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SHARED PREFERENCE NICHE ORGANIZATION:
IMPLICATIONS FOR COMMUNITY ORGANIZATION AND DIVERSITY

Irene Catherine Wisheu

Thesis submitted to the
School of Graduate Studies and Research
University of Ottawa
in partial fulfilment of the requirements for the
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Université d'Ottawa
en vue de l'obtention de le doctorat ès sciences à

L'Institut de biologie d'Ottawa-Carleton

Irene Catherine Wisheu, Ottawa, Canada, 1996

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ABSTRACT

Patterns of resource partitioning have been widely described, but the causes of these patterns are incompletely understood. To explore how the patterns are formed, I did a quantitative literature survey. In Chapter One, I (1) discuss current misconceptions in the literature, (2) document and describe five ways in which resource partitioning can occur, and (3) establish guidelines for predicting the two most common ways in which patterns of partitioning are formed.

In Chapter One, the most common way in which patterns of resource partitioning were formed was through shared preference niche organization. Centrifugal organization extends shared preference organization from one resource gradient to multiple gradients. In Chapter Two, experimental evidence supporting the validity of the centrifugal organization model is reviewed and predictions of the model are presented.

The centrifugal organization model predicts how the size of species pools changes along a resource gradient. Two other models from the literature make contradictory predictions. The three models were tested in Chapter Three using biomass / species composition data from 33 eastern North American wetlands. The resulting 640 quadrats produced a pattern of pool size consistent with a previously untested model, the species pool model. This model states that the pattern of pool size is the same as the pattern of alpha diversity along a biomass gradient. This suggests that (1) the more easily measured alpha diversity values can be used to predict where large species pools occur and (2) ecological processes that are associated with changes in alpha diversity may also influence the species pool.

RESUMÉ

La répartition des ressources démontre plusieurs patrons qui ont été largement étudiés mais dont les causes sont toujours inconnues. Afin de comprendre la formation de ces patrons, une revue littéraire a été entreprise. Au cours du premier Chapitre, Je (1) discuterai des differentes conceptions retrouvées au sein de la littérature, (2) présenterai et documenterai cinq cas où la répartition des ressources est présente et (3) établirai des lignes directrices qui permettront de prédire les deux cas les plus fréquents de partition des ressources.

Le premier Chapitre nous a permis de déceler que le modèle des préférences partagées explique le plus communément les patrons observés au sein de la répartition des ressources. Le modèle de l'organisation centrifuge élargie pour sa part, l'organisation des préférences partagées à plusieurs gradients. Le Chapitre Deux présente des preuves expérimentales supportant l'exactitude du modèle des préférences partagées.

Le modèle de l'organisation centrifuge prédit des changements de taille, au sein d'un réservoir d'espèces, suivant un gradient de ressources. Deux autres modèles retrouvés au sein de la littérature, proposent pour leur part, des prédictions contraires. Les trois modèles existants ont été évalué grâce à des données sur l'abondance et la composition d'espèces retrouvées au sein de 33 milieux humides de l'est de l'Amérique du nord. Les résultats obtenus sont presentés au cours du Chapitre Trois. Ces derniere ne supporte pas le modèle de l'organisation centrifuge mais sont toutefois cohérent avec le modèle du réservoir d'espèces. Ce modèle suggère que les patrons observés au sein des réservoirs de tailles sont

similaires aux patrons de biodiversité existants le long d'un gradient de biomasses. Ceci suggère que (1) des mesures simples de diversité peuvent être utilisées afin de prédire des changements au sein des reservoirs de taille et que (2) les processus écologiques associés aux changements de biodiversité peuvent également influencer les réservoirs d'espèces.

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I wish to thank my supervisor, Paul Keddy, for not only guidance and leadership with my thesis but for years of friendship and advice. My experiences as a student and as an associate in his lab have helped me immensely in both the completion of this project and in the realization that research is what I want to do.

