AN ABSTRACT FOR THE DISSERTATION OF

Roland B. Russell for the degree of Doctor of Philosophy in Zoology presented on April 14, 2005.

Title: Biodiversity: Illustrations of Some Concepts, Causes, and Consequences.

Abstract approved:

Redacted for Privacy

Bruce A. Menge

Jane Lubchenco

Careful analysis and thoughtful synthesis will be necessary for expanding the envelope of ecological understanding. This work is my attempt at communicating both of these, in relation to three questions about our understanding of the structure and dynamics of biological diversity. These questions focus on a) advancing our understanding of the relations of organismal form and physiological process, b) explaining the overwhelming influence of ecological context on the relationship between local ecological processes and regional evolution and dispersal processes in driving local species richness patterns, and c) demonstrating the causal effect of biological trait diversity on community photosynthetic processes. Chapter two addresses how we conceptualise diversity, and concludes that although simple (i.e., univariate) morphologically-based functional group models for macroalgae are not functionally predictive, morphology does play a key role in ecophysiological responses. Using morphological attributes to successfully infer macroalgal behaviour would be a remarkable advance for marine ecology, and appears attainable. Chapter three demonstrates the overwhelming importance of ecological context in altering the predictions of theory. Specifically, we demonstrate that regional species pools have reduced influence on local richness at small local scales, within interactive groups of species, and in higher intertidal zones. We conclude with a synthesis of how ecological competition, abiotic stress, and positive interactions may act in concert to influence local richness. Chapter four analytically investigates the role of diversity in changing how ecosystems function. I argue that all effects of diversity must act through species traits, and that the current debate regarding
the influence of species richness *per se* versus species traits is misguided. Instead, I propose a focus on the roles of the presence of, versus interactions between, traits. I provide empirical evidence that five tidepool communities each containing five species have a higher average photosynthetic rate than the same total biomass of each of the five species arranged into five monocultures. This mechanism, detected in photosynthetic rate (one of the most fundamental ecological functions), should be common to ecosystems other than marine intertidal pools. Finally, chapter five concludes with a recap of the key results from these studies, and a look to the future.

APPROVED:

Redacted for Privacy
Co-Major professor, representing Zoology

Redacted for Privacy
Co-Major professor, representing Zoology

Redacted for Privacy
Chair of the Department of Zoology

Redacted for Privacy
Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature authorizes release of my dissertation to any reader upon request.

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Roland B. Russell, Author
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Clichéd though it may appear, I would not have completed this dissertation if it were not for the friends, family, and colleagues that have kept me afloat. My deepest and most sincere thanks, to all of you.

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CONTRIBUTION OF AUTHORS

Spencer Wood helped with data collection, analysis, interpretation, synthesis, and writing (in other words, all parts) of Chapter 3. Gary Allison helped with design, data collection, interpretation of the results, and synthesis of Chapter 3. Bruce Menge and Jane Lubchenco helped with design, instigating data collection, supported the research, and provided advice on interpretation of the results of Chapter 3.
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Dedication

This work is dedicated to four stunning people whom I miss dearly, and wish that I could share my current existence with:
Calvin Russell, Gus Leitner, Sam Hicks, and Franz Dolp.
Preface

(an alternative definition of the reality of diversity)

"Now when I write of paradise I mean Paradise,
not the banal Heaven of the saints.
When I write "paradise" I mean not only apple trees and golden women
but also scorpions and tarantulas and flies,
rattlesnakes and Gila monsters,
sandstorms,
volcanoes and earthquakes,
bacteria and bear, cactus, yucca, bladderweed,
ocotillo and mesquite, flash floods and quicksand,
and yes--disease and death and the rotting of the flesh."

"... the Paradise of which I write and wish to praise is with us yet,
the here and now,
the actual, tangible, dogmatically real earth
on which we stand."

Edward Abbey
(1968).
Biodiversity: Illustrations of Some Concepts, Causes, and Consequences.

Chapter 1 ~ General Introduction

How do ecosystems work? This overarching question has guided the research that I presented in this thesis. I pose three sets of questions under this broad conceptual umbrella.

1) How should we identify types of diversity? Specifically, can we develop a predictive functional understanding of organisms based on easily assessed descriptive characteristics?

2) What causes diversity? Specifically, do local ecological interactions trump historically derived regional species pools in determining local species richness?

3) What are the consequences of diversity for system dynamics? Specifically, do biologically diverse systems function differently than biologically depauperate ones? How do we mechanistically expect diversity to influence the functioning of an ecosystem?

Various permutations of these questions have been and continue to be persistent foci of ecological science. Intellectual giants of the past such as Lamarck (1809), Wallace (1858), and Darwin (1859) all focused their energy on understanding morphological adaptation of organisms to ecological environments. This work has evolved into an active field of research attempting to understand the role of organismal morphology in predicting ecological function (Koehl 1996, Westoby 2002, Lavorel and Garnier 2002). Efforts to understand the factors underlying the ecological causes of biological diversity at a community scale have similarly occupied the time of most of the ecological icons, and has received sustained attention through the years (e.g. Hutchinson 1959, Connell and Orias 1964, MacArthur and Wilson 1967, Paine 1969, Lubchenco 1978, Menge and Sutherland 1987, Huston 1994). In addition, at least as far back as Darwin (1859), ecologists have been, and continue to be, intrigued by the potential consequences of biological diversity in communities (MacArthur 1955, Elton 1958, May 1973, McNaughton 1977, Cottingham et al. 2001, Worm and Duffy 2003). Recently this latter interest

Conceptualisations of diversity and functional utility

"The environment affects the shape and organization of animals, that is to say that when the environment becomes very different, it produces in course of time corresponding modifications in the shape and organization of animals."

J. B. Lamarck. (1809)

Question

Can morphological diversity be used to infer ecological function? The products of the incessant evolutionary play in the ecological theatre around us (Hutchinson 1965) are manifest as morphologically different types of organisms (Lamarck 1809, Wallace 1858, Darwin 1959). Adopting some circular causal inference, we can thus predict that knowing morphological form of an organism should grant us, to some extent, the ability to predict ecological behaviour (Hutchinson 1948). It is this goal—being able to describe diversity in terms of types of species, and use this description to some useful ends allowing for the prediction of ecological function—which has motivated my work on function-form relations in New Zealand macroalgae (Chapter 2).

Over thirty years ago, MacArthur predicted that a key advance in the ecology of species coexistence would come with a more lucid understanding of how organisms of type A interact with organisms of type B (MacArthur 1972). I argue that the same prediction still holds and has only become more pertinent and pressing in the intervening years. Although we are making definite advances in predictive functional ecology in terrestrial plant systems (Diaz and Cabido 2001, Lavorel and Garnier 2002, Cornelissen et al. 2003), in many other systems (e.g. marine ecosystems in general) we are sorely lacking in an operational understanding of predictive functional-form relationships. My second chapter is directed at helping take marine ecology closer toward this long-standing goal.

Rather than describing the types of organisms in a system (as both Hutchinson [1948, 1959] and MacArthur [1972] touted the merits of), the currently accepted approach to describing the
biological diversity in an ecosystem is to resort to quantifying and communicating the number of species in the system, and perhaps the evenness (relative equity of relative abundances) of these species. I believe that if we wish our description of diversity to represent some functionally relevant aspect of the ecosystem, a revision of this approach is necessary. I propose that in order to more appropriately describe diversity, we need to actively invest energy in the development of approaches to predict and describe how organisms behave, based on easily assessed morphological descriptions or classifications of these organisms (Westoby et al. 2002, Cornelissen et al. 2003). Can we effectively make this leap from descriptive structural characteristics to explaining functional behaviour, that is, the leap from morphological form and structure to ecophysiological responses to abiotic and biotic gradients? Or, perhaps more aptly, how do we most effectively make this step?

State of the science

Evidence indicates that the currently existing hypotheses linking form with function in marine macroalgae (Littler and Littler 1980, Gaines and Lubchenco 1982, Steneck and Watling 1982, Steneck and Dethier 1994) have met with only moderate success for predicting general ecological function (Padilla and Allen 2000). Other morphologically based models exist, yet their physiological explanatory power remains untested (e.g. Dring 1982). One explanation for the failure of these models is that the dramatic plasticity in macroalgal morphological form allows for extremely disparate mechanistic means to similar ends. For example, coping with desiccation by heavy cortication (i.e., a robust layer of cells, the cortex, on the portions of an alga exposed to the external environment) and retention of internal water versus densely branched non-corticated forms retaining external water. This mechanistic variation, in turn, renders the current one-dimensional classification systems relatively ineffective at predicting multi-dimensional physiological responses. That is, the focus on a classification scheme that classifies each taxon into a nominal category (e.g. apples, oranges) seems likely to be unresponsive to alternative morphological solutions to a problem such as desiccation. I predict, however, that a less linear classification system, rooted in a multi-dimensional set of readily assessable descriptors of macroalgal characters, should do a more effective job at providing a functionally predictive system based on algal form (Johansson and Snoeijs 2002).

Approach

No broad multi-species tests of the of these morphological models for predicting ecophysiological responses to abiotic gradients exist (Padilla and Allen 2000). Johansson and Snoeijs (2002) get closest to this goal by analyzing the static (e.g. non-stressed) photosynthetic behaviour of 32 species as a function of depth. Nonetheless, a generic link between
morphological form and ecophysiological stress responses remains tenuous. To test the prediction of a broad-scale linkage between functional-form models and ecophysiological stress responses, I studied the physiological photosynthetic response to desiccation of 51 New Zealand algal taxa. These taxa span all defined functional-form groups of multicellular algae, all major phyla and classes of marine algae, three orders of magnitude in size, and occupy the entire range of intertidal habitats. This substantial increase in the number of species assessed relative to past studies improves both the resulting generality of conclusions and the statistical ability to tease apart relationships in broad, multivariate physiological and morphological space. Using repeated pulse-modulated fluorometry and weight measurements, I was able to represent strategies of resilience and resistance of marine macroalgae to desiccation stress in multidimensional physiological space. Functional-form groups were then analyzed for ability to explain variation in these physiological response strategies. Finally, a set of easily assessed morphological variables was derived and tested as a multi-dimensional explanatory model for this complex ecophysiological behaviour. These analyses have the potential to provide substantial and novel insight into the link between the structural composition of organisms, particularly marine macroalgae, and their consequent ecological response to physiological stress.

Causes of diversity and contextual constraints

"[W]hy are there so many kinds of animals?"

G. E. Hutchinson (1959)

Question

My third chapter attempts to illuminate some of the factors that determine how many species exist in a particular place. An additional facet of this question is how we expect this relationship to change as we alter the spatial scale, habitat, and focal species of our observations. Given our vast understanding of the potential importance of local ecological interactions on influencing local communities (e.g. Tansley 1917, Clements et al. 1926, Gause 1934, Paine 1969, Lubchenco 1978), and our only slightly less long-established understanding of the potential influence of regional species pools on local community richness (MacArthur and Wilson 1967, Terborgh and Faaborg 1980), can we demonstrate the conditions under which we expect to see local interactions being relatively more important than regional species pools, and vice versa? This work, done in collaboration with colleagues, addresses three questions. First, how strong is the influence of ecological context in dictating expected predictions of these relationships between local and regional species richness? Second, can we identify under what contexts
local interactions dominate regional species pools in driving local richness? Third, can we provide a novel conceptual model and updated ecological framework with which to reconcile past discrepancies in published conclusions from investigations of local interactions versus regional species pools as drivers of local richness? These questions form an important foundation for ecological research approaches in general: how important is context, what are the relative effects of alternative hypotheses, and can we reconcile past disagreements with careful logic and synthesis?

State of the science

The birth (Terborgh and Faaborg 1980), growth (e.g. Cornell 1993) and eventual, from my perspective, mistreatment (see Westoby 1998, Huston 1999, Srivastava 1999, and Loreau 2000 for reviews of inappropriate applications) of the techniques in this subfield of ecology (biodiversity-ecosystem function studies) have produced an intriguing history. Given their hypothesis that local ecological interactions could place an upper ceiling on the number of species in a system, Terborgh and Faaborg (1980) utilized a simple graphical approach to test a suite of predictions relating to this hypothesis. In the quarter century since, a number of analyses of this particular pattern have utilized these techniques but have paid little regard to the ecological context in which their observations took place (Srivastava 1999, Hillebrand and Blenckner 2002). A number of large-scale surveys (often based on literature reviews and range maps, rather than observations of actual communities) have reached, I believe, conclusions that can be explained ultimately by ecological context rather than ecological interactions.

For example, Caley and Schluter (1997), reached the conclusion that local diversity patterns were dominated by regional species pools, but the data they analyzed assessed ‘local’ communities approximately the size of counties (25,000 km²), and their estimates of local richness were collated from overlapping distributions on large-scale range maps. However, this scale is far larger than the scale on which most organisms interact. For example, competition or predation typically occur between individuals or aggregations of individuals, which can thus be assumed to occur on spatial scales that are closer to the sizes of individuals or patchy aggregations of these individuals. Rarely do these scales of interaction approach areas as large as thousands of square kilometres. Clearly we do not generally predict local ecological interactions will limit local richness on these spatial scales (Loreau 2000), nor can we expect to detect signatures of local ecological interactions when the data utilized do not contain the signatures of such local interactions, for example when using range maps to estimate local richness (Hurlbert and White 2005). A substantial portion of the existing confusion surrounding this topic, I predict, can be eliminated by more explicit recognition of the ecological context of
these experiments, and appreciation of the influence of these contextual effects on predictions of ecological theory.

**Approach**

We analyse, in this third chapter, large scale patterns in species richness in intertidal communities across the US coast of the northeast Pacific Ocean, from northern Washington to southern California. Predictions are made, rooted in our novel conceptual framework relating spatial scale and species groupings to detection of potential effects of local ecological interactions on local species richness. We then analytically partition these data into different species groupings (e.g. trophic levels) and different habitats (e.g. low, mid, and high intertidal zones), and analyse observed relationships between local and regional species richness across different 'local' spatial scales. Given the contextual breadth of our empirical approach, we are able to demonstrate how the likelihood of seeing the signature of local interactions limiting local richness is dependent on focal spatial scales, habitat types, and species groupings. This analysis is relatively unique in its utilization of such a spatially extensive and fine-grained empirical ecological survey to explicitly test contextual factors and their relation to ecological theory. We believe that these analyses will provide a useful predictive model that can reconcile past differences evident in the existing literature.

**Consequences of diversity to system functioning.**

"It has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can be raised in the latter than in the former case ... the truth of the principle that the greatest amount of life can be supported by the great diversification of life, is seen under many natural circumstances"

Darwin (1859)

**Question**

After exploring the factors underlying the ecological causes of biological diversity, it seems pertinent to turn my attention to the potential consequences of diversity. I specifically focus on whether there are systemic functional consequences of variation in species richness. Given the well-documented alteration of diversity around the world by humans (Global Biodiversity Assessment 1995, Vitousek et al. 1997, Millennium Assessment 2005), a link between diversity and ecosystem functioning implies that we may be altering the fundamental fabric of
ecosystems in more insidious ways than we are currently aware. As such, gaining a better understanding of the mechanics of this relationship between diversity and system functioning are potentially extremely important if we care to understand and mitigate our anthropogenic impacts on natural systems.

State of the science

Evidence is accumulating which appears to strongly support a link between species richness (one metric of biological diversity) and the functioning of ecosystems (i.e. transfers of mass or energy through ecosystems; Naeem 2002, Hooper et al. 2005, Spehn et al. 2005). I believe that the recent bloom in analyses of the relationship between ecosystem functioning and diversity (Cameron 2002) has brought with it a profusion of (occasionally, at least) unnecessary debate. Although some elegant attempts have been made to elucidate mechanisms (Caldeira et al. 2001, Hodgson et al. 2002, Jonsson and Malmqvist 2003), the current state of biodiversity and ecosystem functioning theory is not as mechanistic as it should be given the amount of energy that has been devoted to analysis of the topic in recent years. The novelty of my approach to this question illuminates some important mechanistic aspects of the relationship, and identifies potential pitfalls of experimental analyses in this field. Based on logic and empirical evidence, I argue that all effects of diversity on ecosystem functioning must act via variation in traits, and that the debate regarding strength of effects of species richness per se versus effects of functional traits of species is misguided and not productive.

Approach

Diane Srivastava (unpub. MS) presents a three-phase description of biodiversity research: is biological diversity able to affect ecosystem process, is biological diversity likely to affect ecosystem process, and is biological diversity important for ecosystem process. In Chapter 4 I address the ability of diversity to influence system processes, and touch on the importance (relative to community biomass) of biodiversity. In this fourth chapter I present my analytical deconstruction of the relationship between macroalgal community photosynthetic rates and species richness. This analysis allows me to attribute variation in this ecosystem process to a) the presence of particular species traits versus b) the interaction between different traits. In addition, novel application of existing statistical approaches provided a method to estimate the amount of the relationship between photosynthetic rates and species richness that could be attributed hypothetically to differential resource overlap between inter- versus intra-species individuals. These assessments offer new insight into the relationship between species richness, variety in traits, and system functioning. Specifically, I illustrate how partitioning the effect of species richness into effects of trait uniqueness versus trait interactions allows for a
substantial advance in our understanding of this relationship between species richness and ecosystem functioning. Most importantly, I feel, this chapter provides some recommendations as to how we could refocus our attention to increase the productivity of our explorations of this ecological paradigm.

Summary

The following three chapters deal with three fundamental aspects of our understanding of the structure and dynamics of biological diversity. Chapter two addresses how we classify diversity, and the importance and difficulty of developing a more functionally-based ecological perspective. Chapter three demonstrates the overwhelming importance of ecological context in altering the predictions of theory, and provides a new conceptual approach for understanding the relative influences of ecological interactions, regional species pools, and abiotic stress in driving local species richness. Chapter four analytically investigates the role of diversity in changing how ecosystems function, demonstrates some new ideas about how we should think about and empirically address this relationship, and reiterates the prevalent influence of organismal traits on ecosystem functioning. Finally, chapter five concludes with a recap of the key results from these studies, and a look to the future.
Chapter 2 ~

Why appearances matter: macroalgal morphology explains desiccation tolerance in 49 intertidal species.

Roland B. Russell

To be submitted to Ecology
Abstract

An ability to predict ecological function, based on form, is an appealing notion in ecology. Marine macroalgal systems lack an adequately predictive model that infers general function from form. By assessing the desiccation tolerance of a large number of diverse macroalgal taxa (49 species and 2 morphotypes), I was able to explicitly test three hypotheses. 1) Morphology influences macroalgal response to desiccation. This was supported. 2) Morphological functional-form models for marine macroalgae, as they currently exist, explain functional desiccation responses. This was supported, but the data indicate that this relationship is weak and that these categorical functional-form models provide negligible predictive power. Lastly, 3), it is possible that a simple multi-dimensional suite of easily assessed macroalgal descriptors can more adequately predict functional behavior than these functional-form models. This hypothesis was also supported. I argue, in conclusion, that current one-dimensional approaches to functional-form classification systems are inadequate and should be replaced with multi-dimensional approaches that stress ease and speed of information acquisition. Deriving and understanding such models to create a more predictive functional ecology should be a more active focus of marine ecology.
Introduction

"A visitor arriving in the tropics notices first, perhaps from the plane window, the rather light metallic green on the foliage compared to temperate foliage. On landing he smells the various fungi that make the tropics smell like a moist greenhouse. On closer examination, the leaves of the forest trees are puzzlingly uniform to one used to using leaf shape to identify temperate trees. Very few leaves of trees of the forest interior have lobed leaves like our oaks, or stellate leaves like our sweet gums, or leaves with toothed margins like our elms. Instead, almost all the leaves seem to be elliptical with smooth margins and, perhaps, an acute tip. The bark too seems strikingly uniform. In fact, the experienced tropical forester will hack the tree with his machete and note the color and consistency of the sap that oozes out, and the color of the cambium layer. He finds these, plus the forms of the buttresses around the base of the tree, to be the most useful identification points. But why are temperate leaves so irregular? Or why are tropical ones so regular? The question has never been properly answered, but we have some hints."

