixed culture data. Though this prevented us from directly estimating fitness inequality, we estimated the potential fitness inequality between the two species by subtracting the growth rate of each *S. paradoxus* monoculture replicate from the corresponding monoculture replicate of *S. cerevisiae* (Adler et al. 2007), and we assessed changes in the magnitude of fitness inequality by comparing the absolute values of ancestral and post-selection fitness inequalities. Though we recognize that this indirect measure does not examine the potential for the two species to adapt to the environments of selection differently (e.g. if one species adapts by increasing growth rate while the other adapts by lowering mortality), and that our measure could be complicated if the presence of one species dramatically affects the growth rate of the other (e.g. through ethanol inhibition), there is evidence that competition between yeast species is mediated by environmentally dependent fitness differences (Goddard 2008; Arroyo-López et al. 2011) or spatial competition (Nissen et al. 2003; Nissen and Arneborg 2003; Arneborg et al. 2005), both of which are likely to be influenced by growth rate. Though we do not provide a formal analysis of how selection affected carrying capacity (K), as it can also be important in batch culture we provide figures showing its response to our selection envi-

ronments (Appendix 4.2). While we estimated carrying capacity using the same regression methods (and thresholds) as r, there were some data points where the model had clearly produced unrealistic estimates of carrying capacity, and so in cases where the regression estimated K to be greater than 2 we replaced the regression estimate with the final OD read for that culture.

Unfortunately, the inoculation of the fifth replicate of *S. paradoxus* was not successful in the Day 0 assay plates, and consequently we excluded it when calculating any value reliant on Day 0 *S. paradoxus* assay readings. Furthermore, while this replicate was clearly successfully inoculated into the LD, HS, and YPD selection environments, it did not grow in any assay condition after selection in the LD + HS environment, and its OD was low at each transfer point. Given the severity of the LD + HS treatment for *S. paradoxus* it is likely that this replicate simply went effectively extinct in the LD + HS environment after inoculation (*S. paradoxus* LD + HS population 6, which had clearly been present until day 6, was also incapable of growth in any assay condition on day 12), and so we retained it when analyzing day 12 data, but we also present the affected figures (Fig. 4.2, Fig. 4.31 in Appendix 4.4) with *S. paradoxus* replicate 5 from the LD + HS environment omitted (Appendix 4.3), and again found only minor differences from results presented here. Finally, all of the *S. paradoxus* populations assayed in 0 g/L dextrose, 20 g/L NaCl media on Day 0 had extremely high growth rates, which we believe was most likely caused by an incorrect assay medium being added to these wells in the assay plates (Fig. 4.35, Fig. 4.36, Fig. 4.37, Fig. 4.38, Fig. 4.39 in Appendix 4.4). To preserve our ability to compare responses in *S. cerevisiae* and *S. paradoxus* we have removed this assay condition from all following analyses, leaving us with a total of 49 assay conditions.

As each line was assayed under all selection and assay conditions we used repeated mea-

sures ANOVA to analyze the effect of selection background on Day 12 yield, the magnitude of changes in niche size, and the magnitude of changes in fitness inequality across our assay environments. To determine whether niche size, fitness, and magnitude of fitness inequality had changed significantly from the ancestral condition over the duration of selection we assessed the null hypothesis that change in these equalled 0 for each selection treatment with t-tests. To show the impact of selection on each of these we report the quotient of the median post-selection value and the median ancestral value for each comparison alongside its t-test. To control for family-wise error inflation with these t-tests we applied a Holm-Bonferroni correction (Holm 1979) to the tests necessary for each species and response variable combination. Assumptions of normality and heteroskedasticity of variances were assessed using boxplots, and while some variances appeared heterogeneous, ANOVA is robust to violations of these assumptions in balanced designs (Zar 1999). The repeated measures assumption of sphericity was assessed with a Mauchly test, and where significant violations of sphericity were found the Greenhouse-Geisser (GG) correction was used when epsilon was less than 0.75 (Quinn and Keough 2002), and corrected degrees of freedom and p-value were reported alongside the epsilon statistic. All analyses were performed in R 3.0.2 (R Core Team 2013). Assessments of sphericity were performed using the car package version 2.0-24 (Fox and Weisberg 2011), and nonlinear regression was performed using the minpack.lm package version 1.1-8 (Elzhov et al. 2013).

4.4 Results

4.4.1 Response to environments of selection

Yeast yield (OD) on day 12 was clearly influenced by the environment of selection (Fig. 4.1; *S. cerevisiae* $F_{3,15} = 491.6$, p=3.4e-15; *S. paradoxus* $F_{1.13,5.63} = 59.1$, $\epsilon_{GG} = 0.375$, p_{GG} = 3.00e-4). For both species average yield was highest in the YPD selection environment, with *S. cerevisiae* having slightly higher yield than *S. paradoxus*. For *S. cerevisiae* average yield was next highest in the HS selection environment, followed by the LD and LD + HS selection environments, whereas for *S. paradoxus* the LD selection environment had the second greatest average yield followed by the HS and LD + HS selection environments. On average there was a decrease in yield for all species in all treatments over the course of the selection phase, but there were also some cultures that experienced recovery in yield after initial losses. Fitness (r) on Day 0 also clearly differed between the different selection environments for both species, with the highest fitness on average in the YPD environment ($\sim$ 0.53/h - 0.64/h), followed by the LD, HS, and finally the LD + HS environment ($\sim$ 0/h - 0.14/h) (Fig. 4.30 in Appendix 4.4).

4.4.2 The fundamental niche

Originally both species had niches that included most of the environmental conditions we assayed them in (Fig. 4.2). Not surprisingly, the greatest proportion of replicates grew when salt concentrations were low and/or dextrose concentrations were high, with all ancestral populations growing at maximal dextrose in the absence of salt (Fig. 4.31 in Appendix 4.4). As salt concentrations increased or dextrose concentrations decreased both species tended to experience less growth, with no populations growing in the absence of dextrose

and maximal salt, though almost all populations from both species were capable of growing at low dextrose levels when salt concentrations were also low, or at high salt concentrations when dextrose concentrations were high. As expected, for a given salt concentration *S. paradoxus* lines began to cease growth at higher dextrose concentrations than those of *S. cerevisiae*, but surprisingly, some *S. paradoxus* lines also continued growth in high salt, low dextrose environments in which all *S. cerevisiae* lines were incapable of growing.

The environment in which lines were selected had a significant effect on the change in the size of the niche (*S. cerevisiae* $F_{3,15}$=6.386, P=5.29e-3; *S. paradoxus* $F_{1.43,\ 5.74}$=14.92, $\epsilon_{GG} = 0.480$, $p_{GG} = 6.78$e-3). Both species broadly experienced contraction in niche size after selection (Fig. 4.2, Table 4.2): *S. cerevisiae* experienced modest losses in niche size, especially after selection in the HS environment where median post-selection niche size was 78% of the ancestral median, while *S. paradoxus* experienced stronger losses, especially after selection in the LD + HS environment where median post-selection niche size was only 19% of median ancestral niche size. Losses for *S. cerevisiae* were generally due to lost ability to grow at high salt concentrations after selection, even in lines selected in environments containing salt, whereas losses for *S. paradoxus* were due to lost ability to grow in a wider variety of environments, including some benign environments (i.e. with low salt concentrations and relatively high dextrose concentrations), especially after selection in environments that contained salt (Fig. 4.31 in Appendix 4.4).

4.4.3   Fitness

Along with contractions in the niche, our lines generally lost fitness across the assay environments over the course of selection (Fig. 4.3, Table 4.3). The patterns of overall fitness loss were essentially the same as those of niche size loss, with modest declines for *S. cerevisiae*,

and stronger declines for *S. paradoxus*, especially in the LD + HS environment, though the overall change for *S. paradoxus* populations selected in the HS environment were not significant (Table 4.3). At the level of individual assay environments *S. cerevisiae* experienced similar patterns of fitness change across the different selection environments, generally experiencing modest losses in fitness, while retaining pre-selection fitnesses or experiencing moderate fitness gains in some cases (average growth rate change ranging between 0.07/h and -0.23/h) (Fig. 4.32 in Appendix 4.4). *S. paradoxus*, on the other hand, showed marked differences in the pattern of fitness change across the selection environments (Fig. 4.33 in Appendix 4.4). The pattern of fitness change was broadly similar for populations selected in the YPD and LD environments, with moderate to strong losses in most assay environments, though in low salt and high dextrose conditions decreases in fitness were less severe, and even increased slightly in some cases (average growth rate change ranging between roughly 0.03/h and -0.35/h). Populations selected in the HS environment showed retention or increases in fitness in environments with low dextrose and no salt, and moderate to strong losses in most other environments. Selection in the LD + HS environment resulted in strong losses of fitness in many environments (average growth rate declining as much as 0.488/h in the worst case), even in environments that remained within the fundamental niche (i.e. environments with low salt concentrations). Importantly, our populations lost fitness not just on average across the assay environments, but also tended to lose fitness in the environments in which they had been selected (Fig. 4.32, Fig. 4.33, Fig. 4.34, and Table 4.6 in Appendix 4.4), though after Holm-Bonferroni correction this trend was only significant for the *S. cerevisiae* LD and HS populations. *S. cerevisiae* populations selected in the LD + HS environment were an exception to this trend, as ancestral fitness for all replicates in the environment of selection had been 0.

4.4.4 Potential fitness inequality

As expected, the magnitude of initial fitness inequalities were relatively low when salt concentrations were either low or high ($\sim$ 0.05/h on average), but became stronger ($\sim$ 0.10/h - 0.14/h on average) at intermediate salt concentrations, especially when dextrose concentrations were moderate to high (Fig. 4.4). Mean change in potential fitness inequality across all the environmental conditions over the course of selection was significantly impacted by the environment of selection ($F_{3,12} = 21.2$, p=4.36e-5). After selection the magnitude of fitness inequality significantly increased for populations that had been selected in the LD + HS environment but remained relatively unchanged for populations selected in the other three environments (Fig. 4.5, Table 4.4). Despite these trends, all selection treatments resulted in some environments where the magnitude of potential fitness inequality increased, and some environments where it decreased (Fig. 4.6). In particular, there were strong increases in the size of fitness inequality (up to $\sim$0.41/h on average) in lower salt conditions after populations were selected in either the HS or the LD + HS environments due to losses of *S. paradoxus* fitness post-selection in these environments. Selection in low salt conditions tended to result in increases in the size of fitness inequality at intermediate salt, high dextrose concentrations, and declines or lack of change in the size of fitness inequality high salt or low dextrose conditions.

4.5 Discussion

Our results demonstrate that selection in different environmental conditions can affect the form of the fundamental niche, the fitness of populations across the niche, and the fitness inequalities that characterize competitive interactions.

We had expected that selection in stressful environments would lead to adaptation to these environments, and thence to niche expansion, either through evolutionary rescue for environments that were not initially part of the niche (Bell and Gonzalez 2009), or improved performance in similar environments outside the niche if the selection environment was initially in the niche (Gonzalez and Bell 2013). Instead populations of *S. cerevisiae* experienced modest losses of niche size and fitness in most selection conditions, while *S. paradoxus* experienced stronger losses, especially after selection in the LD + HS environment. While these results were unexpected, they are not without precedent, and in many cases populations selected in stressful conditions have been found to experience declines in fitness (Paquin and Adams 1983; Goho and Bell 2000*b*). Such losses in fitness (and consequently niche area) could be due to selection for culture conditions that differ from conditions of assay (Goho and Bell 2000*a*), selection for a different component of fitness (Jasmin et al. 2012), epistatic interactions among beneficial mutations (Paquin and Adams 1983), environmentally enhanced mutation rates (Ram and Hadany 2012; Sharp and Agrawal 2012), epigenetic effects (Jablonka and Raz 2009), or stochastic fixation of deleterious alleles (Whitlock 2000). While we called our four environments 'selection environments' and we refer to the 12 days of our experiment as the 'selection phase' because we expected selection to occur, given the lack of adaptation observed, the relatively short duration of our experiment, and our expectation that initial genetic variation was minimal, our results may not reflect selection so much as epigenetic effects, which are known in fungi (Jablonka and Raz 2009) and can be caused by stress responses in other organisms (Chinnusamy and Zhu 2009). Ultimately, we are unsure of what mechanism(s) are at work in our populations, but our results make clear that even short periods of stress can dramatically affect the fundamental niche of yeast populations.

Initial fitness inequalities suggested that *S. cerevisiae* would have a competitive advantage

134

over *S. paradoxus* when salt concentrations were intermediate and dextrose concentrations were high. Over the course of the selection phase the fitness inequalities between *S. cerevisiae* and *S. paradoxus* changed, resulting in greater inequality between the two species after populations had been selected in environments containing salt, and especially after selection in the LD + HS environment. Importantly, these increases in fitness inequality occurred in assay environments where *S. paradoxus* had its greatest fitness (both before and after selection), and where fitness inequalities had originally been small. Consequently, selection in these environments not only resulted in the collapse of *S. paradoxus*'s fundamental niche, but also potentially a decrease in its competitive ability in the portion of the fundamental niche that remained, effectively eliminating the predicted realized niche for *S. paradoxus* in the presence of *S. cerevisiae* and the absence of strong niche differentiation.

An obvious question remains as to why we saw so little adaptation to the environments of selection. Both *S. cerevisiae* and *S. paradoxus* have previously been shown to adapt to glucose limitation and salt stress (Paquin and Adams 1983; Ferea et al. 1999; Goddard and Bradford 2003; Gonzalez and Bell 2013), yet we saw limited evidence that our lines adapted to either of these stressors. The existence of heritable variation is necessary for selection, and our decision to run a relatively short experiment ($\sim$13 generations) with clonal isolates may have limited both the initial genetic variation and the supply of beneficial mutations. Yet, clear adaptation to environments very similar to our HS environment has previously been observed for *S. paradoxus* in shorter periods than this (Samani and Bell 2010), whereas we actually observed a trend toward declines in fitness. The conditions in which we assayed fitness were slightly different from the environment of selection, but previous research has indicated that growth parameters of yeast cultures are reasonably robust to these kinds of differences in culture conditions (Warringer and Blomberg 2003), suggesting that differences

between the environments of selection and assay are unlikely to have been a cause of our results. *S. cerevisiae* showed similar patterns of change in fitness and niche size over all our selection environments, suggesting that losses in fitness are due to a mechanism independent of these conditions, perhaps some element of the selection environments that differed from the assay environments, or selection for an aspect of fitness we did not assay. Previous research has shown that yeast population yield can decline in a trade-off with growth rate during nutrient limitation (Jasmin et al. 2012), and while we did not see increases in either of these metrics in the environments of selection it is possible that selection was operating on an unmeasured metric (e.g. mortality.). *S. paradoxus* also lost fitness after selection in all of the environmental conditions, suggesting that a similar mechanism as that operating on *S. cerevisiae* may have affected it, but the conditions of selection had much larger impacts on changes in *S. paradoxus* fitness and niche size, indicating that salt stress in particular affected *S. paradoxus* more strongly, as discussed above. It is also worth noting that while we saw relatively little evidence for adaptation when considering growth rate, many of our populations experienced increased yield on Day 12 compared to that on Day 9 or Day 6, most dramatically in the case of two *S. paradoxus* populations in our HS environment that had nearly gone extinct before rebounding. These *S. paradoxus* populations may have experienced evolutionary rescue events (Fig. 4.1), a process in which mutants adapted to stressful conditions appear during what would otherwise be the process of population extinction (Gonzalez et al. 2013). If the recovery of these populations is in fact due to evolutionary rescue it may be that the HS populations experienced it, whereas the LD + HS populations did not, because of the larger population sizes, and thus mutational input, maintained in the HS case.

Despite close phylogenetic ties between our two species (Liti et al. 2009), they responded

differently to our selection environments. In agreement with previous research demonstrating the relative sensitivity of *S. paradoxus* to salt stress (Gonzalez and Bell 2013), on average our populations of *S. cerevisiae* experienced less severe losses in niche size and fitness after selection in the HS and LD + HS environments compared to those from *S. paradoxus.* In addition to having different evolutionary backgrounds (Replansky et al. 2008), our two strains also differed in their ploidy, and while there is evidence that haploid yeast populations may adapt more quickly at high population sizes (Zeyl et al. 2003), yeasts are well known to change their ploidy during experimental conditions (Zeyl et al. 2003; Dhar et al. 2011; Jasmin et al. 2012), and as we never explicitly assessed the ploidy of our populations, nor had access to more than one strain of each species, it is unclear what aspect of their biology set the two apart.

Given the relative dearth of evidence for adaptation, and the short duration of our experiment, the decreases in fitness and the niche contraction observed for our *S. paradoxus* populations after selection in the LD + HS environment are all the more remarkable. While we are unsure about what mechanism(s) affected these populations, the implication is clear: environmental conditions can dramatically alter the outlook for ecological dynamics in a relatively short period of time. If such effects are common it may be that ecological dynamics are frequently determined not only by the environmental conditions in which populations find themselves, but the history of environmental conditions they have experienced, even after substantial periods of time. The lack of a similar persistent decline in fitness of our *S. cerevisiae* populations selected in the same environment highlights that populations and species may respond very differently to stressful environments, with some species experiencing predominantly reversible losses in fitness, while others may bear the burden of 'environments past' for considerable periods of time.

4.5.1 Conclusions

We demonstrated that environmental conditions play an important role in determining the form of the Hutchinsonian niche (i.e. those environments in which $r > 0$), as well as how fitness varies within the niche. Our results show that different populations may respond to a history of environmental stress quite differently, and that these responses can affect fitness across a broad range of environments. Consequently, environmental conditions not only determine the fitness inequalities that are key to ecological dynamics, but also affect how these fitness inequalities will change through time. In our experimental system selection in an environment with two stressors led to increases in fitness inequalities in environments that were part of the both species' fundamental niches and where fitness inequalities had originally been small, suggesting that selection in stressful environmental conditions may reduce the potential for coexistence of these competitors in the absence of strong niche differentiation.

4.6 Acknowledgements

4.7 Literature Cited

Adler, P. B., J. HilleRisLambers, and J. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Arneborg, N., H. Siegumfeldt, G. H. Andersen, P. Nissen, V. R. Daria, P. J. Rodrigo, and J. Glückstad. 2005. Interactive optical trapping shows that confinement is a determinant of growth in a mixed yeast culture. FEMS Microbiology Letters 245:155–159.

Arroyo-López, F., L. Pérez-Través, A. Querol, and E. Barrio. 2011. Exclusion of *Saccharomyces kudriavzevii* from a wine model system mediated by *Saccharomyces cerevisiae*. Yeast 28:423–435.

Bataillon, T., T. Zhang, and R. Kassen. 2011. Cost of adaptation and fitness effects of beneficial mutations in *Pseudomonas fluorescens*. Genetics 189:939–949.

Bell, G., and A. Gonzalez. 2009. Evolutionary rescue can prevent extinction following environmental change. Ecology Letters 12:942–948.

Bridle, J. R., and T. H. Vines. 2007. Limits to evolution at range margins: when and why does adaptation fail? Trends in Ecology & Evolution 22:140 – 147.

Chinnusamy, V., and J.-K. Zhu. 2009. Epigenetic regulation of stress responses in plants. Current Opinion in Plant Biolology 12:133 – 139.

Cooper, V. S. 2014. The origins of specialization: insights from bacteria held 25 years in captivity. PLoS Biology 12:e1001790.

Costantini, C., D. Ayala, W. Guelbeogo, M. Pombi, C. Some, I. Bassole, K. Ose, J.-M. Fotsing, N. Sagnon, D. Fontenille, N. Besansky, and F. Simard. 2009. Living at the edge: biogeographic patterns of habitat segregation conform to speciation by niche expansion in *Anopheles gambiae*. BMC Ecol. 9:16.

Crain, C. M., K. Kroeker, and B. S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters 11:1304–1315.

Dhar, R., R. Sägesser, C. Weikert, J. Yuan, and A. Wagner. 2011. Adaptation of *Saccharomyces cerevisiae* to saline stress through laboratory evolution. Journal of Evolutionary Biology 24:1135–1153.

Elzhov, T. V., K. M. Mullen, A.-N. Spiess, and B. Bolker 2013. minpack.lm: R interface to the Levenberg-Marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds.

Feldmann, H., P. Branduardi, B. Dujon, C. Gaillardin, and D. Porro. 2012. Yeast molecular and cell biology. 2nd edition. Wiley-Blackwell, Weinheim.

Ferea, T. L., D. Botstein, P. O. Brown, and R. F. Rosenzweig. 1999. Systematic changes in gene expression patterns following adaptive evolution in yeast. Proceedings of the National Academy of Sciences USA 96:9721–9726.

Fisher, R. A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford.

Fox, J., and S. Weisberg. 2011. An R Companion to Applied Regression. Second edition. Sage, Thousand Oaks CA.

Futuyma, D. J. 2010. Evolutionary constraint and ecological consequences. Evolution 64:1865–1884.

Gasch, A. P. 2003. The environmental stress response: a common yeast response to diverse environmental stresses. Pages 11–70 *in* S. Hohmann and P. Mager, editors. Yeast stress responses. Springer-Verlag, Berlin.

Goddard, M. R. 2008. Quantifying the complexities of *Saccharomyces cerevisiae*'s ecosystem engineering via fermentation. Ecology 89:2077–2082.

Goddard, M. R., and M. A. Bradford. 2003. The adaptive response of a natural microbial population to carbon- and nitrogen-limitation. Ecology Letters 6:594–598.

Goho, S., and G. Bell. 2000*a*. The ecology and genetics of fitness in *Chlamydomonas*. IX. The rate of accumulation of variation of fitness under selection. Evolution 54:416–424.

Goho, S., and G. Bell. 2000*b*. Mild environmental stress elicits mutations affecting fitness in *Chlamydomonas*. Proceedings of the Royal Society of London B 267:123–129.

Gonzalez, A., and G. Bell. 2013. Evolutionary rescue and adaptation to abrupt environmental change depends upon the history of stress. Philosophical Transactions of the Royal Society B 368:20120079.

Gonzalez, A., O. Ronce, R. Ferrière, and M. E. Hochberg. 2013. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. Philosophical Transactions of the Royal Society B 368:20120404.

Hohmann, S. 2002. Osmotic stress signaling and osmoadaptation in yeasts. Microbiology and Molecular Biology Reviews 66:300–372.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65–70.

Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences USA 106:19659–19665.

Holt, R. D. 2014. Evolution of the ecological niche. Pages 288–297 *in* J. B. Lossos, editor. The Princeton guide to evolution. Princeton University Press, Princeton.

Holt, R. D., M. Barfield, and R. Gomulkiewicz 2005. Theories of niche conservatism and evolution: could exotic species be potential tests? Pages 259–290 *in* D. F. Sax, J. J.

Stachowicz, and S. D. Gaines, editors. Species invasions: insights into ecology, evolution, and biogeography. Sinauer associates, Sunderland.

Holt, R. D., and R. Gomulkiewicz 2004. Conservation implications of niche conservatism and evolution in heterogeneous environments. Pages 244–264 *in* R. Ferrière, U. Dieckmann, and D. Couvet, editors. Evolutionary conservation biology. Cambridge University Press, Cambridge.

Hooper, H. L., R. Connon, A. Callaghan, G. Fryer, S. Yarwood-Buchanan, J. Biggs, S. J. Maund, T. H. Hutchinson, and R. M. Sibly. 2008. The ecological niche of *Daphnia magna* characterized using population growth rate. Ecology 89:1015–1022.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415–427.

Jablonka, E., and G. Raz. 2009. Transgenerational epigenetic inheritance: prevalence, mechanisms, and implications for the study of heredity. The Quarterly Review of Biology 84:131–176.

Jasmin, J.-N., M. M. Dillon, and C. Zeyl. 2012. The yield of experimental yeast populations declines during selection. Proceedings of the Royal Society B: Biological Sciences 279:4382–4388.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350.

Leiby, N., and C. J. Marx. 2014. Metabolic erosion primarily through mutation accumulation, and not tradeoffs, drives limited evolution of substrate specificity in *Escherichia coli.* PLoS Biology 12:e1001789.

Lenski, R. E., and M. Travisano. 1994. Dynamics of adaptation and diversification: a 10,000-

generation experiment with bacterial populations. Proceedings of the National Academy of Sciences USA 91:6808–6814.

Liti, G., D. M. Carter, A. M. Moses, J. Warringer, L. Parts, S. A. James, R. P. Davey, I. N. Roberts, A. Burt, V. Koufopanou, I. J. Tsai, C. M. Bergman, D. Bensasson, M. J. T. O'Kelly, A. van Oudenaarden, D. B. H. Barton, E. Bailes, A. N. Nguyen, M. Jones, M. A. Quail, I. Goodhead, S. Sims, F. Smith, A. Blomberg, R. Durbin, and E. J. Louis. 2009. Population genomics of domestic and wild yeasts. Nature 458:337–341.

Michel, A., R. S. Arias, B. E. Scheffler, S. O. Duke, M. Netherland, and F. E. Dayan. 2004. Somatic mutation-mediated evolution of herbicide resistance in the nonindigenous invasive plant hydrilla (*Hydrilla verticillata*). Molecular Ecology 13:3229–3237.