I am also indebted to fellow graduate students for both friendship and support, most notably to Maureen Toner, Lisa Twolan-Strutt, Joyce Belcher, Kristin Nielsen, and Harold Lee. They all made coming into the lab a pleasure. Evan Weiher deserves special thanks for being a comrade and a friend, and for offering sound scientific advice. He has commented on certain sections of this thesis, as have the following: P. Clarke, D. Currie, L. Olsvig-Whittaker, R. Bornkamm, L. Aarssen, J. Grace, M. Zobel, M. Huston, and G. Guntenspergen. Advice was also received from the members of my committee, S. Findlay and L. Flanagan, and from D. Currie and F. Pick. Members of the examining committe were also supportive (P. Catling, H. Damman, S. Findlay, D. Lean, and J. Picman), as was D. Brown. Thanks to all.

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GENERAL INTRODUCTION

The distribution of organisms along gradients has been a central theme in ecology for well over a century (e.g., Humboldt and Bonpland 1807 (as described in Huston 1994), Cowles 1899). Gradients were central to Gleason's view of community organization, a view that saw communities as assemblages of species acting individually in establishing themselves along particular environmental gradients (Gleason 1926). Whittaker, with his "gradient analysis" of vegetation of the Great Smoky Mountains (1956) not only contributed to the eventual acceptance of Gleason's hypothesis, but he also established the gradient as fundamental to the study of communities. Hutchinson used gradients in his definition of the niche (Hutchinson 1957), which opened up new areas of ecological enquiry. It was therefore inevitable that questions regarding resource partitioning would be raised (Hutchinson 1959).

Resource partitioning, the way in which coexisting species differ in their resource use along gradients (Schoener 1986), is frequently illustrated as shown in Appendix 1. Patterns of resource partitioning have been extensively described (e.g., Diamond 1973, Pianka 1969, Whittaker 1967) but the causes of the patterns are still not fully understood. The manner however, in which patterns of partitioning are formed remains central to many of ecology's current questions. For example, patterns of partitioning can arise in at least two different ways (Rosenzweig 1991), and the importance of competition in producing the pattern will vary depending on which of the two ways is occurring. Therefore, the importance of competition in structuring communities will not be determined until (1) it is widely recognized that patterns of partitioning can be formed in alternative ways, and (2) it can be

determined how patterns are being formed.

The current literature frequently assumes that only one mechanism can produce patterns of resource partitioning. To emphasize that the patterns can be formed in multiple ways, and to determine guidelines for predicting how particular patterns are formed, a quantitative literature survey was carried out. The results of this survey are presented in Chapter One. Here, I (1) discuss current misconceptions in the literature, (2) document and describe five ways in which resource partitioning can occur, and (3) establish guidelines for predicting the two most common ways in which patterns of partitioning are formed.

The literature survey showed that the most common way in which patterns of partitioning were formed was through shared preference niche organization. This is when two species share a preference for the same section of a resource gradient but do not occupy it together. The two species differ in their competitive abilities, so only the dominant species occupies the preferred section. The subordinant species is forced to occupy a secondary, less desirable segment of the gradient. This basic form of niche organization is usually considered as occurring along a single resource gradient but was extended to two resource gradients by Rosenzweig and Abramsky (1986). This new form of organization was called centrifugal organization and is the subject of Chapter Two.

Although originally proposed as occurring along two resource gradients, the concept of centrifugal organization was extended to multiple gradients and to multiple species or vegetation types by Keddy (1990). Keddy proposed that wetlands were centrifugally organized, an idea corroborated by Wisheu and Keddy (1992). This review article has been published in the *Journal of Vegetation Science* and is presented in an edited form as Chapter Two.