(MacArthur 1972)

Why are the trees that surrounded MacArthur, whether in the forests of Vermont or Panama, morphologically different? Morphology must be a manifestation of ecophysiological differences between these trees: if elliptically shaped, smooth-margined, acute-tipped leaves function differently than other shapes, this geographical difference is ecologically expected. Our understanding of the role of a species in an ecosystem, I believe, is substantially informed by visual recognition of morphological variation. In terrestrial plants, for example, our common verbal classifications of trees versus shrubs, or woody versus herbaceous forms, are grounded in distinctions of morphology, and have predictable implications for the functional behaviour of these types of individuals (Diaz and Cabido 2001, Lavorel and Garnier 2001, Westoby et al. 2002). A list of species abundances will tell us less about the functioning of a foreign ecosystem than would a list of abundances of types. A kelp forest is understood, for example, as a system based on certain morphological types of species, rather than particular identities. My goal here is to advance our understanding of the classification of organisms into
morphologically based groups, and illuminate the role of morphological diversity in altering ecophysiological behaviour.

A number of convergent functional-form (a term used hereafter to refer to form-based classifications systems assumed to infer function) classification systems have been proposed for macroalgae, with consequent functional predictions for both algal ecophysiology and community ecology (Littler & Littler 1980, Gaines and Lubchenco 1982, Steneck & Watling 1982, Steneck & Dethier 1994). A unique approach is taken by Dring (1982), who classifies plants morphologically based on structure, ontogeny and growth patterns of algal thalli (hereafter referred to generally as a structure-based system). Most of these functional-form models converge upon a basic categorical morphological system that groups species based on the degree of branching, cortication, and calcification, in concert with the flatness of fronds, robustness, and/or overall size of the plant. Steneck and Dethier (1994), for example, distinguish categories of 1) single cell microalgae, 2) filamentous algae, 3) foliose algae, 3.5) corticated foliose algae, 4) corticated macrophytes, 5) leathery macrophytes, 6) articulated calcareous algae, and 7) crustose algae. Steneck and Dethier (1994) propose a continuous functional-form metric, which is represented by the numbers assigned in the previous list: for example, corticated thalli are scored higher than uncorticated thalli, implying not just categorization, but also rank order of function. Dring’s (1982) structure-based classification system focuses, instead of form, on growth structures and the degree of complexity in general growth patterns (e.g. filamentous growth which can be uniaxial, multiaxial, heterotrichous, or pseudo-parenchymatous). For the purposes of this paper, I make a distinction between structure and form; structure is defined as the way in which parts are arranged or put together to create a whole organism, while form refers to outward appearance and shape of an organism. Links between either form- or structure-based algal classifications and the consequent functioning of these taxa have been demonstrated (Littler and Littler 1980, Gaines and Lubchenco 1982, Gacia et al. 1996, Johansson and Snoeijs 2002), but the relationship does not hold for other ecologically relevant functions (e.g. Dudgeon et al. 1995, Padilla and Allen 2000, Gomez et al. 2004), and none of the available models have been widely adopted as a generic classification system for marine macroalgae that both distinguishes morphologically descriptive types and is simultaneously functionally informative. In order for a morphological macroalgal classification system to be ecologically useful, it must describe ecophysiological species behaviour reasonably well based solely on identified group membership. Although examples of success of functional-form models are becoming more common in terrestrial plant systems (e.g. Lavorel et al. 1999, Garnier et al. 2001), the relationship is not widely applicable to marine plants, and the available approaches are claimed to be inadequate at providing a generic link
from form to function in marine systems (Padilla and Allen 2000). Indeed, Padilla and Allen (2000) make the claim that the ‘paradigm is lost’ and implies that we should refocus our energy on questions relating functionally-defined groups to infer system function. Yet, while marine ecology may be losing a paradigm, plant ecology appears to be gaining ground on the Holy Grail of a trait-based functional ecology (Lavorel and Garnier 2002). If this paradigm is lost in marine ecology, we should be trying harder to find it.

Is it possible to derive a morphological classification system for macroalgae that explains physiological responses? I propose that it is, but as is argued by Johansson and Snoeijis (2002), this will not be simply a novel revision of our current one-dimensional categorization systems. A successful system should provide a categorization system that requires knowledge only of rapidly assessable morphological features, rather than intensive or experimental taxon-specific knowledge, and provide substantial insight into the physiological behaviour of the individual of interest (Lavorel and Garnier 2001, Cornelissen et al. 2003). I predict that such an approach is possible in marine systems, and that a few descriptors of gross morphology (e.g., degree of cortication and/or calcification, ‘branchiness’, ‘bladiness’, robustness, and overall size) will provide substantial power to predict physiological functioning of macroalgae.

Desiccation is an important ecophysiological stress for many organisms, and macroalgal tolerance to desiccation has been cited as a functional response that is expected to demonstrate a strong signature of morphology (Padilla and Allen 2000). Macroalgal desiccation stress in the intertidal is remarkably frequent and extreme, due to the periodic immersion and emersion caused by tidal fluctuations on a generally diurnal or semidiurnal cycle (Harley 2003). Intertidal macroalgae thus repeatedly alternates from being submerged and in a relatively constant temperature regime to being emerged from the ocean, exposed to dramatic fluctuations in temperature, potential nutrient deficiencies, and often extreme water loss (Lipkin et al. 1993). Marine algae exist (predominately) in a seawater medium, which removes key morphological constraints imposed on terrestrial plants by negating the need for substantial internal structural support as well as for disparate photosynthetic and nutrient harvesting organs (Norton 1991, Raven and Edwards 2001). Freedom from these constraints allows for a remarkable plasticity in morphological form within the three phyla (Rhodophyta, Chlorophyta, and Phaeophyta) of common marine algae (Norton 1991). It is therefore expected that the fundamental constraints on macroalgal morphology are imposed by key abiotic gradients (in factors such as desiccation or wave force) and biotic interactions (e.g. herbivory or parasitism), rather than gravity and mass transport. Given that the rapidity of drying increases the potential for damage during desiccation (Bohnert 2000) coupled with the relative morphological freedom
permitted by other physiological constraints, intertidal macroalgal morphology should be an excellent system in which to look for insightful links between form and function.

I pose the following three hypotheses to illuminate answers to the broad question of how macroalgal morphology relates to ecophysiological photosynthetic behaviour.

**Hypothesis.1.** Morphology of marine intertidal macroalgae determines, in part, desiccation tolerance.

*Prediction:* Different morphological types of algae will respond differently to desiccation.

**Hypothesis.2.** Morphological classification systems explain differences in desiccation tolerance of macroalgae.

*Prediction:* Morphological form-based classifications and structure-based classification systems will explain more variation in multivariate photosynthetic response to desiccation than expected by chance.

**Hypothesis.3.** A multi-dimensional suite of easily assessed morphological descriptors is more effective at predicting photosynthetic response to desiccation than one-dimensional function-form classification systems.

*Prediction:* More variation in photosynthetic response will be explained by a suite of estimated morphological parameters than will be by one-dimensional morphological classification systems.

In order to test these predictions, I assess the desiccation response of a suite of 51 taxa (49 species, 2 morphotypes) of intertidal marine macroalgae, and demonstrate how these responses are related to morphological characteristics of the particular taxa and their assigned morphological groups. Photosynthetic yield, as measured by pulse amplitude modulated fluorometry, was used as a measure of photosynthetic health, and patterns of ecophysiological response were assessed by analyzing relationships between relative and absolute water loss rates, photosynthetic yield, desiccation time, and post-desiccation recovery and resilience.

**Methods**

**Definitions**

Functional-form classification systems are taken to refer specifically to models that are based on form and are intended to imply or predict function. The term 'functional groups', is widely and loosely applied in the literature (Lavorel and Garnier 2001). Here it refers specifically to
groups of organisms which functionally respond in a unique way to external gradients (i.e. functional response groups), rather than groups which affect their environment in unique ways (i.e. functional effect groups, sensu Diaz and Cabido 2001). Ecophysiology refers to physiological responses that occur at ecologically relevant scales and are manifest generally as whole-organism ecological responses to physiological stresses, such as photosynthetic response to desiccation. It is used to distinguish other more biochemically specific physiological processes, e.g. photosynthesis per se or reactive oxygen production in response to desiccation stress, which more often act, and are studied, on a sub-organismal level.

**Species analyzed**

51 macroalgal taxa were used for this study, including 49 species and two morphologically distinct types, all found on or near the Kaikoura peninsula on the South Island of New Zealand. The taxa involved are presented in table 2.1. These species span a range of finely-filamentous through thick leathery forms, and include: representatives of all three phyla of macroalgae, from the shallow subtidal through to the upper limits of macroalgae distribution, and taxa inhabiting rocky reef platforms as well as in tidal pools, epiphytic, and free-floating habitats. Collected individuals were selected from what was estimated to be the vertical mid-point of their range, returned to the lab and placed in running seawater tanks immediately (less than 2hrs post-collection). Individual specimens were selected to simulate their morphological habit in situ, so entire individuals were used wherever feasible, representative portions were used from individuals larger than ~25cm, and species that exist in turfs or colonies in the field were tested as groups of individuals representing field habit.

**Morphological information**

The species selected were grouped according to the classification systems proposed by Dring (1982), Littler and Littler (1980), Gaines and Lubchenco (1982), Steneck and Watling (1982), and Steneck and Dethier (1994). A distinction is made between the system proposed by Dring (1982), which is founded in structural growth form, and the remaining publications, which classify species mainly on a convergent set of morphological functional-form types.
Table 2.1: List of species, functional-form group membership, descriptive variables, and phylogenetic affinities. ‘Code 1’ refers to abbreviated species codes used in figures 2.1 and 2.2. ‘Code 2’ refers to abbreviated species codes used in figure 2.3.

Abbreviations: ‘calc.’ is calcification, ‘cort’ is cortication, ‘robu’ is robustness. Structure-based indicates the functional classification system proposed by Dring (1982), (f) is fine resolution, (c) is coarse resolution. Form-based is the functional classifications of Littler and Littler (1980), Steneck and Watling (1982), and Steneck and Dethier (1994), with (c) representing the general classification type, and (m) representing the estimated continuous metric proposed by Steneck and Dethier (1994). [Table continued for two pages horizontally, and two pages vertically.]
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<th>Form-based (M)</th>
<th>Structure-based (C)</th>
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<td>foliose</td>
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<td>parenchymatous</td>
<td>two dimensional</td>
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<td>foliose</td>
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<td>Stictosiphonia arbuscula</td>
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<td>terete</td>
<td>4</td>
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</tbody>
</table>
Dring's 'structure-based' classification model, is rooted in coarse distinctions between (f) filaments, (c) coenocytes, and (p) parenchymatous thalli, with a fine resolution classification nested within this, including (a1) unbranched, (a2) branched, (a3) heterotrichous, (a4) crustose, (a5) pseudo-parenchymatous, (c1) simple, (c2) uniaxial, (c3) multiaxial, (p1) 2-dimensional, and (p2) 3-dimensional structures. These two scales (coarse and fine) are analyzed as two distinct morphological structure-based classification systems in this study.

Filamentous growth refers to cell division in one dimension, producing a long filament that may or may not branch. Heterotrichous filaments are those which differentiate into two distinct 'types', such as prostrate and erect types, within one organism. Crustose filaments are those that are arranged tightly in parallel, and thus form a flat and broad surface that is very thin (i.e. does not extend off of the substrate more than a few millimeters generally). See below for the definition of pseudo-parenchymatous. Coenocytic growth refers to development when cell division are uncommon (or very rare), resulting in a large multinucleate cytoplasm enclosed in a single 'cell'; some large (> 30 cm) marine algae produce morphologically differentiate and complex coenocytic structures. Simple coenocytic growth represents single, globular thalli, uniaxial coenocytic growth is differentiated into branches that are only a single filament in cross section, and multiaxial coenocytic growth contains multiple filaments in cross section of a branch, due to more than one filament extending the length of each branch. True parenchymatous growth refers to cell division in three dimensions, while pseudo-parenchymatous filamentous growth is produced via filamentous cell-divisions (one, or two dimensions) leading to a three dimensional thallus that appears parenchymatous. I follow Dring's (1982) approach and categorize foliose algae such as Ulva as parenchymatous and two-dimensional, although this is not generally accepted as parenchymatous growth (cf. Abbott and Hollenberg 1976).

The form-based approach tested herein will adopt the categorical system described in the introduction. That is: 1) single cell microalgae, 2) filamentous algae, 3) foliose algae, 3.5) corticated foliose algae, 4) corticated macrophytes, 5) leathery macrophytes, 6) articulated calcareous algae, and 7) crustose algae. Steneck and Dethier (1994) propose that their classification system can be considered in a continuous way, by assigning values intermediate to the categorical levels they present, based on the numbers assigned to each group. This continuous approach was also analyzed, as a separate system from the categorical approach.
Some species are not well suited to particular classification schemes, and were placed in the most suitable of multiple groups that they could belong to. Switching these 'borderline' species into other groups made no qualitative differences to conclusions reached in this analysis (results not presented), given the large number of taxa involved.

In order to contrast these one-dimensional classification systems to an analogous multivariate approach, species were quantified on six easily and rapidly assessed descriptive morphological gradients. These descriptors were cortication, calcification, robustness, size, ‘bladiness’, and ‘branchiness’. These particular axes were selected as an attempted distillation of ways in which phycologists describe the morphological gestalt of algal individuals, with attention to particular aspects of morphology that are predicted to be associated with physiological responses, and a strict focus on ease and speed of assessment. These gradients encompass the distinguishing features used most of the morphological classification systems mentioned previously, while avoiding the one-dimensionality of those systems. These descriptors are intended to represent aspects of algal morphology that an algal ecologist could easily estimate, rather than a concrete set of rules instructing how to group individuals. For example, one might describe an alga within Steneck and Dethier's (1994) rubric as a foliose' individual, yet in the system proposed here the same individual might be described as a relatively small, uncalcified, uncorticated, unbranched, and relatively fragile sheet-like alga. Where necessary, I will abbreviate this approach as 'MEAD': multidimensional, easily assessed descriptors.

In order to test the relative effectiveness of this 'gestalt' approach against the form- and/or structure-based morphological classification systems, these intuitive qualitative morphological gradients must be converted to quantitative metrics. Thus, 51 taxa were described using these six axes that were quantitatively approximated in the following ways:

1. **Calcification** (binary): yes or no.
2. **Cortication** (binary): yes or no.
3. **Robustness** (ordinal): Indexed to 5 degrees, from 0 (fragile), to 4 (tough). Levels correspond roughly to 0 (extremely fragile, difficult to handle without thallus breakage), 1 (easily torn), 2 (breaks, but not easily), 3 (substantial energy required to break thallus tissue), and 4 (nigh impossible to pull apart).
4. **Size** (ratio). Ranging from "small" to "large". Operationalized as height plus the average of width and depth of the individual. A ten centimeter high spherical individual (*e.g.* *Colpomenia bullosa*) would thus be given a value of 20 \((10 + (10+10)/2 = 20)\) for this analysis, while for contrast a round and flat ten centimeter high individual (*e.g.* *Ulva fenestrata*) would be given a value of 15 \((10 + (10+0.1)/2\).
= 15.05), and a ten centimeter high uniaxial filamentous individual would have a value of 10 \((10 + (0.1+0.1)/2 = 10.1)\).

5. 'Bladiness' (ordinal): Categorized into 5 degrees, from 0 (cylindrical in cross section), to 4 (entire thallus sheet-like). Levels correspond with ratios of cross sectional width to depth \((w:d)\) of thalli: 0 \((w:d = 1\); filaments or larger cylindrical thalli), 1 \((w:d = 2\); oblong in cross section), 2 \((3 < w:d < 9\)), 3 \((w:d > 10\); thick sheets), and 4 \((w:d approaching \infty\); a single thin sheet).

6. 'Branchiness' (ordinal): Categorized into 5 degrees, from 0 (unbranched) to 4 (profusely branched). Intermediate levels include 1 (one to five branches), 2 (six to twenty branches) and 3 (twenty one to forty branches). This measure is, as much as possible, estimated independently from bladiness, whereby an individual with bladed fronds could be unbranched (0) or highly branched (3 or 4).

**Desiccation gradient**

Desiccation was selected as the ecophysiological stress to analyze for this study, given the ecological realism of this physiological stress gradient, and the fact that physiological response to this stress is expected to be associated with the morphological variation (Padilla & Allen, 2000). A gradient of desiccation was established indoors in low artificial light (3 to 7 \(\mu\)Em\(^2\)s\(^{-1}\) PAR), moderate temperatures (~20 °C), and moderate humidity (72\%, +/- 5% std. dev.). I used a rotating fan to simulate a moderate and heterogeneous breeze. Each specimen was placed on a small plastic platform, to allow for monitoring of specimens without disturbing their positioning. The start of each desiccation treatment involved placing an individual, or clump of individuals, directly from seawater onto the plastic platforms. No excess water was shaken, dripped, or spun off of the individuals, in order to better create an ecologically relevant desiccation experience. Total desiccation time for each specimen was 4 hours (220 to 265 minutes), chosen to represent a reasonable length of desiccation stress that some of the species involved would regularly experience.

The experiment was repeated nine times in austral spring 2004. Individual specimens of each species involved were measured on multiple occasions, with a goal of five replicate desiccation trials for each species. Given experimental losses (for example, specimens dropped during the experiment, or batteries dying during fluorometry measurements) and occasional collection difficulties, each species involved had three or more individual replicates.
Weight loss was measured by repeatedly measuring the mass of each individual through time. By dividing the observed weights by pre-treatment weight measurements, relative weight loss can be assessed. Weights were recorded, on average, eight times including initial and final measures (thus approximately every half an hour). Immediately after the final weight measure, specimens were relocated into flowing seawater tanks and left for a 48 hour period of recovery. This recovery period is not appropriate for some of the species involved that require emersion from the ocean (i.e. some algal species adapted to the high intertidal will 'drown if kept submerged for many days). I assumed that a 48 hour period of submersion would not substantially adversely affect these taxa, and although the treating species differently may be appropriate in other situations, e.g., Skene (2004), treating species differently post-desiccation was deemed inappropriate for the intended assessment of relative comparisons among species. All species were thus treated equally to permit desired physiological contrasts.

Measurements of photosynthetic yield were undertaken approximately every twenty to thirty minutes during desiccation, as well as 48 hours after cessation of desiccation experiments. Photosynthetic yield was estimated using a pulse-modulated fluorometer (Opti-Sciences OS5-FL), and measurements were taken in constantly maintained ambient artificial low light (3 - 7 µEm⁻²s⁻¹ PAR, measured with an Apogee PAR sensor). Although different species may have independent responses to this light level, there is no reason to assume that relative trends would not be consistent; comparisons across species are thus warranted. Photosynthetic yield—referred to simply as 'yield' herein—is operationally defined as the estimated variable fluorescence (Fᵥ) divided by maximal fluorescence (Fₘ), with variable fluorescence calculated as the difference between ambient fluorescence (Fₒ') and maximal fluorescence (thus Fᵥ = [Fₘ-Fₒ']/Fₘ; see Schreiber (1986)). Each yield measurement occasion (every 20 to 30 minutes) involved three to five measurements taken at stratified haphazardly placed points on the individual. This provided measurements of photosynthetic yield that included all portions of the algal thalli, including less photosynthetically active regions (e.g. stipes).

Constructing the response matrix: physiological parameter estimation

The response of each taxon to desiccation was parameterized by multiple interdependent regressions, which resulted in 17 different facets of physiological response to desiccation tolerance. These variables were estimated as follows.

First, the taxon-wide rate of absolute water loss was estimated from a linear random-effects regression, modeling the natural log of water loss as a function of time desiccated:

\[ \ln(\text{Mass} + 1) = i + \text{time desiccated} \times s \]
The intercept ($i$) and slope ($s$) were allowed to vary randomly for each individual monitored (i.e. random effects), providing a final estimate of taxon-wide water loss rate (slope) with desiccation time, as well as an instantaneous water loss rate (the intercept). This model, upon back-transformation, is equivalent to $\text{Mass} = e^i e^{s \text{time}(\text{t})}$, with $e^i$ simplifying to a new constant. Thus, it is pertinent to note that the $i$ term is not simply a weight loss intercept, but contributes to the realized slope of this relationship. Both the weight loss with time constant ($i$), and the time coefficient ($s$) were added to the physiological response matrix.