Moore, J. A. 1952. Competition between *Drosophila melanogaster* and *Drosophila simulans*: II. The improvement of competitive ability through selection. Proceedings of the National Academy of Sciences USA 38:813–817.

Mueller, L. D. 1988. Evolution of competitive ability in *Drosophila* by density-dependent natural selection. Proceedings of the National Academy of Sciences USA 85:4383–4386.

Nissen, P., and N. Arneborg. 2003. Characterization of early deaths of non-*Saccharomyces* yeasts in mixed cultures with *Saccharomyces cerevisiae*. Archives of Microbiology 180:257–263.

Nissen, P., D. Nielsen, and N. Arneborg. 2003. Viable *Saccharomyces cerevisiae* cells at high concentrations cause early growth arrest of non-*Saccharomyces* yeasts in mixed cultures by a cell-cell contact-mediated mechanism. Yeast 20:331–341.

Osmond, M. M., and C. de Mazancourt. 2013. How competition affects evolutionary rescue. Philosophical Transactions of the Royal Society of London B: Biological Sciences 368:20120085.

Ostrowski, E. A., C. Ofria, and R. E. Lenski. 2007. Ecological specialization and adaptive decay in digital organisms. The American Naturalist 169:E1–E20.

Paquin, C. E., and J. Adams. 1983. Relative fitness can decrease in evolving asexual populations of *S. cerevisiae*. Nature 306:368–371.

Pulliam, H. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rainey, P. B., and M. Travisano. 1998. Adaptive radiation in a heterogeneous environment. Nature 394:69–72.

Ram, Y., and L. Hadany. 2012. The evolution of stress-induced hypermutation in asexual populations. Evolution 66:2315–2328.

Replansky, T., V. Koufopanou, D. Greig, and G. Bell. 2008. *Saccharomyces sensu stricto* as a model system for evolution and ecology. Trends in Ecology & Evolution 23:494 – 501.

Samani, P., and G. Bell. 2010. Adaptation of experimental yeast populations to stressful conditions in relation to population size. Journal of Evolutionary Biology 23:791–796.

Sharp, N. P., and A. F. Agrawal. 2012. Evidence for elevated mutation rates in low-quality genotypes. Proceedings of the National Academy of Sciences USA 109:6142–6146.

Turner, P. E., and S. F. Elena. 2000. Cost of host radiation in an RNA virus. Genetics 156:1465–1470.

Urban, M. C., B. L. Phillips, D. K. Skelly, and R. Shine. 2007. The cane toad's (*Chaunus*

[Bufo] marinus) increasing ability to invade Australia is revealed by a dynamically updated range model. Proceedings of the Royal Society B 274:1413–1419.

Warringer, J., and A. Blomberg. 2003. Automated screening in environmental arrays allows analysis of quantitative phenotypic profiles in *Saccharomyces cerevisiae*. Yeast 20:53–67.

Whitlock, M. C. 2000. Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. Evolution 54:1855–1861.

Winsor, C. P. 1932. The Gompertz curve as a growth curve. Proceedings of the National Academy of Sciences USA 18:1–8.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Pages 356–366 *in* Proceedings of the sixth international congress of genetics.

Wright, S. 1948. On the roles of directed and random changes in the genetics of populations. Evolution 2:279–294.

Zar, J. 1999. Biostatistical Analysis. Fourth edition. Prentice Hall, Upple Saddle River.

Zeyl, C., T. Vanderford, and M. Carter. 2003. An evolutionary advantage of haploidy in large yeast populations. Science 299:555–558.

Table 4.1. Selection environments used. All environments (except YPD) consisted of YPD modified to the following salt and dextrose concentrations.

Treatment name	[Dextrose] (g/L)	[NaCl] (g/L)
LD + HS	1.6	80
LD	1.6	0
HS	20	80
YPD	20	0

Table 4.2. t-test results assessing H$_o$: change in niche size = 0, and quotient of medians (post-selection niche size divided by ancestral niche size), for each species and environment of selection. p-values in bold are significant after Holm correction.

	t	df	p	Median quotient
S. cerevisiae				
LD + HS	-5.36	5	**3.05e-3**	0.82
LD	-5.42	5	**2.89e-3**	0.82
HS	-8.64	5	**3.44e-4**	0.78
YPD	-3.50	5	**1.72e-2**	0.93
S. paradoxus				
LD + HS	-8.07	4	**1.28e-3**	0.19
LD	-7.73	4	**1.51e-3**	0.48
HS	-3.20	4	**3.30e-2**	0.52
YPD	-7.17	4	**2.00e-3**	0.50

Table 4.3. t-test results assessing H_o: change in fitness (r) averaged over the 49 assay conditions = 0, and quotient of medians (averaged post-selection fitness divided by averaged ancestral fitness), for each species and environment of selection. p-values in bold are significant after Holm correction.

	t	df	p	Median quotient
S. cerevisiae				
LD + HS	-12.07	5	**6.88e-5**	0.82
LD	-10.88	5	**1.14e-4**	0.81
HS	-11.30	5	**9.49e-5**	0.77
YPD	-8.73	5	**3.27e-4**	0.85
S. paradoxus				
LD + HS	-8.69	4	**9.66e-4**	0.18
LD	-10.06	4	**5.48e-4**	0.45
HS	-2.74	4	5.17e-2	0.63
YPD	-7.93	4	**1.37e-3**	0.53

Table 4.4. t-test results assessing H_o: change in potential fitness inequality magnitude averaged over the 49 assay conditions = 0, and quotient of medians (post-selection fitness inequality magnitude divded by ancestral fitness inequality magnitude), for each environment of selection. p-values in bold are significant after Holm correction.

	t	df	p	Median quotient
LD + HS	9.20	4	**7.74e-4**	1.88
LD	0.01	4	9.96e-1	0.95
HS	2.07	4	1.07e-1	1.34
YPD	0.66	4	5.42e-1	1.07
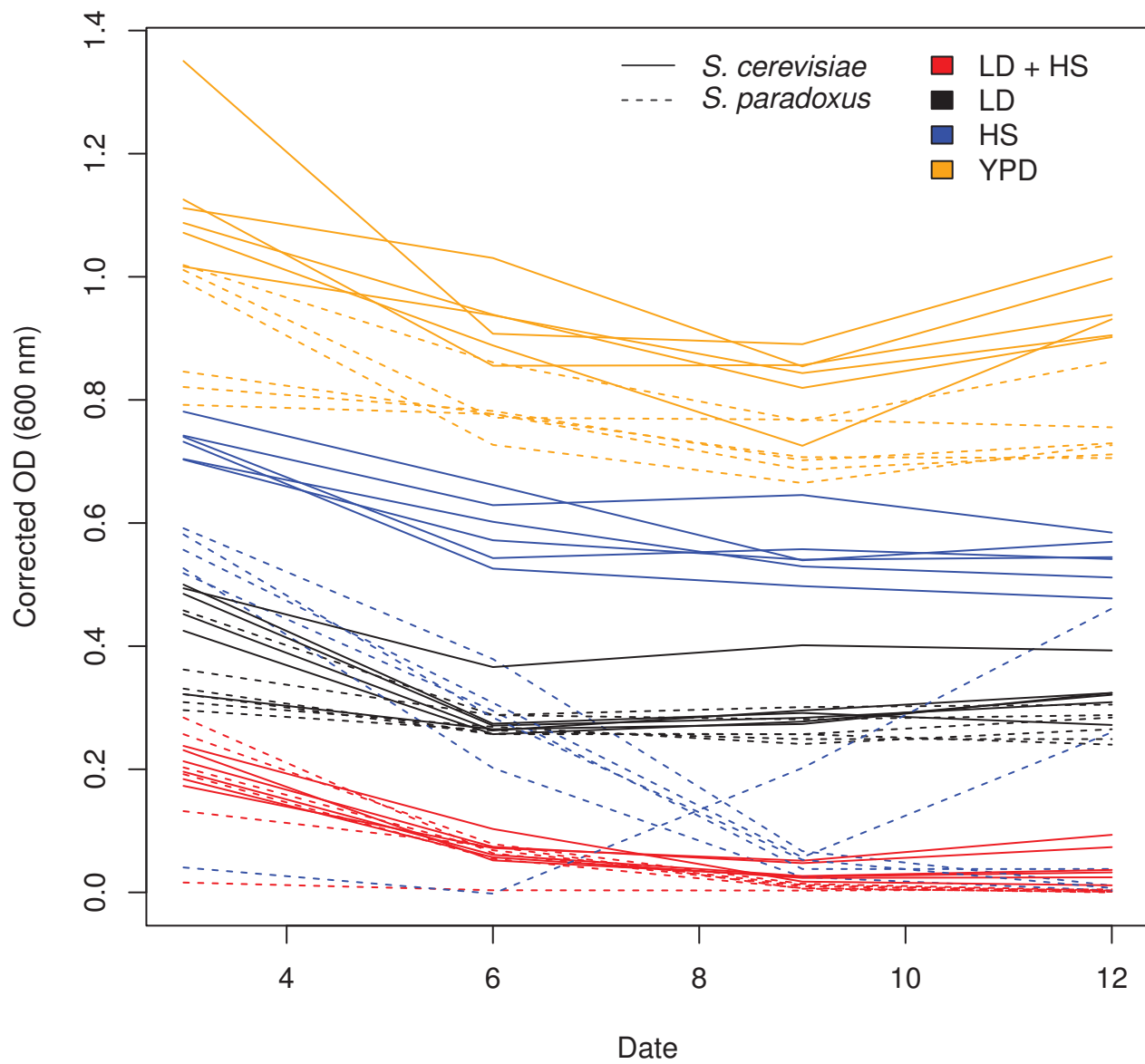
Fig. 4.1. Optical density (OD) of each selection line (100 μL) at each transfer point (Days 3, 6, 9, 12). Selection environments described in Table 4.1.
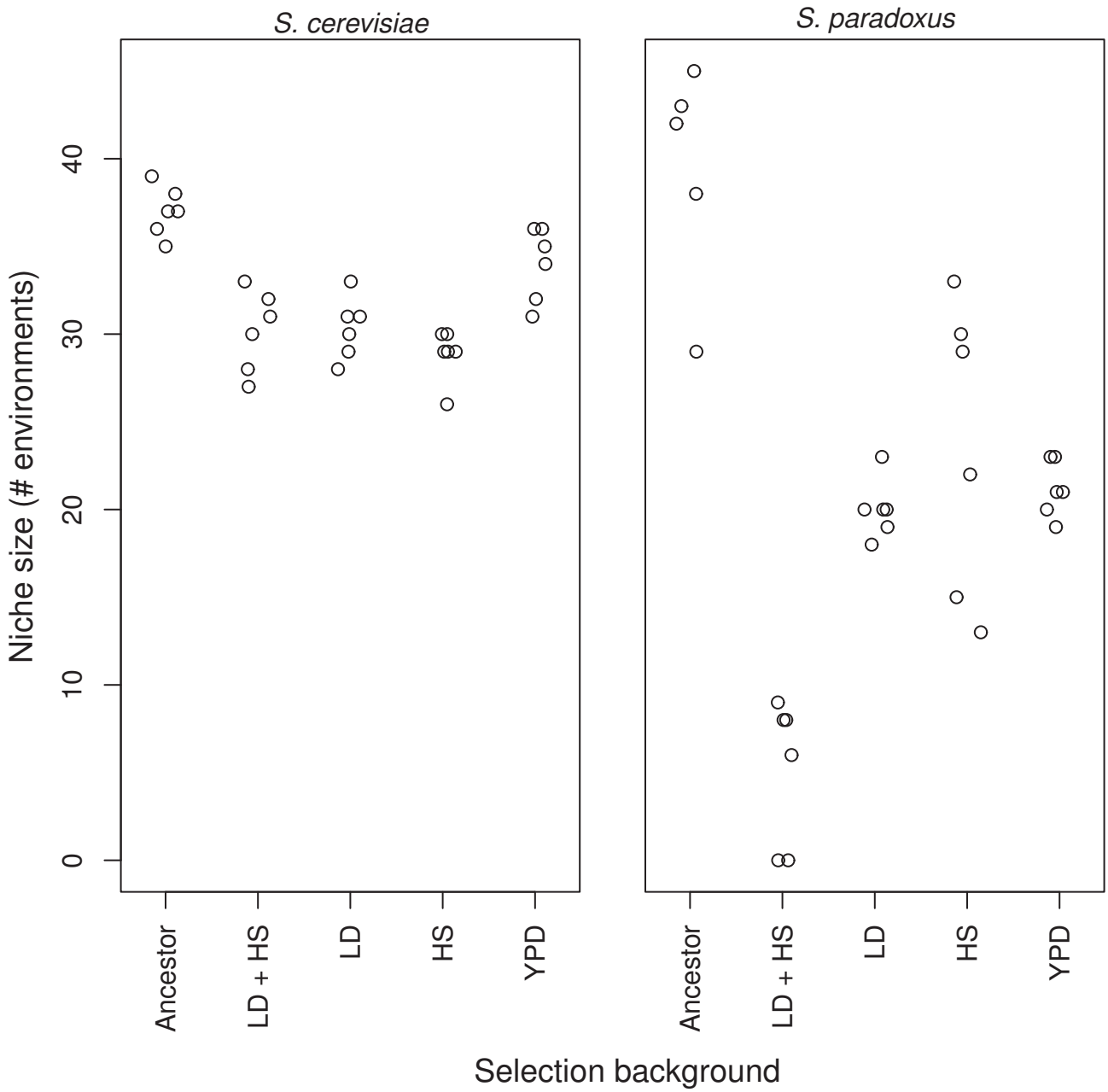
Fig. 4.2. Number of environmental conditions (niche size) along our dextrose and salt gradients (49 environments total) in which each experimental line can grow before selection (ancestor), or after selection in one of our four selection environments (Table 4.1). For the ancestral condition *S. cerevisiae* n=6, *S. paradoxus* n=5, and for the post-selection condition n=6 for both species in all environments.
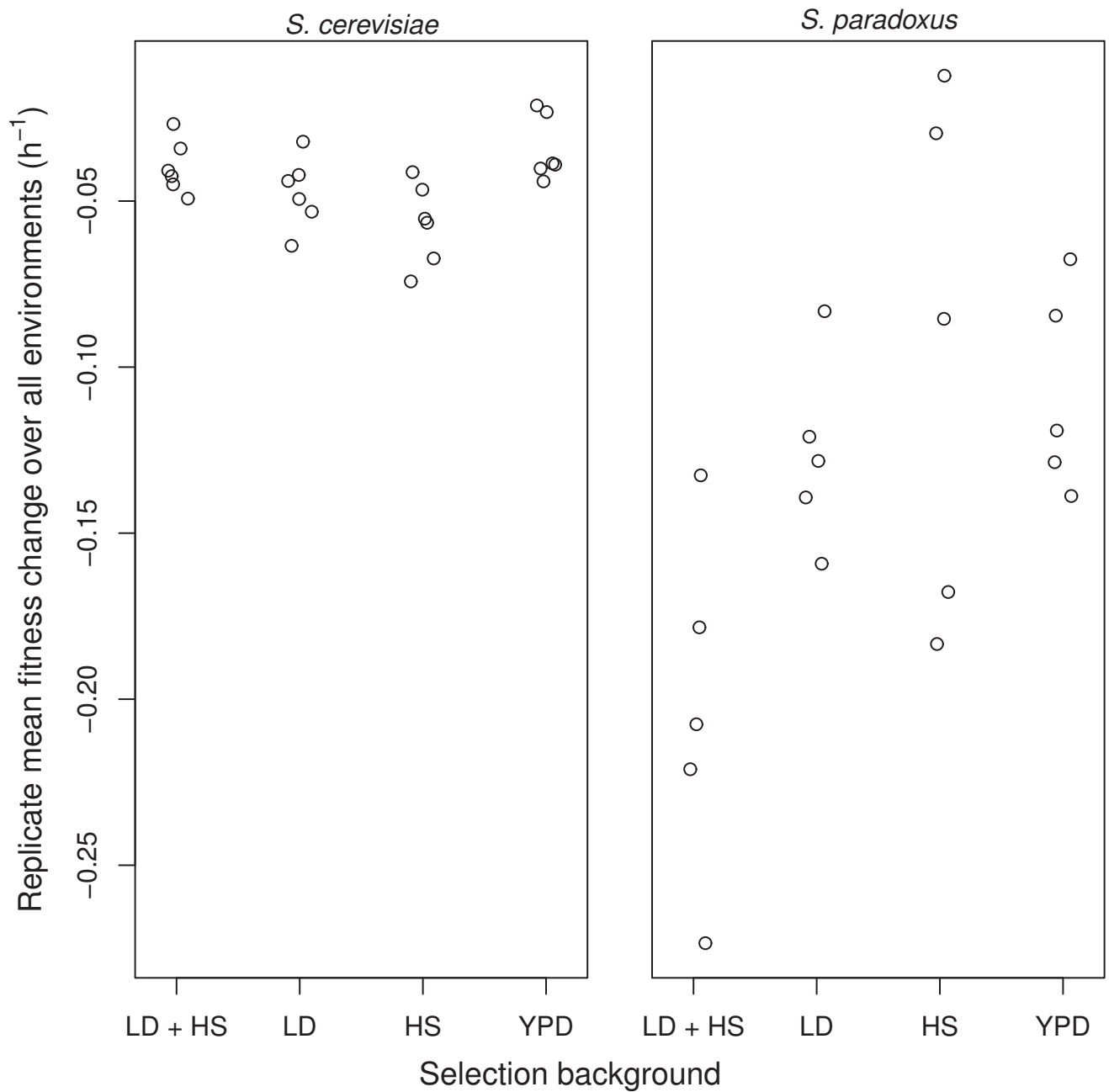
Fig. 4.3. Change in fitness (r) for each replicate, averaged over 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). *S. cerevisiae* n = 6; *S. paradoxus* n = 5.
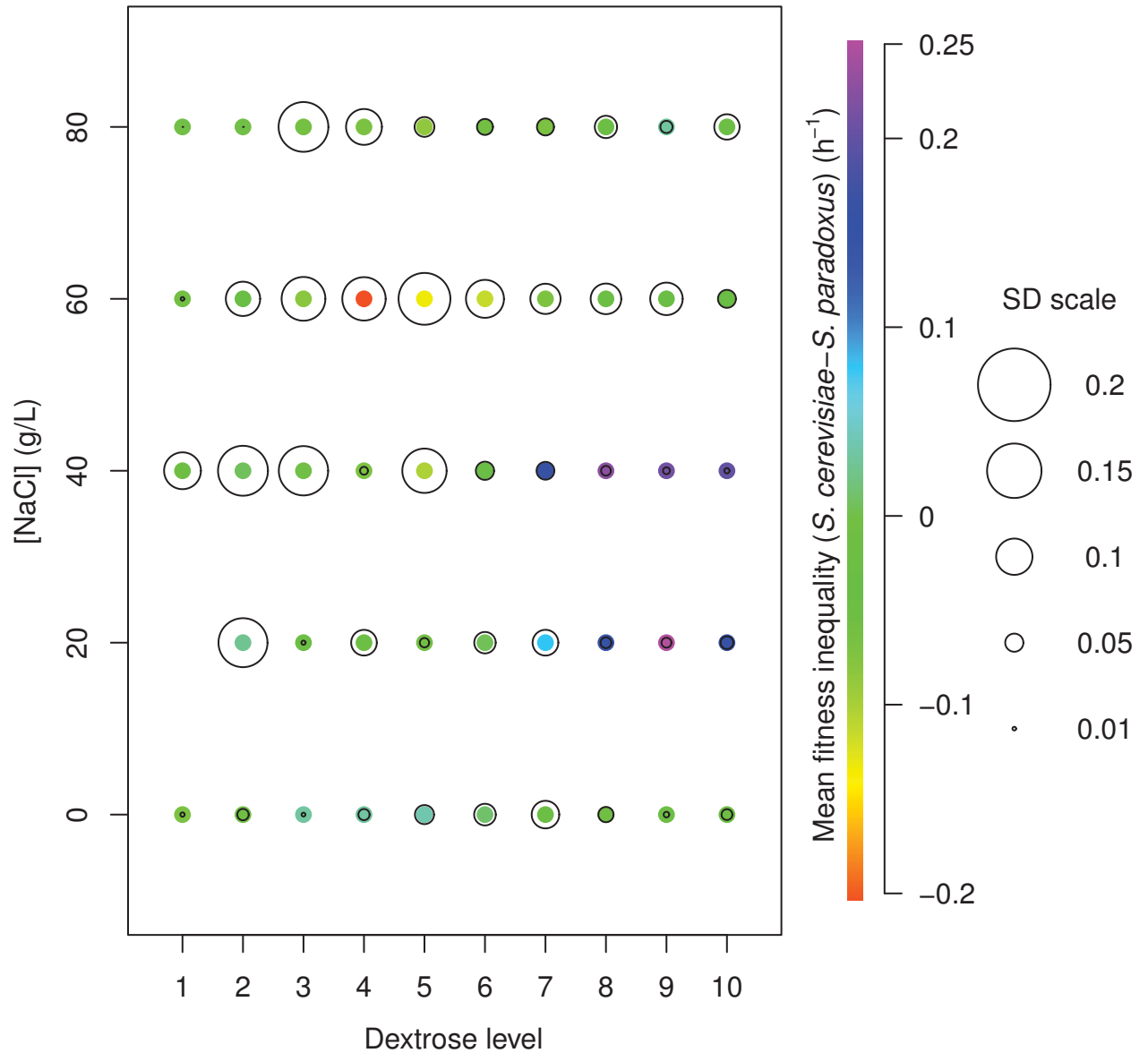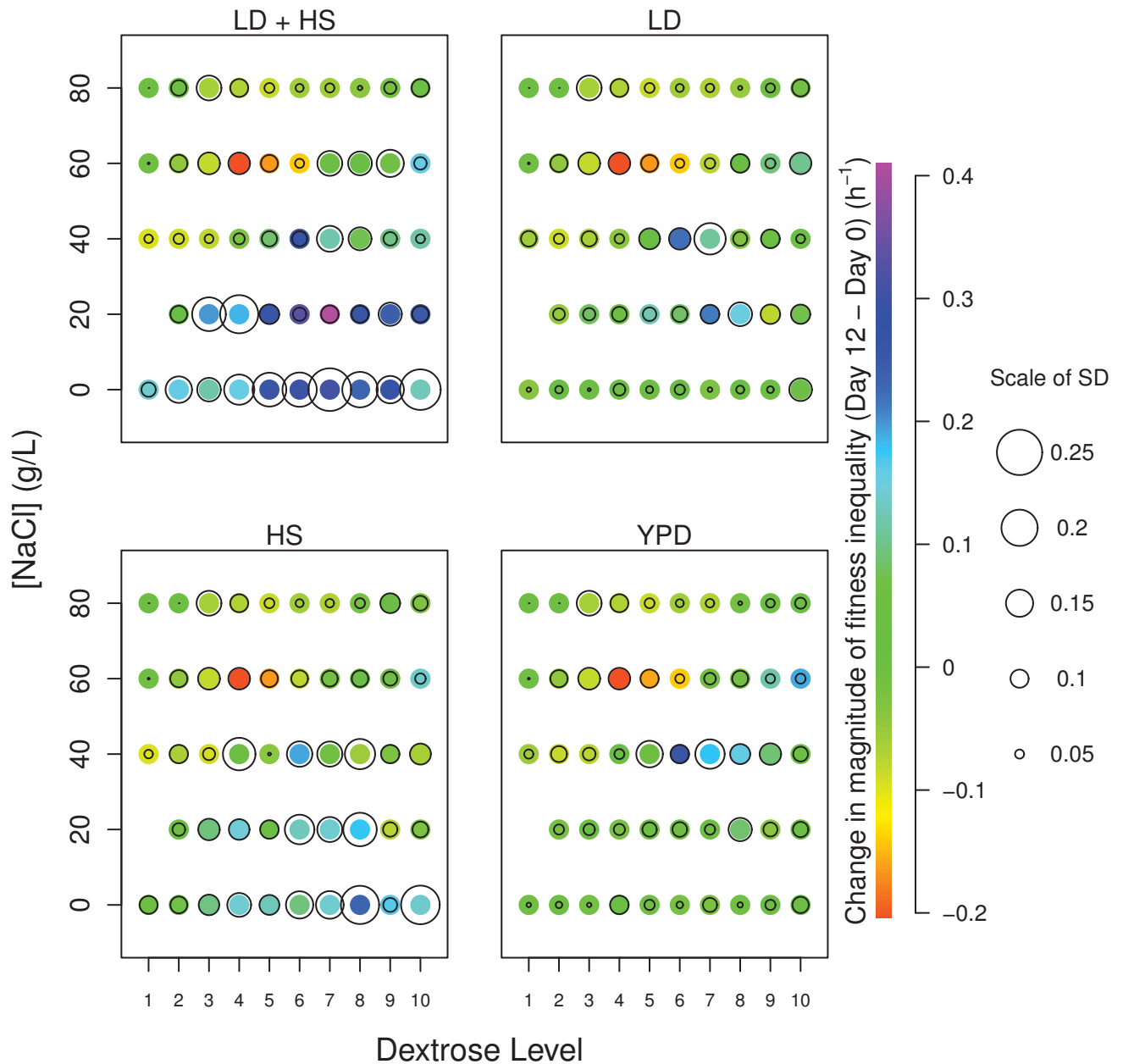
Fig. 4.4. Mean ancestral potential fitness inequality between *S. cerevisiae* and *S. paradoxus* in 49 different assay conditions along dextrose and salt gradients (Table 4.1). Mean fitness inequality is indicated by the colour of the point, and the standard deviation of fitness inequality is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 5.
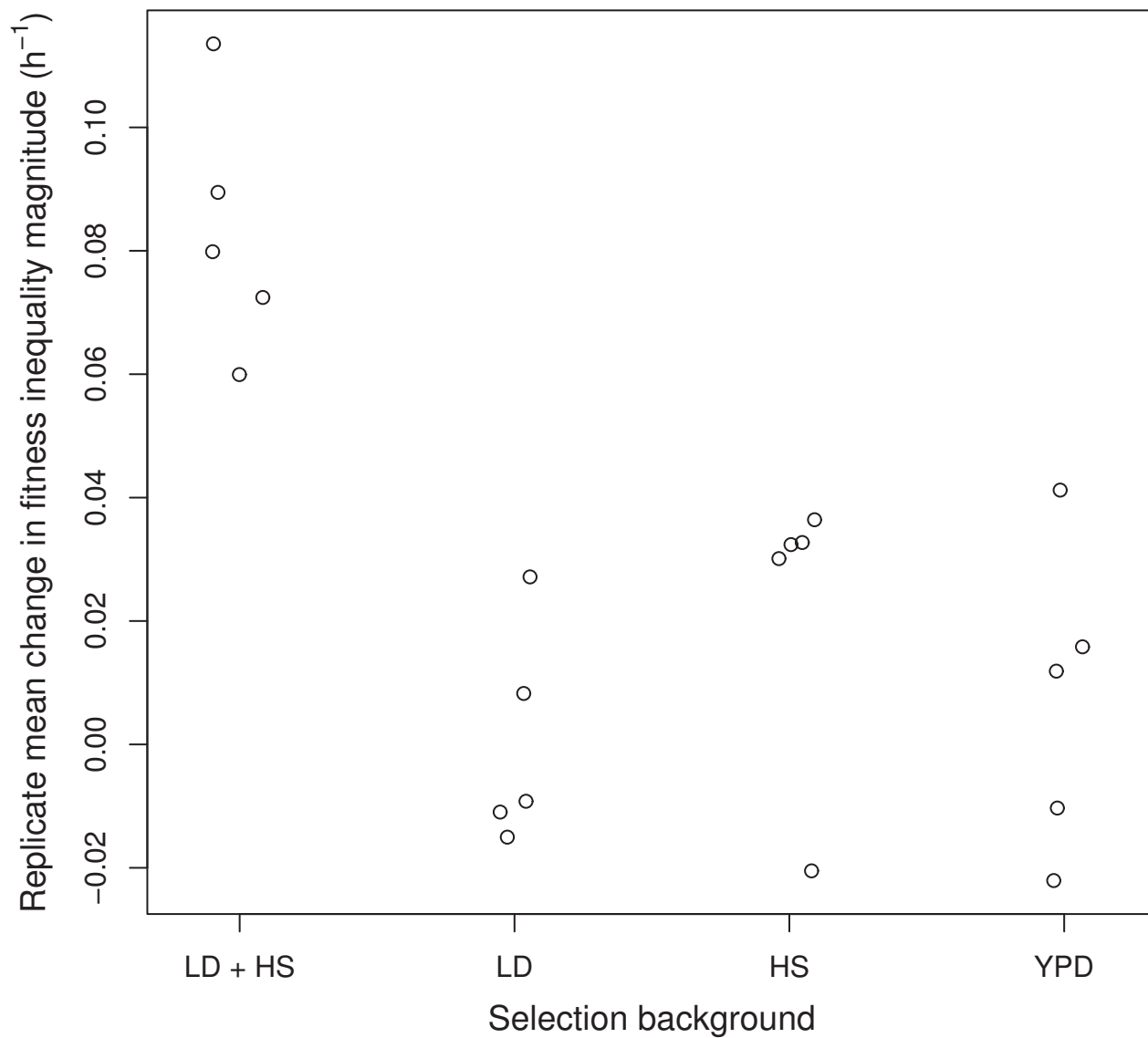
Fig. 4.5. Mean change in the strength of potential fitness inequality for each replicate between *S. cerevisiae* and *S. paradoxus* over 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). n = 5.