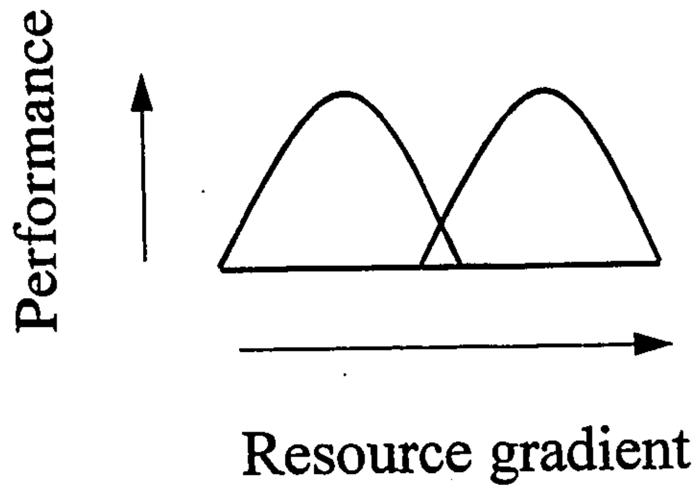
If wetlands are centrifugally organized, then biodiversity in wetlands should be highest near the low end of the biomass gradient (Chapter Two). Biodiversity is here defined as the pool of species available to colonize a given habitat. Alpha diversity, the most commonly studied measurement of diversity, is the number of species in a small sample of uniform habitat (Whittaker 1975). The prediction that the centrifugal organization model makes regarding the size of species pools is an important prediction because there is growing public interest in protecting biodiversity and because few other models make predictions regarding the size of species pools.

Two other models that make predictions of how pool size changes along a biomass gradient were found in the literature and were compared to the centrifugal organization model. Their contradictory predictions were tested in Chapter Three. Few opportunities exist to address questions regarding the species pool, since a large amount of data from geographically diverse habitats is required. However, I had participated in a large surveying exercise and could assemble the required data. Chapter Three is the first time that two of the three models have been tested, and is as well, the first documentation of how alpha diversity and pool size change along a biomass gradient. Chapter Three has been accepted by *Oikos* and is here presented in an edited form.

APPENDIX 1

The pictorial representation of resource partitioning. The two curves represent the distributions of two species along a resource gradient. The height of each curve represents a species' performance. Performance can be measured as a species' abundance or as an organism's fitness or rate of resource consumption. In this hypothetical situation, each species has optimal performance at a different point along the resource gradient. Zones of curve overlap show areas where the two species coexist.

Appendix 1



CHAPTER ONE

PREDICTING HOW PATTERNS OF RESOURCE PARTITIONING ARE FORMED

ABSTRACT

Patterns of resource partitioning have been widely described, but the causes of these patterns are as yet incompletely understood. The same pattern of resource partitioning can be produced by different types of niche organization (distinct versus shared preferences), but we are as yet unable to predict which type of organization will be structuring a particular gradient or habitat. To establish guidelines for predicting the occurrences of the different types of niche organization, I surveyed the literature to find examples of resource partitioning. I then identified, characterized, and tabulated occurrences of the different types of organization. In ten years of *Ecology*, there were 114 instances of resource partitioning accompanied by explanations of how the patterns were formed. Shared preference and distinct preference niche organization were most commonly cited as creating patterns of resource partitioning, but there were also examples of one-sided preferences, centrifugal organization, and niche organization consistent with optimal foraging theory. Shared preferences were demonstrated twice as often as were distinct preferences (x^2 = 11.9, d.f. = 1, $p < 0.001$), indicating that shared preferences are either more common in nature or that distinct preferences are harder to demonstrate. Shared preferences occurred more frequently than distinct preferences among autotrophs (x^2 = 7.014, d.f. = 1, p = 0.008). Among different aged individuals of the same species (n = 5), the type of niche organization was always that of shared preferences. Distinct preferences occurred when organisms were partitioning "hosts", i.e., when organisms were partitioned on different hosts rather than along gradients (n = 5). This chapter confirms that different types of niche organization can

create the same pattern, and also offers guidelines for predicting how a particular pattern of resource partitioning is being formed.