Second, the relationship between length of desiccation time and photosynthetic yield was estimated with cubic regression models. Photosynthetic yield was modeled as a function of time desiccated. Quantile regression (Koenker and Bassett 1978, Cade and Noon 2003) was utilized to allow quantification of intra-taxon ranges in photosynthetic yield. The estimated percentage drop in yield after half an hour and after 240 minutes were added as physiological responses, as well as the estimated initial photosynthetic yield. Some taxa exhibit uniformity in response to desiccation with the entire individual affected homogeneously, whereas other taxa exhibit patchier intra-individual responses, with portions of the thallus severely affected and other portions only minimally affected. Comparing quantile regressions through the $95^{th}$ quantile and the $5^{th}$ quantile of photosynthetic yield provided an estimate of the range of yield expected between those portions of an alga that are most substantially depressed by desiccation, versus those portions of an alga that are least depressed, and an estimate of this range was added to the response matrix. Description of regression through the $95^{th}$ quantile of yield also allows for an assessment of the photosynthetic response of the most photosynthetically active portions of the thallus (Cade and Noon 2003), and the percentage drop in maximal yield estimated after four hours of desiccation was added to the response matrix.

Third, the relationship between yield and relative water loss was estimated by linear quadratic regression. Since I am modeling yield as a function of relative (rather than absolute) water loss, all effects in these regressions were modeled as fixed effects. The parameters from these regressions allowed estimation of the estimated median and maximal percent drop in yield after loss of 10% and 50% of total wet weight (four parameters). In addition, relative weight lost after four hours desiccation, and the estimated yield at 50% water loss, were added to the physiological response matrix. The coefficients from this regression (the rate and acceleration of yield change with water loss) were also included as response variables.
Finally, the ability of these individuals to recover after this period of desiccation was estimated by measuring the photosynthetic yield of desiccated individuals after 48 hours (+/- 6hrs) of recovery in flowing seawater tanks. These yield measurements allowed for estimation of photosynthetic resilience expressed as a proportion of final yield after desiccation (i.e., how plastic is photosynthetic yield?), and photosynthetic resistance expressed as a function of initial pre-desiccation photosynthetic yield (e.g. what is the chronic depression in yield?). For each species, these two parameters (chronic yield depression measured as the drop in desiccation between initial and final yield, and yield plasticity measured as the recovery of yield upon rehydration) were added to the physiological response matrix.

**Statistical approaches**

The statistical approach I use is a novel approach, loosely based on a hybridization of the methods of Johansson and Snoeijjs (2002) and McIntyre and Lavorel (2001). Johansson and Snoeijjs (2002) simplify photosynthesis-irradiance curves using principal component analysis, and use this condensed metric (e.g. PCA axes) of photosynthetic relationship to light as a metric to distinguish physiological types, and then assess the relationship between this physiological gradient and morphological types or depth distributions. Maclntyre and Lavorel (2001) use a different approach to address a similar but different question. They define stress-related species response groups, and use correlations between traits to identify function-related species response ‘syndromes’. They then identify syndromes that change across a particular stress gradient (e.g. grazing), and utilize the presence of particular syndromes and their response to stress to describe functional species types. I use PCA to simplify physiological response to a condensed number of measures of desiccation response (analogous to ‘syndromes’ sensu Maclntyre and Lavorel (2002)). I then model this distilled, but still multivariate, response as a function of various morphological classification systems. This essentially provides an estimate of how strongly these morphological classification systems describe functional behaviours of algal taxa.

Principal Components Analysis (PCA) was used to reduce the dimensionality of variation in taxon-specific physiological responses to desiccation by identifying composite linear responses. The axes from this principal components analysis indicate which combinations of physiological responses account for the greatest variation in multivariate desiccation response. Ecophysiological responses to morphology are expected to be linear, so this is the ideal method to maximize the variance in the physiological matrix that can be presented in a low-dimensional space. The correlation matrix of physiological response was utilized, due to different scales of measurement (e.g., fluorescence per percent total weight lost vs. weight lost per minute).
species scores in this physiological ordination space were then used as a response for further analyses, focusing on the first four principal components due to space constraints (these four axes represent the greatest amount of variation in the response).

Multivariate Analysis of Variance (MANOVA) was used to test whether the morphological defined classification systems (e.g. form-based, structure-based, or the multidimensional easily assessed descriptors) represented groups of algae that were more unique physiologically than expected based on random assortment of physiological traits (James and McCulloch 1990, Venables and Ripley 2002). Thus, for each classification system, desiccation tolerance was modeled as a response to functional group membership. MANOVA tests were computed using the first four dimensions of the PCA of the physiology matrix as a response. Univariate analyses from those relationships identified as statistically significant in the MANOVA demonstrated which of the physiological responses (PCA axes) were explained by variation in morphological functional groups and by the easily assessed descriptors.

All statistical analyses were computed using R, an open-source software package (R Development Core Team 2004). Additional packages used for R included MASS (Venables and Ripley 2002) and vegan (Oksanen 2005). All variables in the ecophysiological matrix were checked for normality and log transformed, and/or were normalized before analyses, where necessary.
Results

Dynamics of photosynthetic desiccation tolerance in macroalgae

Different taxa exhibited a large range of physiological desiccation response strategies (Figs. 2.1 and 2.2). Some species resisted weight loss during desiccation, and simultaneously maintained high photosynthetic yield during desiccation (*Hormosira banksii*, *Lophothamnion hirtum*, and *Porphyra* spp.), which in some cases was coupled with nearly full recovery post-desiccation (*e.g.* *Hormosira banksii*). In other species, however, this short-term resistance was coupled with chronic declines and lack of resilience in photosynthetic yield post-desiccation (*e.g.* *Lophothamnion hirtum*). This chronic effect would not have been detected during desiccation stress given the lack of photosynthetic or visual cues of stress, but post-desiccation effects were clear from the drop in photosynthetic yield and severely atrophied tissue. Some species resisted desiccation initially, then suffered dramatic declines followed by near full recovery upon rehydration (*e.g.* *Cladophoropsis herpestica*), while others suffered immediate and chronic drops in photosynthetic yield (*e.g.* coralline crust, *Pterocladia lucida*, and *Rhodymenia linearis*). Some taxa demonstrated uniformity in photosynthetic yield during desiccation (*e.g.* *Splachnidium rugosum*, or *Caulocanthus ustulatus*), while others show enormous variability as desiccation progressed (*Duvillaea willana*, *Enteromorpha ramulosa*, or *Glossophora kunthii*). In some taxa this latter effect was associated with heterogeneous rates of intra-individual dehydration; the protrusions of *Enteromorpha ramulosa*, for example, showed clear visual and photosynthetic signs of rapid drying while the central portions of the thallus remained well hydrated with minimally reduced photosynthetic yield.
Figure 2.1: Plots of yield against desiccation time for all species. Lines represent cubic regressions fit through every percentile between the 5th and 95th percentile, color-coded to legend in bottom right. Scale in bottom left is consistent across all plots. The box plot represents post-desiccation photosynthetic yield after two days of recovery. Abbreviated species names are listed above each plot, and codes are listed with full names in table 2.1.
Figure 2.1 (continued):

Photosynthetic yield (Fv/Fm)
Figure 2.2: Plots of yield against relative water loss for all species. Abbreviated species names are listed above each plot, and codes are listed with full names in table 2.1. Quadratic quantile regressions are fit through every integer quantile between 5 and 95 percentiles. Lines represent cubic regressions fit through every percentile between the 5th and 95th percentile, color-coded to legend in bottom right. Scale in bottom left is consistent across all plots.
Figure 2.2:

![Figure 2.2: Graphs showing photosynthetic yield (Fv/Fm) vs. weight lost (proportion) for various species.](image)
Figure 2.2 (continued):

![Graph showing photosynthetic yield (Fv/Fm) vs. weight lost (proportion) for various species.](image-url)
The loadings for the first four axes of the principal components analysis (PCA) of species in physiological space are presented in Table 2.2. The two crustose species (*Ralfsia verrucosa* and coralline crust) were omitted from the analysis, due to difficulties in adequately estimating proportional weight loss given their permanent attachment to the substrate, leaving 49 taxa in the analysis (47 species and two morphotypes). The first two axes of the PCA are plotted in figure 2.3. The first axis is associated with slow drops in yield with relative weight loss, slow drops in yield over time, and stronger resistance to chronic effects of desiccation (Table 2.2). Axis two is associated with greater acceleration of yield decrease with time, greater plasticity or resilience in yield post-desiccation, larger declines in yield after 4 hours of desiccation, and a larger intra-taxon range (patchiness) of photosynthetic yield. These first two axes correspond with manifestations of stability and resistance strategies (increasing resistance along axis one), and plasticity and resilience strategies (increasing resilience along axis two). Axis three is a related to taxa with greater resistance to water loss (not yield) and a large drop in yield once 10% of water has been lost. Axis 4 distinguishes species that start with lower photosynthetic yield, and suffer declines in relative and absolute photosynthetic yield quickly with water loss.

**Table 2.2:** Loadings of the first four principal components calculated by PCA on the physiological desiccation responses. Also lists all 17 variables incorporated in the physiological response matrix. Loadings less than 0.1 absolute value are not show, and values greater than 0.3 absolute value are show in bold. Symbols beside physiological variables indicate the expected sign of the loading if correlated with resilience and/or resistance; (+) is positive correlation, (-) is negative correlation, and (.) indicates no expected relationship.

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<th>Axis 2</th>
<th>Axis 3</th>
<th>Axis 4</th>
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<td>percent drop in yield after 10% relative weight loss (-)</td>
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<td>-0.19</td>
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<tr>
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<td>0.23</td>
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<td>percent drop in maximal yield after 10% rel. weight loss (+)</td>
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<td>0.32</td>
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<td>proportional weight lost after four hours (-)</td>
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Figure 2.3: PCA biplot of species in physiological space. Given incompatible measurement scales, physiological variables are standardized and the correlation matrix is used. Codes are presented in Table 2.1. Plot on the left is axis one versus two, and on the right is three versus four.
Effectiveness of functional-form models

Form-based classification systems, in general, explain desiccation tolerance in marine macroalgae moderately well (Table 2.3; MANOVA). Categorical form-based classification systems were shown to respond physiologically differently to desiccation stress (MANOVA, F = 1.801, d.f. = 20, 133.6, p = 0.026). The continuous classification system proposed by Steneck and Dethier (1994), however, was a weak predictor of desiccation tolerance (MANOVA, F = 2.125, d.f. = 4, 44, p = 0.094). The categorical form-based classification system explains 15%, 19%, 25%, and 11% of the variation (df = 5) in each of the first four PCA axes (Table 2.4; univariate analyses).

The rarely cited morphological classification system based on algal growth structures proposed by Dring (1982) was an effective predictor of this ecophysiological response at fine resolution (Table 2.3: MANOVA, F = 2.772, d.f. = 16/116.7, p = 0.001). Three groups (uniaxial, multiaxial, and unbranched filaments) only had one member in this suite of species, and were removed from the MANOVA analysis. Dring’s coarse resolution grouping shows no differences in physiological responses. Of the first four PCA axes, Dring’s fine grouping system accounts for 22%, 31%, 33%, and 17% of the variation (df = 4) in each, respectively. This categorization system thus explained more variance on all axes, with fewer degrees of freedom, than the form-based model.

The groups defined by both form-based classifications (figure 2.4a) and structure-based classifications (figure 2.4b) do not strongly distinguish physiologically distinct responses to desiccation in a low-dimensional categorizations. In other words, functional-form systems with only one dimension (e.g., the univariate categorical grouping of Littler and Littler (1980)) do not neatly separate different physiological behaviours. If these univariate groupings were effective, we expect to see unique occupation of particular regions of the ordination space by a particular morphological group, and we would expect to see individual and sharp peaks in figure 2.4. Furthermore, the peak for each group of species would occupy a unique position (relative to other groups) in the ordination space. In fact, we see broader, less distinct peaks spread
Table 2.3: Multivariate analysis of variance (MANOVA) of functional-form models with physiological PCA axes 1:4 as the response. Wilk's test statistic is used to assess multivariate significance. The following models are tested: Form-based models, categorical (Steneck and Watling 1982, Littler and Littler 1980) and continuous (Steneck and Dethier 1994); Structure-based models (Dring 1982), coarse and fine; and a small suite of multi-dimensional easily assessed descriptors (MEAD).
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<th>( df(\text{den}) )</th>
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Figure 2.4: Density plots indicating the location and clustering of groups classified under (4a) a form-based grouping system (e.g. Littler and Littler 1980, or Steneck and Dethier 1994), or (4b) a structure-based grouping system (e.g. Dring 1982). Height indicates relative density of points. Strong predictive power of form on function would predict that the peaks would be discrete from one another based on their position on the x and y axis. Lack of this distinction indicates that these morphological groups do not represent distinct physiological behaviours.
Figure 2.4a: Form-based groups

articulated calcareous  corticated foliose  filamentous

foliose  leathery  terete
Figure 2.4b:

**Structure-based groups**

- **branched filaments**
- **heterotrichous**
- **pseudo-parenchymatous**
- **three dimensional**
- **two dimensional**
across the ordination space, and a lack of uniqueness in the space occupied by peaks of
different groups (figure 2.4). This indicates that these morphological classification systems
contain substantial overlap in physiological response between groups, and thus poor predictive
ability. Therefore, although the mean physiological response of these functional-form groups
are different (MANOVA results, table 2.3), evidence supporting any practical predictive
relationship with function is weak.

Effectiveness of descriptive variables

The multidimensional easily assessable descriptive variables also effectively distinguished
ecophysiological responses (MANOVA; Table 2.3). The MEAD analysis indicates that
cortication (F = 2.848, d.f. = 4/33, p = 0.039), 'branchiness' (F = 4.111, d.f. = 4/33, p = 0.008),
and the 'bladiness' by size interaction (F = 2.4.023, d.f. = 4/33, p = 0.009), all influence
physiological desiccation response. Inclusion of intertidal zone into the analysis (another easily
assessed and common descriptor for algae) added robustness (F = 3.019, d.f. = 4/30, p =
0.033) and zone (F = 2.830, d.f. = 12/79.7, p = 0.003) to the variables already mentioned as
potential drivers of physiological desiccation tolerance. Univariate ANOVA tests (Table 2.4)
from this full model showed evidence of association between resistance to desiccation (i.e. PCA
axis 1) and cortication (p=0.032), robustness (p = 0.016), bladiness (p = 0.048), and intertidal
zone (p = 0.004). Resilience (i.e., PCA axis 2) was explained by cortication (p = 0.025), size
(p = 0.020) and the bladiness by branchiness interaction (p = 0.020). These multivariate
descriptors cumulatively explain 57%, 48%, 58%, and 38% of the variance (100% total variance
minus the percent unexplained, listed in table 2.3: 43%, 52%, 42%, and 62% for axes one
through four, respectively) in the PCA scores for the first four axes (df = 15). These analyses
indicate that this multivariate morphological approach relates broadly to functional desiccation
tolerance.
Table 2.4: Univariate analyses (ANOVA tables) for each of the first four principal components assessed as a response to the form-based models, structure-based models, and MEAD-based models. The percent variance (un) explained represents the Sum of Squares for that effect as a proportion of the total amount. As such, residuals sums of squares (i.e. 'unexplained' rows) represent the proportion of variation that it not explained in the various models. Annotation on the right indicates significance levels; '*' < 0.05, '**' < 0.01, and '***' < 0.001.
Table 2.4:

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Discussion

Desiccation response strategies and morphology

These results illuminate certain strong connections between morphology and physiological response to desiccation. This diverse suite of species demonstrated remarkably different strategies for coping with desiccation. The first prediction I made was that morphological attributes would be associated with desiccation response. As is demonstrated by the univariate ANOVA tables (Table 2.4) demonstrating the explanatory power of morphology for the PCA scores, most of the estimated aspects of morphology (i.e. all of the multivariate descriptors, other than calcification and some interactions) are associated with ecophysiological responses of macroalgae to desiccation. Thus, as expected, morphological characteristics of macroalgal species are clearly associated with physiological responses, and my first hypothesis is broadly and strongly supported.

Algal morphology should be directly responsive (evolutionary) to gradients in environmental stresses (e.g. desiccation, wave forces), diffusion potential (to acquire nutrients, generally in absence of a mass transport system), biotic interactions (Norton 1991), and/or trade-offs between these factors. Algae should be more responsive to these factors than land plants, because of the relative freedom of algae from the morphological constraints imposed on land-plants by mass transport (land plants need to move water from roots to leaves, and photosynthate from leaves to roots; Raven and Edwards 2001) and structural support requirements (land plants need to cope with the need for more substantial structural support systems, given the low viscosity of air relative to water; Niklas 1992). As such, I predict that we should see morphology relating more directly to physiological response to abiotic stress in algae than in terrestrial plants. A number of diverse morphological strategies for coping with desiccation are observed in this study. Those species with extremely heavy cortication (that is, substantial development of the tougher cell-types on the interface between the organism and the environment, the cortex; e.g. Durvillaea willana or Hormosira banksii) tended to maintain high photosynthetic yield during desiccation. This strategy is associated with a strong resistance to internal water loss (Brown 1987, Ji and Tanaka 2002). Other species, for example Lophothamnion hirtum and Halopteris virgata, utilize a nearly opposite strategy to arrive at the same end: both are uncorticated and finely branched, resulting in an extremely high affinity for external water retention. The cost of this 'sponge structure' strategy is partially evident in the
observed low resilience of photosynthetic yield of these species in contrast to *Hormosira banksii* or *Durvillaea willana*.

Further support for the role of morphology in driving functioning is presented by the fact that variation between congeners is as great as variation between species from different genera. Two examples are *Enteromorpha* and *Cystophora*. Both *Enteromorpha ramulosa* and *Cystophora retroflexa* are more finely and profusely branched than their respective congeners, and I observed (in figure 2.1, for example) that both of these more finely branched species (neither of which are branched nearly as finely or profusely as *Lophothamnion hirtum* and *Halopteris virgata*) tended to have greater rates of decline of photosynthetic yield with desiccation. Indeed, the extreme dehydration of these morphological extremities was visually apparent during the experiment, while the main portions of the algal thalli remained hydrated. The bimodal appearance of photosynthetic yield of *Enteromorpha ramulosa* through time is due to this tendency for relatively binary (dehydrated or not) response in this alga; the shift from photosynthetically active to inactive tissue with dehydration is abrupt, and more of a threshold in this species than in others examined.

Contrarily, morphology does not always adequately represent physiology. For example, two crusts were analyzed in this study: *Ralfsia verrucosa* and an unidentified coralline crust. The difference in rate of yield decrease with time is almost as large between these two as between any other two species investigated; the coralline crust suffered an immediate precipitous decline in photosynthetic yield and showed minimal to no recovery, while *Ralfsia verrucosa* maintained relatively high photosynthetic yield during desiccation, and nearly complete recovery. Although the coralline crust is calcified, there is no *a priori* reason to predict that calcification would negatively influence resilience or resistance of photosynthetic yield. A better explanation comes from observing the fact that these two species differ dramatically in their intertidal habitat, with *Ralfsia verrucosa* occupying an high intertidal zone habitat that is emerged almost constantly, and the coralline crust occupies a nearly always submerged habitat in the extreme low intertidal zone. These differences in tidal height are likely to impose strong evolutionary constraints (and concurrently strong selective pressures) on physiological desiccation tolerance, as has been noted elsewhere (Abe et al. 2001, Skene 2004). I have shown that the effect of intertidal zone is, as expected, an important explanatory factor in explaining physiological desiccation tolerance (tables 2.3 and 2.4). Although some argue that intertidal zone may trump the role of

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1 Coraline crusts in New Zealand are, as a group, very poorly studied. Efforts to document and identify the diversity of species in the country are currently underway (through NIWA).
morphology in explaining physiological desiccation responses (e.g. Abe et al. 2001, Gomez et al. 2004, but see Ji and Tanaka 2002), my analysis indicates that morphology plays a strong role in explaining physiological desiccation response (tables 2.3 and 2.4; note the percent variance explained). This conclusion is possible because of the large number of taxa included in my study, and the resulting statistical power remaining after accounting for the effect of habitat. It is also worth noting the difficulty in untangling the potential confounding fact that algae in higher intertidal habitats tend to be morphologically different (more highly corticated, and smaller, for example) than taxa low in the intertidal.