Fig. 4.6. Mean change in the strength of potential fitness inequality between *S. cerevisiae* and *S. paradoxus* in 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). Mean change in fitness inequality magnitude is indicated by the colour of the point, and the standard deviation of change of fitness inequality magnitude is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 5.

Appendices to Chapter 4

Appendix 4.1: Figures produced after omitting final OD read on day 12 from Pedruski et al. *Selection in stressful environments leads to niche contraction in an evolutionary model system*
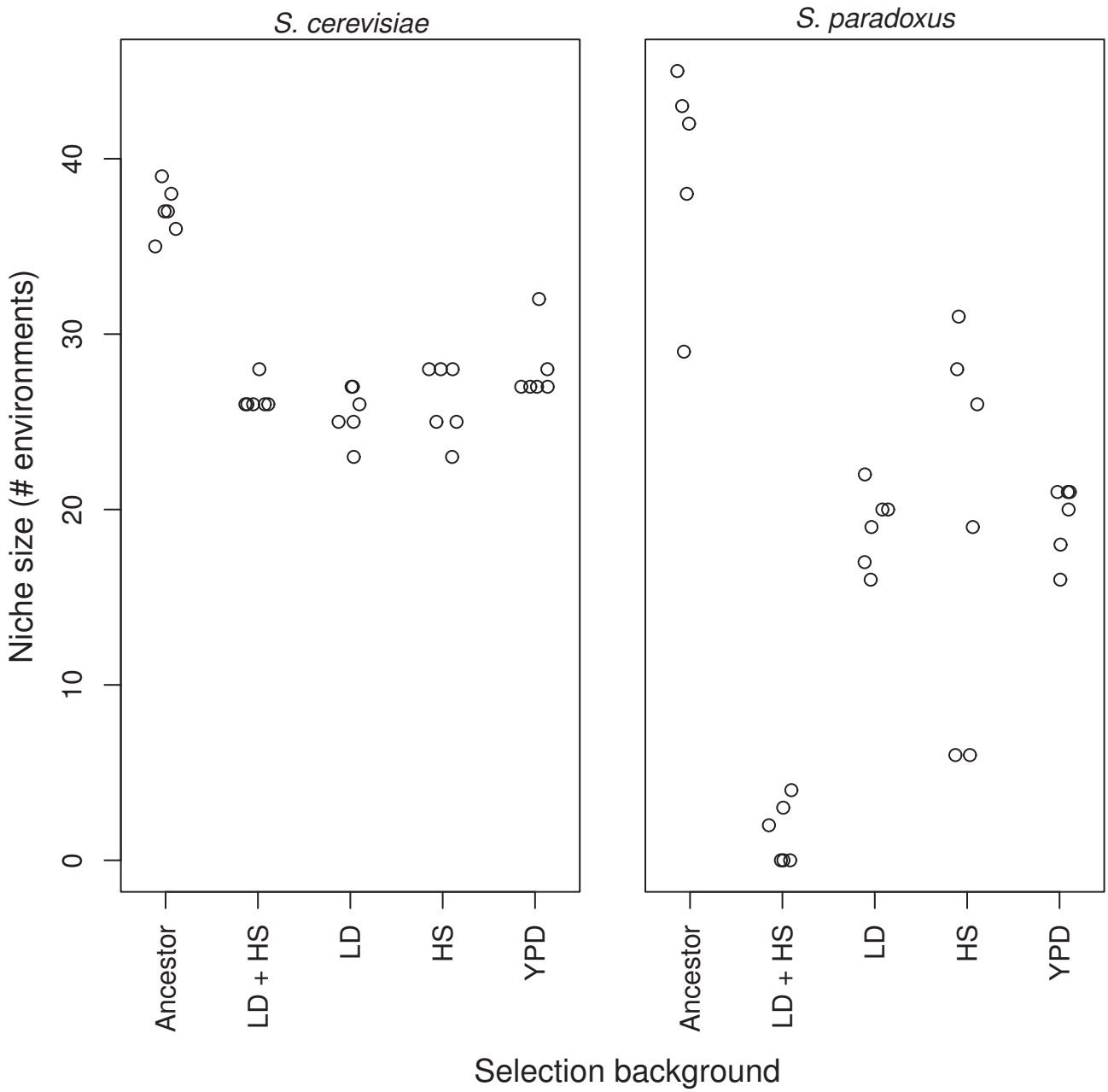
Fig. 4.7. Number of environmental conditions (niche size) along our dextrose and salt gradients (49 environments total) in which our experimental lines can grow before selection (ancestor), or after selection in one of our four selection environments (Table 4.1). For the ancestral condition *S. cerevisiae* n=6, *S. paradoxus* n=5, and for the post-selection condition n=6 for both species in all environments.
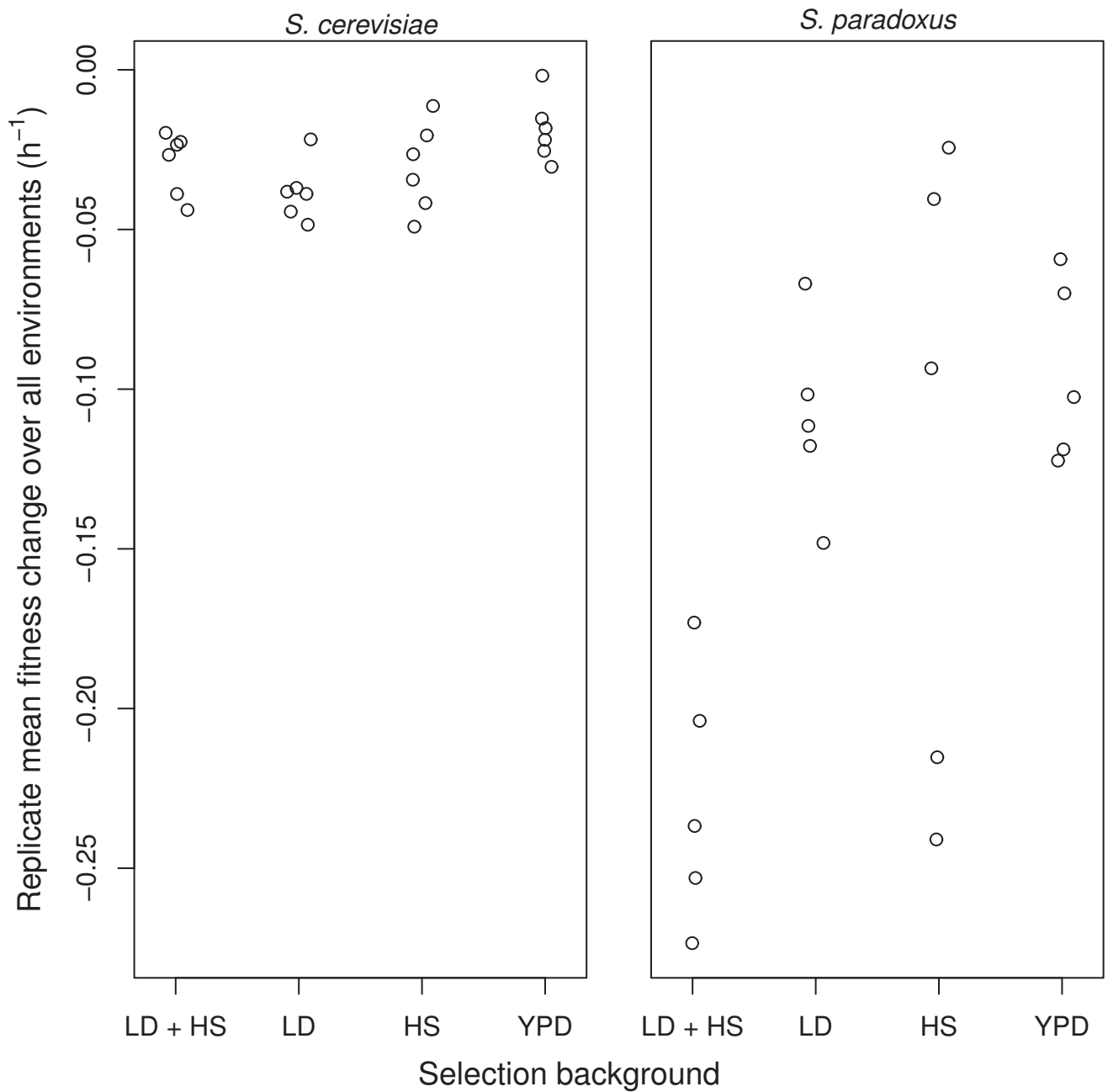
Fig. 4.8. Change in fitness (r) for each replicate, averaged over 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). *S. cerevisiae* n = 6; *S. paradoxus* n = 5.
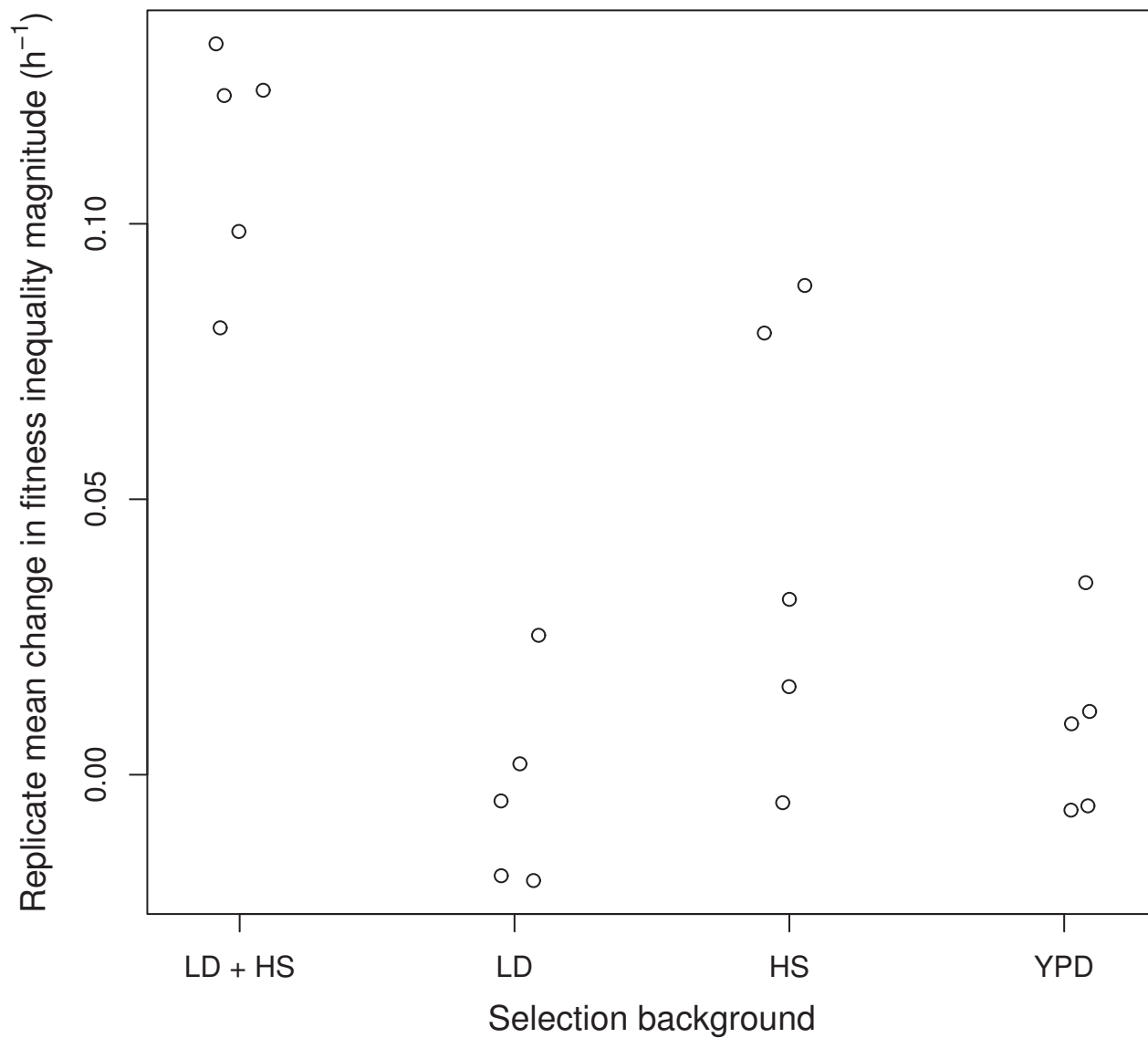
Fig. 4.9. Mean change in the strength of potential fitness inequality for each replicate between *S. cerevisiae* and *S. paradoxus* over 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). n = 5.
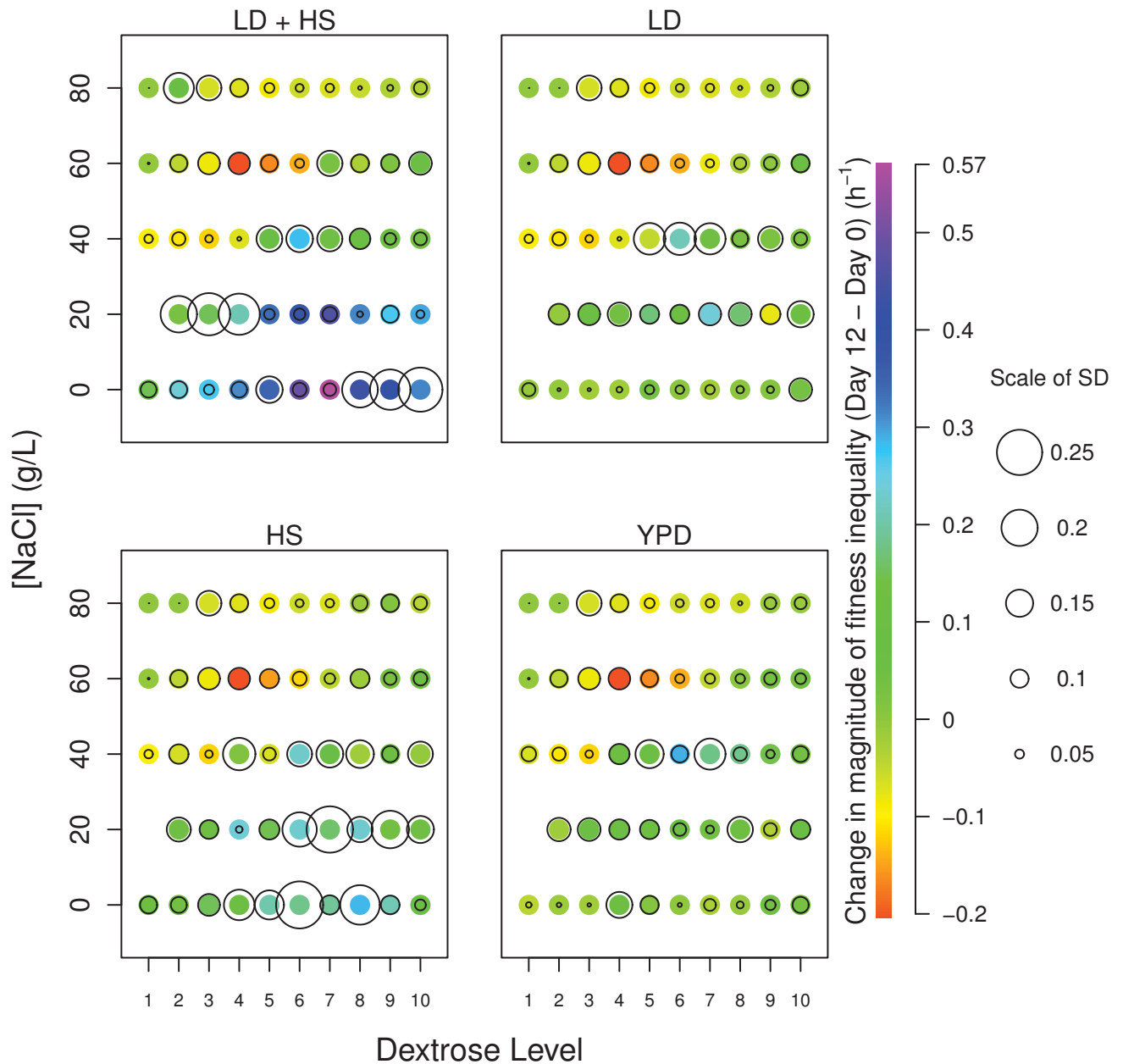
Fig. 4.10. Mean change in the strength of potential fitness inequality between *S. cerevisiae* and *S. paradoxus* in 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). Mean change in fitness inequality magnitude is indicated by the colour of the point, and the standard deviation of change of fitness inequality magnitude is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 5.
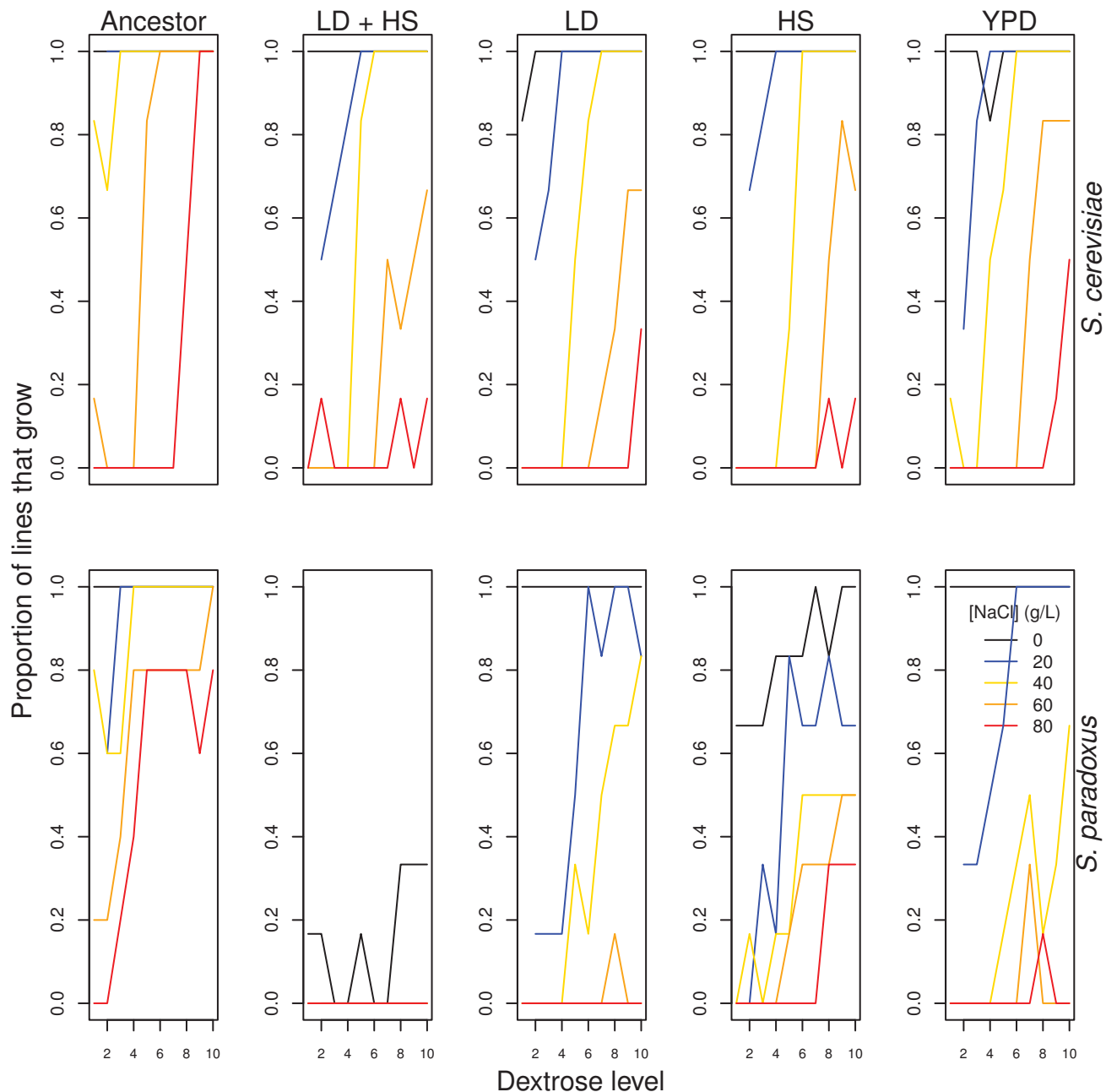
Fig. 4.11. Proportion of replicates capable of growing across our dextrose and salt gradients in the ancestral condition or after selection in our four environments (Table 4.1). Dextrose levels: $1 = 0$ g/L, $2 = 0.1$ g/L, $3 = 0.2$ g/L, $4 = 0.4$ g/L, $5 = 0.8$ g/L, $6 = 1.6$ g/L, $7 = 3.2$ g/L, $8 = 6.4$ g/L, $9 = 12.8$ g/L, $10 = 20$ g/L. For the ancestral condition *S. cerevisiae* n=6, *S. paradoxus* n=5, and for the post-selection condition n=6 for both species.
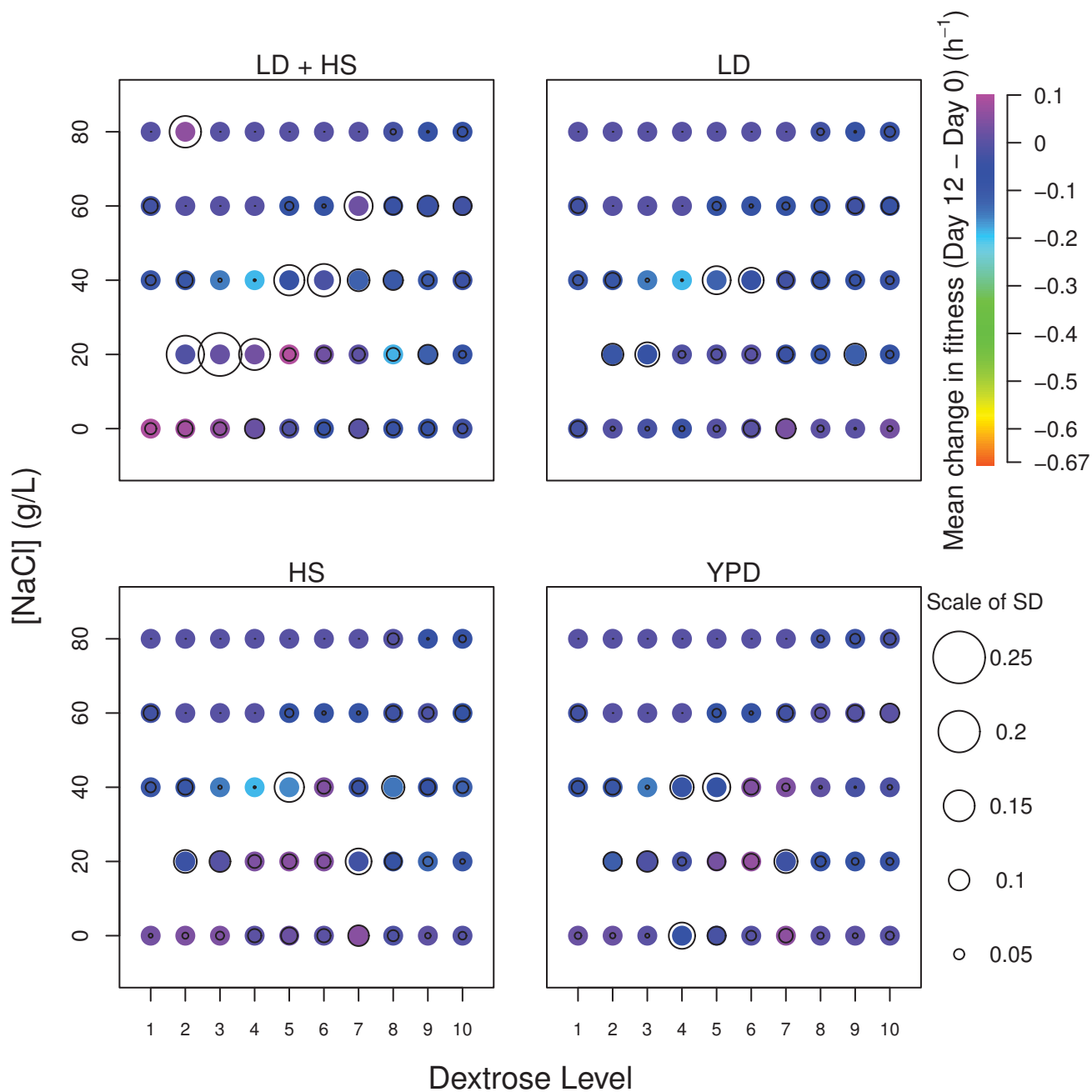
Fig. 4.12. Mean change in *S. cerevisiae* fitness (r) in 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). Mean fitness change is indicated by the colour of the point, and the standard deviation of fitness change is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 6.
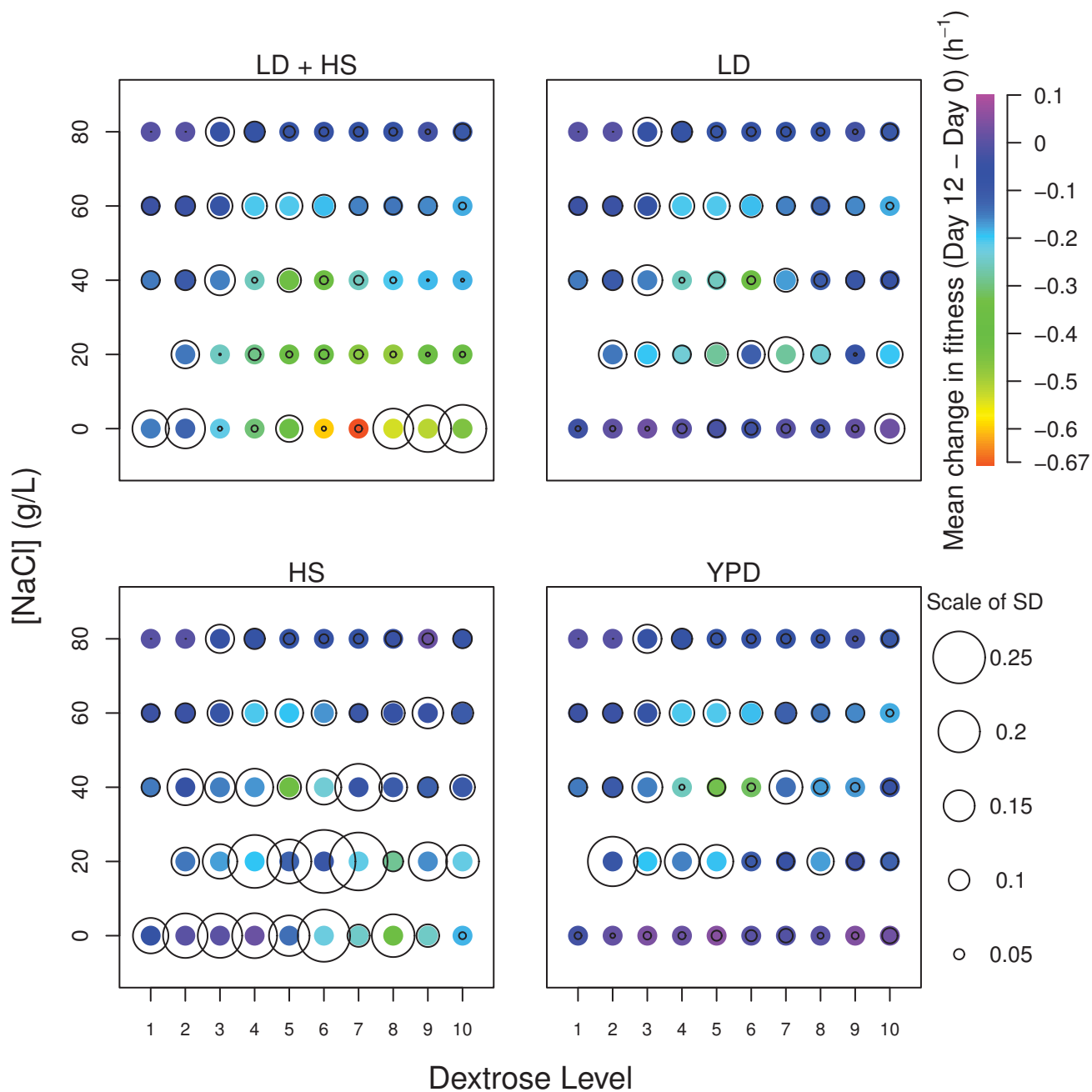
Fig. 4.13. Mean change in *S. paradoxus* fitness (r) over 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). Mean fitness change is indicated by the colour of the point, and the standard deviation of fitness change is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 5.
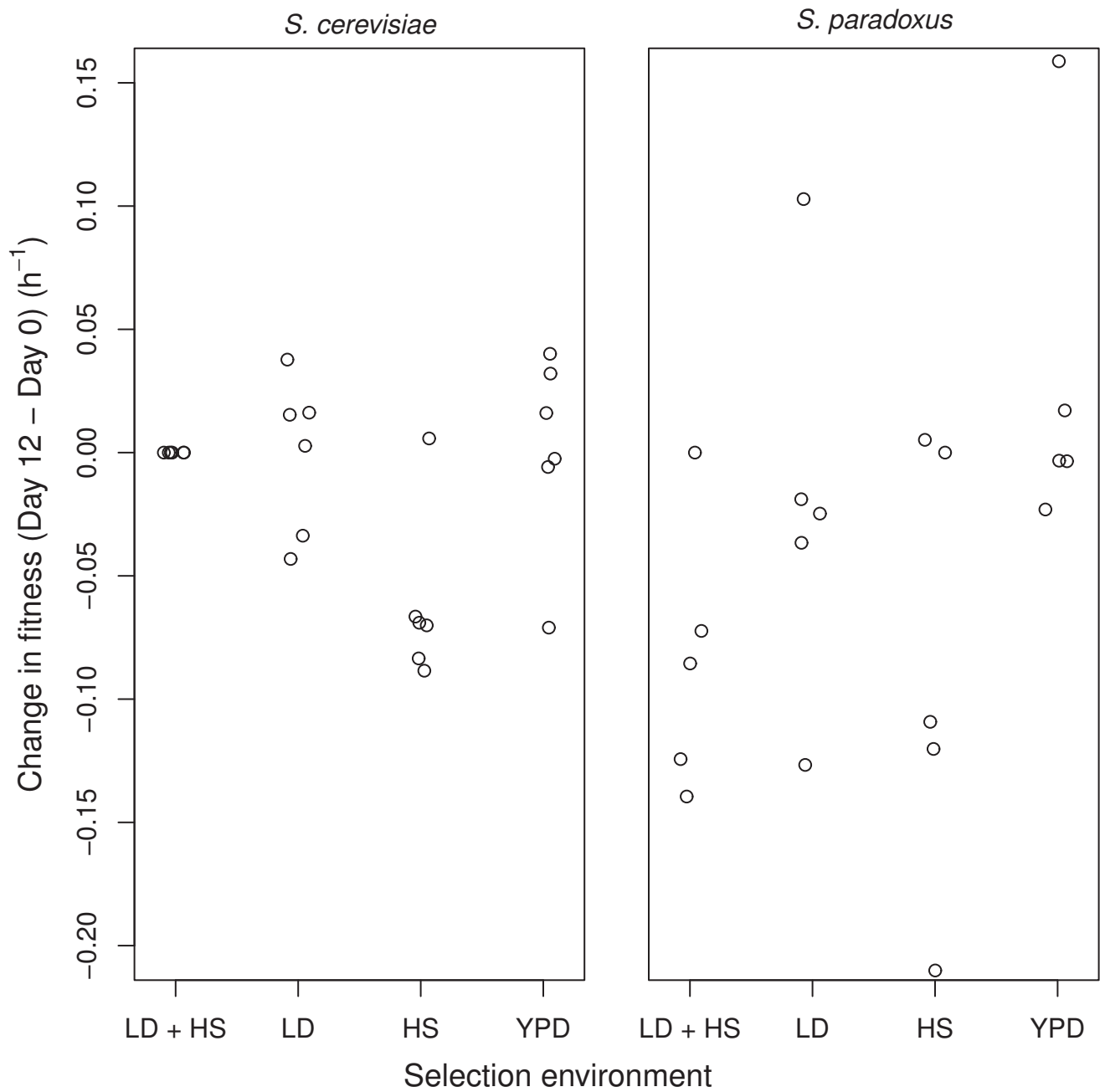
Fig. 4.14. Change in fitness (r) for each replicate strictly in the environment of selection after 12 days in four different environments (Table 4.1). *S. cerevisiae* n=6, *S. paradoxus* n=5.