INTRODUCTION

"The absence of terrestrial halophytes in the non-halophytic terrestrial flora is due only to their *incapacity to struggle* successfully; the absence of aquatic halophytes in fresh water depends on their *unfitness to exist* there."

Schimper 1903

When Schimper published this description in 1903, he was acknowledging that one pattern of distribution can come about by two different means. He saw that both terrestrial and aquatic halophytes were restricted to saline soils, but that the organisms were so distributed for different reasons. He proposed that terrestrial halophytes could occupy fresh soils but that competitive inferiority was forcing them onto saline soils. With the aquatic halophytes however, physiological limitations were preventing them from occurring where soils and water were fresh (Figure 1.1).

The pattern of halophytes and non-halophytes being differentially distributed along the salinity gradient is resource partitioning (Figure 1.2). The two types of niche organization that Schimper described are termed shared preferences and distinct preferences (Rosenzweig 1991, Figure 1.2, bottom right). To describe these two types of organization, it is necessary to identify the habitat that a species "prefers". A habitat is preferred if it is the habitat in which the species occurs in highest density, in which it has greatest fitness, or that it actively chooses when given a choice.

Shared preference niche organization is when both species share a preference for one

end of the resource gradient. For example, both terrestrial and aquatic halophytes might grow best on non-saline soils (Figure 1.2). However, species differ in their tolerances and their competitive abilities, so they become differentially distributed along the gradient as determined by their position within a competitive hierarchy. Intolerant, competitive dominants occupy the preferred end of the resource gradient while tolerant, subordinant species occupy regions with lower levels of resource. With shared preferences, competition between dominants and subordinants creates the observed patterns of resource partitioning.

Distinct preference niche organization is the situation where both species have a preference for different segments of the resource gradient (Figure 1.2, bottom left). For example, aquatic halophytes might prefer saline soils and might be unable to occupy fresh water areas even when in the absence of competing species (Figure 1.1). Competition is therefore **not** the underlying mechanism to the pattern. With distinct preference niche organization, physiological, morphological, or behavioural attributes of the species determine species distributions.

Determining How Patterns of Resource Partitioning are Formed

In this thesis, resource partitioning will be defined as the way in which coexisting species differ in their resource use along resource gradients (Schoener 1986). Also known as niche partitioning, resource utilization, and habitat selection (Hutchinson 1957, Schoener 1974, Rosenzweig 1991), resource partitioning is often illustrated as resource utilization curves (Figure 1.2, top, see also Appendix 1). Patterns of resource partitioning are

frequently described in the literature (e.g., Whittaker 1967, Pianka 1969, Diamond 1973), but how the patterns are formed is not fully understood.

Distinct preference niche organization is most commonly suggested as creating the pattern of resource partitioning (Rosenzweig 1991). First modeled by MacArthur and Levins (1967) and MacArthur (1972), distinct preference organization has also been termed niche differentiation and reciprocal niche overlap (Colwell and Fuentes 1975, Keddy 1989)[1]. To distinguish distinct preference niche organization from shared preference organization, both fundamental and realized niches must be known.

A fundamental niche is the potential distribution of a species along a resource gradient (Hutchinson 1957). This was termed the physiological response by Ellenberg in 1953, 1954 (as described in Mueller-Dombois and Ellenberg 1974, see also Austin 1980, Austin and Smith 1989). Fundamental niches can only be determined by allowing species to occur along gradients in the absence of competition from other species. Reciprocal removal experiments, during which both species are allowed to occur along the gradient in the absence of the other, must be performed before fundamental niches can be determined. In contrast, a realized niche can be determined without experimentation. The realized niche is the actual distribution of a species along a resource gradient in the presence of competition (Hutchinson 1957). Ellenberg referred to this as the ecological response (Mueller-Dombois and Ellenberg 1974).