Utility of morphological functional-form models for macroalgae

Although morphologically-based functional groups are associated with physiological responses (table 2.3), they are not able to faithfully predict ecophysiological tolerance to desiccation of intertidal marine macroalgae (figure 2.4). Furthermore, they explain relatively minimal variation in desiccation tolerance. Note that the amount of variation explained by the functional form models can generally be explained by only one or two of the easily assessed descriptors (table 2.4). My second hypotheses was thus supported, but weakly so; the available morphological functional-form grouping systems do better at explaining physiological response than expected by random assignment to functional groupings (MANOVA; table 2.3). Given the large variation in physiological response within particular groups, these classifications do not accurately provide predictive power for physiological response (e.g. figure 2.4). Of the functional-form models available, the structure-based classification system of Dring (1982), appears to perform as well, or better, then the more often cited form-based models2. To my knowledge the physiological relevance of this alternative classification system has not been demonstrated, or tested, previously.

All available functional group classification systems for macroalgae are in essence one-dimensional, in the sense that they attempt to classify algae into one unordered, or ordered in the case of Steneck and Dethier (1994), categorical gradient. Given that gross morphology is important in mitigating desiccation stress in physical systems, I propose that these grouping systems are oversimplistic and do not provide substantial predictive power for desiccation tolerance (also discussed by Johansson and Snoeijs 2002). As mentioned previously, the same

2 Citation frequencies for the most popular macroalgal function-form models, as of April 2005, are 169 times for Steneck and Dethier (1996), 252 times for Steneck and Watling (1982), and 352 times for Littler and Little (1980), while Dring (1982) is cited only 97 times, even though it is an entire book, rather than a more specific journal article.
end-result in an ecophysiological response such as desiccation resistance can be attained through vastly divergent morphological strategies (e.g. profuse fine branches and no cortication, or heavy cortication with few branches). Morphology drives these responses (hypothesis one is valid), but the same end result is reached by dramatically different morphological means. Thus although these one-dimensional morphological classification models are associated with physiological response to desiccation, they are weak predictors of desiccation tolerance (hypothesis 2 is valid, but not strongly so). Certainly, they do not explain as much total variation in ecophysiological response as the set of multidimensional descriptors (table 2.4). Thus an easily assessed suite of descriptors of macroalgae does a better job of predicting desiccation tolerance than functional-form models as they currently exist and therefore my third hypothesis is supported.

Padilla and Allen (2000) call for a revision of our functional-form classification system of macroalgae to more closely match those terrestrial classification systems in which functional groups are defined based on a particular function, rather than morphological form. I argue that although this is an important focus in our attempts to ecologically understand ecosystems, it fails to satisfy one of the primary goals of macroalgal functional-form models—to predict function based on form. Thus the energy that should be dedicated to developing a more robust suite of classification systems for function-specific responses of macroalgae (for example, response to herbivory (Steneck and Watling 1982)) should not detract from our attempts to produce a more robust predictive model of generally how morphology influences ecophysiological functioning. A goal of developing a classification system based on morphological form that enables us to predict function is not mutually exclusive of, nor less insightful than, a goal of developing more inherently labor-intensive functionally based models that predict function. I believe that logically there will always be a decrease in functional predictive ability in shifting from fine to coarse scales: for example, individual organism to species to functionally defined group to morphologically defined group. It is also important to recognize that this drop in predictive ability is associated with a corresponding decline in the amount of information required for classification (e.g. it is generally easier to identify phylum than species of an alga, but knowing phylum tells us less than species about physiological behaviour). This trade-off between specificity and generality is generally recognized and accepted at a species level. For example, we assume that understanding the physiological behaviour of an entire species is generally effective at predicting physiological function of an individual of that species. By making this assumption, we incur a cost; we recognize that our knowledge of that individual’s physiological behaviour would be more accurate if we experimentally assessed that specific individual. Nonetheless, we accept that the benefit of not
needing to undertake this individual-specific physiological analysis is worth the cost of reduced
certainty of physiological behaviour. Whether we can produce the analogous situation with
meta-species groups of macroalgae based on morphology and explaining functional behaviour
remains an open question. My experimental analysis shows that a shift from one- to multi-
dimensional classification systems would provide an important step in this direction. In sum,
morphological variation appears to be a vehicle for extremely disparate mechanistic strategies
of coping with desiccation stress, ranging from stubborn resistance (minimal dehydration with
time desiccated, and minimal depression of photosynthetic yield with dehydration) to plastic
resilience (substantial depression in yield followed by full recovery after alleviation of stress).
Although morphological groups may capture some variation in physiological stress responses,
the fact remains that more fundamental morphological variation is necessary in order to explain
such responses.

General implications form-function relations.

As MacArthur stated thirty-three years ago, the future principles of the ecology of coexistence
will be general statements "... of the form 'for organisms of form A in environment of structure B,
such and such a relationship will hold" (MacArthur 1972). Today, I feel that the MacArthur's
comments directed at the ecology of coexistence could be appropriately reapplied to ecosystem
functioning, among other key ecological foci. In the intervening third of a century since this
remark, ecology appears to have moved only slowly in this direction, with a profusion of
Descartian reductionism, a persistent conceptual focus on a species-based ecology, and a
rather slow approach toward the more difficult goal of a truly functional ecology. I suggest that
advancing our understanding of morphological types and their functional importance (Diaz and
Cabido 2001, Lavorel and Garnier 2001, Westoby et al. 2002) should be a more active focus of
ecology in a world with more species than will ever be independently understood functionally.
Although terrestrial plant functional grouping systems have met with success (Reich et al. 1998,
Sagers 2003), attempts to provide a similar conceptual framework for the functional ecology of
macroalgae (Littler and Littler 1980, Steneck and Dethier 1994) are lacking in operational value
for predicting ecophysiological responses (Padilla and Allen 2000). The research presented
here reiterates the tight connection between morphological form and ecophysiological function,
while at the same time illuminating the critical flaws in the attempt to apply one-dimensional
classification schemes to a more complex, multidimensional reality. The relevance of
morphology to physiology, as shown here, is more adequately explained by qualitative multi-
dimensional and easily assessable descriptions. This argues that we should explicitly endorse
the reality of multivariate complexities over a classification focused system forged to fit into the linear constraints of our conceptual processes. I believe that if ecologists—marine ecologists especially—put more energy into advancing our understanding of how we can predict ecological function at scales beyond individual species, our science would be dramatically improved.
Acknowledgements

I express my thanks to C. Carlson, F. Chan, A. Guerry, J. Lawler, S. Lilley, J. Lubchenco, B. Menge, and S. Wood for their assistance. I also extend my deep appreciation to the Andrew W. Mellon Foundation and D. Schiel for making this research logistically possible. This work was also supported by a Mamie Markham award, a Hanlon Venture Fund, a National Sciences and Engineering Research Council of Canada award, a Fulbright Fellowship, and grants from the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation. This is contribution number XXX from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans funded primarily by the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation. This is a contribution from the Marine Ecosystems Dynamics Consortium (MEDC; http://intertidalweb.org).
Literature cited (chapter 2)


Chapter 3 ~

Scale, Environment, & Trophic Status: The Context-Dependency of Community Saturation in Rocky Intertidal Communities.

Roly Russell, Spencer A. Wood, Gary Allison, Jane Lubchenco, & Bruce A. Menge

To be submitted to American Naturalist
Abstract

Our understanding of the relative influence of different ecological drivers on the number of species in a place remains limited. Assessing the relative influence of local ecological interactions versus regional species pools on local species richness should help bridge this conceptual gap. Plots of local species richness versus regional species pools have been used to address this question, yet after an active quarter century of research on the relative influence of local interactions versus regional species pools, consensus remains elusive. We propose a conceptual model explicitly incorporating spatial scale and ecological interaction strength to reconcile current disparities. We then test the model using a survey of marine rocky intertidal algal and invertebrate communities from the Northeast Pacific. We reach two main conclusions. First, these data show that the signature of saturation will more likely be observed a) at small spatial scales coincident with the scale of biological interactions, b) when studying ecologically interactive groups of species, and c) in generally more abiotically-driven habitats (e.g., the high intertidal). Second, conclusions of past studies asserting that the regional species pool is the primary driver of local species richness may be artifacts of large spatial scales or ecologically non-interactive groups of species.
Introduction

For decades, ecologists have documented the roles of individual factors in determining how many species exist in a place. From local-scale empirical studies on the influences of competition, disturbance, or predation, up to continental scale macroecological and epoch-long evolutionary drivers, ecologists can say with uncommon certainty that numerous factors can influence local diversity, including predation (Paine 1966), herbivory (Lubchenco and Gaines 1981), competition (Gurevitch et al. 1992), recruitment (Gaines and Roughgarden 1992), facilitation (Bruno et al. 2003), dispersal (Huffaker 1958), disturbance (Mackey and Currie 2000), and biogeography (Caley and Schluter 1997). However, we still have a poor understanding of the relative influence of multiple factors acting in concert on the number of species in a place. An important step in this effort is to assess the relative influence of local constraints (e.g., biological interactions, such as competition) versus regional historico-evolutionary drivers (e.g., speciation) on local diversity (Ricklefs 2004).

Plots of the regional species pool against local species richness have been used to test this contrast (Terborgh and Faaborg 1980). If regional species pools (manifestations of evolutionary history) do not influence local species richness, no significant relationship is expected. On the other hand, if regional species pools are driving local species richness, we expect to see a linear relationship; increases in regional species pools should be associated with concomitant increases in local species richness. Following the publication of Terborgh and Faaborg's seminal paper, numerous (>100) studies have addressed this relationship, cumulatively spanning a large range of taxonomic groups, habitat types, and spatial scales (see Cornell (1999), Hillebrand and Blenckner (2002), and Srivastava (1999), for reviews). Despite such intensive study, conclusions continue to expound the primacy of both local ecological interactions (Munguia 2004; Winkler and Kampichler 2000) or regional species pools (Caley and Schluter 1997; Witman et al. 2004) in driving local richness, and a widely applicable theoretical interpretation of these conclusions is still rudimentary.

This graphical approach is controversial. The technique is imperiled by its statistical shortcomings (Srivastava 1999), incongruence between spatial scales of mechanisms and observations (Huston 1999; Loreau 2000), and overly simplified dichotomous nature which excludes abiotic hypotheses. An unacknowledged and recurring disjunction between the scales at which the theoretical mechanisms act and the scales of the empirical data applied (e.g., 'local' communities defined at scales far larger than expected scales of competitive interaction), will alter theoretical predictions. To illuminate these discontinuities, we use empirical data to analyze how conclusions reached from local-regional plots depend on three
potentially influential contextual factors: spatial scales, taxonomic groupings, and habitat type.

By regressing local species richness against regional species pools, we are testing if local species richness is determined by the regional species pool. If ecological interactions can saturate local communities with species (i.e., set an upper limit to species richness), an asymptotic relationship should be observed. However, the reverse is not true: observing an asymptotic relationship implies only that factors other than regional species pools are driving local richness. That local ecological interactions are limiting local richness is only one of a suite of potential alternative hypotheses.

Ecological theory provides a simple prediction for saturation of communities: if species are interacting then saturation is often predicted, and if species are not interacting then saturation is rarely predicted (Huston 1999; Loreau 2000; Shurin and Allen 2001). Even accepting interaction-based ecological theories (Elton 1927; Hutchinson 1959; Menge and Sutherland 1987; Oksanen et al. 1981) and assuming that saturation does limit local species richness, we do not predict saturation at spatial scales beyond those at which individuals interact, nor among groups of species which are weakly interactive or not interactive (Figure 3.1). For example, sponges living under boulders in wave-sheltered low intertidal areas are not expected to influence the abundance of barnacles living on nearby wave-exposed high intertidal open rock surfaces. Furthermore, communities that do appear saturated have been shown both theoretically (Mouquet et al. 2003) and empirically (Munguia 2004) to conceal saturation patterns during intermediate stages of community assembly. Ecological models that are in essence non-interactive or explicitly neutral in terms of species interactions (Bell 2000; Caswell 1976; Hubbell 1997; Hubbell 2001) cannot predict that local competitive interactions will limit local richness. Therefore, even if communities are ecologically saturated, to observe this relationship we must look in the right place at the right time, and at the right group of species.

Here, we propose a relatively simple conceptual framework that we believe reconciles some ongoing controversies, and then test this framework empirically. Our framework incorporates explicitly the influences of the defined spatial scale of the 'local' community (Huston 1999) and the groups of species studied on the capacity for species to interact and therefore on the potential to discern ecological saturation (Figure 3.1). Even if species interactions saturate community membership at a particular scale, increasing the spatial breadth of the defined
Figure 3.1: A conceptual model demonstrating the spatial scale and species grouping dependency of predictions from local-regional theory. When a survey chooses a large, ecologically heterogeneous area as a local scale, or when group of species investigated are not interactive, we would not expect to find saturation. Only when species groupings and local scale both incorporate interacting species should we expect saturation potential. The darker shading in this diagram signifies higher potential to detect saturation of communities. For example, a study assessing ecological saturation at very large local scales and across various taxonomic groupings might fall into the large region bounding the letter ‘A’ (e.g., Caley and Schluter 1997), and we would not predict to see saturation, even if the hypothesized mechanisms are acting to saturate communities at smaller local scales. An experiment at an ecologically interactive local spatial scale, however, and with a highly interactive group of species (area bounding ‘B’; e.g., Munguia 2004), would allow us to predict saturation, if the mechanisms are in fact operating.

Local community should eventually incorporate heterogeneous abiotic environments and lead to a shift from an asymptotic relationship into a linear relationship (i.e., apparent dominance by the regional species pool). Likewise, groups of species that interact strongly may demonstrate ecological saturation, whereas species richness of ecologically non-interactive groups of species will, regardless of spatial scale, never saturate due to ecological interactions. Our proposed framework predicts that if species assemblages produced by a particular combination of spatial scale and species identities are not strongly interactive, we will see linear relationships between the regional species pool and local species richness. Likewise, we expect to see potential asymptotic relationships only where spatial scales of
interactions match those of field observations, and where the group of species assessed (determined by habitat as well as operational taxonomic focus) includes strongly interacting species.

Empirically contrasting the influence of scale, species groupings, and habitat on the frequency of asymptotic relationships, and thus potential ecological saturation of communities, should provide insight into the factors underlying the tension between local constraints and regional species pools on species richness. Here we use a spatially extensive set of surveys of marine rocky intertidal communities along the West Coast of the USA to address empirically how these three elements—scale, species groupings, and habitat— Influence the relative dominance of the evolved regional species pool and local species interactions on local species richness. We address three predictions; we should see an increased influence of regional species pools (quantified here by a saturation index, relating the most speciose local community to the estimated asymptote) as we assess 1) increasingly large local spatial scales, 2) groups of species that are only weakly competing, and 3) habitats with weakly interacting species.

Methods

Ecosystem description

Marine rocky intertidal ecosystems along the west coast of the United States, ranging from northern Washington (48.4N, 124.7W) to southern California (32.7N, 117.3W), compose the empirical focus of this study. Vertical zones in the intertidal are characterized by gradients in environmental factors and potential stress levels, ranging from a nearly continuously submerged benthic marine community, low in the intertidal, to nearly terrestrial communities high in the intertidal (Lewis 1964). We focus on communities at three tidal heights: Mean Lower Low Water (MLLW), Mean Sea Level (MSL), and Mean Higher High Water (MHHW), referred to hereafter as the ‘low’, ‘mid’, and ‘high’ zones, respectively. As has been documented repeatedly at sites along the West Coast (Connolly and Roughgarden 1998; Dayton 1971; Menge et al. 1994; Paine 1966; Paine 1974; Sanford and Menge 2001), zones at wave-exposed sites are dominated respectively by macrophytes (low zone), mussels (mid zone), and barnacles and macrophytes (high zone).
Figure 3.2: Map of surveyed regions on the west coast of the United States. At the largest scale, points represent regions within which three sites were surveyed, within which three sets of transects were placed in each of the Low, Mid, and High intertidal zones, in which ten quadrats were sampled.

The organisms in this study were identified to species whenever possible, although coarser groupings were necessary in cases where key identifying features were not expressed at the time of sampling (see appendix 2, table A2.1, for a complete list of taxa). Most taxa observed in this study are sessile in their mature stages and may interact indirectly via mobile species (predators, herbivores or habitat modifiers; Menge 1995) or directly via competition for space or facilitation (Connell 1961; Connell 1983; Menge et al. 1997; Paine 1966). Many invertebrate species in these systems have mobile larval stages, and potentially relatively long distance dispersal (Kinlan and Gaines 2002; Grantham et al. 2003; Kinlan and Gaines 2003).
Data Collection

The survey data herein were obtained using a nested sampling scheme. At the largest scale, we sampled within 16 regions spread across 16 degrees of latitude (from 32° to 48° North). Regions were, on average, 168 kilometers apart. Within each of these regions, three sites were nested a few kilometers apart. Within each site, three sets of 50 m transects were placed in each of three zones (high, mid and low), for a total of nine transects in each site, and thus 27 transects in each region (Figure 3.2). In each transect, community composition was quantified in ten randomly placed 0.25 m² quadrats. Within each quadrat, we identified and estimated the percent cover and/or density of all macroscopic organisms (appendix 2, table A2.1 for a complete list of taxa). These surveys were repeated annually from 2000 to 2004. Survey sites were selected a priori using aerial photos and specific criteria, including the presence of suitable open coast intertidal habitats with wave exposed and moderately sloping rocky platforms. The purpose of these selection criteria was to limit sampling to intertidal habitats that were as physically similar as possible. These criteria and sampling methods are described in more detail in Schoch and Dethier (1996).

Local and Regional Pool Estimation

Definitions of 'local' and 'regional' in the literature vary dramatically and are clearly context-dependent. For example, local scales used in the literature range from the flesh of a fig (Hawkins and Compton 1992) or the gut of a fish (Aho and Bush 1993) to areas over half the size of Switzerland (e.g., Caley and Schluter 1997). A simple and appropriate, but still not empirically operational, definition of local species richness that we adopt is 'the number of species living in a small, ecologically homogenous area'. Here we empirically test three local scales. We define samples taken at the quadrat scale of 0.25 m² as the smallest local community, samples taken at the transect level, on a scale of tens of meters, as an intermediate-sized local community, and samples taken at the site level, across several transects, a scale of a few kilometers, as the largest local community. Since most species included in this study are rather small and sluggish or sessile when mature, and competition for space occurs on small spatial scales, we believe that this range of scales provides a reasonable test of these patterns. To operationalize these local scales, we use the observed number of species, at each scale, to estimate local species richness.

Determining the regional species pool is a more formidable challenge. Ideally, we would calculate the regional pool directly as we define it: 'the number of species that can disperse to a locality in ecological time and survive the physical environment in the absence of
ecological interactions'. The latter half of this definition is critical, since our definition must exclude, from the low intertidal for example, taxa such as caecilians and cetaceans that may disperse to—but cannot reside in—the intertidal. Thus, unlike the theoretical bounds of the local scale, the regional species pool is an actual number that must be estimated, based on the defined local community.

Regional species pools have been estimated in the past primarily by either of two methods: literature-based range maps (e.g., Caley and Schluter 1997) or cumulative species lists from field observations (e.g., Terborgh and Faaborg 1980). Both methods have associated pros and cons. Range maps, for example, offer the advantage of a temporally integrated measure of all species present in an area over many years. However, range maps rely upon interpolation, at least at some spatial scales. Many obscure intertidal species have been recorded at only a handful of locations along the coast, with published ranges spanning the coastline between these points. These coarse estimates overestimate the regional pool (Hurlbert and White 2005), and produce biased measures of local richness which logically lack the signature of local ecological interactions. Alternatively, cumulative counts of species observed in an area, the method we use here, provide a more direct measure of the species actually extant within the defined region. This method is able to provide more study-specific estimates of regional species pools than range maps, at the expense of underestimating the actual number of species in the regional pool. This method also ensures that only species detectable by our survey methods are included in the estimated regional species pool.

Mechanistically, we approximate the regional species pool as the total number of species that were observed in the surveys within each of the 16 regions (see Figure 3.3). For example, assessing the regional species pool for filter feeders in the mid intertidal requires calculating the total number of filter feeder species that were actually observed in the 90 quadrats surveyed in the mid zone within that specific region. These regional estimates were calculated independently for each species grouping.

For each region, we compared the observed richness values to rarified asymptotic richness estimates, calculated using the jackknifed technique (Heitshe and Forrester 1983; Rumohr et al. 2001; Zahl 1977) and the S metric (Karakassis 1995). These estimates were only slightly higher than the observed regional richness values (i.e., sampling intensity was approaching asymptotic numbers of species), and analysis using these extrapolated estimates of total species richness gave similar results to using observed richness. We therefore use observed richness in the analyses, to allow more direct interpretation. All of
the above computations were performed using the SAS System for Windows v.8.0 (SAS Institute, Inc., Cary, NC, USA).