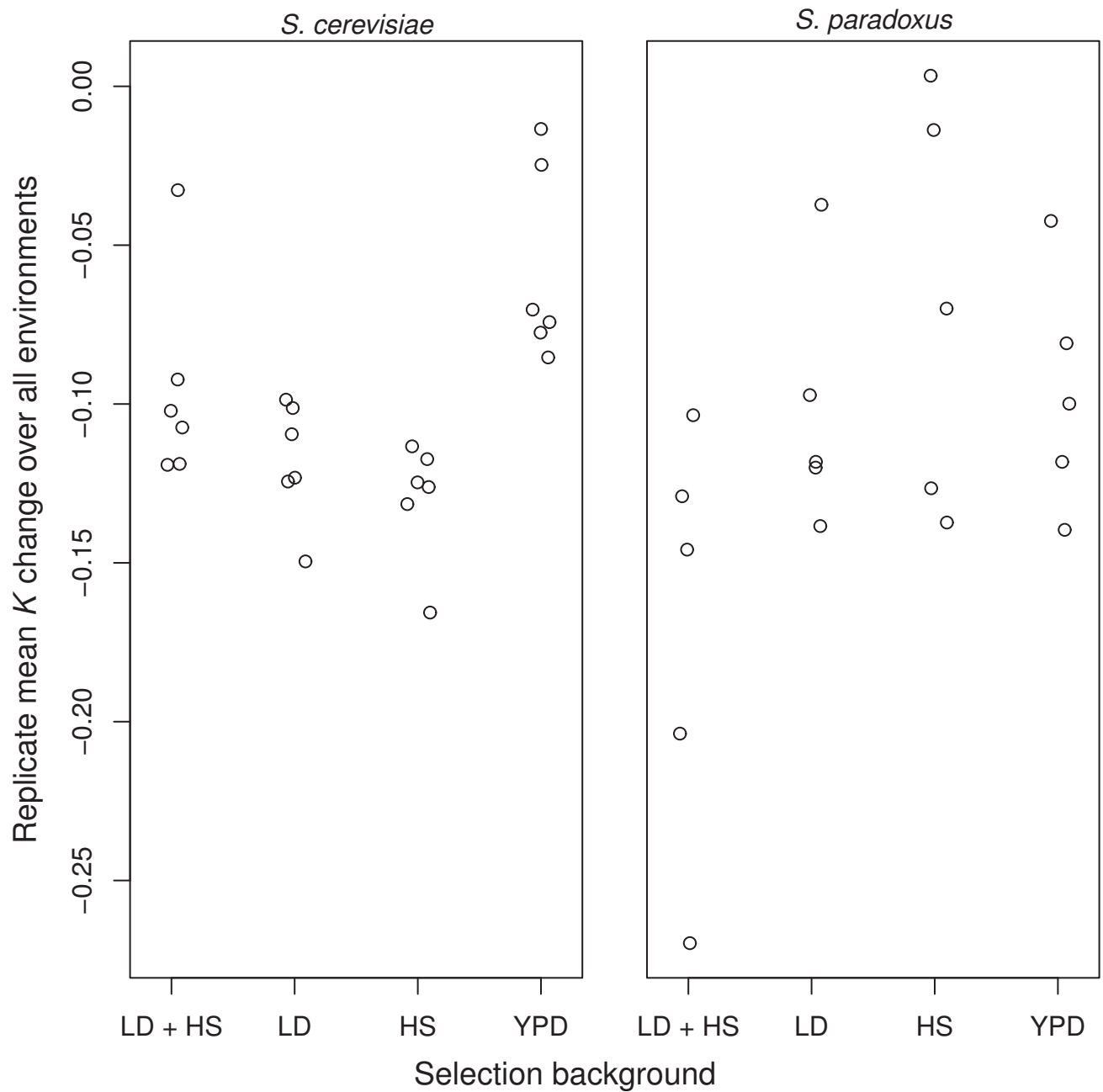# Appendix 4.2: Figures produced with K as metric of fitness.

Fig. 4.15. Change in K for each replicate averaged over 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). *S. cerevisiae* n = 6; *S. paradoxus* n = 5.
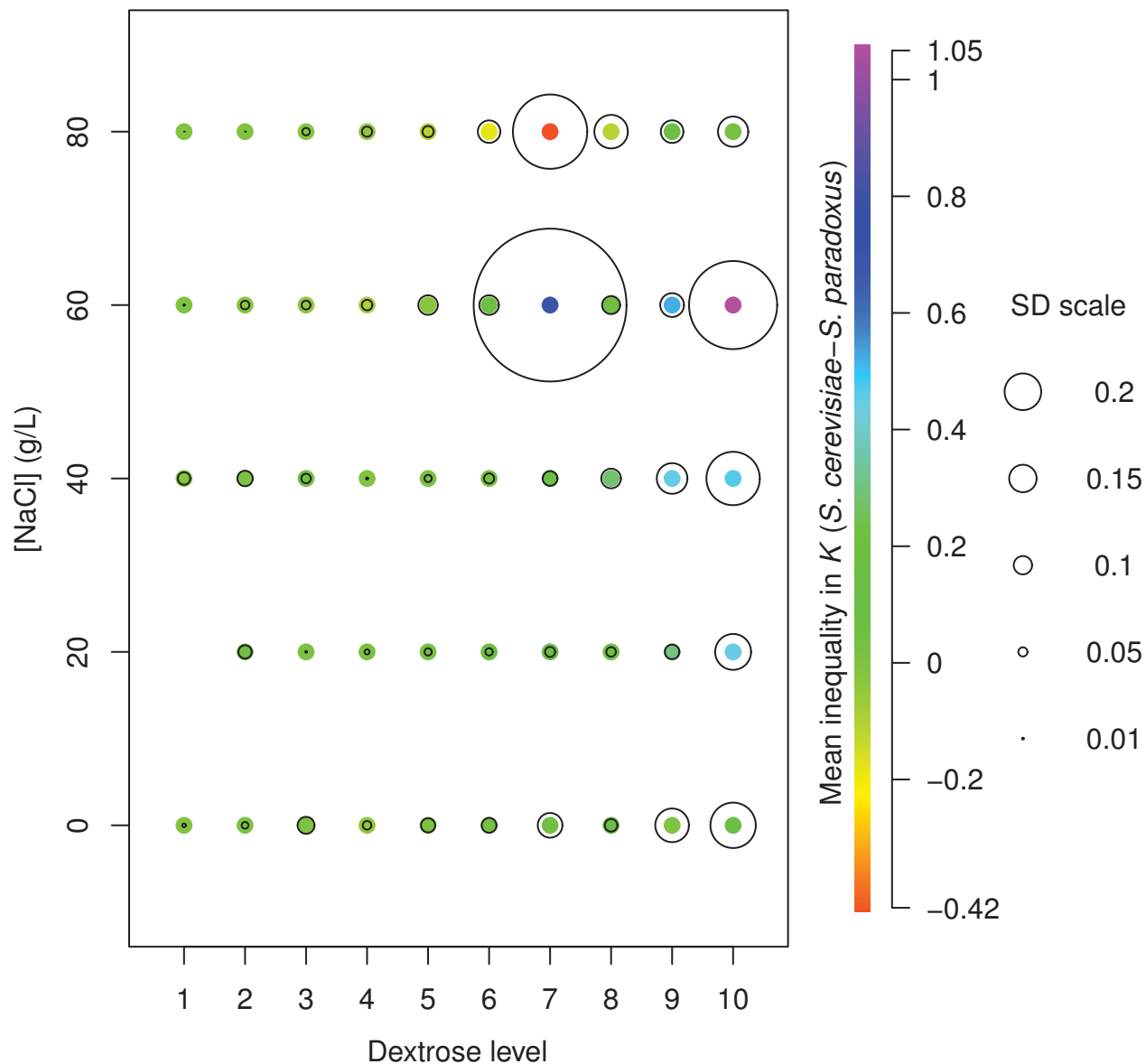
Fig. 4.16. Mean ancestral inequality in K between *S. cerevisiae* and *S. paradoxus* in 49 different assay conditions along dextrose and salt gradients (Table 4.1). Mean fitness inequality is indicated by the colour of the point, and the standard deviation of fitness inequality is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 5.
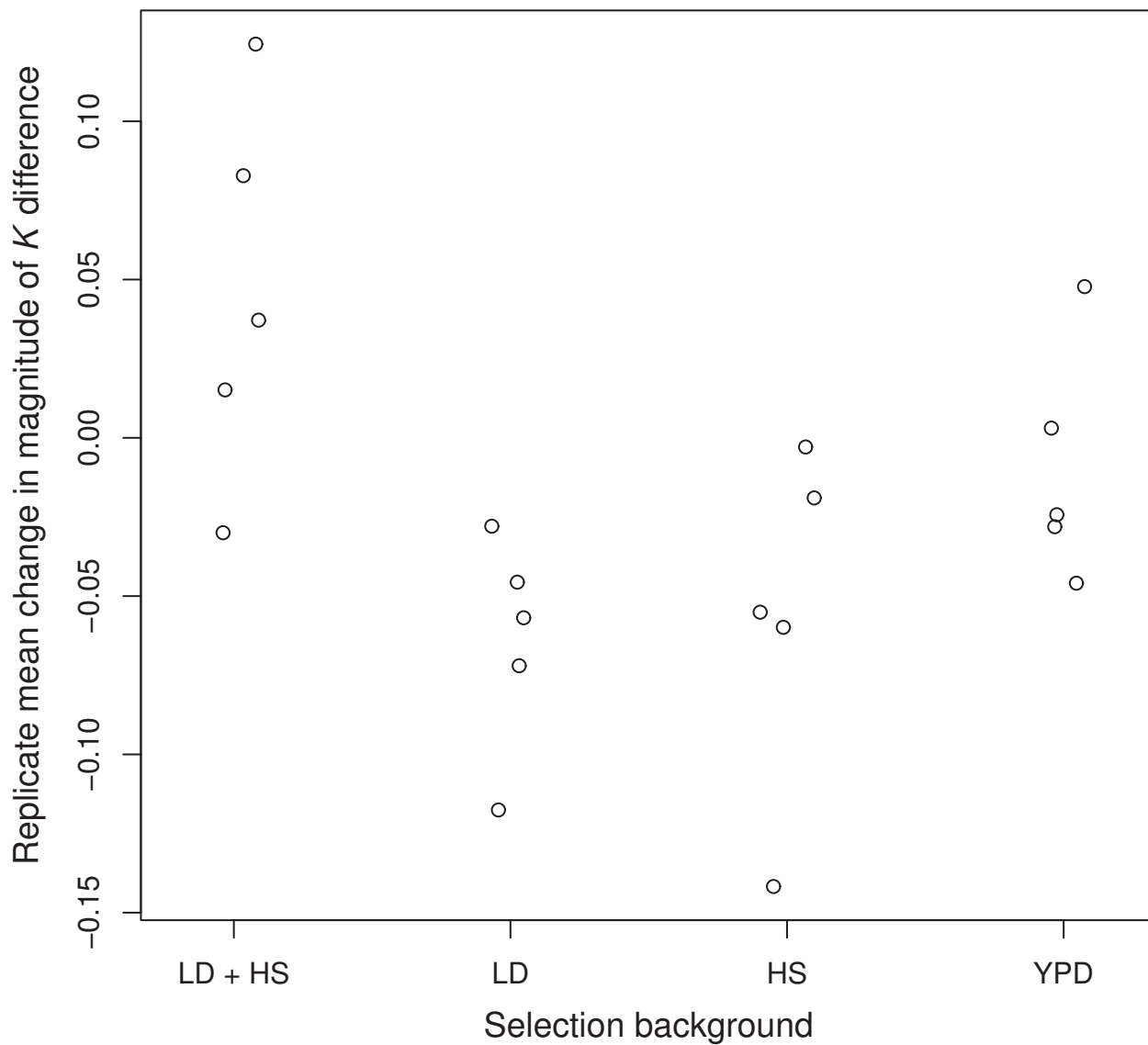
Fig. 4.17. Mean change for each replicate in the magnitude of the difference in K between *S. cerevisiae* and *S. paradoxus* over 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). n = 5.
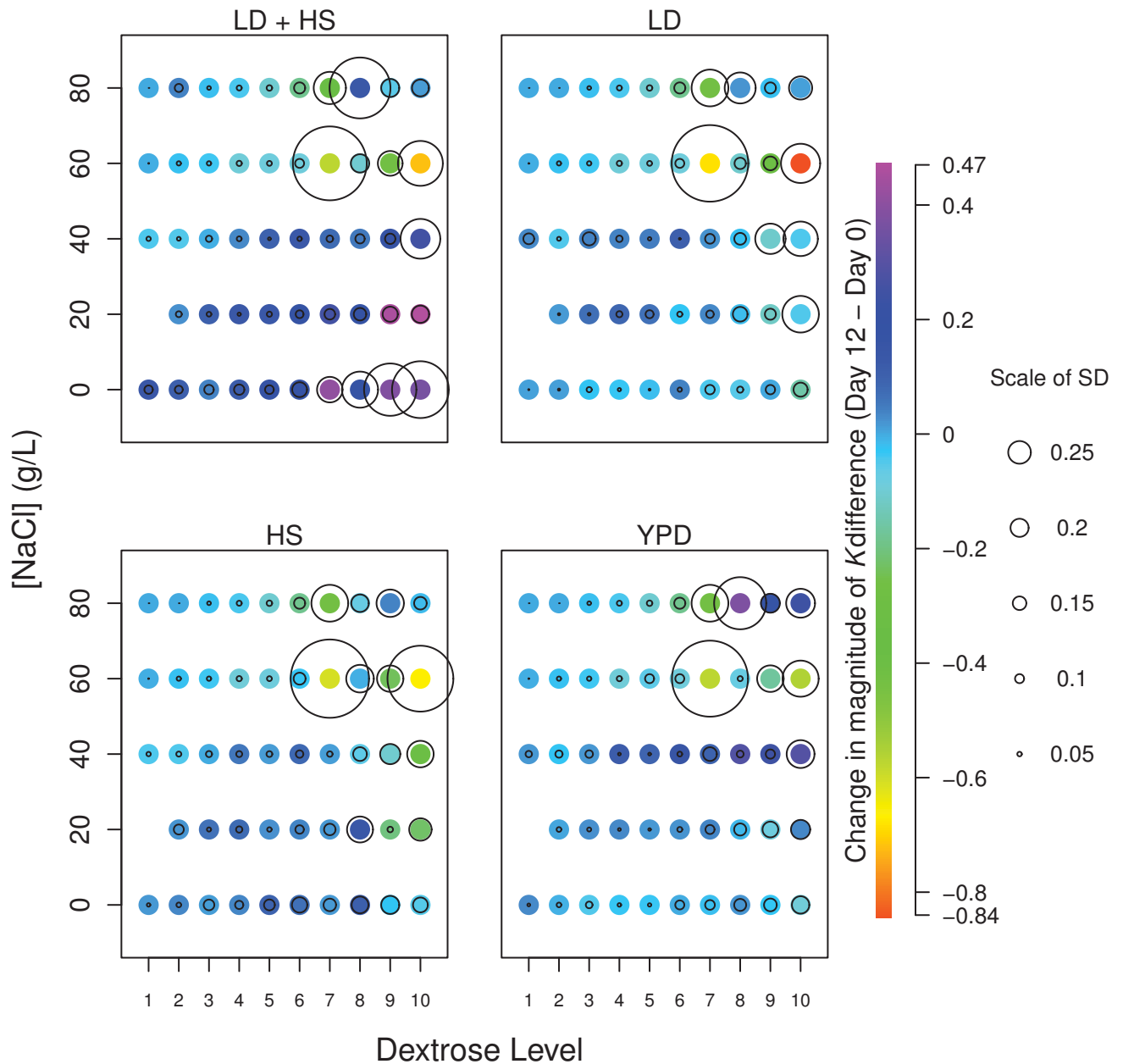
Fig. 4.18. Mean change in the magnitude of the difference in K between *S. cerevisiae* and *S. paradoxus* in 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). Mean change in fitness inequality magnitude is indicated by the colour of the point, and the standard deviation of change of fitness inequality magnitude is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 5.
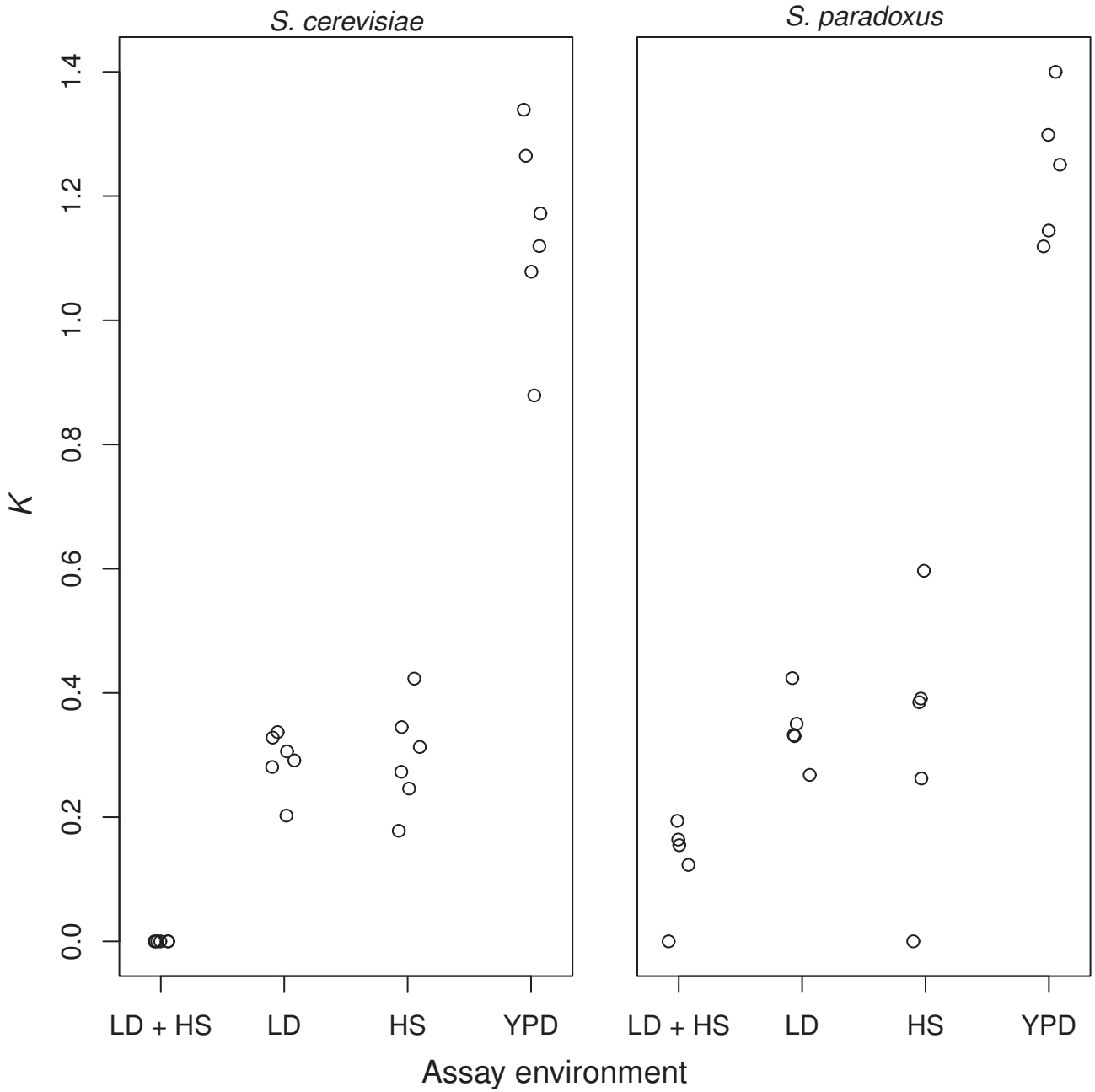
Fig. 4.19. *K* of each ancestral yeast population in the assay conditions corresponding to our four environments of selection (Table 4.1). *S. cerevisiae* n=6, *S. paradoxus* n=5.