With distinct preference organization, fundamental niches approximate realized niches

[1] To add to the confusion, it seems that distinct preferences have also been referred to as resource partitioning (e.g. Goldberg and Barton 1992, Paine 1984).

(Figure 1.2). Each species does best or has optimal performance at a different point along the resource gradient even when competition has been removed. Niche expansion may occur during a competitive release experiment, but the preferred habitats will remain distinct. In contrast, with shared preferences, a removal experiment will reveal the presence of inclusive fundamental niche (Miller 1967, Colwell and Fuentes 1975). That is, both species will prefer the same segment of the resource gradient and their fundamental niches will overlap.

To distinguish shared preference from distinct preference niche organization, the fundamental niches of the species must be experimentally demonstrated. Since competition can occur at the boundaries of both shared and distinct preferences, demonstrations of competition between species are insufficient. At present, it is not known how frequently shared preferences and distinct preferences occur or how we might predict their occurrences (Rosenzweig 1991). It is also unclear as to what other types of niche organization might exist.

Types of Niche Organization

In addition to shared and distinct preferences, there are indications in the literature that other situations can also produce patterns of resource partitioning. For example, centrifugal organization occurs when there are shared preferences along two or more resource gradients. Species share a preference for the same segment of the resource gradient, but they have secondary preferences that are distinct (Figure 1.3D, E). When resources are in short supply, they will each expand out along resource gradients along which

they are the best competitor (see also Chapter Two, Figure 2.2). This situation will produce patterns of partitioning, but it is unknown how commonly this type of niche organization occurs.

One-sided preferences, first modeled by Colwell and Fuentes (1975, Figure 1.3F, G), will also produce a pattern of resource partitioning, but the mechanism remains little explored. Colwell and Fuentes (1975) also commented on occasions when fundamental niches contract during removal experiments but this situation does not appear to have been developed further in the literature. I will refer to this type of organization as optimal foraging since it is irreconcilable with competition theory but is consistent with optimal foraging theory (Pyke et al. 1977, Figure 1.3H).

Current Misconceptions

It has been over 90 years since Schimper first recognized that the same pattern of resource partitioning can arise as the result of two different forms of niche organization (Schimper 1903), yet considerable confusion still remains regarding how patterns of resource partitioning are generated. Foremost is a widespread failure to recognize that patterns of distribution (or realized niches) are not the same as fundamental niches. This obscures the distinction between pattern and process, and questions regarding how patterns are generated are overlooked and not considered.

When there is recognition that pattern and process are separate, problems may still occur. The form of niche organization generating a pattern of resource partitioning is often

assumed to be that of distinct preferences (Rosenzweig 1991). This assumption causes some researchers to (1) give no consideration to alternative types of niche organization and (2) inadequately test for the situation they believe to be generating the observed patterns. For example, results indicative of organisms with shared preferences have been dismissed as inconclusive because researchers were unaware that alternatives to distinct preferences exist.

Consequences of the recurring oversight that multiple forms of niche organization exist may include the following: (1) Review articles that do not distinguish between the opposing forms of niche organization (e.g., Schoener 1974, 1983, Connell 1983, Gurevitch et al. 1992) may base their conclusions on patterns formed in different ways. For example, the question of how competition affects biomass (Gurevitch et al. 1992) will probably have a different answer depending on whether resources are partitioned by shared or distinct preferences. (2) Mathematical models which may assume one form of niche organization, are perhaps being tested with communities that are structured by another form. (3) Discussions of how patterns of resource partitioning arose do not consider that alternative types of organization generating patterns of partition may themselves have different evolutionary origins. For example, the ghost of competition past (the coevolutionary shaping of competitors' niches, Connell 1980) might be present with organisms partitioned through distinct preferences, but the ghost need not be invoked when preferences are shared. Also, (4) the importance of competition (or alternatives such as predation) in creating patterns of resource partitioning may not be determined until it is recognized that the role of competition changes depending on the type of niche organization (e.g., Schoener 1983, Connell 1983). For example, competition may be central to the formation of a community where species

have shared preferences, but competition may play little or no role in a community where organisms have distinct preferences.