Statistical Analyses

We use non-linear asymptotic regressions to test local-regional relationships, since the hypotheses predict an asymptotic relationship and not a quadratic relationship. In this paper we present a Michaelis-Menten (MM) type function (eq. 1), chosen because of the ecological interpretability of the parameters. Rather than traditional tests for a dichotomous presence or absence of saturation, we analyze the quantitative degree of saturation, which we argue is a more ecologically realistic paradigm of actual communities.

\[
\text{Local Richness} = \frac{(V_{\text{max}} \times \text{Regional Pool})}{(K_m + \text{Regional Pool})}
\]  

Eq. 1

Km is an estimated parameter that describes the curvature of the relationship. Vmax provides an estimate of the asymptote, which approaches infinity as the relationship becomes more monotonically linear (regionally dominated). This asymptote represents a quantitative measure of saturation: if the asymptote is estimated within the range of local richness observed, we interpret this as a saturated system. If the estimated asymptote is infinite, or occurs at an unattainably high local richness, the community is not saturated. Since we are interested specifically in factors constraining the upper limits to local richness (rather than the mean local richness), we use nonlinear quantile regression (Cade and Noon 2003; Scharf et al. 1998) to regress the 90th percentile of local richness on the regional species pool, and use all observations, rather than mean observed richness values. Quantile regression minimizes least absolute differences rather than least squared differences. Data are necessarily spatially auto-correlated, and measures of curve fit are neither presented nor analyzed: we are interested in the relationship between the asymptote and local richness data, not in measures of fit. These analyses were performed using the statistical program R (R Development Core Team 2004) and the 'quantreg' package for quantile regression (Koenker 2004).

We use a calculated metric of percent saturation for comparing saturation patterns across species groups and scales that vary in total number of species. This metric presents the most speciose local community as a proportion of the estimated asymptote of local richness. An index of 100% saturation indicates that some local communities contain the same number of species as the estimated asymptote, while 0% saturation indicates that the observed maximal local richness is negligible relative to the estimated asymptote of local richness (i.e.,
the regression is a straight line). Thus, a saturated community should be 100% saturated, while a regionally-dominated community would be 0% saturated. This saturation index is bounded between 0 to 100 percent.

Percent saturation was calculated, as above, for each of the possible permutations of local scale (3: quadrats, transects, and sites), taxonomic resolution (8: All species combined, Kingdoms - algae or invertebrates, and trophic levels - filter feeders, primary producers, herbivores, omnivores, and carnivores), habitat types (3: low, mid, and high intertidal), and years (5: 2000-2004). This equates to assessment of saturation for 360 permutations, from which estimated parameters were used to calculate the saturation index. The relationship between the saturation index and spatial scale, zone, and species groupings was estimated using a linear model (mixed effects, estimated by residual maximum likelihood, using R) incorporating all main effect and interaction terms, nested within the repeated measures each year. Each main effect (scale, habitat, and species grouping) was modeled as an ordinal factor, to correspond to our null hypotheses of saturation levels changing as we increased spatial scales (quadrats ≤ transects ≤ sites), tidal height (low ≠ mid ≠ high), or ecological resolution (all ≥ kingdoms ≥ trophic levels) of species groupings. Qualitative conclusions are not different between this ordinal approach versus a categorical approach (both methods presented in appendix 2, table A2.3); the ordinal approach is presented herein for ease of interpretation.

Variance of saturation index for explanatory groups (e.g., spatial scale) was calculated by randomly permuting (10,000 times) the observed association between saturation indices and each contextual factor (i.e., scale, habitat, and species groupings), pooled across years, calculating the variance in observed data relative to variance in random permutations as our test statistic and its distribution. These probabilities provide a test of whether observed differences in variation of saturation indices between groups are different from expected given a null hypothesis of no relationship between saturation and spatial scale, habitat, and species groupings.

Results

Local-regional plots

Modeling the saturation index as a function of contextual factors demonstrates (regression coefficients presented in Table 3.1) increased saturation at smaller local scales, higher in the
intertidal, and among trophic species groupings, as opposed to linear—and thus regional species pool driven—relationships at larger local scales, lower in the intertidal, and in coarser groupings of species. Appendix 2, figure A2.1 graphically presents the regressions of each of the 360 permutations of scales, habitats, taxonomic groups, and year. Summaries of parameters estimated from the regressions are presented in appendix 2, table A2.2. Figure 3.3 presents an example comparison of local and regional richness for each of the eight species groupings, in one intertidal habitat (mid intertidal), at one local scale (0.25 m²), in one year (2003), across the Pacific Coastline of the contiguous United States.

Table 3.1: Regression of community saturation index as a function of resolution, scale, and habitat. Terms are ordered factors, each with three levels, and thus the linear components test for a linear change across the gradient (e.g. low to high zone habitat), while the quadratic terms indicate whether the relationship levels off or is unimodal across each gradient. Resolution refers to species groupings (all, kingdom, or trophic level), scale refers to the size of the local scale (quadrat, transect, or site), and habitat refers to intertidal zone (low mid, or high). Terms with p < 0.05 are in bold.

<table>
<thead>
<tr>
<th>Regression term</th>
<th>Value</th>
<th>Std. Error</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.346</td>
<td>0.022</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>resolution</td>
<td>0.121</td>
<td>0.025</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>resolution²</td>
<td>0.005</td>
<td>0.023</td>
<td>0.831</td>
</tr>
<tr>
<td>scale</td>
<td>-0.321</td>
<td>0.024</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>scale²</td>
<td>0.069</td>
<td>0.024</td>
<td>0.004</td>
</tr>
<tr>
<td>habitat</td>
<td>0.251</td>
<td>0.024</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>habitat²</td>
<td>-0.073</td>
<td>0.024</td>
<td>0.002</td>
</tr>
<tr>
<td>resolution * scale</td>
<td>-0.102</td>
<td>0.043</td>
<td>0.018</td>
</tr>
<tr>
<td>resolution² * scale</td>
<td>0.024</td>
<td>0.040</td>
<td>0.544</td>
</tr>
<tr>
<td>resolution * scale²</td>
<td>-0.031</td>
<td>0.043</td>
<td>0.471</td>
</tr>
<tr>
<td>resolution² * scale²</td>
<td>0.015</td>
<td>0.040</td>
<td>0.707</td>
</tr>
<tr>
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<td>0.107</td>
</tr>
<tr>
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<td>0.040</td>
<td>0.808</td>
</tr>
<tr>
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<td>0.806</td>
</tr>
<tr>
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<td>0.040</td>
<td>0.533</td>
</tr>
<tr>
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<td>&lt;0.001</td>
</tr>
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<td>scale² * habitat</td>
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</tr>
<tr>
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<td>0.022</td>
</tr>
<tr>
<td>scale² * habitat²</td>
<td>-0.023</td>
<td>0.034</td>
<td>0.497</td>
</tr>
</tbody>
</table>
Figure 3.3: Local species richness versus regional species pool regressions from intertidal communities on the West Coast of the United States. The black dashed line is a nonlinear asymptotic model fit through the 90th quantile. These results demonstrate the number of species in local communities at the scale of a single quadrat (1/4 m²) in the mid intertidal (Mean Sea Level). The regional pool is calculated as the number of species that were observed in a surveyed region surrounding each local community, which is on the order of 10's of kilometers. Points have been jittered to aid in visualization of data density.

Effects of Spatial Scale

As local scale increases, communities become dominated by regional species pool effects (negative coefficient in Table 3.1). At the smallest local scale, richness reached, on average, 73% of the estimated asymptote of local richness, dropping to 39% in the intermediate transect scales, and to only 18% at the site-level, the coarsest spatial resolution (Figure 3.4).

Small local scales also demonstrate a broader range of potential saturation levels. Permutation of the variance of saturation indices associated with each local scale indicate that variance tends to decrease as local spatial scales increase: quadrat-level variance is greater than transect-level ($p_{(1\text{ tail})} < 0.001$), and transect-level variance is greater than site-level ($p_{(1\text{ tail})} < 0.001$).
Figure 3.4: Saturation indices across various 'local' scales of observation. The 'small' scale refers to the average number of species within ¼ meter squared quadrats, 'medium' relates to 50 meter horizontal transects, and 'large' represents groups of three nested transects across approximately 1 km of shoreline. Data are calculated from groups of different trophic status, and different habitats (High, Mid, and Low intertidal communities), and thus each point represents the saturation of a particular trophic level in a particular zone at each spatial scale (e.g., all filter feeders in the low intertidal would be one point at each scale).
**Effects of Species Groupings**

Incorporation of all taxa in one analysis results in a predominately regionally-dominated relationship (mean saturation index = 18%), while finer and potentially more interactive species groupings show progressively higher levels of saturation: 30% with kingdoms as groups, and 39% with trophic levels as groups (Figure 3.5). The positive coefficient ($p < 0.001$) of species groupings indicates that saturation potential increases as we shift from grouping all taxa to grouping taxa into trophic levels.

Different groups do not exhibit different variability of saturation indices. The variance in the saturation index of all-inclusive groupings is not less than in kingdom-level groups ($p_{(1 \text{ tail})} = 0.152$) or trophic-level groupings ($p_{(1 \text{ tail})} = 0.073$).
Figure 3.5: Demonstration of the range of saturation indices across a range of taxonomic resolutions. ‘all’ refers to a grouping of all species; ‘kingdom’ refers to a kingdom-level division, parsing species in two groups (i.e., Protista, and Animalia). ‘trophic’ refers to groups of species based on trophic status, including primary producers, suspension/filter feeders, herbivores, omnivores, and carnivores. Data are calculated from communities at different habitats (high, mid, and low intertidal). Each point represents the saturation of the grouping resolution indicated on the x-axis in a particular tidal height, using transects as the local spatial scale (e.g., one of the points in the all-inclusive category represents the saturation level of an analysis counting all species found in quadrats in the low intertidal).
Figure 3.6: Saturation levels of intertidal communities at different intertidal heights. 'high' refers to Mean Higher High Water (MHHW), 'mid' is Mean Sea Level (MSL), and 'low' is Mean Lower Low Water (MLLW). Data are calculated from groups of different trophic status. Each point represents the saturation of a particular trophic level in transects, given the intertidal zone indicated on the x-axis (e.g., the saturation of filter feeders found in transects is one point in each intertidal zone).
Effects of Intertidal Zone

Saturation is less common in habitats lower on the shore than in habitats higher on the shore (Figure 3.6; Appendix 2, table A2.2). Mean saturation in the low, mid, and high zones is 19%, 42%, and 56%, respectively. The regression coefficients for habitat \( p < 0.001 \) and habitat\(^2\) \( p = 0.002 \) indicate that each of the three habitats is different (Table 3.1). Variation in saturation indices is not different between habitats \( p (2 \text{ (a)}l) > 0.05 \).

Discussion

Our conceptual framework predicts that as the potential strength of local ecological interactions decreases, there should be concomitant increases in the potential for the regional species pool to determine local species richness. We analyzed data along three axes along which we might expect such a shift in the relative strength of local ecological interactions: spatial scale, taxonomic grouping, and habitat type.

Scale influence

Our prediction that smaller spatial scales should be more saturated was supported by the data: mean saturation dropped from 73% at the smallest local scales to only 18% at the largest spatial scales. Thus, increases in the spatial scale of 'local' communities were associated with an increase in dominance by the regional species pool, as predicted theoretically (Huston 1999; Loreau 2000; Westoby 1998) and from empirical meta-analyses (Hillebrand and Blenckner 2002). There has been a disparity in previous research between the scale at which the proposed mechanism for saturation (e.g., ecological interaction) operates and the scale of observation (Huston 1999). Observations at spatial scales greater than that within which species interact will lead us to conclude that the regional pool has a dominant effect, regardless of whether or not local interactions determine local richness at smaller scales. For example, at abnormally large local scales (e.g., 2,500 km\(^2\) and 25,000 km\(^2\) in Caley and Schluter 1997) we expect to—and do—see an apparent prevalence of the regional species pool in determining 'local' community composition. Studies at local scales that match scales of ecological interactions do, also as predicted, demonstrate saturation potential (Borges and Brown 2004; Munguia 2004; Winkler and Kampichler 2000). If the goal
is to compare the relative influence of the regional species pool versus local ecological interactions in driving local species richness, as the tool was originally presented and used (Terborgh and Faaborg 1980), then local scales must be small enough for the encompassed populations to be able to interact.

On the other end of the local-scale spectrum, sampling areas that are too small may lead to a pseudosaturated relationship in which there are too few individuals to sample the relative abundance distribution properly, and rare species are not assessed adequately (Caley and Schluter 1997; Karlson and Cornell 2002). The large numbers of individuals sampled at even the smallest scales surveyed in this study (a mean of 318 mobile individuals and 133% cover of sessile individuals per quadrat) make it unlikely that small sample size drives the relationships we observed.

**Group membership influence**

Our prediction that coarser species groupings should be more regionally-dominated than finer groupings was supported, with percent saturation more than doubling (from 18% when all taxa were combined to 39% when trophic levels were analyzed separately) when species were grouped into ecologically defined trophic levels. The majority of species in these food webs have weak or undetectable interactions (Berlow 1999; Menge 1995); how we define membership in the groups of taxa that we investigate will, in large part, determine whether we expect species to interact or not. For example, breaking an ecological community into phylogenetic groups, rather than mutual resource users (e.g., analyzing all ‘ant taxa’, as opposed to ‘granivores’, in a system), should lessen the potential strength of the focal mechanism (in this case, competitive interactions and niche packing) proposed to drive the pattern. Relative mobility of different groups of species can also influence expected patterns resulting from ecological interactions by changing historical and contemporary dispersal patterns (Munguia 2004; Williams et al. 2003). In the present analysis we see an increased magnitude and variation of saturation patterns within groups at a finer resolution, such as trophic levels (Figure 3.5). Again, when designing studies to assess the relative importance of local species interactions and regional species pools, we must ensure that the observed taxa have the necessary potential to functionally interact.

**Habitat influence – biotic interactions**

Because environmental stress and potential productivity vary across habitats, the average strength of interactions among habitats is expected to vary and thus influence predictions of
ecological saturation. We assessed the prevalence of saturation patterns across different intertidal habitats, ranging from high intertidal zones where thermal stress should be higher to the low zone where such stress should be lower (Harley 2003). Interestingly, we see differences, yet the low intertidal is where we see the strongest signature of regional dominance (19% saturation in the low intertidal, in contrast to 42% in the mid and 56% in the high intertidal). Given the documented increase in general abiotic stress levels higher in the intertidal (Bertness and Leonard 1997; Hacker and Gaines 1997), this result appears inconsistent with our prediction that higher stress would decrease the importance of biotic interactions as a determinant of community composition (Connell 1961; Menge and Sutherland 1987) and lead to more regionally-dominated communities higher in the intertidal. One alternative hypothesis is that increased predation lower in the intertidal could decrease the relative role of competition (Connell 1961; Menge and Sutherland 1987), allowing for an increase in the influence of the regional species pool in the low zone. Similarly, facilitation has been documented to become increasingly important at higher levels of abiotic stress (Bertness and Leonard 1997; Bruno et al. 2003; Hacker and Gaines 1997). Facilitation could drive these observed patterns (Shurin and Allen 2001), if we hypothesize that once a threshold number of species are present in the regional pool, the community is released from determination by abiotic conditions and stabilizes at some local richness level dictated by the presence of stress-ameliorating species in the local community.

**Habitat influence – abiotic stress**

If abiotic factors, however, drive local species richness in the high intertidal (Menge and Sutherland 1976), we expect to see a decrease in the relative importance of the regional species pool on local richness in this habitat, as we observed. Note that this prediction is founded on a hypothesized decrease in the influence of the regional species pool due to increased influence of locally acting abiotic factors, rather than the traditionally assumed increased influence of local ecological interactions. Our data indicate that low in the intertidal zone the regional species pool appears to have a significant influence on local species richness (only 19% saturated on average). Higher in the intertidal zone our data show that variables other than the regional species pool have increased potential to structure local communities (greater than 40% saturated); this relationship could represent an increase in the importance of local ecological interactions, or alternatively could be an expression of an increase in the importance of local abiotic stress in determining local richness.
Incorporation of abiotic stress and facilitation into traditional local-regional models

By wedging the traditional model from local-regional literature (i.e., local species richness is driven by either local ecological interactions or the regional species pool) to environmental stress models, we can provide explanations for the differences in species richness observed between habitats. Environmental stress models generally predict that as the influence of abiotic stress increases (cf. increased intertidal elevation: Bertness and Callaway 1994; Bertness and Leonard 1997), the relative influence of predatory interactions declines, competitive interactions follow with an increase and then decrease in importance, followed by compensatory increase in the relative influence of facilitation and then direct abiotic stress (Bertness and Callaway 1994; Bertness and Leonard 1997). The influence of the regional pool will be strongest under conditions away from those engendering strong competitive interactions, and away from conditions where facilitation ameliorates stress levels: for example, the low intertidal. Our results, which indicate that regional dominance is decreased higher in the intertidal, could thus be interpreted as an increase in importance of facilitation, a decrease in predation, or an increase in direct abiotic stress, rather than exclusively as a function of competitive ecological interactions.

Conclusions

Our results yield three main points. First, the relative importance of multiple alternative hypotheses must be assessed empirically in order to understand ecosystem dynamics, a difficulty given the requisite spatially and taxonomically broad surveys necessary for such macroecological analyses (e.g., Wootton 2005). Furthermore, descriptions of complex systems such as ecosystems are necessarily not scale-invariant (Bar-Yam 1999), and thus the role of ecosystem drivers must be assessed at multiple scales to produce generally applicable systemic knowledge (Rahbek and Graves 2000). Our study provides such an empirical and cross-scale assessment. By quantifying the observed relative importance of local ecology versus regional species pools across spatial scales, habitat types, and species groupings, we have gained new insight into the general dynamics of drivers of local richness. Local species richness is driven by multiple scale-variant factors: even if our goal is to interpret the ecological significance of a single driver, we gain more applicable ecological insight if we couch our influence of interest (e.g., the regional species pool) within a diverse assemblage of potential drivers and across spatial scales.
Secondly, as a future direction, we emphasize that plots of local species richness versus regional species pools are not always an adequate tool to assess the relative influence of local ecological interactions and regional species pools (Huston 1999; Srivastava 1999). Regression of one response (i.e., local richness) against one explanatory variable (i.e., regional species pool richness) implies that the regional species pool and local ecological interactions are the only two relevant variables influencing local richness in these contexts. This traditional approach tells only part of the ecological story, while veiling others. Our results indicate that additional factors such as facilitation and abiotic stress may have dramatic influences on the relationship between local richness and regional species pools.

In future research, a more insightful approach would be to simultaneously test the influence of local ecological interaction strengths, the richness of the regional species pool, and abiotic variables. We concede that such broad scale quantification of the strength of local ecological interactions concurrently with abiotic information would be a major challenge. We hope that further tools may be developed that allow us to advance in this direction.

Lastly, this study emphasizes the volatility of predictions of ecological theory due to the ecological context. We will only see saturation where species can be expected to interact, which is dependent on, among other factors, temporal and spatial scales, habitat types, and operational species groupings (see Figure 3.1). We argue that plots of local richness against the regional species pool have been misinterpreted due to lack of attention paid to the potentially overwhelming influence of ecological context (Berlow 1997; Menge 2003). If we assess patterns at landscape scales, we should not expect to see—and do not see, in our results—strong signatures of local ecological interactions, regardless of their potential relevance at smaller scales. We have also demonstrated that we are more likely to detect the signature of ecological saturation when observing ecologically, rather than taxonomically, defined groups of species. Lastly, we demonstrated that even at small local scales and within ecologically defined groups of species, the characteristics of the habitat we are studying can dictate whether we observe saturation dynamics or not. With more explicit incorporation of experimental context into predictive theory, we have the potential to constructively reconcile the disjunct conclusions of past studies, and gain more complete insights into the general behaviour of ecological systems.
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Literature Cited (Chapter 3)


Chapter 4 ~

Biodiversity and ecosystem processes: species, traits, and interactions.