Fig. 4.20. Mean change in *S. cerevisiae K* in 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). Mean change of *K* is indicated by the colour of the point, and the standard deviation of *K* change is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 6.
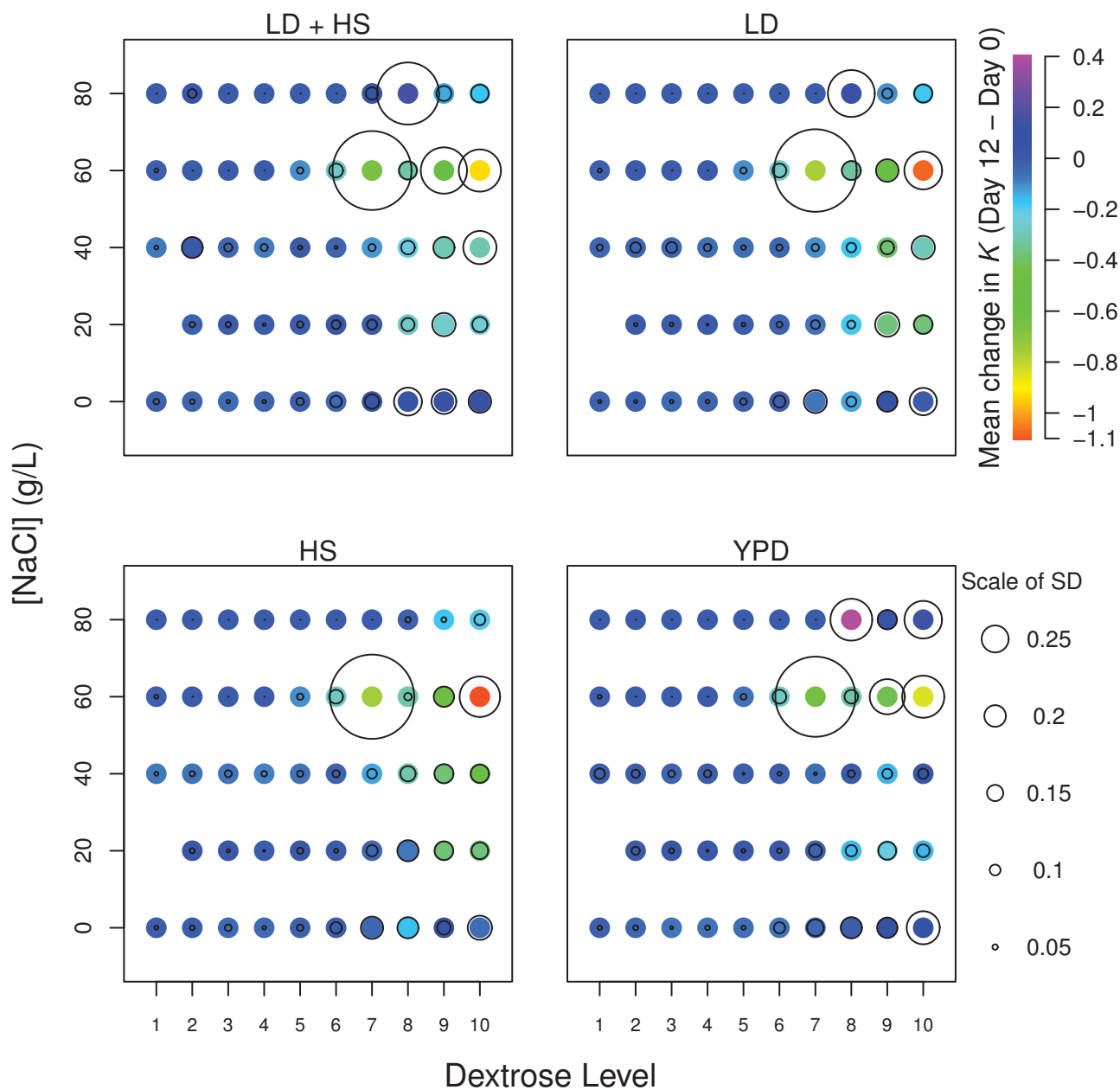
Fig. 4.21. Mean change in *S. paradoxus K* over 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). Mean change of K is indicated by the colour of the point, and the standard deviation of K change is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 5.
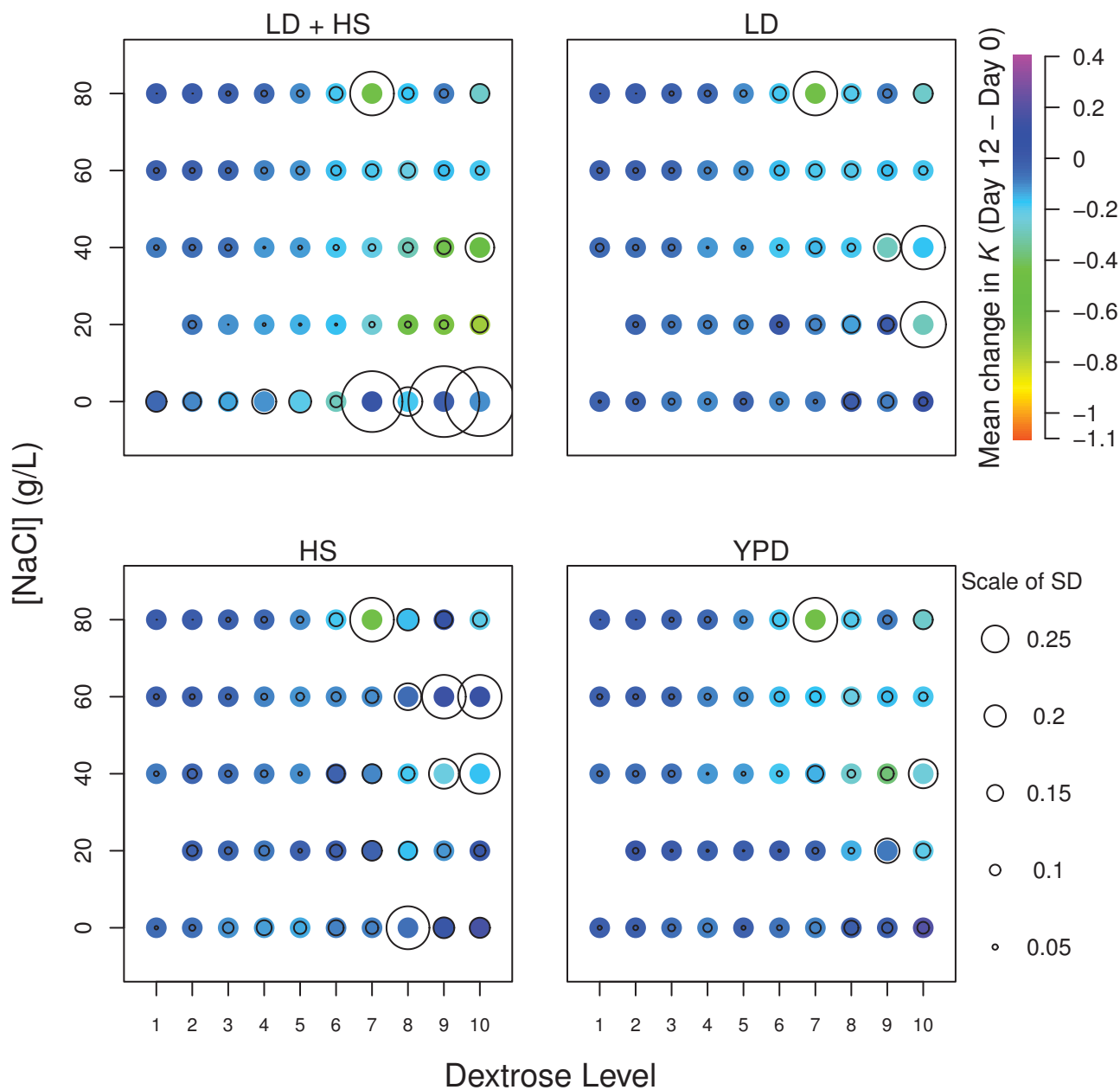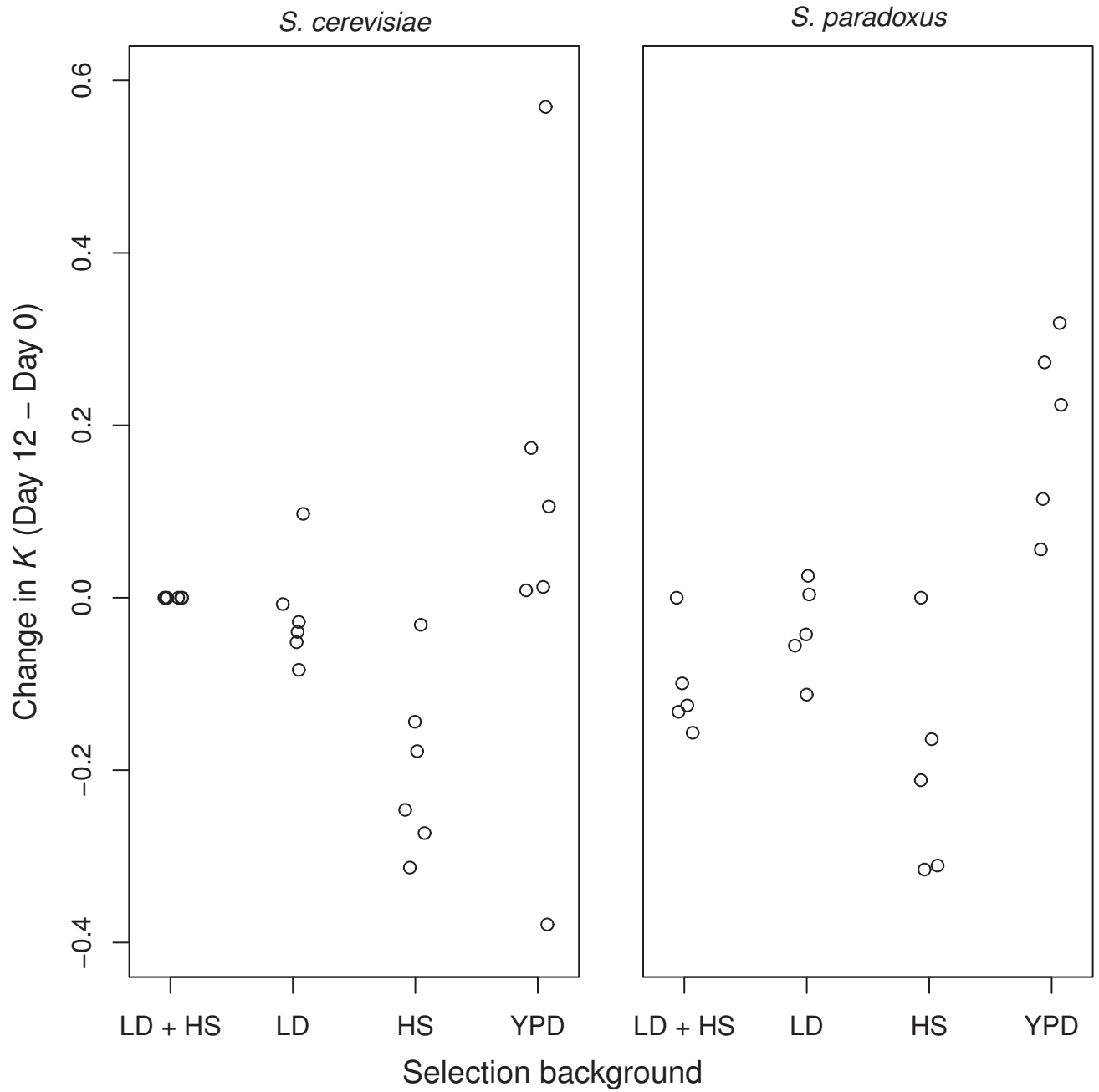
Fig. 4.22. Change in K for each replicate strictly in the environment of selection after 12 days in four different environments (Table 4.1). *S. cerevisiae* n=6, *S. paradoxus* n=5.
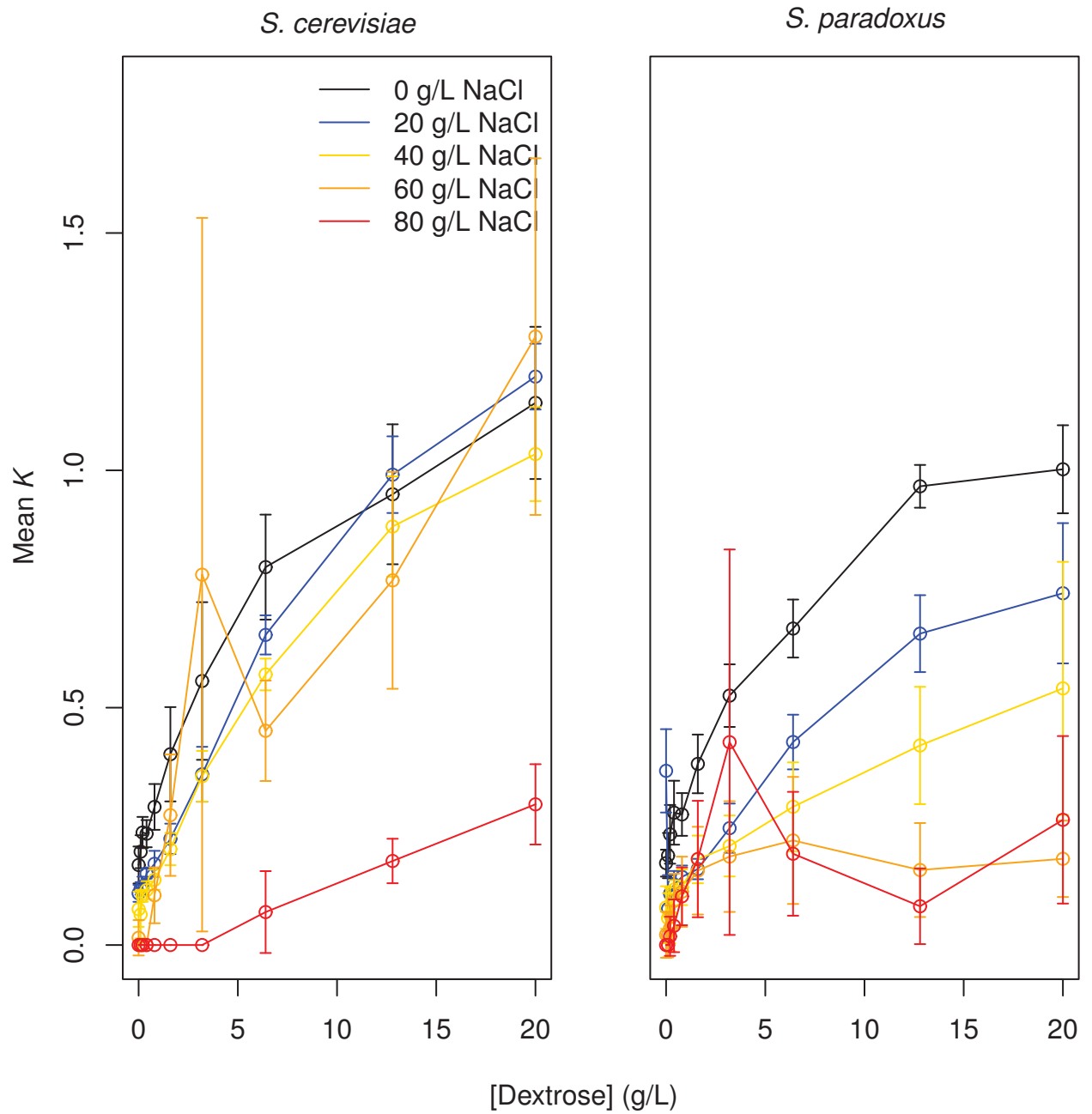
Fig. 4.23. Mean carrying capacity (K) of the ancestral populations in each assay environment. n=6 for *S. cerevisiae*, and n = 5 for *S. paradoxus*. Error bars +/- 1 standard deviation.

Fig. 4.24. Mean carrying capacity (K) of the populations in each assay environment after selection in the LD + HS environment. n=6 for both species. Error bars +/- 1 standard deviation.