Roland B. Russell

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Abstract

At all ecological scales, the numbers and identities of species in ecosystems are changing. Although these changes certainly can influence the functioning of ecosystems, the mechanistic basis for this relationship remains unclear. I logically pose and empirically defend a conceptual model stating that all influences of species richness must act through variation in traits: either through presence of, or interactions between different traits. Given this model, I argue that the debate about species richness versus composition as drivers of ecosystem processes is misguided. I empirically show, using photosynthetic rates of marine macroalgal communities, that beyond observing a positive effect of species richness (via the consequent increase in trait diversity) on community photosynthetic rates, this effect can be mechanistically decomposed into components associated with the presence of, versus interactions between, particular traits. This provides an important advance in our understanding of the mechanistic foundations of the observed pattern between species richness and the functioning of ecosystems.
Introduction

On the planetary scale, species are disappearing faster than they are appearing (GBA 1995; MA 2005). Similarly, translocation of species by humans is homogenizing composition of biological communities around the globe (Elton 1958; Olden et al. 2004). On finer scales, this translocation is increasing the number of species (i.e., species richness) in some locales (Sax & Gaines 2003) and decreasing species richness at other locales (e.g., Piazzi et al. 2001). Simultaneously, global climate change is shifting and changing local distributions of species (e.g., Parmesan & Yohe 2003; Schiel et al. 2004). In addition, pervasive anthropogenic habitat alteration is shifting the suitability of habitats toward more cosmopolitan suites of species. These changes beg the question of whether changes in biodiversity are expected to change how ecosystems are functioning. In my view, the answer is unequivocally yes. Certain species are known to have dramatic influences on ecosystem functioning. Examples include ecosystem engineers (e.g., the dam-building beaver Castor canadensis, which creates wetlands; Naiman et al. 1986; Wright et al. 2002), dominant species (e.g., the abundant periwinkle Littoraria irrorata, which can turn salt marshes into mudflats; Silliman & Bertness 2002) and keystone species (e.g., Pisaster ochraceus, a sea star that can dramatically influence community structure despite relatively low abundance; Paine 1969; Power 1996). Clearly the loss of these species as their associated functional traits would lead, or has led to concomitant dramatic changes in some ecosystem processes. I thus modify my initial question to ask how, not whether, diversity influences ecosystem functioning.

Initial observations and experiments that indicated that species richness influences the functioning of ecosystems (e.g., Naeem et al. 1994; Tilman & Downing 1994; McGradySteed et al. 1997; Tilman et al. 1997; Hector et al. 1999) have been actively disputed (Grime 1997; Huston 1997; Hodgson et al. 1998; Wardle 1999) and defended (Naeem & Li 1998; Risser 1999; van der Heijden et al. 1999; Loreau & Hector 2001; Hector et al. 2002) in the literature. These discussions have stimulated a profusion of empirical studies addressing this relationship (Cameron 2002; Naeem 2002). The core of the debate rests on whether the influence of species richness is primarily through the positive correlation of species richness with diversity of species’ functional traits, or whether species richness, per se, influences ecosystem processes. I believe that this polarization is misguided: if species are not different, then diversity does not exist and we would not predict any influence on functioning. Biological diversity at the species level can be defined by variation in traits between species, so logically all effects of biological diversity must act directly or indirectly via variation in species traits. As stated by Grime (1997)
in reference to the results of (MacGillivray et al. 1995), “it is the biological characteristics of the
dominant plants rather than their number that control ecosystem productivity and
biogeochemistry”. This point seems obvious, but the segue taken by Grime leads to his
conclusion that “So far, neither evolutionary theory nor empirical studies have presented
convincing evidence that species diversity and ecosystem function are consistently and causally
connected.” Similarly, with papers titled like Hooper and Vitousek’s 1997 publication—“The
effects of plant composition and diversity on ecosystem processes”—it appears that both ‘sides’
of this debate seem to be fostering the unfortunate notion that composition of communities is
distinct from and exclusive of the grander concept of biological diversity. Rather than arguing
about whether it is species richness per se or species composition that influences ecosystem
functioning, I believe that we should put our energy into advancing understanding of how
variation in traits mechanistically underpins the observed patterns between diversity and
ecosystem function (e.g., Diaz & Cabido 2001; Diaz et al. 2003; Duffy 2003; Hooper & Dukes
2004).

**Conceptual Development**

Diversity theoretically influences ecosystem processes via two overarching mechanisms:

1. **Trait uniqueness hypothesis**: if all species were functionally homogenous (i.e., no
   functional diversity existed), ecosystems would function differently than they currently
do. For example, without organisms with differences in their abilities to metabolise
inorganic versus organic forms of nitrogen, the biogeochemical nitrogen cycle would
function differently. In grassland ecosystems, for example, it is clear that traits
particular to certain groups of species, such as nitrogen fixers, have important
ramifications for the biogeochemical nitrogen cycle in these systems (Hooper &
Vitousek 1997; Tilman et al. 1997). In essence, this can be distilled down simply to the
fact that different traits, by definition, do different things. This mechanism is well
documented and indisputable, and relies only on the existence of particular traits (arrow
2 in Figure 4.1).

   a. **Bet-hedging** is a subset of this mechanism: an increase in diversity increases
the odds of some species having traits leading to tolerance, resistance, or
resilience to shifting environmental conditions (McNaughton 1977; Walker
1992; Walker et al. 1999; Yachi & Loreau 1999). This bet-hedging aspect relies
on increased numbers of species probabilistically leading to increases in the
likelihood that particular traits are present in more speciose communities (arrow 1 in Figure 4.1).

2. **Trait interaction hypothesis:** inter-individual variation in traits implies that individuals of one species may function differently when neighboured by individuals of different, versus the same, species. In other words, new dynamic properties could emerge from the structure, or pattern, of diversity. This pathway is supported by complex systems theory relating structure or arrangement of components to altered functioning of an aggregate whole *(e.g., Levin 1998, 2000; Capra 2001)*, and relies on interactions between diverse components of a system *(e.g., traits)* leading to changes in system behaviour (arrow 3 in Figure 4.1).

All else being equal, increased species richness will be correlated with increased diversity of species traits, and thus be indirectly associated with ecosystem processes through the first mechanism described above. This has been described as a ‘confounding’ sampling effect in previous research *(see Huston 1997)*. I argue that this is an important valid causal connection between diversity in the broader sense *(e.g., variety of form and function)* and ecosystem functioning, yet recognize that this ‘sampling effect’ is a confounding effect when focusing strictly on the effects of species richness *per se* on ecosystem processes. Logically, if species are added to a system without loss of existing species, more speciose systems will include a greater diversity of traits (even if the whole system is functionally bounded *(sensu Hooper and Dukes 2004)*, in that there are ultimate constraints to the presence of traits, imposed by abiotic filters during community assembly for example; Lavorel and Garnier 2002). These functionally diverse systems should operate differently than functionally depauperate systems *(Schmid et al. 2002)*.

A mechanistic foundation for the trait interaction hypothesis arises from ecological first principles, even for a fundamental ecosystem process such as photosynthesis. If any resource *(e.g., nutrients, light, or space)* limits the rate of a process *(e.g., photosynthesis)*, and if, as assumed in basic competition theory *(MacArthur 1972)*, intra-specific resource demands overlap more than inter-specific resource demands, I predict that the variety of interactions
Figure 4.1: A simplified conceptual model of the relationships between biological diversity and ecosystem processes. The nesting of 'numbers of species' and 'variety of traits' within biological diversity indicates that these are subcomponents of the grander concept that is 'biological diversity'. Arrows indicate relationships addressed in this study. Arrow 1 represents the inevitable positive influence of increased trait diversity in systems with increased numbers of species. Arrow 2 represents the standard influence of the presence of particular traits on biogeochemical cycles. Arrow 3 represents the influence of interactions between traits, and thus the influence of spatial or temporal patterning of the arrangement of these traits, on ecosystem functioning.
between species, and thus species richness, must influence in some way the system-wide rate of that process (i.e., mechanism two above). Hypothetically, a fixed amount of biomass of a number of species could be spatially partitioned into either a set number of monospecific patches, or the same number of multi-species patches (Figure 4.2; row A versus B). Given the two postulates above (that some resource is limiting, and there is more overlap in intra- than inter-specific resource demands), having lower biomass of each individual species implies that a resource-limited rate (e.g., nutrient uptake, light capture, space acquisition) would be less reduced when neighboured by interspecific individuals (i.e., in a more diverse system) than by conspecific individuals. In situations where we might see a static total community standing biomass (Hubbell 2001), and perhaps even energy (Enquist & Niklas 2001), partitioned between the species present, we thus predict a multi-species arrangement of individuals (Figure 4.2B) to a have higher total photosynthetic rate (i.e., be making more efficient use of available energy) than average monospecific arrangements (Figure 4.2A).

Figure 4.2: Two possible arrangements of five individuals each of five different species. Row A represents five monoculture arrangements in five 'communities', while row B represents five communities that each contain equal amounts of each species. The total amount (e.g., biomass or numbers) is fixed for each set of communities, but the ratio of intraspecific to interspecific neighbours changes entirely, from 1:0 in row A to 0:1 in row B. If some resource (nutrients, light, space) is limiting, and if resource use overlap is less between interspecific individuals than it is between intraspecific individuals, then I predict that the communities in row B will more efficiently utilize the available resources.

This present study teases apart the relative magnitude by which each of these two mechanisms, acting through species richness, influences ecosystem processes (Figure 4.1). Specifically I examine the influences on ecosystem functioning of particular traits (assessed by species identities; the trait uniqueness hypothesis), and of interactions between traits (assessed by species richness: the trait interaction hypothesis). By fixing the total biomass of experimental
communities and partitioning biomass of each species equally between all possible combinations of species, I simultaneously test the importance of both the presence of particular species (the trait uniqueness hypothesis) and the importance of interactions between species (the trait interaction hypothesis) in driving the average photosynthetic rate of these experimental communities.

**Materials and Methods**

*Definitions*

Biological diversity, as defined in this study, refers to variation in biological form or function. Commonly, a simple count of species number (species richness) is used as an imperfect proxy of this conceptual construct, although ideally, measurement of biological diversity would be based on variation in form and function within and between individual species. In the absence of this ideal, I deconstruct biological diversity into two key operational components: species richness and species identity. Species identities here are used as a proxy for trait diversity, following the logical assumption that a number of individuals of different species have cumulatively more unique traits than the same number of conspecific individuals. This allows for the presence of particular traits (the trait uniqueness hypothesis) to be accounted for by species identities. After parsing out this species-specific trait influence, any remaining effect that is attributed to species richness must represent an effect attributable to interaction between species (the trait interaction hypothesis). Verification that this effect is acting through interactions between traits can demonstrated by showing a difference in how individuals are responding differently to inter- versus intra-specific individuals.

Ecosystem functioning is defined as the summation of all transfers of mass or energy through an ecological system (species and their encompassing environment). An ecosystem process (analogous to one ecosystem function) is defined as one subcomponent of ecosystem functioning, specifically associated with a biogeochemical process, such as carbon fixation or nitrate uptake. Herein I focus on photosynthetic rate as an ecosystem process, given that this is the fundamental process by which energy enters ecological systems.

*Experimental design*

Marine intertidal pools were used the model ecological system for this study, and groups of marine macrophytes varying in both numbers and identities of species were assembled to test
the model presented in Figure 4.1. Tidal pools form ideal and tractable model systems for assessing ecosystem dynamics due to their relatively discrete nature and small size (e.g., Nielsen 2001; Nielsen 2003). In addition, tidepool communities vary substantially in macroalgal species richness, ranging from monocultures to relatively speciose algal communities (e.g., up to ~25 species; Lubchenco 1978). Tidal pools also may contain relatively high algal biomass to pool volume ratios (e.g., 30% algal biomass to 70% water volume Klugh 1924), with consequential rapid changes in dissolved oxygen caused by photosynthesis of the algal community (Morton & Miller 1968; Goss-Custard 1979). These high photosynthetic rates, in concert with relatively small resource pools (e.g., nutrients or space) due to isolation when emerged from the ocean, can lead to resource limitation. Finally, macroalgae are convenient for such studies because of their unusual tractability: the lack of a true vascular system and generally reduced structural support systems enables relatively easy manipulation of both total mass and numbers of individuals. This range of diversity and fast response time, coupled with discrete community boundaries (pool edges) and robust tractable individuals provides an ideal natural model for studying the consequences of biological diversity.

To test the generality of the mechanisms tested, I replicated these experiments in two ecosystems with relatively independent evolutionary histories: rocky shores in the vicinities of Newport, Oregon, U.S.A., and Kaikoura, Canterbury, New Zealand. Species selected for these experiments were chosen from among suites of species occurring in the respective local communities. Experimental communities were then created from these groups of species in the laboratory. New Zealand species included Lophothamnion hirtum, Halopteris virgata, Cystophora torulosa, Hormosira banksii, and Porphyra sp., while United States species included Ulva sp., Mastocarpus papillatus, Mazzaella splendens, Fucus gardneri, and Sargassum muticum. For each synthetic community, total biomass was fixed at either 40 (New Zealand) or 15 grams (U.S.A.) wet weight of algae. The different fixed biomasses were determined by the relatively larger sizes of species used in New Zealand. Given the five species chosen for each run of the experiment, every permutation of those five species was a treatment: five monocultures, ten unique combinations of two species, ten unique combinations of three species, five unique combinations of four species, and only one unique combination including all five species. Treatments with no algal biomass were included with each run, to control for measurement error and background changes in dissolved oxygen. Each species was allocated an even proportion, by weight, of the total community biomass, and the actual biomass of each species in each pool was used in the statistical models, to account for the variation in individual algal sizes that led to realized biomass of each species (actual masses were +/- 2.5% of expected biomass on average).
Community-level photosynthetic rate was the measured ecosystem process. Photosynthetic rate was estimated by evolution of dissolved oxygen, using a YSI 95 dissolved oxygen meter. Incubations of algal assemblages were done using one litre water volumes in glass Mason jars in the United States, and one and a half litre water volumes in plastic tubs (ice-cream containers) in New Zealand. Experiments were repeated in dark and light environments providing estimates for respiration rates and net photosynthetic rates which allow for calculation of estimated gross photosynthetic rate. Incubations were not stirred, which would alter estimated absolute photosynthetic rates, but should not influence the predictions of the two key hypotheses tested here. These differences in incubation chamber materials and water to biomass ratios were imposed due to logistical constraints, and in order to accommodate different morphologies of algae, specifically differences in algal volume to mass ratios, at the two locations. These differences result in different water to biomass ratios in different locations (15 grams per 1 litre in the U.S., and 40 grams per 1.5 litre in New Zealand), and thus differences in potential resource limitation rates, with the Oregon experiments potentially being less resource limited than the New Zealand experiments. Nutrient levels, in addition, tend to be higher near Newport, Oregon than they do near Kaikoura, New Zealand (e.g., Menge et al. 1999, Menge 2000, Menge et al. 2003), further adding to the potential for the New Zealand pools to be more nutrient limited. Photosynthetic rate for each assemblage was repeatedly assessed across a range of typical environmental conditions, ranging from bright sun and hot weather to cloudy, low light and cool conditions. In addition, I generated experimental conditions such as brief desiccation (2 hrs in full sun at 29 °C) and low salinity (2 hrs in 0 % NaCl) exposure. These different environmental conditions, including those experimentally generated, are hereafter referred to as ‘climates’. These climates were established to ensure the generality of the observed responses discussed herein, as well as to address questions regarding stability of photosynthetic rates across various levels of species richness, results from which will not be discussed in this paper. The climates under which the experiment was run were as follows: in the USA, ‘cloudy’ (heavy cloud cover; PAR (photosynthetically active radiation) = 750 μEm⁻¹s⁻¹), ‘low light’ (using shade cloth; PAR =10 μEm⁻¹s⁻¹), ‘low salinity a & b’ (immediately, and two hours, after a two hour exposure to freshwater, respectively; PAR = 1000 μEm⁻¹s⁻¹), ‘moderate sun’ (clear sky; PAR = 1400 μEm⁻¹s⁻¹), and ‘underwater’ (incubated under 60 cm of seawater; PAR = 50 μEm⁻¹s⁻¹). In New Zealand, climates were ‘cloudy’ (heavy cloud cover; PAR = 900 μEm⁻¹s⁻¹), ‘desiccation low light’ (immediately after two-hour desiccation in full sun; PAR = 125 μEm⁻¹s⁻¹), ‘desiccation moderate light’ (24 hours post-desiccation; PAR = 700 μEm⁻¹s⁻¹), ‘low light’ (at dusk; PAR = 30 μEm⁻¹s⁻¹), ‘full sun a & b’ (full sun, = 25 °C; PAR = 2000 μEm⁻¹s⁻¹), and ‘cool sun’ (full sun, 17 °C; PAR = 2000 μEm⁻¹s⁻¹). All PAR measurements were averaged from multiple measurements using an Apogee PAR-SUN sensor.
**Statistical analyses**

Community photosynthetic rate was measured under a range of environmental conditions. Using repeated measures mixed effect linear models, this community photosynthetic rate was modeled as a response to species richness and biomass of each species in each assemblage (i.e., species identities):

$$PS_{comm} = B0 + B1(\text{richness}) + B2(\text{sp1}) + B3(\text{sp2}) + B4(\text{sp3}) + B5(\text{sp4}) + B6(\text{sp5}) + \text{error} \quad (eq.1)$$

'PS_{comm}' represents the community-level photosynthetic rate, 'richness' represents species richness, and the 'spX' terms represent the biomass of each species in the community. The coefficients B2 through B6 signify the trait uniqueness hypothesis, and B1 signifies a manifestation of the trait interaction hypothesis. All independent variables are nested within climate (a random factor), with repeated measures taken on each pool. As opposed to methods using an estimated over-yielding or relative-yielding approach (e.g., Vandermeer 1989; Spehn et al. 2005) which focus specifically on a calculation of estimated yield of polycultures based only on total observed yields of monocultures, my approach specifically incorporates the identities and biomass of each species involved in every treatment. The variance explained by the species richness term is thus loosely analogous to relative yielding approaches, but the species-specific photosynthetic rates are being estimated robustly from all available treatments. The species richness term specifically tests whether species richness has any influence on community photosynthetic rate after accounting for identities and weights of all species in the community. This point made in the last phrase is vital: "after accounting for identities and weights of all species in the community." If a model fits better with this species richness term than without (based on a test accounting for increased parameterization of the richer model; Akaike Information Criterion, AIC, for example), this indicates that species richness somehow influences photosynthetic rates above and beyond species identities, supporting the trait interaction hypothesis. This analysis is possible only because the stablished treatments include all possible permutations of every species involved.

In an attempt to better model the potential role of resource limitation of each species in these assemblages, I further tested the changes corresponding with a more elaborate model that incorporates species-specific photosynthetic responses as quadratic functions of biomass.

$$PS_{comm} = B0 + B1(\text{richness}) + B2(\text{sp1}) + B3(\text{sp1}^2) + B4(\text{sp2}) + B5(\text{sp2}^2) + B6(\text{sp3}) + B7(\text{sp3}^2) + B8(\text{sp4}) + B9(\text{sp4}^2) + B10(\text{sp5}) + B10(\text{sp5}^2) + \text{error} \quad (eq.2)$$

This elaboration allows for each species' photosynthetic rates to decrease as biomass increases. If interactions between species are mitigating average resource limitation, we expect...
a drop in the explanatory power of the species richness term in this model relative to equation 1, to account for variation that is explained instead by quadratic (limiting) species identity terms in the quadratic model (eq2). In other words, species richness may increase (or decrease) photosynthetic rate of communities relative to estimated species-specific influences (eq1), and this species-richness associated increase may be explained, in part, by modeling each species as having independent rates of photosynthetic limitation at increased biomass levels (eq2).