Fig. 4.25. Mean carrying capacity (K) of the populations in each assay environment after selection in the LD environment. n=6 for both species. Error bars +/- 1 standard deviation.
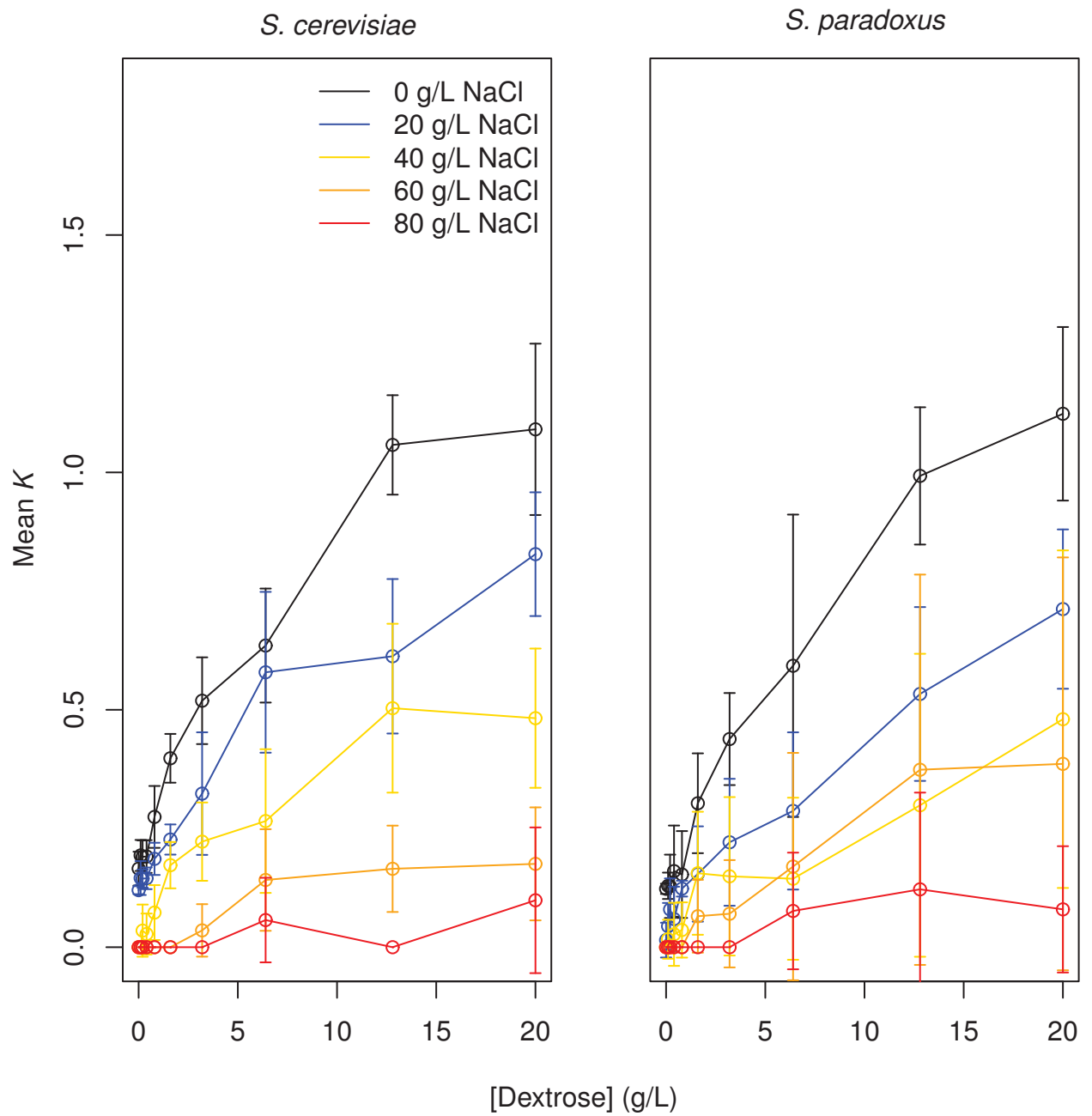
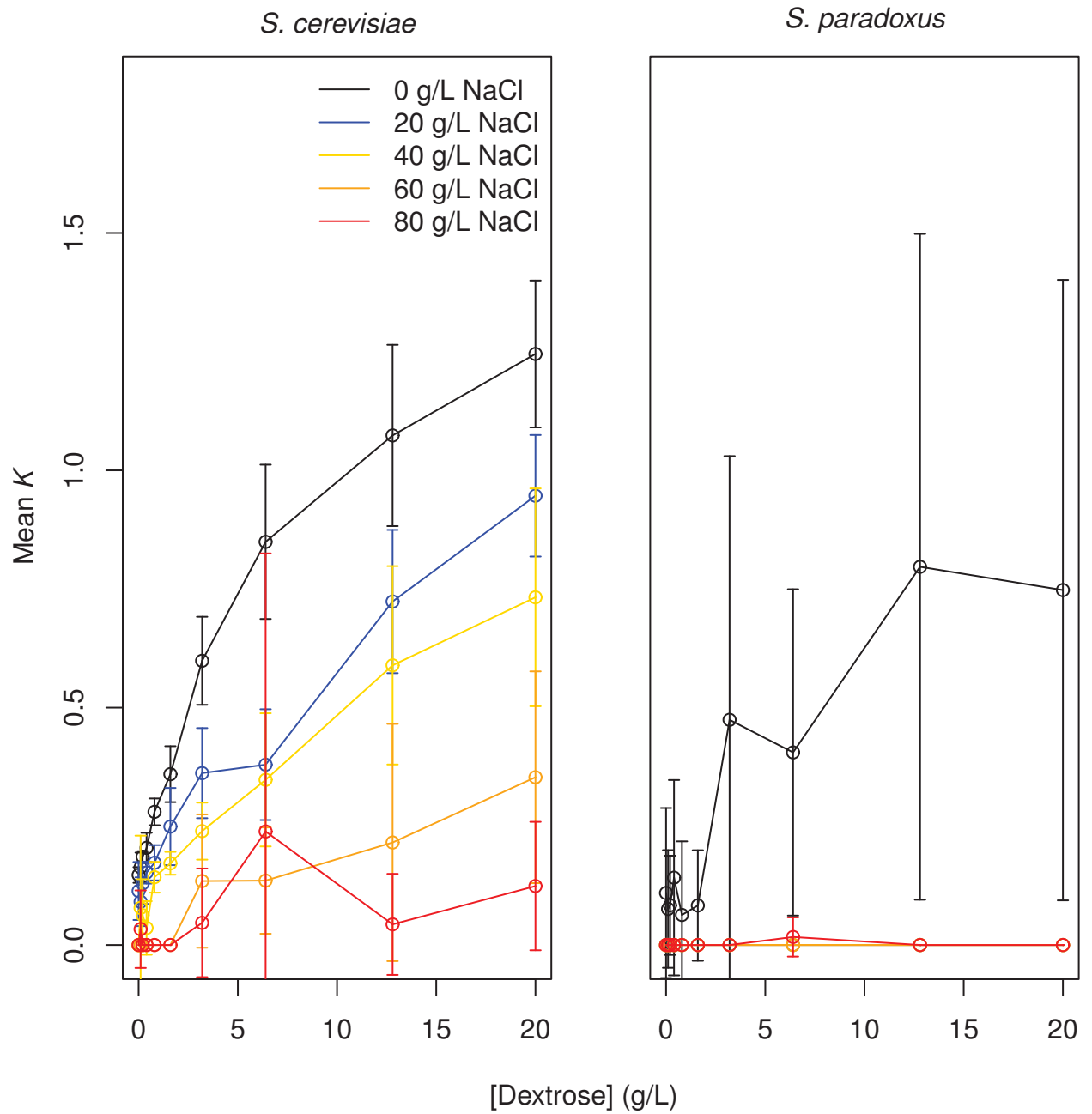Fig. 4.26. Mean carrying capacity (K) of the populations in each assay environment after selection in the HS environment. n=6 for both species. Error bars +/- 1 standard deviation.
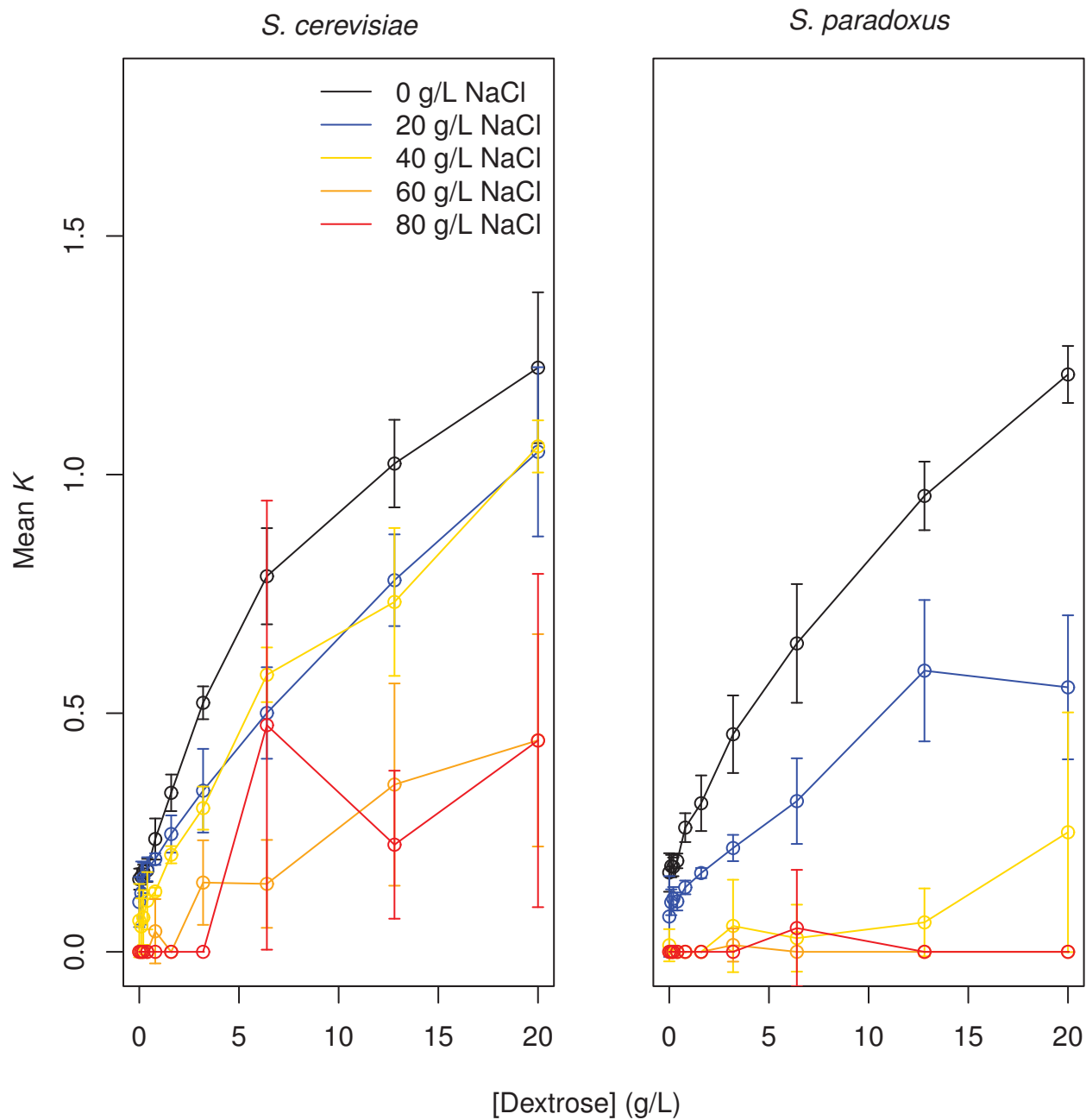
Fig. 4.27. Mean carrying capacity (K) of the populations in each assay environment after selection in the YPD environment. n=6 for both species. Error bars +/- 1 standard deviation.

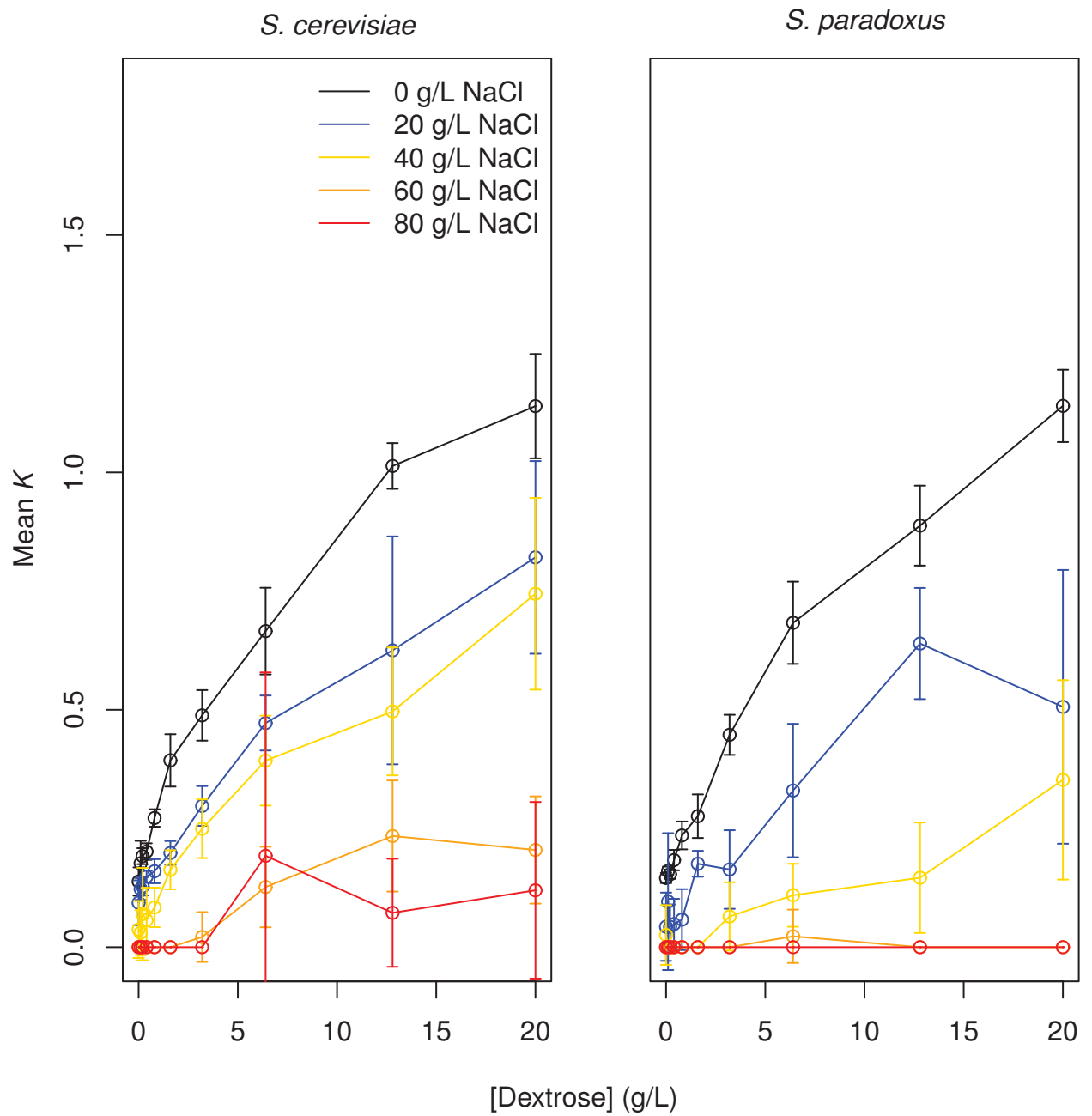**Appendix 4.3:** **Figures produced after removing fifth**
S. paradoxus **population selected in LD + HS environ-**
ment from Pedruski et al. *Selection in stressful envi-*
ronments leads to niche contraction in an evolutionary
model system
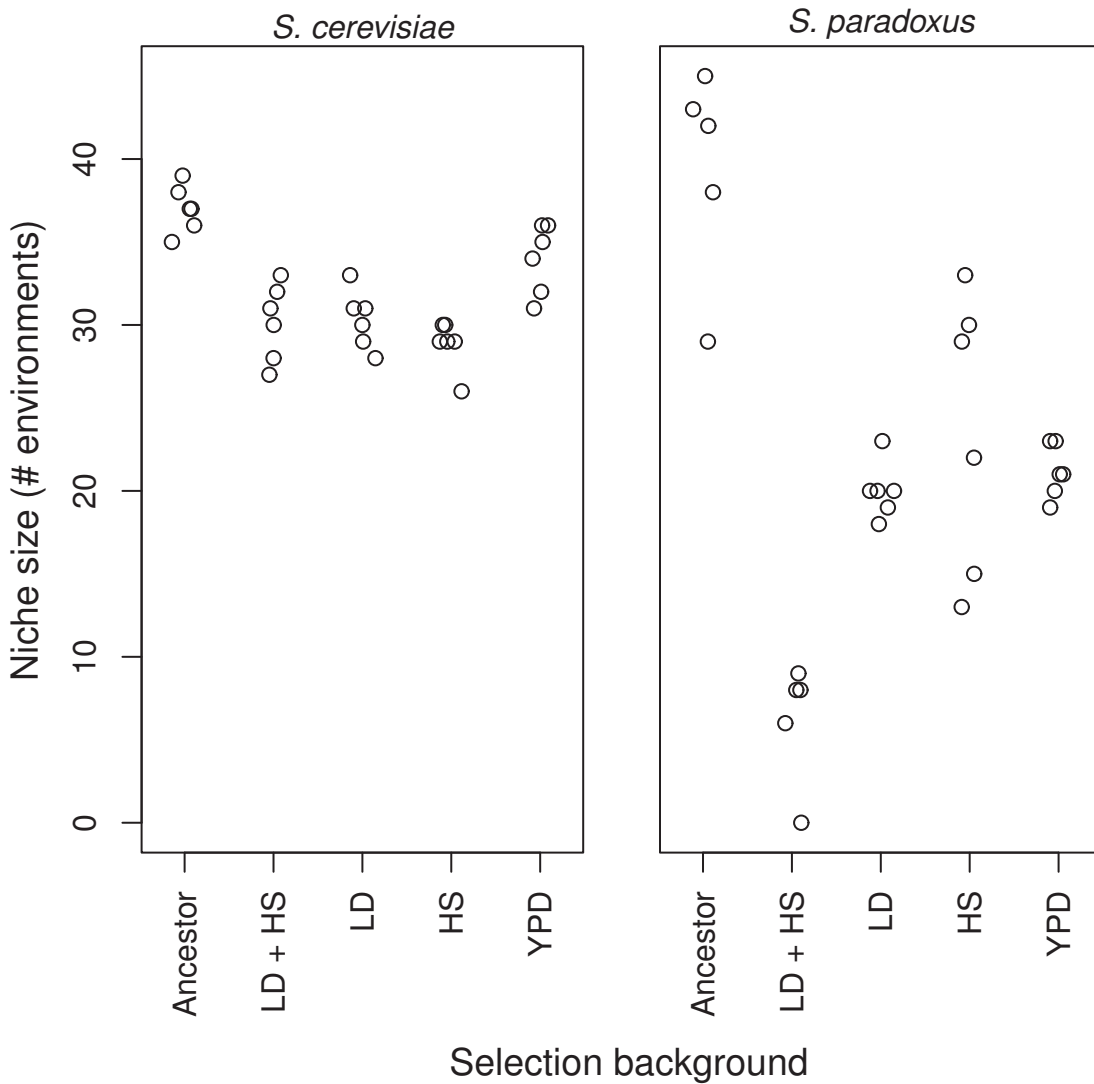
Fig. 4.28. Number of environmental conditions (niche size) along our dextrose and salt gradients (49 environments total) in which our experimental lines can grow before selection (ancestor), or after selection in one of our four selection environments (Table 4.1). n = 6 for *S. cerevisiae* in the ancestral and post-selection condition, n=5 for the ancestral *S. paradoxus* and post-selection LD + HS environments, n=6 in all other post-selection environments.

Fig. 4.29. Proportion of replicates capable of growing across our dextrose and salt gradients in the ancestral condition or after selection in our four environments (Table 4.1). Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 6 for *S. cerevisiae* in the ancestral and post-selection condition, n=5 for the ancestral *S. paradoxus* and post-selection LD + HS environments, n=6 in all other post-selection environments.

Appendix 4.4: Supplemental Figures and Tables from Pedruski et al. *Selection in stressful environments leads to niche contraction in an evolutionary model system*

Table 4.6. t-test results assessing H$_o$: change in fitness = 0, and median quotient (post-selection fitness divided by ancestral fitness) in each environment of selection for populations selected in that environment. In the LD + HS environment all ancestral and selected *S. cerevisiae* populations had a fitness of 0. p-values in bold are significant after Holm correction.