It is possible to quantitatively partition the variance in community photosynthetic rate into independent components associated with species richness or species identity components of diversity (Figure 4.3). Variance partitioning methods (Legendre & Legendre 1983; Whittaker 1984) provide ecological insight in situations where distinguishing the relative roles of various drivers of a response is desired; the tool has been applied primarily to distinguish between the roles of environmental, biotic, and/or spatial factors in driving various multivariate and univariate ecological responses (e.g., Borcard & Legendre 1994; Magnan et al. 1994; Økland & Eilersen 1994; Heikkinen & Birks 1996; Anderson & Gribble 1998; Ohmann & Spies 1998; Roche et al. 1998; Hedenas 1999; Boone & Krohn 2000; Real et al. 2003; Cleary & Genner 2004; Smith & Wiser 2004). Here, this approach is adapted to partition the variance of this univariate ecosystem process (community photosynthetic rate) into three components: variance uniquely explained by species richness, variance uniquely explained by species identity, and variance that is shared between these two explanatory factors (i.e., can be explained by either factor). The regression presented in equation 1 provides an estimate of the total variation (Vt; white region in Figure 4.3C) that is accounted for by a ‘full’ model including both richness and identity (variance in photosynthetic rate explained from the regression model [model sum of squares] divided by the total variance of photosynthetic rate [total sum of squares of response]; equivalent to $r^2$ in a regression). Removing species identities (all the species-specific terms) from this full model provides an analogous calculation for the total variance explained by species richness (Vr; black region in Figure 4.3B). Similarly, removing species richness from the full model (eq. 1) provides an estimate of the total variance explained by species identities (Vi; white region in Figure 4.3A). Subtraction then provides an estimate of the amount of overlap (technically called the ‘intersection’ of richness and identity, ‘$\cap$’, in probability set notation) between these two predictors (overlapping region in Figure 4.3D, shaded dark grey).

$$V_r + V_i - V_t = V_r \cap V_i$$  \hspace{1cm} (eq.3)

This intersection can thus be accounted for by three different regression models. Modeling community photosynthetic rate as a function of a) species richness, b) species identities, or c)
Figure 4.3: An example of variance partitioning for diversity effects. The area of each shape is a quantitative representation of variance explained. The light grey background in each case (A-D), represents the total variance of the response, in this case community photosynthetic rate, normalized to equal 100%. The relative size of the other shapes thus indicates how much of the total variance in the response is explained by the respective models (i.e., an r² in a regression). If we regress community photosynthetic rate on the identities of each species (i.e., modeling how the biomass of each species involved explains community photosynthetic rate) we get an estimate of how much of the variance in community photosynthetic rate is explained by variation in species identities (sum of squares from the model divided by total sum of squares). This percentage of the total variance is represented in ‘A’, with the white square representing the variance in community photosynthetic rate that is accounted for by variation in species identities (Vₗ). We can then repeat this process, modeling photosynthetic rate as a function of species richness only, and produce box ‘B’. The black square quantitatively represents the variance in community photosynthetic rate that is accounted for by variation in species richness (Vᵣ). If we then regress community photosynthetic rate on a model containing both species richness and species identities, we produce an analogous estimate of the total variance explained, but by this rich model instead of only species richness or identities (Vₜ; the white area in box ‘C’). Importantly, this rich model may explain more, less, or the same amount of variance as does the sum of the two independent regressions. In this example, it explains less. This indicates that these two explanatory variables (species richness and species identities) share a portion of the variance that they each explain independently. This amount that is shared (the dark grey area in ‘D’; termed the ‘intersection’ and symbolized as Vᵣ ∩ Vₗ in probability set notation) can be quantified by adding the two independent estimates together (Vᵣ and Vₗ), and subtracting the rich model estimate (Vₜ). If the result is positive (as it is in this example) this component of the variance can be explained by either species richness or species identities when modeled independently. If this amount is negative, this indicates that a model including both species richness and species identity accounts for variance in the response that cannot be explained by either explanatory variable independently.
Figure 4.3
both species richness and species identities, will account for this particular component of the variation in community photosynthetic rate. This overlap in variance accounted for by identity or richness \((V_r \cap V_i)\); dark grey in Figure 4.3D) is the component of the overall species richness effect that is acting via species identities, since it is explained either by numbers or identities of species. Similarly, the variation explained by richness \((V_r)\) minus this intersection \((V_r \cap V_i)\) provides an estimate of the variation in community photosynthetic rate that is associated only with species richness, and cannot be accounted for without including species richness into a regression model (black region in Figure 4.3D).

As an example, if we model ecosystem process as a function of only species richness, as is often done in diversity-ecosystem function studies, we are only able to identify the \(V_r\) component of variation. If, in this example, all of this variation could also be explained by the identities of the species involved, the intersection \((V_r \cap V_i)\); grey area in Figure 4.3D) would be equal to \(V_r\) (black area in Figure 4.3B), and there would be no variation in the ecosystem function that could be attributed uniquely to species richness. Thus, although species richness would be correctly identified as a driver of the ecosystem process, this conclusion would be veiling the mechanistic role of species identities in moderating this influence of species richness on ecosystem functioning. For both equation 1 and 2, observed variance in community photosynthetic rate was partitioned into components explained by species richness \((V_r)\), by species identities \((V_i)\), and shared by both richness and identity \((V_r \cap V_i)\), using these variance partitioning methods.

By comparing variance components with species identities being modeled as linear functions of biomass (eq. 1) with the analogous components with species identities modeled to include resource limitation (quadratic functions of mass; eq. 2), we can derive some insight into the relative role of potential resource limitation in driving the relationship between species richness and community photosynthetic rate. The increased amount of variance explained exclusively by species richness \((V_r - V_r \cap V_i)\); black region in Figure 4.3D) in the simple linear models (eq. 1) over the quadratic models (eq. 2) identifies the amount of variation accounted for by species richness that is mechanistically explained by some type of species-specific resource limitation. If there is little overlap between variance components of richness and identity in the linear models, this indicates that these effects are predominately distinct. An increase in overlap seen with quadratic models then indicates that this portion of the variation is associated specifically
Figure 4.4: Quantitative partitioning of variance in community photosynthetic rates. The two rows labelled 2a represent a linear identity-specific biomass model, while the two rows labelled 2b represent a quadratic model of species-specific biomass dependent photosynthetic rate. The subheadings represent the different climates (see text for details) in which experiments took place. The area covered by the white, grey, or black color represents the amount of variation explained by each model, where white areas represent variance explained by species identities, black areas represent variance explained by species richness, and grey areas represent variance that may be explained by either species identities or species richness (i.e., variance that is shared by both identity and richness). The white regions of 2a correspond with arrow 2 in Figure 4.1, and the black regions correspond with arrow 3. Cases where grey squares (shared variance) do not overlap the white squares (identity) represent situations where a model including both species richness and species identity accounted for more variation than the sum of variance accounted for by both factors independently (i.e., shared variance is above and beyond the sum of variance explained by the two components alone). The legend (right box in middle row) is a scale for how the size of each box relates to the percentage of total variation in community photosynthetic rate that is accounted for by that factor. Asterisks indicate where the species richness component of the regressions was significant at $p < 0.05$. Most past studies of biodiversity and ecosystem functioning attribute the grey area of 2b purely to species richness, or purely to trait diversity, rather than the more mechanistic explanation provided in the text (it is an effect of species richness, mechanistically explained by interactions between interspecific traits).
Figure 4.4
with the limiting terms imposed by the quadratic model. In other words, the species identity model that includes a potential for resource limitation is explaining variation that was uniquely attributed to species richness, and thus this element of the species richness effect is, in reality, driven through the quadratic terms.

Results

The relative partitioning of variation explained by species identities, species richness, and shared by both is presented in Figure 4.4, and Table 4.1. The area of each square in Figure 4.4 quantitatively represents variance in community photosynthetic rates accounted for by experimentally imposed variation in the variable of interest. In Figure 4.4, white shaded areas indicate the amount of variation in community photosynthetic rates explained exclusively by species identities, black squares represent variation explained exclusively by species richness, and grey areas represent variation explained by either richness or identities (cases where the grey area is not embedded into the corner of the white region represent variance accounted for by identity and richness that is not attributable to either variable alone; a negative intersection, see Figure 4.3). Table 4.1 presents the calculations of these shared components of variance, including the percentage of the variance in photosynthetic rate accounted for by species richness that is shared with species identities (negative values represent variation explained by richness and identity together that are not attributable to either independently). As is shown, the average percentage of the variation attributed to species richness that is shared with species identity \((V_r \cap V_i / V_r)\) varies dramatically from the nearly none in the linear models (average of 9% shared; Table 4.1) to nearly all in quadratic models (94% shared).

As expected, particular species identities influenced ecosystem functioning in my study. Species identities accounted for a substantial component of variation in community photosynthetic rates (white plus grey areas in Figure 4.4a; Table 4.1). Likewise, in the typically applied univariate model of ecosystem process as a response to species richness alone, we see that species richness affects community photosynthetic rate, although to a lesser extent (black plus grey areas in Figure 4.4a; Table 4.1). Unexpectedly, a model including species identity is improved upon sequential addition of species richness (black area in Figure 4.4a; model D fits better than E in Table 4.2, \(p < 0.05\)). Species identities account for, on average in linear fixed effects models, 67% of the observed variance in community photosynthetic rate (white plus grey area in Figure 4.4), while community species richness accounts for 9% of the variation in photosynthetic rate (black plus grey area in Figure 4.4; Table 4.1). Very little (0.4%) variation, on average, is shared between species richness and species identities (grey area in
Table 4.1: Partitioning of variance components. Variance components are estimated from individual fixed effects models for each 'climate'. 'richness' indicates the percent of variation in the response (community photosynthetic rates) explained by a model only including species richness (\( V_r \)), 'richness & identity' indicates that variation explained by a model including both species richness and species identities simultaneously (\( V_t \)). 'ident' indicates the percent of variation explained by a model that only contains species identities (\( V_i \)). 'shared' indicates the variance that is explained by either species richness or species identities (\( V_r \cup V_i \)), and 'shared %' indicates the proportion of the variance explained by species richness that can also be explained by species identities (\( V_r \cup V_i / V_r \)). In the right half of the table (where indicated), species-specific photosynthetic rates are modeled as a quadratic function of biomass. The p-values presented represent the statistical significance of the species richness term in mixed effects models (eq1 and eq2 in the text) that include both species richness and species identities. Climate abbreviations represent the various climates under which the experiments were run; see text for details. USA = United States of America, NZ = New Zealand.

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<th>rich (( V_r ))</th>
<th>shared (( V_r \cup V_i ))</th>
<th>% shared ( V_r \cup V_i / V_r )</th>
<th>p-value</th>
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Table 4.2: Model comparisons for models including only climate (A), climate and species richness (B), climate and species identities (C), climate, species identities and species richness (D), climate, species identities as quadratics, and species richness (E), and climate and species identities as quadratics (F). Log Likelihood Ratio (LLR) test statistics are presented as comparisons between the nested models. These test statistics are computed as 2 times the differences in log likelihood between the two models being tested. The LLR test statistic is then compared with a chi-squared distribution using the difference in degrees of freedom between the two models. The presented p-values represents the probability that the increased fit of the richer model is due to random effects of increased parameterisation. The Akaike Information Criterion (AIC) is provided as an additional test controlling for the number of parameters; models with lower AIC scores are preferred (AIC = 2*d.f. – 2*log likelihood). The comparison between models E and F indicates that if species identities are included as quadratic functions of biomass, including species richness does not improve the model substantially (i.e., model F fits better than model E).

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<td>0.8102</td>
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| New Zealand                  |       |      |       |                |       |      |      |         |
| intercept                    | A     | 9    | 3199  | -1590.38       |       |      |      |         |
| species richness only        | B     | 16   | 3177  | -1572.40       | A vs B | 35.95 | 7   | <.0001  |
| species identity only        | C     | 44   | 2918  | -1415.20       | B vs C | 314.41 | 28  | <.0001  |
| species richness and identity| D     | 51   | 2814  | -1355.96       | C vs D | 118.48 | 7   | <.0001  |
| species richness and quadratic identity | E | 86 | 2789 | -1308.43 | D vs E | 95.05 | 35 | <.0001  |
| quadratic identity only      | F     | 79   | 2780  | -1311.18       | F vs E | 5.49  | 7   | 0.5999  |
Table 4.3: Estimated coefficients from regressions of community photosynthetic rate on species identities and species richness. Species richness is abbreviated 'richness', and is bold where the term was significant in the regression (see Table 4.1). The 'est. magnitude' column presents the estimated size of the coefficient. In the case of species identities, this represents the predicted increase in photosynthetic rate per gram of biomass; in the case of species richness, it indicates the expected increase (since they are all positive coefficients) in photosynthetic rate with the addition of one species. Upper and lower bounds of estimated 95% confidence intervals are also presented. Climate indicates the environmental conditions for that particular run of the experiment (see text for details).
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Figure 4.4); 8.6% (9% - 0.4%; total attributed to species richness minus amount shared with identity) of the variation is uniquely explained by species richness (black area in Figure 4.4).

The magnitude of coefficients from regression of community photosynthetic rates on species richness and species identity (Table 4.3) represent the estimated influence of an increase in one species, or one gram of biomass, on community photosynthetic rate. The positive coefficients of species richness demonstrate that species richness increases community photosynthetic rates even while accounting for species identities (species richness coefficients in Table 4.3). This indicates that in these synthetic communities, five tide-pools with biomass divided evenly between five species are predicted to have a higher community photosynthetic rate (cumulatively or on average), than the same total biomass of each of the five species partitioned into five mono-specific tide-pools.

Table 4.2 presents the comparisons between fit of six different models: (A) a model including an intercept only (these are all nested within climates, so this represents estimation of mean community photosynthetic rates for each climate), (B) a model including an intercept and species richness, (C) a model including intercepts and species identities, (D) a model (eq.1) including both species richness and species identities, (E) a model (eq.2) including species richness and species identities allowing for species-specific resource limitation, and (F) model E without the species richness term. Each richer model is tested for an improved fit to the data relative to the preceding model using the log-likelihood ratio (LLR) test statistic. These LLR statistics are used to test of whether the increased parameterisation in richer models in a nested set of models is warranted. LLR statistics are compared with a chi-squared distribution, with the difference in degrees of freedom between the two compared models as the test statistic degrees of freedom. When the fit of a model is not improved upon addition of extra parameters more than expected by chance, the simpler model is favoured. For example, comparisons between a model that includes species identities (model C) and a model that includes species identities as well as species richness (model D) show a LLR with a probability of falsely supported a null hypothesis (models are no different) of less than 5%, indicating the addition of the extra parameters (for species richness) is a statistically warranted improvement based on the explanatory power of the model.

Including the potential for some sort of resource limitation by regressing community photosynthetic rates against quadratic models of each species' biomass-specific photosynthetic rate increases the explanatory power of the models. Log-likelihood ratio (LLR) test statistics show that adding species richness to a model that already includes species identities
substantially improves the fit of these models (LLR statistics for the contrast between model C and model D are 98.64 \([p < 0.001]\) and 95.05 \([p < 0.001]\) in the USA and New Zealand, respectively; Table 4.2). We see that quadratic models of identity-specific photosynthetic rates accounted for 85% of the observed variation (as opposed to 67% in linear models) in community photosynthetic rates (white and grey areas in Figure 4.4b; Table 4.1). This increase in explanatory power of species identity (increase in the shared grey area in Figure 4.4b vs. 2a) entirely, or nearly so, consumes the effects previously attributed to species richness (reduced black area in Figure 4.4b vs. 2a), leaving nearly no species richness terms significant and ascribing only 1% (9% richness minus 8% shared) of the total variance in community photosynthetic rate exclusively to species richness (\(V_r - V_r \cap V_i\); black area in Figure 4.4b; Table 4.1). There is no difference between the fit of the quadratic model with, or without, inclusion of the species richness term (the increased parameterisation of model E over model F is not justified; \(p > 0.05\), Table 4.2) indicating that species richness is an unnecessary addition to these models. There is a stronger signature of species richness in New Zealand experiments than in U.S.A. experiments; this correlates with a greater biomass to water volume ratio in New Zealand experiments (i.e., resources were likely more quickly limiting in the NZ versus US experiments).

The variance explained by species richness in the linear models (Table 4.1), coupled with the positive species richness coefficients (Table 4.3), indicates that increased species richness increases community photosynthetic rates. In other words, polycultures have higher average photosynthetic rate than the average of the five monocultures; the arrangement presented in Figure 4.2B does, in fact, result in a higher average photosynthetic rate than that of Figure 4.2A.

The fact that the variance component attributed to species richness is, in turn, explained by quadratic models of individual species' responses ('% shared' columns in Table 4.1) indicates that this effect is likely due to differential levels of resource limitation by different species. Regardless of the exact physiological mechanism, across these sets of five species, the average reduction in photosynthetic rate of an individual is less when surrounded by interspecific neighbours than when surrounded by conspecific neighbours.

Discussion

Three key conclusions emerge from these results. First, as expected, species identity—a tractable realization of unique assemblages of traits—was a major factor in driving ecosystem processes in this system. Statistical models incorporating species' identities account for a substantial amount of the variance in community photosynthetic rates (white plus grey areas in
Figure 4.4). Thus knowing the identities and biomass of each species tells us a great deal about the photosynthetic rate of these communities. Species' traits, by definition, drive key global biogeochemical cycles. It seems apparent that this will be a pervasive fact in studies of biodiversity and its relationship with ecosystem processes whether addressed explicitly or not. This conclusion reiterates the strong influence of the presence of unique traits on ecosystem process (arrow 2 in Figure 4.1); as expected, the trait uniqueness hypothesis is supported.

Second, I conclude that species richness influences ecosystem functioning even after accounting for individual species-specific characteristics (black areas in Figure 4.4a), and that this effect can be explained by interactions between individuals (decrease in black area from Figure 4.4a to 2b). The hypothesized mechanistic cause is differential resource limitation by different species, by implying that the average reduction in photosynthetic rate of an individual is less when surrounded by interspecific rather than by conspecific individuals. This is logical, as noted initially, whereby resource overlap by interspecific individuals must be less than resource overlap by intraspecific individuals. The short duration of this study and the fact that the biomass to water ratio was higher in New Zealand where the response was stronger support the hypothesis that the communities probably became limited by either nutrient or light levels, although there could be alternative explanations. The arrangement, in this case spatial, of traits into more diverse subsets increases the rate of this ecosystem process. This conclusion indicates that the 'pattern' of species (or traits, more accurately) will have an influence on the rates of this ecosystem 'process' (see figures 1 and 2). Although this effect is relatively secondary to the influence of species identity (presence of particular traits, or 'matter'), it is shown to be relevant and detectable. Thus, the trait interaction hypothesis (arrow 3 in Figure 4.1) is also supported.

Third, as logically argued and empirically verified in this study, the influence of species richness on ecosystem functioning is entirely, or nearly entirely, modulated by the relationship between variety of traits and ecosystem functioning. Although species richness can increase the descriptive power of a model including species identities, a further addition of saturating biomass-specific photosynthetic rates for each species substantially improves the models and simultaneously renders the species richness terms non-significant (Table 4.2). Thus, the often vaguely ascribed effect of 'species richness' on ecosystem functioning (process) can be mechanistically explained entirely by variation in traits of individuals, either through unique effects associated with the presence of particular traits (matter: grey area in Figure 4.4a), or through effects associated with interactions between traits (pattern: black area in Figure 4.4a). Here, after detecting a 'species richness effect', I attribute 94% of this effect, on average (Table
4.1), to the proposed mechanism of differential resource limitation (e.g., nutrient, light or space) between conspecific individuals.

This study highlights the importance of mechanistic understanding of the relationship between biodiversity and ecosystem functioning. In this case, community-level photosynthetic rate increased in more speciose communities, and this effect was partitioned into two distinct pathways—presence of particular traits, or suites of traits (the trait uniqueness hypothesis), and interactions between species or traits (the trait interaction hypothesis). Without incorporating species identity into statistical models, only the summation of all effects due to richness would have been detected (all pathways in Figure 4.1; model B in Table 4.2; grey plus black areas in Figure 4.1), and this would lead to the mechanistically vague conclusion that species richness is driving community photosynthetic rate. Thus, if the role of species identity is not included in models of how species richness affects ecosystem processes, the effects of species identities will become partially or entirely embedded into the effects of species richness on the process, clouding interpretation of results (grey areas in Figure 4.4 would be interpreted as black areas). By drilling deeper into the dynamics of this relationship, this empirical analysis demonstrates that this relationship is mediated by individuals behaving—or interacting—differently in species-rich versus species-poor communities. This present analysis goes beyond demonstrating the existence of this grey area (Figure 4.4) by partitioning it into effects of the presence of unique traits versus interactions between these traits. I have also hypothesized, with empirical support, some of the mechanistic underpinnings (proposed to be driven by intra- vs. inter-specific overlap resource limitation) of this now commonly observed effect of species richness on ecosystem processes (e.g., Loreau et al. 2001; Kinzig et al. 2002; Loreau et al. 2002).