	t	df	p	Median quotient
S. cerevisiae				
LD + HS	NA	NA	NA	NA
LD	-8.38	5	**3.97e-4**	0.82
HS	-3.37	5	**1.99e-2**	0
YPD	-0.25	5	0.81e-1	0.98
S. paradoxus				
LD + HS	-3.46	4	2.59e-2	0
LD	-3.57	4	2.34e-2	0.69
HS	-2.01	4	1.14e-1	0
YPD	0.78	4	4.78e-1	0.73
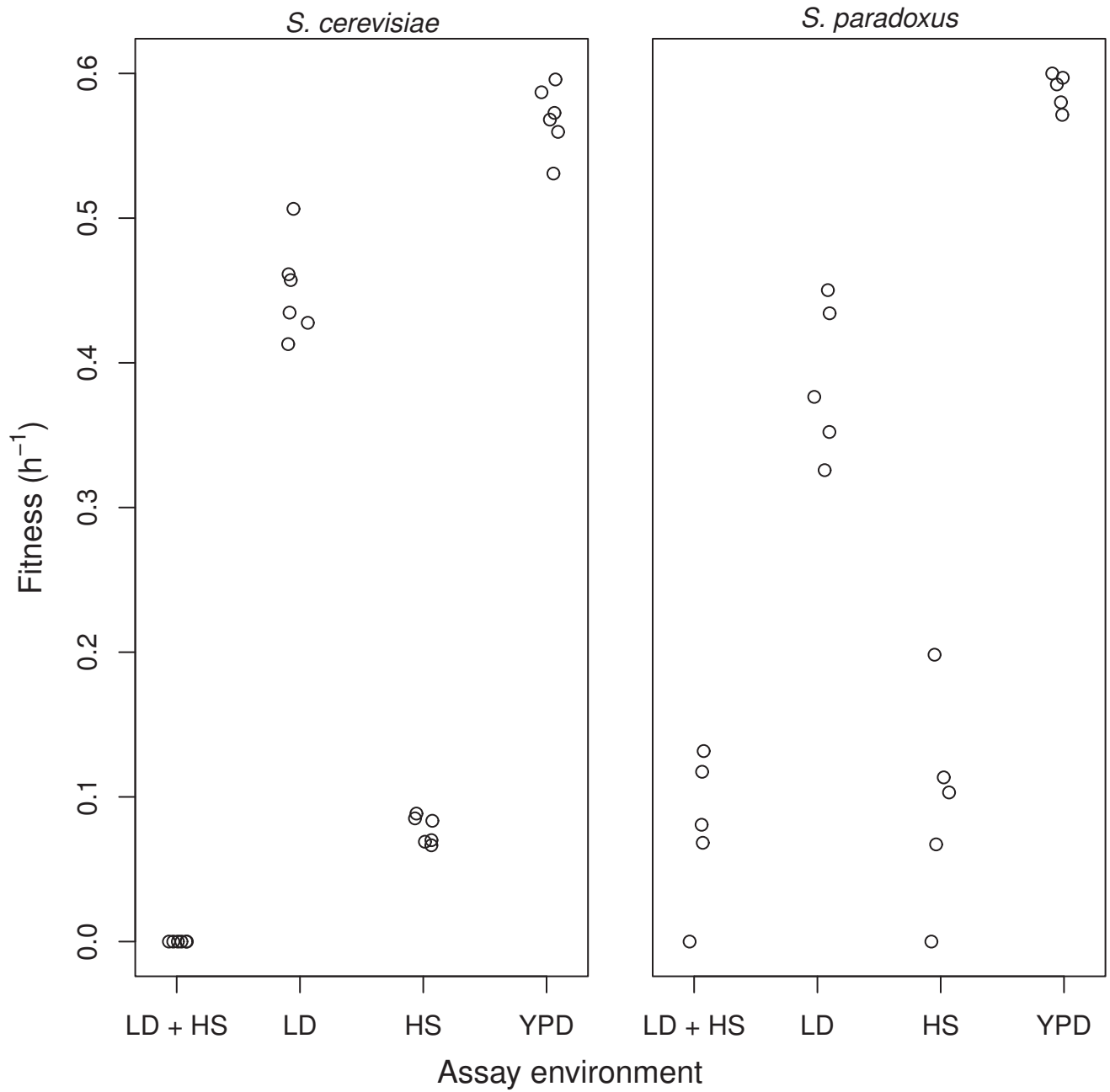
Fig. 4.30. Fitness (r) of each ancestral yeast population in the assay conditions corresponding to our four environments of selection (Table 4.1). *S. cerevisiae* n=6, *S. paradoxus* n=5.
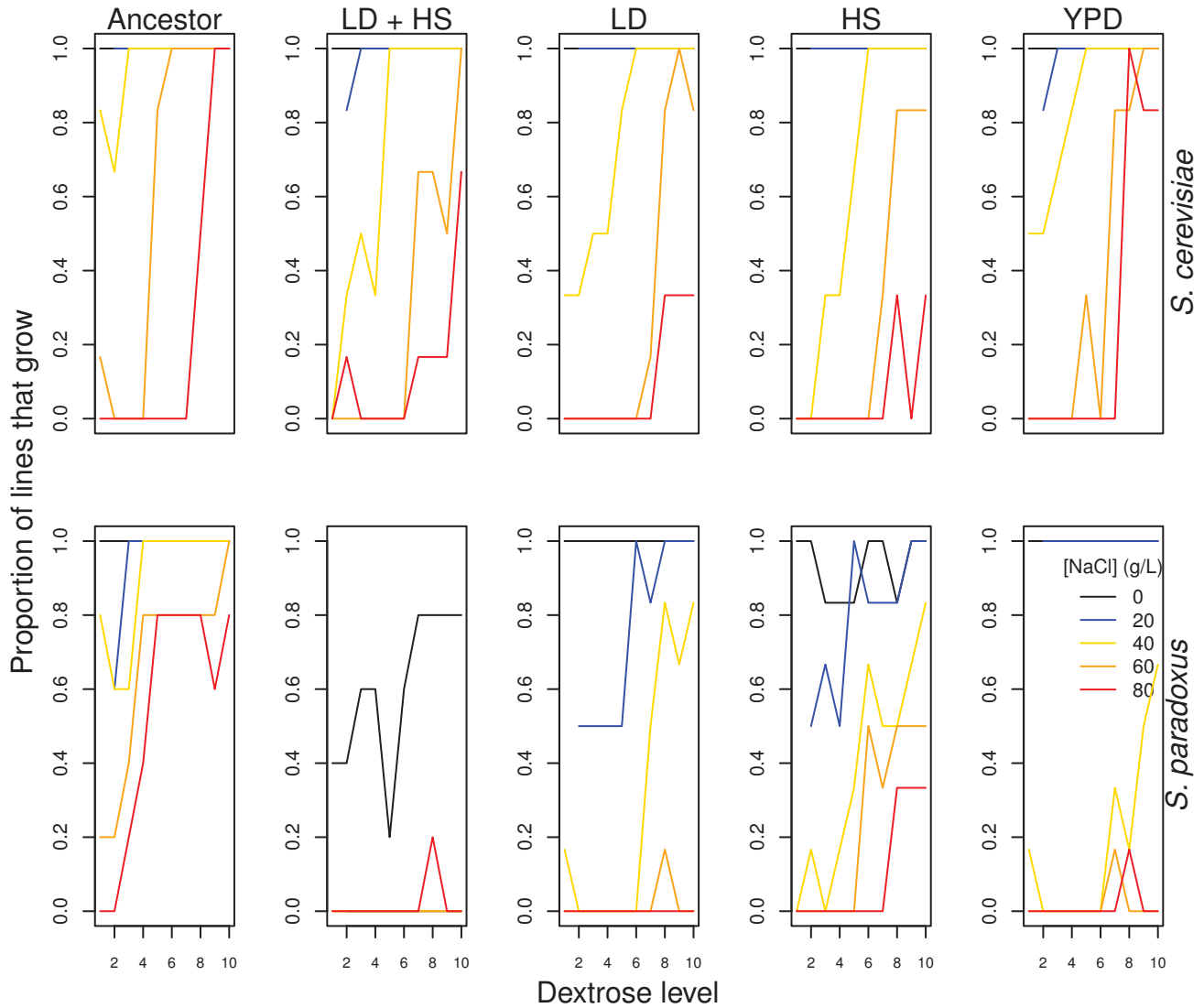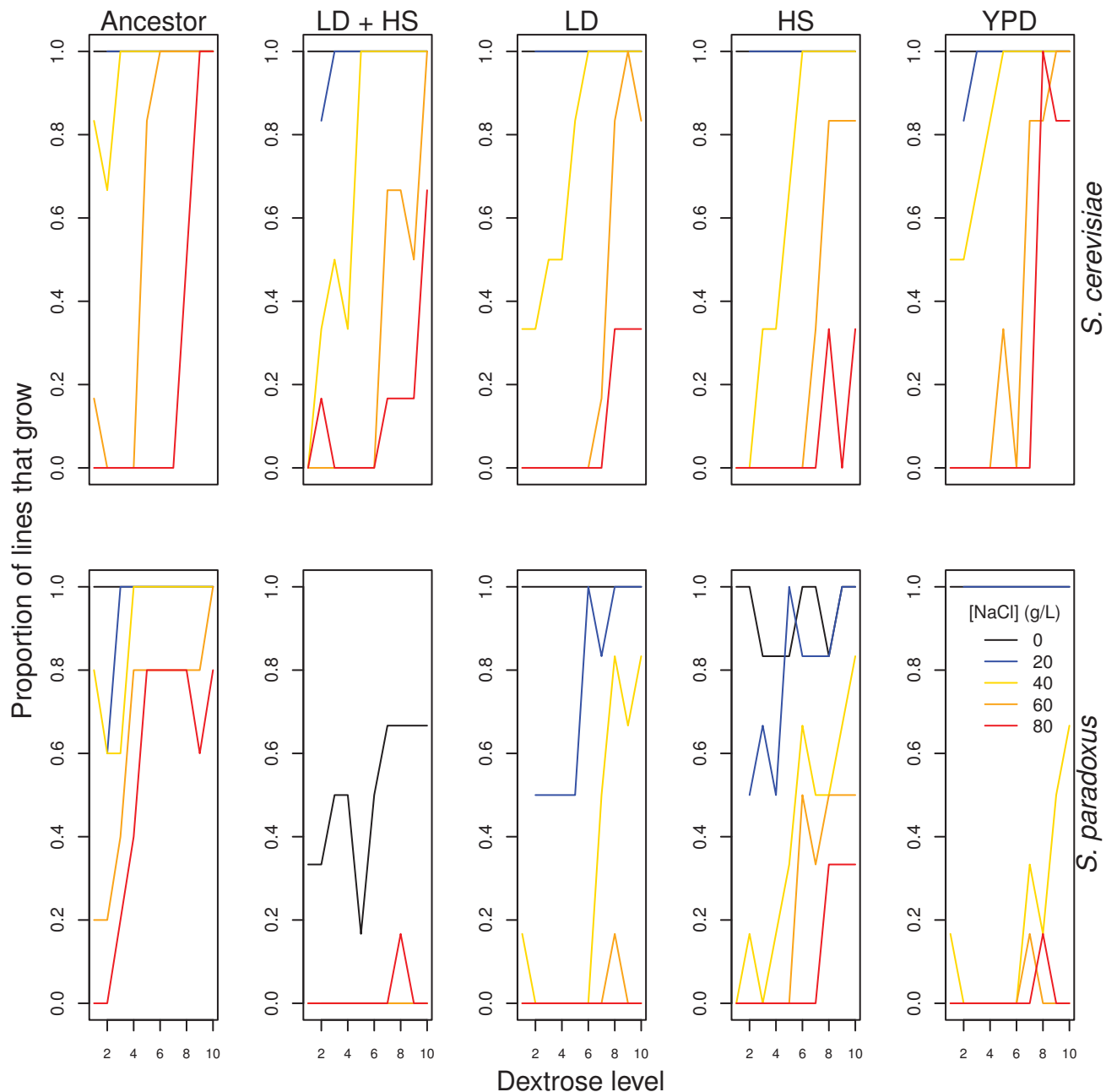
Fig. 4.31. Proportion of replicates capable of growing across our dextrose and salt gradients in the ancestral condition or after selection in our four environments (Table 4.1). Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. For the ancestral condition *S. cerevisiae* n=6, *S. paradoxus* n=5, and for the post-selection condition n=6 for both species.
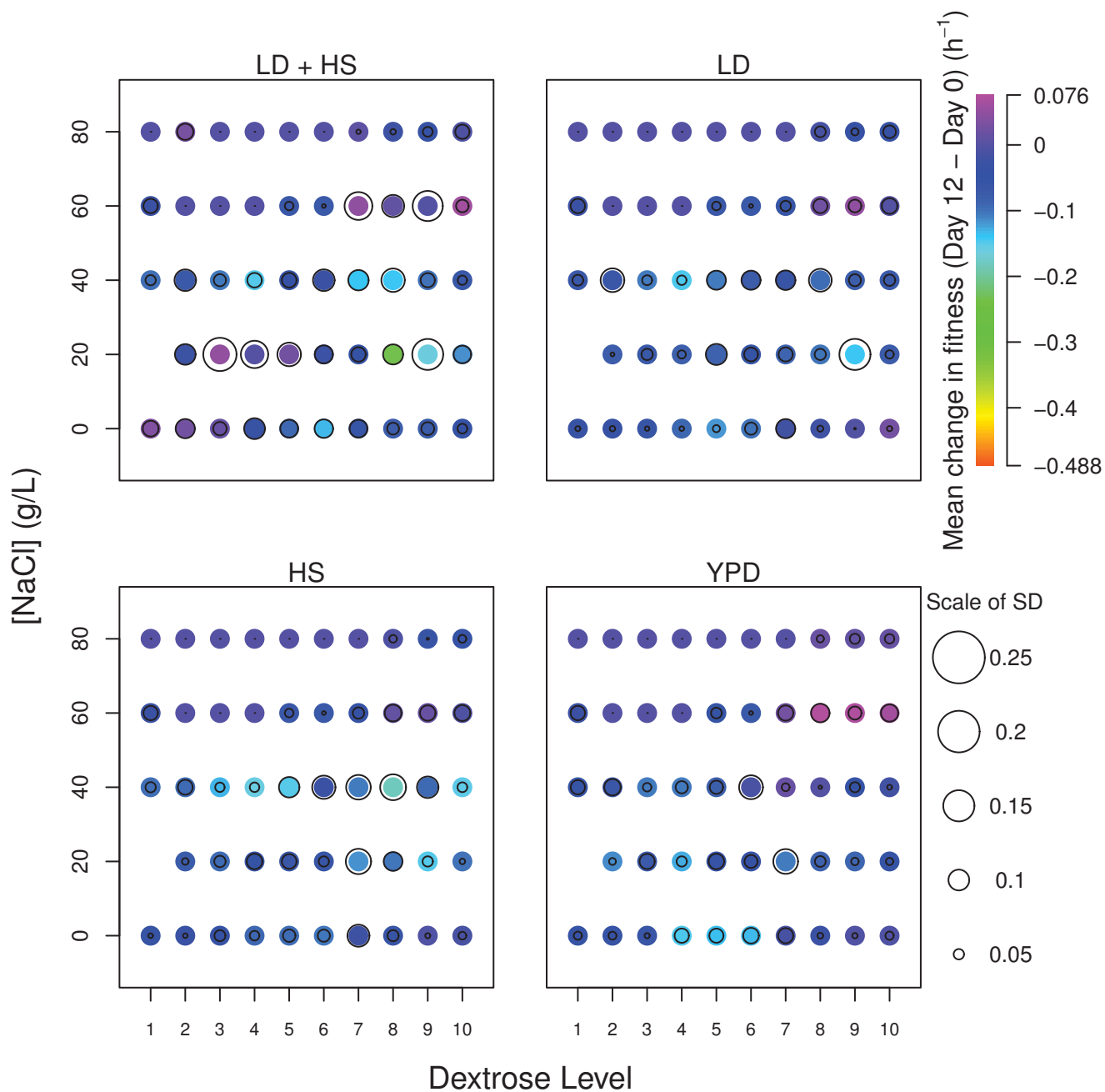
Fig. 4.32. Mean change in *S. cerevisiae* fitness (r) in 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). Mean fitness change is indicated by the colour of the point, and the standard deviation of fitness change is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 6.
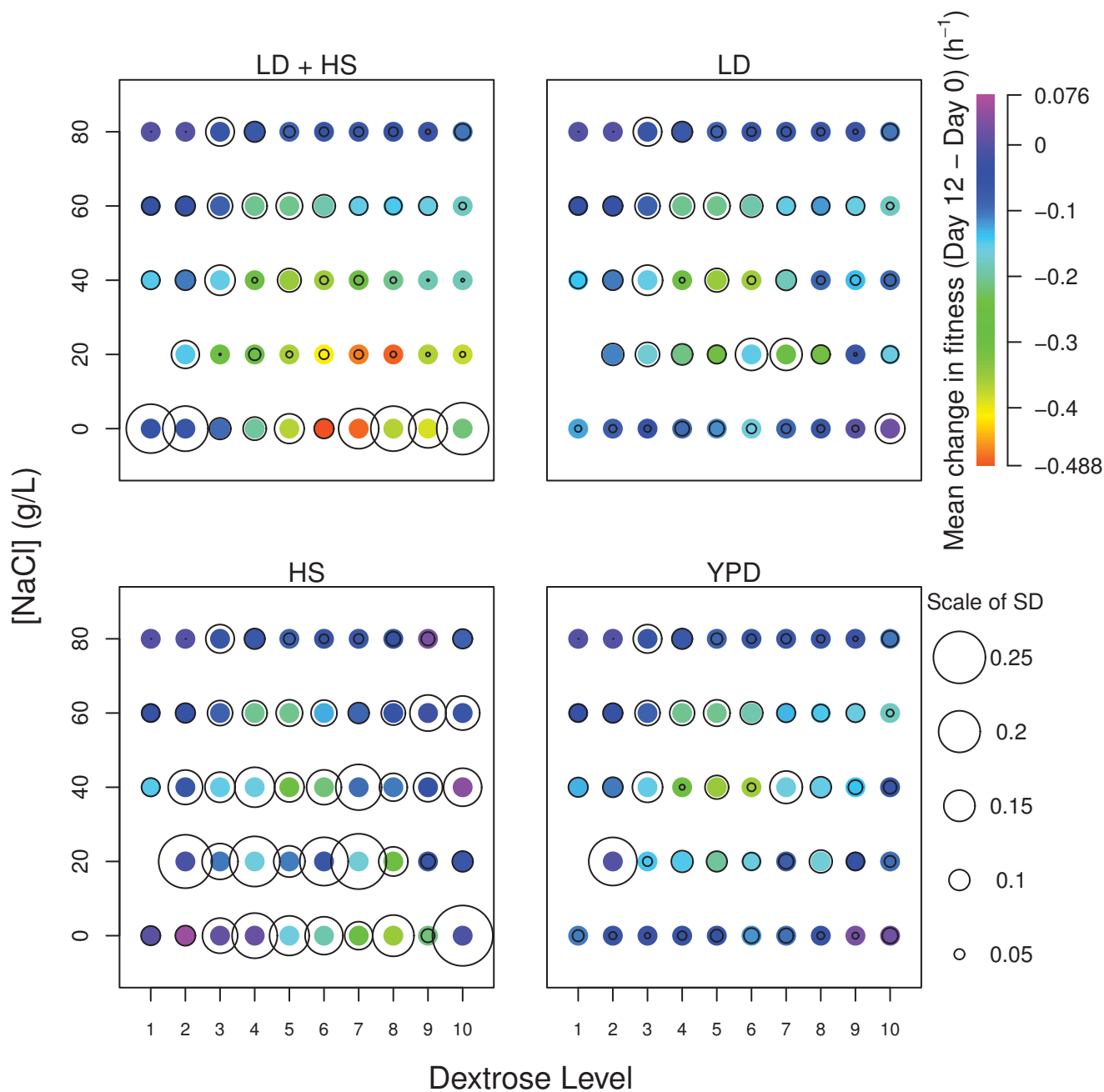
Fig. 4.33. Mean change in *S. paradoxus* fitness (r) over 49 different assay conditions along dextrose and salt gradients, after selection in four different environments (Table 4.1). Mean fitness change is indicated by the colour of the point, and the standard deviation of fitness change is indicated by the width of the accompanying circle. Dextrose levels: 1 = 0 g/L, 2 = 0.1 g/L, 3 = 0.2 g/L, 4 = 0.4 g/L, 5 = 0.8 g/L, 6 = 1.6 g/L, 7 = 3.2 g/L, 8 = 6.4 g/L, 9 = 12.8 g/L, 10 = 20 g/L. n = 5.
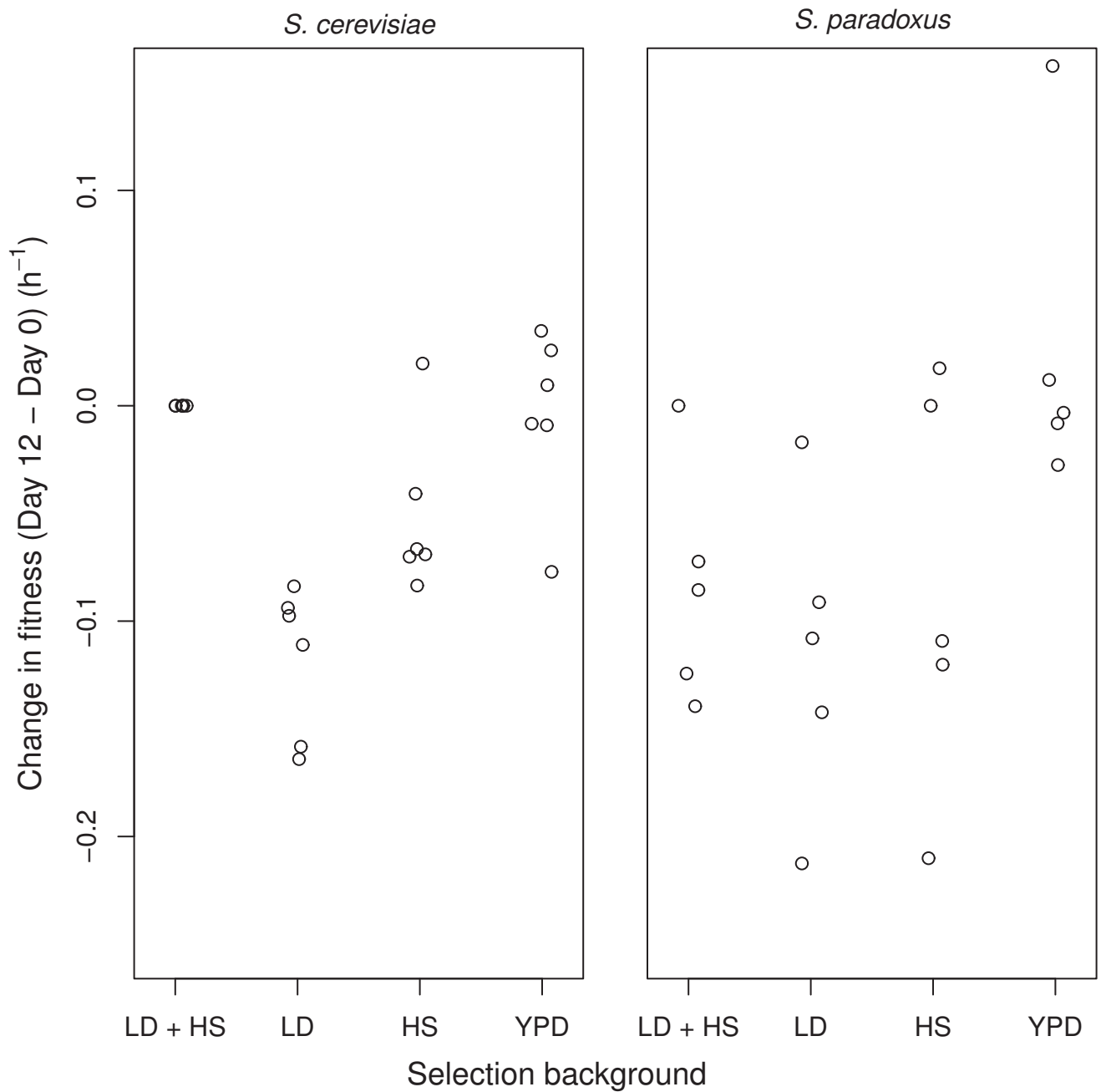
Fig. 4.34. Change in fitness (r) for each replicate strictly in the environment of selection after 12 days in four different environments (Table 4.1). *S. cerevisiae* n=6, *S. paradoxus* n=5.
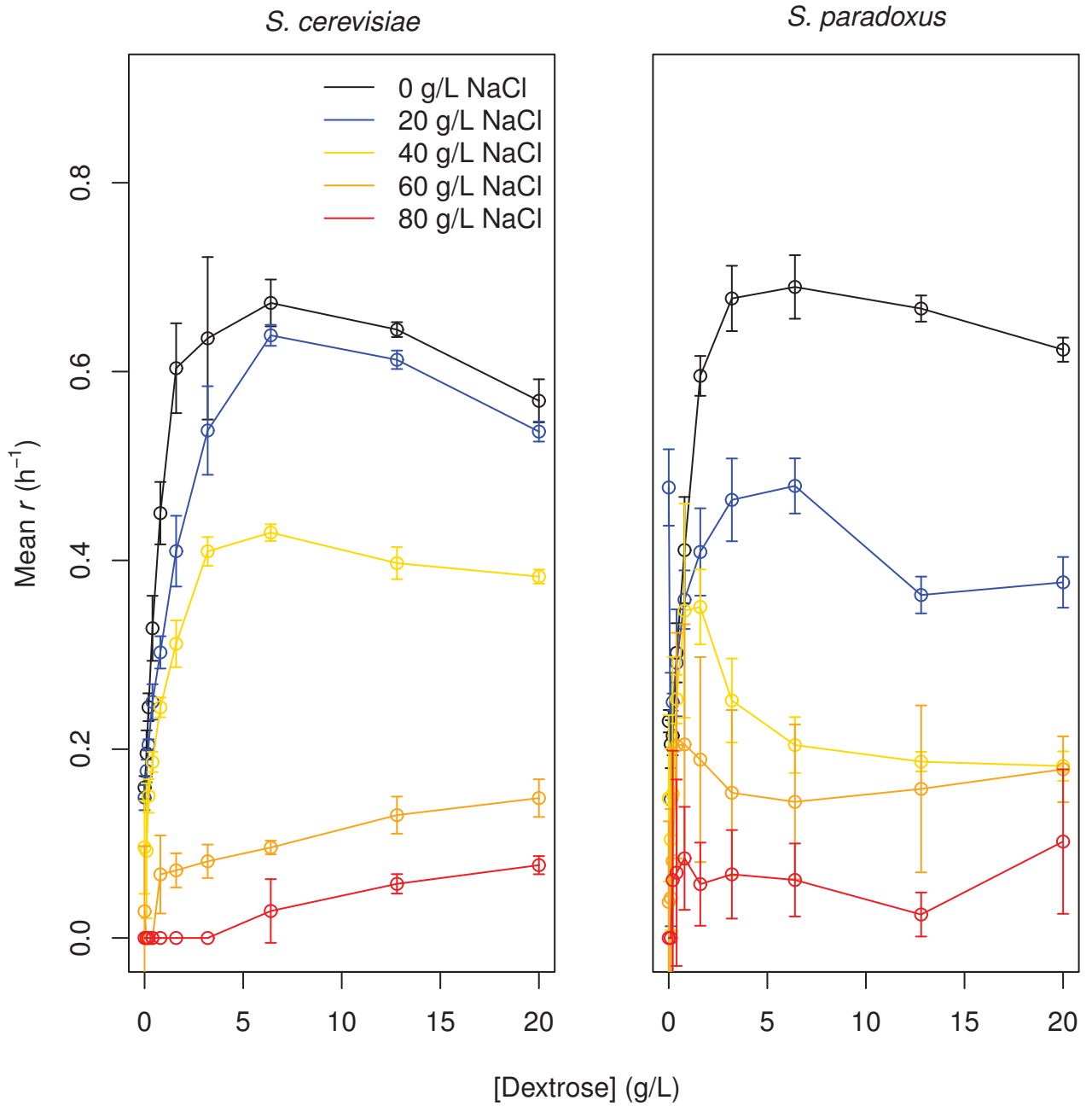
Fig. 4.35. Mean intrinsic growth rate (r) of the ancestral populations in each assay environment. n=6 for *S. cerevisiae*, and n = 5 for *S. paradoxus*. Error bars +/- 1 standard deviation.
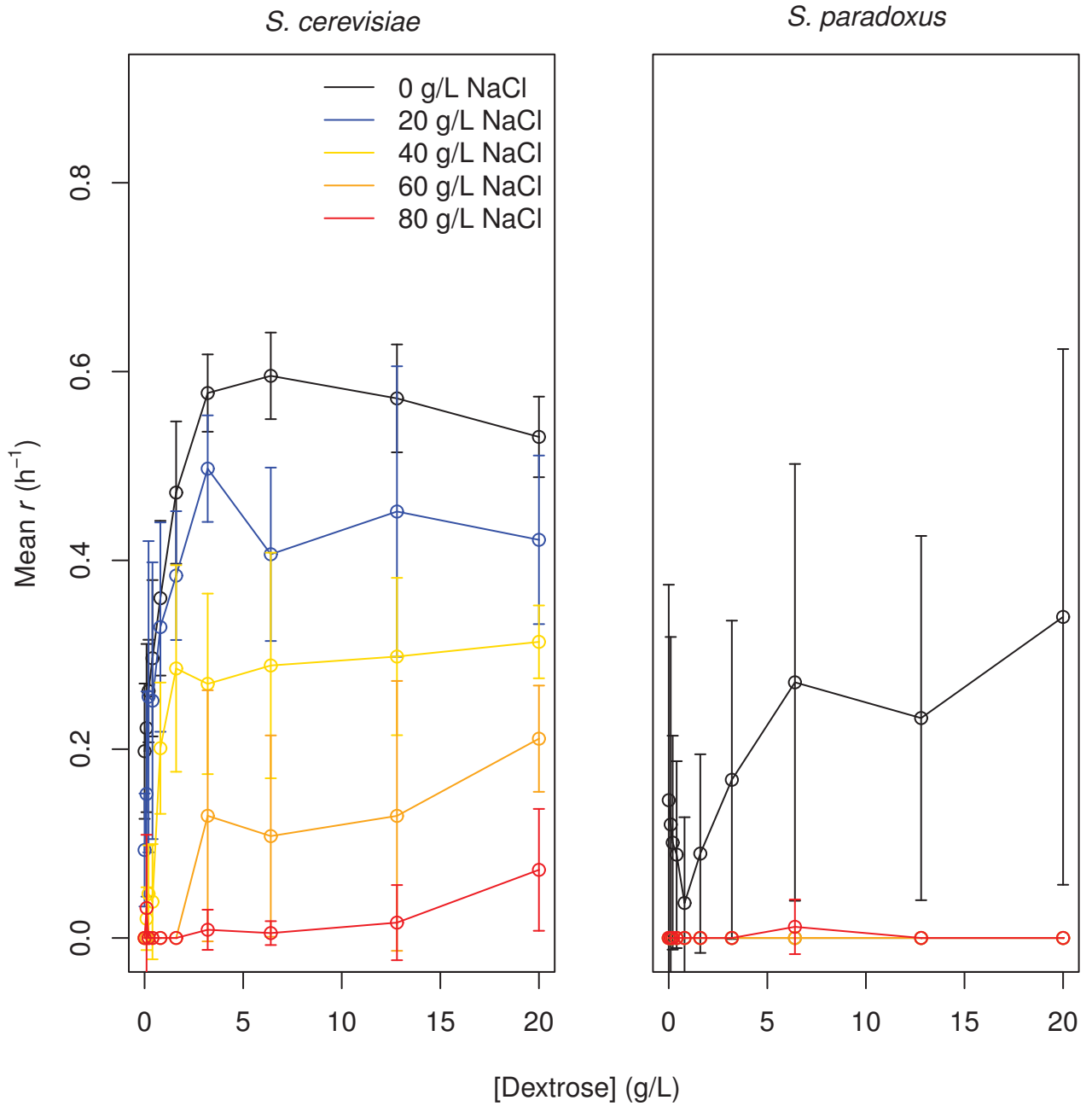
Fig. 4.36. Mean intrinsic growth rate (r) of the populations in each assay environment after selection in the LD + HS environment. n=6 for both species. Error bars +/- 1 standard deviation.
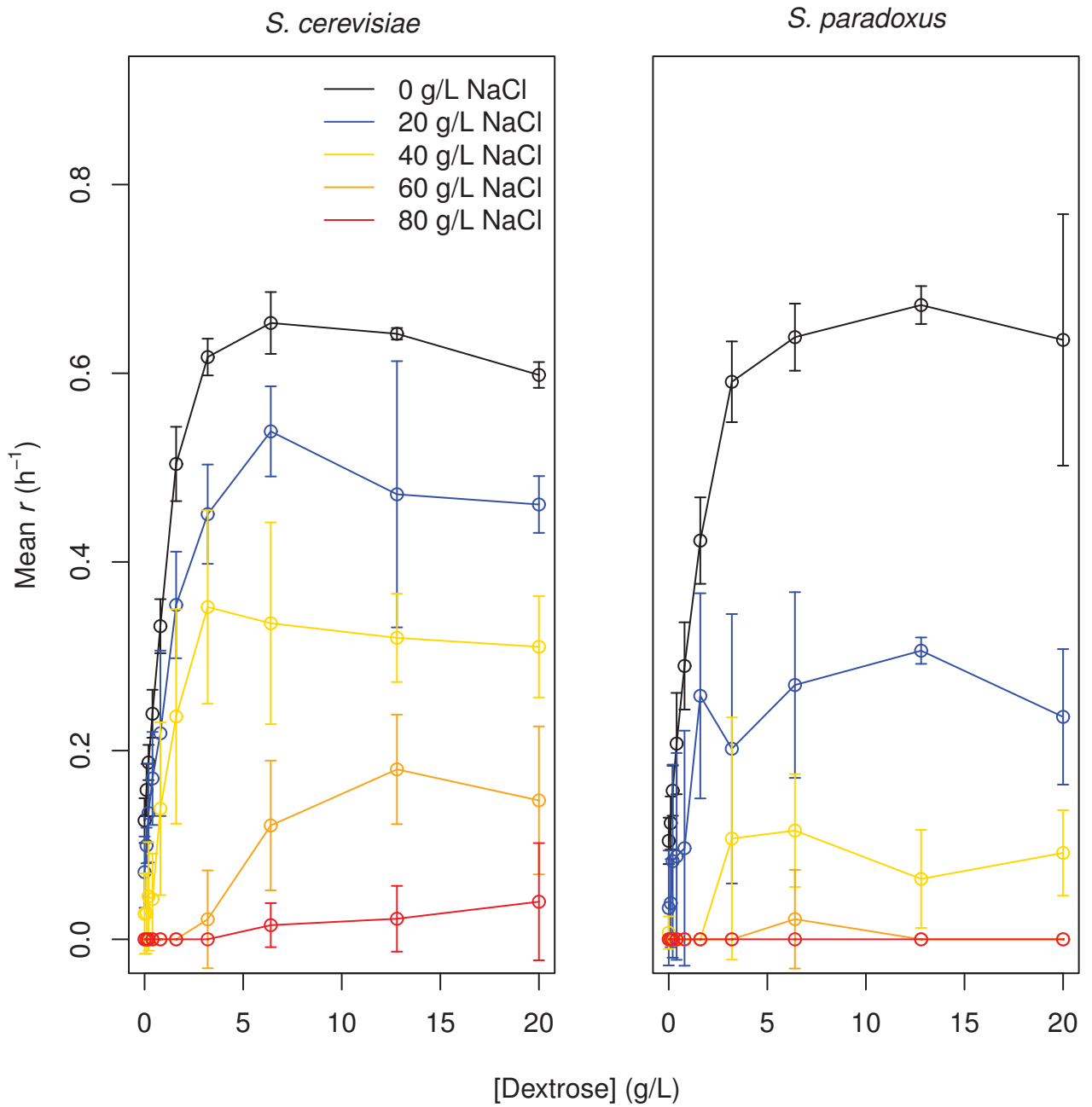
Fig. 4.37. Mean intrinsic growth rate (r) of the populations in each assay environment after selection in the LD environment. n=6 for both species. Error bars +/- 1 standard deviation.
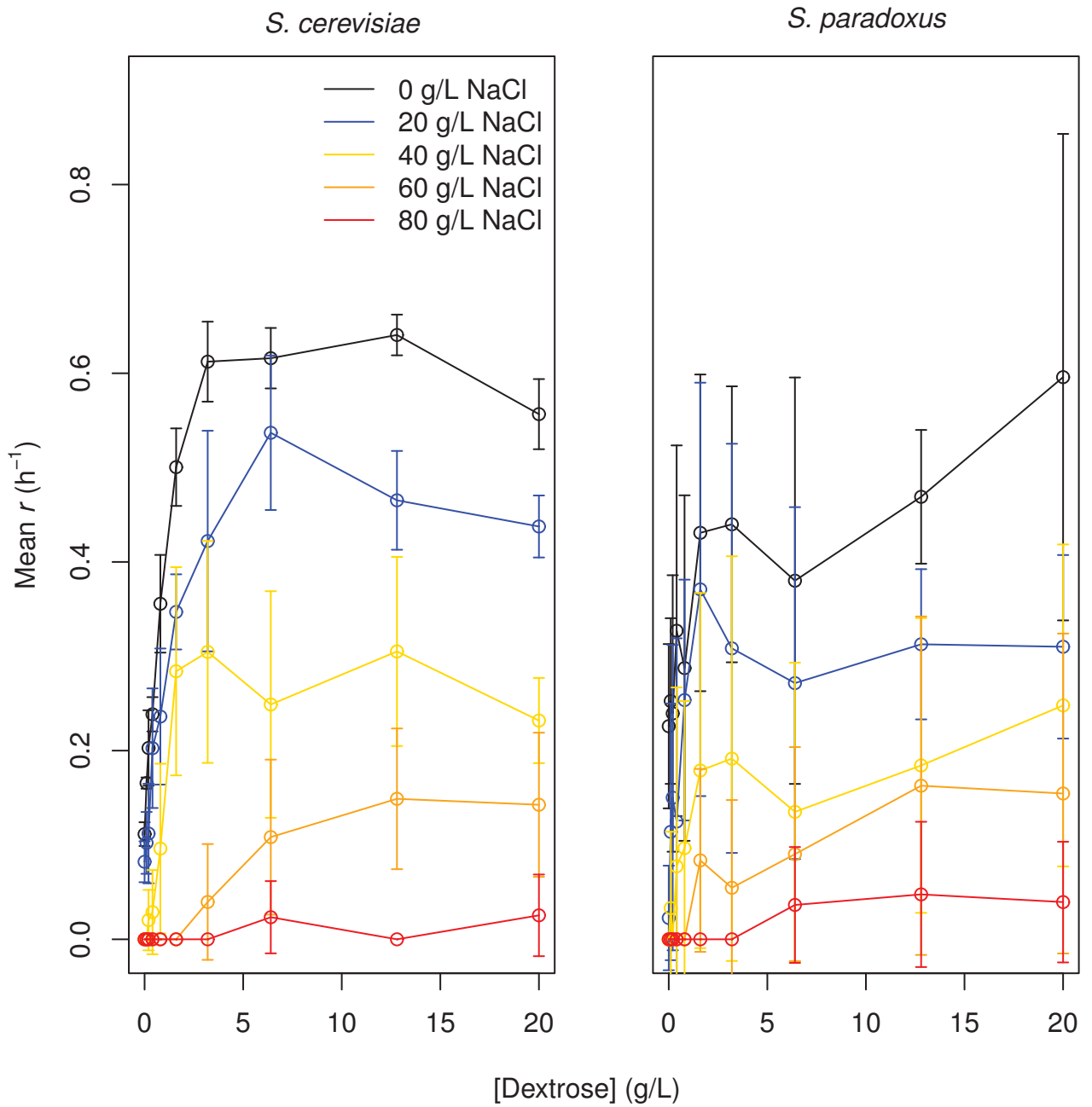
Fig. 4.38. Mean intrinsic growth rate (r) of the populations in each assay environment after selection in the HS environment. n=6 for both species. Error bars +/- 1 standard deviation.