Biological diversity is valued by humanity for a wealth of reasons, including cultural importance, aesthetics, and tangible ecosystem goods (MA 2005). Given the globally pervasive human alteration of biodiversity, understanding the less overt aspects of the ecological relationship between diversity of species, variation in traits, interactions between individuals, and how these affect ecosystem functioning is potentially of substantial consequence. If these global changes in the structure of communities are changing the dynamics of ecosystems in non-obvious ways, we have added incentive to pay attention to our influences on biological diversity. This study demonstrates how the influence of diversity on community photosynthetic rate is mediated through the presence of and interaction between traits. Hopefully my study also helps illuminate some important intricacies of the relationship between diversity and ecosystem functioning. Specifically, by clarifying the two key and often confused mechanistic pathways through which diversity influences ecosystem functioning, and by elucidating some general connections
between matter (i.e. numbers of species and consequent diversity of traits), pattern (i.e. interactions between individuals), and a fundamental ecological process, I believe these experiments have provided new insight into the complex role of species in ecosystem functioning.
Acknowledgements

For their sage intellectual guidance, much needed tips on clarity, and occasionally physical assistance as well, I thank C. Carlson, F. Chan, A. Guerry, J. Lawler, S. Lilley, J. Lubchenco, B. Menge, and S. Wood. I extend my deep appreciation to the Andrew W. Mellon Foundation and D. Schiel for making this research logistically possible. This work was also supported by a Mamie Markham award, a National Sciences and Engineering Research Council of Canada award, a Fulbright Fellowship, and a grant from the David and Lucile Packard Foundation. This is contribution number XXX from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans funded primarily by the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation. This is also a contribution from the Marine Ecosystems Dynamics Consortium (MEDC; http://intertidalweb.org).
Literature cited (Chapter 4)


Chapter 5 ~ General Conclusions

Careful analysis and thoughtful synthesis will be necessary for expanding the envelope of ecological understanding. This work is my attempt at communicating both of these, in relation to three questions relating to our understanding of the structure and dynamics of biological diversity. These questions focused on a) advancing our understanding of the explanatory power of organismal form on physiological process, b) reiterating and explaining the overwhelming influence of ecological context on the relative relationship between local ecological processes and regional evolution and dispersal processes in driving local species richness patterns, and c) demonstrating the mechanistic underpinnings of the causal effect of patterns in distribution of traits (e.g. species richness) on community photosynthetic processes. It is my hope that I have done more to clean the ecological shop of knowledge than to clutter it.

A recap

Chapter two demonstrated that although morphologically-based functional form models for macroalgae are not functionally predictive, morphology does play a key role in ecophysiological responses. This potential to predict function from form, I feel, is an important step toward a more lucid understanding of ecological functioning. The acceptance of needing a more multidimensional approach to develop functionally explanatory classification systems is an important part of this advance. I disagree with Padilla and Allen (2000) in their claim that we have lost the functional-form paradigm, and should focus instead on deriving functional groupings based on specific functional responses. Although function-based grouping systems are an important research focus, I believe that simultaneously with acting upon Padilla and Allen's call for research on function-based groupings, we should be actively pursuing a functionally informative classification system that is based purely on easily assessed descriptions of organisms. If the functional-form paradigm is lost in marine systems, I believe we are obliged to actively rediscover and redefine it. We know that morphology matters for physiology; we now need a better understanding of how to utilize this relationship to predict functional behaviour. Given the overwhelming numbers of species estimated to exist on earth (ten to thirty million, perhaps), and our inability to identify them all (let alone assess their functional behaviour!), even a crude functional understanding of little-known species would be valuable. Such a predictive model is theoretically possible with generic functional-form models,
and appears within reach in certain systems (Koehl 1996, Lavorel and Gamier 2002). My results lend conceptual support to the approach taken in terrestrial systems, where attempts are being made to identify suites of key morphological variables that are of functional importance (McIntyre et al. 1999, Lavorel and Gamier 2002, Westoby et al. 2002). A similar set of key morphological attributes that could assess macroalgal behaviour would be a remarkable advance for marine ecology, and given my results, should be attainable.

Our analysis, in chapter 3, of how the relative importance of local ecological interactions versus regional species pools changes across spatial scales, species groupings, and habitat types provides insights into how ecological context affects theoretical predictions. As an obvious and trivial example, we do not expect to see a signature of local ecological interactions in a situation where our 'local' community of interest is half the size of Switzerland. Similarly, using range maps is an attractive approach to sampling large coarse-scale distributions of species, but we cannot expect to glean insights into intricacies of small-scale ecological processes from such data (Hurlbert and White 2005). By utilizing the expected gradients in strength of ecological interactions across spatial scales and species groupings, this third chapter hypothesised a conceptual model of where we would predict to see dynamics that represent strong local interactions (i.e. small local scales and groups of species expected to biologically interact). Indeed, these predictions were supported by our empirical analysis. This conceptual model may also provide a useful tool for interpretation and reconciliation of disparate conclusions of past studies. Finally, we provided some important additions to the existing theory of local-regional interactions, in attempting to describe how we expect this conceptual model to incorporate ecological stress models and positive biological interactions.

Lastly, my fourth chapter attempts to explain how diversity influences functioning of ecosystems through both the presence of unique traits and interactions between traits. We know that diversity does change how systems function, and this study attempted to help discern how diversity changes the functioning of systems. Specifically, I argue that all effects of diversity (species richness per se, species composition effects, or otherwise) must act through variation in individual traits. A mechanism for interactions between traits to influence system functioning was logically posed, and empirically supported. In essence, if we make the two assumptions that resource demands are more similar between intraspecific individuals than interspecific individuals, and that there is some limiting resource in a system, we expect interactions between traits to matter. I show that the effect of interactions between species (a proxy for
traits), although relatively secondary to the presence of unique species (a proxy for traits, once again), has a detectable influence on the photosynthetic rate of simulated tidepool communities. Indeed, five tidepool communities containing each of five species are predicted to have a higher average photosynthetic rate than the same total biomass of each species arranged into five monocultures. This mechanism, detected in photosynthetic rate (one of the most fundamental ecological functions), should be common to ecosystems beyond marine intertidal pools.

'Forward the path'

"However desperate the situation may be into which mankind has brought itself, the development of this new kind of growth [of scientific knowledge] gives a reason for hope, a reminder that on looking back the seemingly impossible appears to have been transcended, and that in looking forward the path, however difficult, need not again prove impassible."

G. E. Hutchinson, on the growth of scientific knowledge (1948)

I believe that ecology, now more than ever before, is in need of thoughtful synthetic work. Over 50 years ago, and in typical prescient fashion, G. Evelyn Hutchinson noted the astonishing lack of slowing—indeed the acceleration—of the exponential rate of increase of the corpus scientiarum, the 'knowledge of science' (Hutchinson 1948, Lotka 1945 cited therein). The rate of increase in our abilities to produce analytical scientific information is certainly increasing in many fields (Greene 2005). There is an important distinction, however, between the corpus scientiarum and the more rudimentary mass of 'scientific information'. Contrary to Hutchinson's optimism, I feel that there is no a priori reason to expect that our aptitude for synthesis is increasing at a comparable rate to our production of analytical information (Shenk 1997).

Indeed, access to ecological information was at a premium in the recent past, and yet the relative majority of progressive and enduring conceptual synthesis appears to have taken place in those 'information-limited' generations. I believe that the extraordinary conceptual advances made by such inimitable sages as G. Evelyn Hutchinson and Robert MacArthur were deeply rooted in their remarkable ability for clear conceptual distillation of ideas, their experience with natural history, and the value they placed on insightful ecological synthesis. Since the time of their—albeit not simultaneous—youth, however, the science of ecology seems to have become more absorbed by a desire to produce, as succinctly stated by the slogan of the Eagle Hardware® store, "More of Everything". I believe that it is not only more information that we need in ecology now, but also a better understanding of the information we already have procured. Indeed, I feel as though we are shifting from a science where access to information
was the limit to intellectual advance into a science where insightful synthesis of unfathomable volumes of information has become the bottleneck in the extension of our *corpus scientiarum*.

It is my hope that rather than simply adding more clutter to the already busy shop of ecological information production, that this work helps—at least in some small way—make some sense of extant information by providing a few novel and clear conceptual ideas about the structures and dynamics of ecosystems, some redressing and revising of past analyses, and enough empirical and logical support to build a convincing case.


--- (1965). The ecological theater and the evolutionary play. New Haven, CT, Yale University Press.


Appendices
Table A1.1: Univariate fixed-effect regression model analyses of variance for community photosynthetic rate as a function of species richness and species identities. Squared species names (in the 'Source of variation' column), indicate that the model was fit with photosynthetic rate (the response in all cases) as a quadratic function of each species' biomass. 'Climates' represent different environmental conditions (described in detail in the text). The differences in the degrees of freedom (i.e., 'd.f.') between the USA and New Zealand experiments are due to a triplicate replication, in New Zealand but not the USA, of the monoculture and five-species pools. The asterisks represent a code of the probability of observing the relationship observed if that the effect was due to random variation (i.e., 'p-value'), whereby '*' indicates that the probability is less than 5%, '*' indicates less than 1% probability, and '***' indicates less than 0.1% probability.
Table A1.1: (continued for the next 7 pages) USA linear models

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### Table A1.1 (continued): New Zealand quadratic models

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Table A1.1 (continued): New Zealand quadratic models continued

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Appendix 2
Table A2.1: List of taxa surveyed, with their ascribed trophic and phylogenetic affinities.

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<th>Trophic Group</th>
<th>Phylum</th>
<th>Species Type</th>
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3 *Phyllopadix* sp. is included, for the purposes of the kingdom-level analyses, with the Protista.
Table A2.2: Parameters estimated from the nonlinear Michaelis-Menton regression of local species richness on the regional species pool. Grouping level refers to the subgroup with this taxonomic groupings ("A" = All, "K" = Kingdom, "T" = Trophic levels). Locale refers to the scale of local communities (quadrats, transects, or sites), and Habitat is tidal height (low, mid, high). Saturation index refers to the percentage of the asymptote that the maximal datum reached, used here as a measure community saturation. Vmax and Km are the parameters estimated from the non-linear MM model, and when estimated parameters approach infinity, the notation '→∞' is used. Maximum local richness and maximum regional pool refer to the maximum number of species of each group observed in any of the local communities and in the regional pool, respectively.
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Note: The table continues with more entries, but they are not fully visible in the image provided.
Figure A2.1: Local species richness versus regional species pool regressions from intertidal communities on the West Coast of the United States. The black dashed line is a nonlinear asymptotic model fit through the 90th quantile. These results demonstrate the number of species in local communities at the local scales of quadrats (½ m), transects (50 m), and site (~1000 m) in the low, mid, and high intertidal. Taxa are grouped in various ways: all taxa combined, kingdom level groupings (Algae, Invertebrates), and trophic level groupings (Primary Producers, Suspension feeders, Herbivores, Omnivores, Carnivores). The regional pool is calculated as the number of species that were observed in a surveyed region surrounding each local community, which is on the order of 10 kilometers. Points have been jittered to aid in visualization of data density.
Figure A2.1:

2000 - Low zone

local species richness vs. regional species pool for different groups:
- All
- Alga
- Invert
- Susp
- Carn
- Herb
- Prim
- Omni
Figure A2.1 (Continued)

2001 - Low zone

[Graph showing local species richness vs. regional species pool for different categories: All, Alga, Invert, Susp, Carn, Herb, Prim, Omni]
Figure A2.1 (Continued)

2003 - Low zone

local species richness

regional species pool

quadrat size

transplant

digress

All  Alga  Invert  Susp  Carn  Herb  Prim  Omni
Figure A2.1 (Continued)

2004 - Low zone

local species richness
quad app
0 20 40 60 80 120
0 10 30 50

local species richness
trans app
0 20 40 60 80 120
0 10 30 50

local species richness
site app
0 20 40 60 80 120
0 10 30 50

regional species pool
0 0 2 4 6 8 10
0 5 10 15 20

- All
- Alga
- Invert
- Susp
- Carn
- Herb
- Prim
- Omni
Figure A2.1 (Continued)

2000 - Mid zone

local species richness

regional species pool
Figure A2.1 (Continued)

2001 - Mid zone

local species richness vs. regional species pool

- All
- Alga
- Invert
- Susp
- Carn
- Herb
- Prim
- Omni

transpp vs. quadapp
Figure A2.1 (Continued)

2002 - Mid zone

local species richness

regional species pool

All
Alga
Invert
Susp
Carn
Herb
Prim
Omni

quadopp
transopp
elevsopp
Figure A2.1 (Continued)

local species richness

- site spp
- trans spp
- quad spp

All
Alga
Invert
Susp
Carn
Herb
Prim
Omn

2003 - Mid zone
2004 - Mid zone
Figure A2.1 (Continued)

2000 - High zone

[Diagram showing scatter plots for different categories (All, Alga, Invert, Susp, Carn, Herb, Prim, Omni) with local species richness on the y-axis and regional species pool on the x-axis.]
Figure A2.1 (Continued)

2001 - High zone

local species richness

regional species pool
Figure A2.1 (Continued)

2002 - High zone

local species richness

regional species pool
Figure A2.1 (Continued)

2003 - High zone

(local species richness vs. regional species pool)
Figure A2.1 (Continued)

2004 - High zone

local species richness

regional species pool

site spp

trans spp

quad spp

All

Alga

Invert

Susp

Carn

Herb

Prim

Omni
Table A2.3: Comparison between categorical and ordinal linear mixed effects models of saturation index as a function of spatial scale, species grouping, and habitat. Both models are repeated measures regressions. Spatial scale is represented by 'scale' or 'S', with three levels (quadrat, transect, and site). Habitat is represented by 'habitat' or 'H', and includes three levels (low, mid and high intertidal zones). Species groupings are represented by 'resolution' or 'R', and include three levels (all species grouped, kingdom-level groups, and trophic level groups). Three way interactions were not significant, and were removed from the models. Saturation index is the response in both cases, but the contextual factors (scale, habitats, and resolution) are treated as ordinal (e.g. levels are low zone = 1, mid zone = 2, and high zone = 3) in one model, and categorical (e.g. levels = low, mid, and high) in the other. In the categorical tests, the specific category being modeled is indicated in the brackets. Terms that are statistically significant at $p < 0.05$ are shown in bold. The results are similar; for example, notice the resolution term in the ordinal model is significant, yet the resolution2 is not. This corresponds in the categorical model with 'kingdom' resolution not being significantly different from the 'all' resolution (the reference resolution), yet 'trophic' resolution is significantly different. Likewise, where both main effects of spatial scale are significant in the ordinal model, both scale categories (transects and sites) in the other model are also significantly different from quadrats (the reference spatial scale).
Table A2.3:

<table>
<thead>
<tr>
<th>Ordinal term</th>
<th>Value</th>
<th>Std. Error</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.346</td>
<td>0.022</td>
<td>15.417</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>resolution</td>
<td>0.121</td>
<td>0.025</td>
<td>4.885</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>resolution²</td>
<td>0.005</td>
<td>0.023</td>
<td>0.213</td>
<td>0.831</td>
</tr>
<tr>
<td>scale</td>
<td>-0.321</td>
<td>0.024</td>
<td>-13.401</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>scale²</td>
<td>0.069</td>
<td>0.024</td>
<td>2.864</td>
<td>0.004</td>
</tr>
<tr>
<td>habitat</td>
<td>0.251</td>
<td>0.024</td>
<td>10.468</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>habitat²</td>
<td>-0.073</td>
<td>0.024</td>
<td>-3.057</td>
<td>0.002</td>
</tr>
<tr>
<td>resolution * scale</td>
<td>-0.102</td>
<td>0.043</td>
<td>-2.380</td>
<td>0.018</td>
</tr>
<tr>
<td>resolution² * scale</td>
<td>0.024</td>
<td>0.040</td>
<td>0.608</td>
<td>0.544</td>
</tr>
<tr>
<td>resolution * scale²</td>
<td>-0.031</td>
<td>0.043</td>
<td>-0.721</td>
<td>0.471</td>
</tr>
<tr>
<td>resolution² * scale²</td>
<td>0.015</td>
<td>0.040</td>
<td>0.376</td>
<td>0.707</td>
</tr>
<tr>
<td>resolution * habitat</td>
<td>-0.069</td>
<td>0.043</td>
<td>-1.615</td>
<td>0.107</td>
</tr>
<tr>
<td>resolution² * habitat</td>
<td>-0.010</td>
<td>0.040</td>
<td>-0.243</td>
<td>0.808</td>
</tr>
<tr>
<td>resolution * habitat²</td>
<td>-0.010</td>
<td>0.043</td>
<td>-0.246</td>
<td>0.806</td>
</tr>
<tr>
<td>resolution² * habitat²</td>
<td>0.025</td>
<td>0.040</td>
<td>0.624</td>
<td>0.533</td>
</tr>
<tr>
<td>scale * habitat</td>
<td>-0.253</td>
<td>0.034</td>
<td>-7.474</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>scale² * habitat</td>
<td>0.004</td>
<td>0.034</td>
<td>0.107</td>
<td>0.915</td>
</tr>
<tr>
<td>scale * habitat²</td>
<td>0.078</td>
<td>0.034</td>
<td>2.301</td>
<td>0.022</td>
</tr>
<tr>
<td>scale² * habitat²</td>
<td>-0.023</td>
<td>0.034</td>
<td>-0.679</td>
<td>0.497</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Categorical term</th>
<th>Value</th>
<th>Std. Error</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.7595</td>
<td>0.0768</td>
<td>9.892</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>R[kingdoms]</td>
<td>0.0931</td>
<td>0.0872</td>
<td>1.068</td>
<td>0.287</td>
</tr>
<tr>
<td>R[trophic levels]</td>
<td>0.1793</td>
<td>0.0780</td>
<td>2.298</td>
<td>0.022</td>
</tr>
<tr>
<td>S[sites]</td>
<td>-0.5463</td>
<td>0.0872</td>
<td>-6.262</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>S[transects]</td>
<td>-0.3832</td>
<td>0.0872</td>
<td>-4.392</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>H[low]</td>
<td>-0.6730</td>
<td>0.0872</td>
<td>-7.714</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>H[mid]</td>
<td>-0.1896</td>
<td>0.0872</td>
<td>-2.173</td>
<td>0.031</td>
</tr>
<tr>
<td>R[kingdoms] * S[sites]</td>
<td>-0.1441</td>
<td>0.0956</td>
<td>-1.508</td>
<td>0.132</td>
</tr>
<tr>
<td>R[trophic levels] * S[sites]</td>
<td>-0.2034</td>
<td>0.0855</td>
<td>-2.380</td>
<td>0.018</td>
</tr>
<tr>
<td>R[kingdoms] * S[transects]</td>
<td>-0.0227</td>
<td>0.0956</td>
<td>-0.237</td>
<td>0.813</td>
</tr>
<tr>
<td>R[trophic levels] * S[transects]</td>
<td>-0.0483</td>
<td>0.0855</td>
<td>-0.565</td>
<td>0.572</td>
</tr>
<tr>
<td>R[kingdoms] * H[low]</td>
<td>0.0520</td>
<td>0.0956</td>
<td>0.544</td>
<td>0.587</td>
</tr>
<tr>
<td>R[trophic levels] * H[low]</td>
<td>0.1380</td>
<td>0.0855</td>
<td>1.615</td>
<td>0.107</td>
</tr>
<tr>
<td>R[kingdoms] * H[mid]</td>
<td>0.0728</td>
<td>0.0956</td>
<td>0.762</td>
<td>0.447</td>
</tr>
<tr>
<td>R[trophic levels] * H[mid]</td>
<td>0.0872</td>
<td>0.0855</td>
<td>1.020</td>
<td>0.308</td>
</tr>
<tr>
<td>S[sites] * H[low]</td>
<td>0.5051</td>
<td>0.0676</td>
<td>7.474</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>S[transects] * H[low]</td>
<td>0.2588</td>
<td>0.0676</td>
<td>3.830</td>
<td>0.000</td>
</tr>
<tr>
<td>S[sites] * H[mid]</td>
<td>0.1179</td>
<td>0.0676</td>
<td>1.744</td>
<td>0.082</td>
</tr>
<tr>
<td>S[transects] * H[mid]</td>
<td>0.0276</td>
<td>0.0676</td>
<td>0.409</td>
<td>0.683</td>
</tr>
</tbody>
</table>