Fig. 4.39. Mean intrinsic growth rate (r) of the populations in each assay environment after selection in the YPD environment. n=6 for both species. Error bars +/- 1 standard deviation.

Chapter 5

General conclusion

Early definitions of ecology demarcated a science dedicated to understanding the distribution and abundance of organisms (Elton 1927). Important to this goal is the relationship between organisms and their environment, not just in the ways that environments cont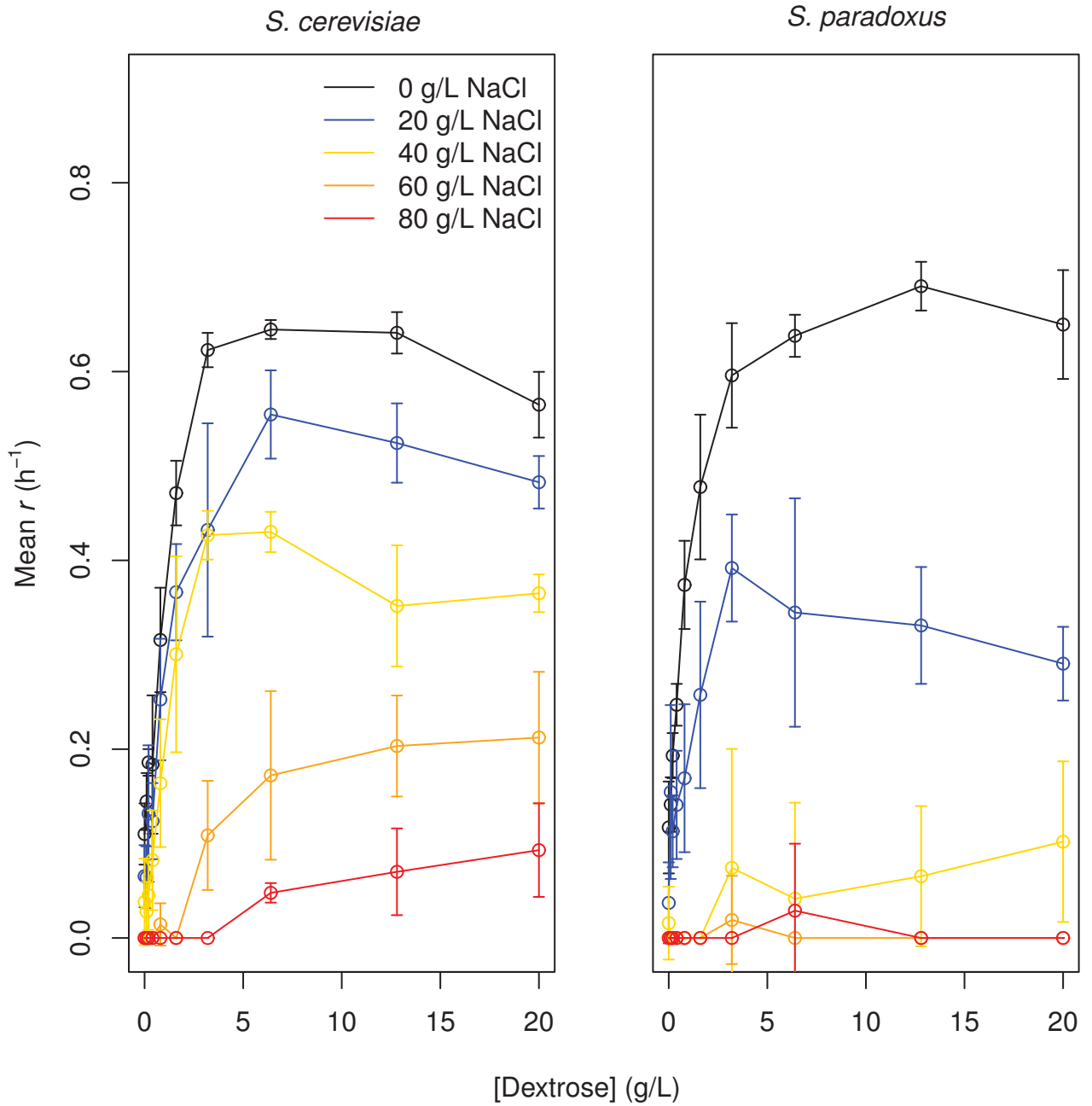rol distributions (Grinnell 1917; Hutchinson 1957), but also in the ways that organisms impact those environments (Leibold 1995; Odling-Smee et al. 2003). The ecological niche has been central to ecological understandings of these relationships.

The success of the niche concept in ecology is, at least partially, attributable to its generality. All organisms need an ecological opportunity to exploit, all organisms impact their communities through their functional roles, and fitness is defined by these relationships. Furthermore, the niche's association with competition (Chase and Leibold 2003), which has been a strong focus of evolutionary biologists and ecologists since the modern development of both disciplines, likely aided its success.

Yet despite claims to generality and associations with key concerns in ecology, the applicability of the niche has been questioned on a number of fronts. Different organisms may relate to the environment differently (Allen and Hoekstra 1992), and the receptivity of ecologists to general theories, as opposed to approaches grounded in natural history, has shifted through ecology's history (Kingsland 1985; Slack 2010). Doubts about the extent of competition's impact on ecological communities have assailed the competitive exclusion principle, one of the niche's key claims to predictive power, and, more recently, the claim that some competitors may be effectively equivalent (Hubbell 2001) has challenged the assumption that competitive biodiversity is tied to functional differences among competitors.

Ultimately each chapter in my thesis addresses how the niche guides ecological thought, and questions about the generality of the niche concept in ecology are inherent to this. Consequently, my thesis not only examines the niche literature, competitive dynamics, and the

evolution of the niche in response to stressful environments, but also provides an exploration of the generality of the niche either in how it has been used by ecologists, or in assessing the extent to which predictions derived from the niche are reliable in the face of environmental variation.

5.1 Specific conclusions and contributions to knowledge

The complex history of the niche and its central place in ecological thought have resulted in an extensive literature devoted to parsing its meaning, but relatively little attention has been paid to how different research communities have used it. To address this gap in knowledge in Chapter 2 I used a citation analysis framework to generate quantitative data on the ways in which the niche has been used, and I demonstrated that the niche spread from animal researchers first to sub-disciplines with a relatively broad focus before moving into relatively specialized sub-disciplines later in the 20th century. Despite my expectation that the different niche definitions would facilitate the spread of the niche concept I found no evidence to suggest that the existence of multiple definitions was essential to the niche's spread among ecological sub-disciplines. Finally, given the common use of the niche concept, I had expected the niche literature to be well integrated across sub-disciplinary boundaries. My examination of a number of sub-disciplines key to the history of the niche revealed, however, that connections between sub-disciplines were often weaker than would be expected due to chance, suggesting that the niche literature remains relatively un-integrated despite its common conceptual core. This tendency for under-citation of research from other sub-disciplines may indicate that the emergence of a truly integrated, and thus general, niche

literature had yet to form by the close of the 20th century. Such a lack of integration naturally limits the insight that ecologists might derive from research in related disciplines, and stands in opposition to ecology's search for unifying and general principles. Consequently, my research not only uses quantitative techniques to examine the history of a central ecological concept, but suggests that changes in how ecologists approach research literature may prove fruitful for future progress in ecology.

The ongoing debate in ecology about how to integrate niche and neutral perspectives on competition has led to a shift in how competition theory addresses competitive coexistence. My third chapter combined a classical model from niche theory with this emerging perspective in competition theory to assess the extent to which competitive outcome reflects the predictions of niche theory. I found that the extent to which competition resulted in the outcome predicted by niche theory was dependent on both the magnitude of fitness inequality and strength of stochasticity acting in the community. Consequently, my research contributes to the ongoing debate in contemporary ecology about the extent to which competitive dynamics are driven by niche or neutral processes, and suggests that the answer is likely to be context dependent. This result not only contributes to the dialogue in theoretical ecology about the forces that drive competitive dynamics, but also has implications for empirical research programmes, suggesting that research dedicated to uncovering how the fitness of competitors relates to environmental variation is essential to further advances in competition theory.

Human activities are accelerating many forms of environmental change, and consequently understanding how organisms respond to novel environments, and particularly stressors, is an increasingly important question. In Chapter 4 I examined how populations of yeast (*Saccharomyces cerevisiae* and *S. paradoxus*) responded to selection in four different envi-

ronments that offered different levels of stress. A major focus of this research was applying the methodologies of experimental evolution to questions at the heart of ecology, and consequently, along with fitness and the niche, this chapter also considered how fitness inequality, an essential, but relatively neglected component of competitive coexistence (Lankau 2011), would be affected in stressful environments. I found that instead of leading to niche expansion through adaptation, selection in some stressful conditions led to contraction of the fundamental niche and losses of fitness in the remaining portions of the fundamental niche for *S. paradoxus*, but not *S. cerevisiae*. This demonstrates that the niche's response to stressful novel environments may be population specific, and may result in both diminished species distributions and diminished potential for co-existence in those distributions. These results offer a disturbing outlook for the response of biodiversity to changing environments, as it suggests the negative impact of competitors may strengthen after selection in stressful environments, further restricting species distributions that are simultaneously restricted by increased sensitivity to abiotic conditions.

5.2   Future work

I examined the pattern of spread of the ecological niche in chapter 2, yet no concept exists in isolation, but is linked to other ideas. Through this thesis I have noted the strong association that has existed between the niche and competition, but the niche concept is also heavily intertwined with that of the ecological community. Both Grinnell (Grinnell and Swarth 1913; Grinnell 1917) and Elton (1927) effectively defined niches that represent the atomic units from which communities are built, and a major application of all the central niche definitions has been to explain community composition. Despite being the primary object

of study for community ecologists, most histories of the community concept have focused primarily on plant ecology (Allen and Hoekstra 1992; but see Clements and Shelford 1939), and so the time seems ripe for a history of the community concept that examines how it has been used in a variety of ecological sub-disciplines. Such a history would not only illuminate the chief unit of study for community ecology (i.e. the community), but, by comparing and contrasting the patterns of disciplinary spread of the community with that of the ecological niche, it would also examine the relationships between these two concepts.

My modelling and experimental work focused on the role of fitness inequality in ecological dynamics, and how evolutionary processes affect fitness inequality. In Chapter 3 I demonstrated that the ecological consequences of competition are dependent on the magnitude of fitness inequality between competitors, and suggest that this may signal that the characterization of competition as a niche or neutral process may be environmentally contextual. Such a claim rests on the assumption that competitive systems do in fact exist along environmental gradients where the relevant fitness inequalities that structure competition vary. Addressing this assumption will be an important step in assessing the nature of competition; theoretically ecology appears to be arriving at a synthesis between neutral and niche theories, but the question about the applicability of these perspectives in nature is an empirical one that must be answered through a range of environmental conditions.

There is an increasing recognition that studying ecology and evolution in simple systems may yield results quite different from studies conducted in more complex communities. In particular, there is increasing awareness of the importance of biodiversity on the evolution of competitive systems, as research demonstrates that biodiversity may provide selection pressures that encourage diversification, but also may prevent diversification through niche pre-emption (De Mazancourt et al. 2008; Bailey et al. 2013). Theoretical work has suggested

that neutrality is more likely to evolve in diverse communities (Holt 2006; Hubbell 2006), but relatively little empirical work has examined an effect of biodiversity on average fitness inequalities within competitive systems.

Fitness inequality is just one part of contemporary competition theory, however, and competitive coexistence is also determined by niche differentiation. Theory predicts that in some cases competition should lead to niche divergence, but in cases where niches are not substitutable it may lead to niche convergence (Abrams 1987). Such niche convergence is a possible source of equalizing mechanisms (Lankau 2011), and it would be interesting to examine whether competition for non-substitutable resources is a particularly rich evolutionary source of neutral and near-neutral competitive systems.

5.3 General conclusions

Ultimately my thesis demonstrates that, though there may be limitations to the generality of at least certain understandings of the niche concept, the niche has been a productive concept in many fields of ecology, and continues to usefully guide research in ecology and evolution. This perspective is supported by the resurgence of interest in niche theory in the wake of neutral theory's advent.

Each of my chapters demonstrated some limitation to the generality of niche thought. In Chapter 2 I demonstrated that while the niche had become a conceptual tool used across ecology, it has not led to a fully integrated literature, suggesting that a truly integrated niche literature had yet to arise. My third chapter showed that niche theory is unlikely to be able to consistently predict the outcome of competitive dynamics in all situations. Finally, in Chapter 4 I demonstrated that the response of the niche to environmental stressors may

201

differ greatly between different populations.

These limitations to the generality of niche theory do not, however, fundamentally impact the importance of the niche in ecology. Ecologists have long realized that the predictions of niche theory are limited, and have productively used deviations from niche theory as useful starting positions to more deeply illuminate ecological processes (Hutchinson 1961). The niche concept has itself changed through time to respond to these challenges, such that today it arguably not only includes the ways in which species differ in their response to environmental variation, but also the ways in which species are similar. Such a vision of the niche is not new, but the emergence of an acceptance on the part of ecologists that competitive similarity may impact the form of competitive dynamics, is ongoing. The juxtaposition and synthesis of traditional niche and neutral perspectives appears to have been immensely productive for community and evolutionary ecology, and the niche will no doubt continue to inspire thought as new questions take the forefront of ecological inquiry.

5.4   Literature Cited

Abrams, P. A. 1987. Alternative models of character displacement and niche shift. I. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. Evolution 41:651–661.

Allen, T. F. H., and T. W. Hoekstra. 1992. Toward a unified ecology. Columbia University Press, New York.

Bailey, S. F., J. R. Dettman, P. B. Rainey, and R. Kassen. 2013. Competition both drives and impedes diversification in a model adaptive radiation. Proceedings of the Royal Society B 280:20131253.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches linking classical and contemporary approaches. University of Chicago Press, Chicago.

Clements, F. E., and V. E. Shelford. 1939. Bio-ecology. J. Wiley & sons, inc., New York.

De Mazancourt, C., E. Johnson, and T. G. Barraclough. 2008. Biodiversity inhibits species' evolutionary responses to changing environments. Ecology Letters 11:380–388.

Elton, C. S. 1927. Animal ecology. Macmillan Co., New York.

Grinnell, J. 1917. The niche relationships of the California Thrasher. Auk 34:427–433.

Grinnell, J., and H. S. Swarth. 1913. An account of the birds and mammals of the San Jacinto area of southern California: with remarks upon the behavior of goegraphic races on the margins of their habitats. University of California Press, Berkeley.

Holt, R. D. 2006. Emergent neutrality. Trends in Ecology & Evolution 21:531–533.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press., Princeton.

Hubbell, S. P. 2006. Neutral theory and the evolution of ecological equivalence. Ecology 87:1387–1398.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415–427.

Hutchinson, G. E. 1961. The paradox of the plankton. The American Naturalist 95:137–145.

Kingsland, S. E. 1985. Modeling nature: episodes in the history of population ecology. University of Chicago Press, Chicago.

Lankau, R. A. 2011. Rapid evolutionary change and the coexistence of species. Annual Review of Ecology, Evolution, and Systematics 42:335–354.

Leibold, M. 1995. The niche concept revisited: mechanistic models and community context. Ecology 76:1371–1382.

Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 2003. Niche construction: the neglected process in evolution. Princeton University Press, Princeton.

Slack, N. G. 2010. G. Evelyn Hutchinson and the invention of modern ecology. Yale University Press, New Haven.