The considerable confusion regarding how patterns of resource partitioning are generated can be illustrated by considering the persistent but faulted notion that niche overlap is a measure of competition intensity (MacArthur 1972, Schoener 1974, 1983). The idea is that the greater the zone of overlap between the distributions of two species, the greater the intensity of their competition. In actual fact, the degree of niche overlap does **not** indicate the intensity of interspecific competition (Keddy 1989). The pattern of partitioning has been inappropriately interpreted as implying process. Fundamental niches have not been considered, so no distinction can be made between shared and distinct preference organization. In spite of this, competition is assumed to be determining the distributions of the species, with no consideration given to how else a pattern of partitioning might be formed.

Understanding how patterns of resource partitioning are formed might not only help clarify questions such as the role of competition in structuring communities, but such understanding would have important conservation implications as well. For example, if the halophytes described by Schimper (1903) were rare or economically important species, and one wanted to increase the numbers of aquatic halophytic plants, then it would be necessary to increase the amount of saline habitat available (Figure 1.1 bottom left). However, if shared preferences occur, as with the terrestrial halophytes, then a second option would exist. Non-halophytic species could be removed and the halophytic plants would perform better on the non-saline soils from which they had been previously excluded (Figure 1.1 bottom right).

Being able to predict the occurrences of the different types of niche organization would be an important management tool.

Objectives Of This Study

There were two objectives to this study. The first was to document the alternative types of niche organization that can create patterns of resource partitioning. The second was to establish guidelines for predicting when patterns of resource partitioning are being created by distinct preferences as opposed to shared preferences. To accomplish these goals, I posed the following questions.

(1) In the literature, what is the relative frequency of distinct preferences, shared preferences, or something else?

(2) How frequently is the type of niche organization demonstrated experimentally?

(3) Can the type of niche organization be predicted by considering characteristics of the study species?

(4) Can the type of niche organization be predicted by considering characteristics of the resource gradient?

METHODS

A survey was made of all articles in *Ecology* (1983 to 1993, including special features, award lectures, and notes and comments). *Ecology* was chosen for the survey

because removal experiments are often reported and because the journal publishes studies on all types of organisms. Abstracts or opening paragraphs were read and when a pattern of resource partitioning was presented, the article itself was reviewed with the following questions in mind:

(1) Is the example of niche organization that of distinct preferences, shared preferences, or something else?

(2) Is the example of niche organization demonstrated experimentally?

(3) What is the study organism?

(4) What is the resource gradient?

In two instances, articles from other journals were consulted in order to identity underlying gradients.

Each type of niche organization was considered as occurring a maximum of once per article regardless of whether its presence was described repeatedly or not. For example, three occurrences of shared preferences with three different pairs of insectivorous mammals (Dickman 1988) were counted as one occurrence. Similarly, when the same type of organization was described for the same organisms but in different articles, it was again considered as having occurred only once. For example, shared preferences in different aged sunfish were demonstrated by Mittelbach (1984), Werner and Hall (1988), and Mittelbach and Osenberg (1993) but was considered one example. This conservative method of counting was used to ensure that more easily manipulated organisms did not bias the survey results.

An example was considered as 'demonstrated' when removal experiments established the fundamental niches of species. For example, if an animal moved into a habitat type

recently vacated by its potential competitor, then shared preferences were demonstrated. If a plant grew better where its competitor once occurred than in its usual habitat, shared preferences were again demonstrated. Whenever possible, T-tests and confidence intervals were used to measure "better". Otherwise, the measurements and interpretations of the researchers were taken at face value and accepted. Shared preferences can be demonstrated by removing both species in turn (a reciprocal removal experiment) or by removing only the dominant species (a simple removal experiment, the removal of one species).

To demonstrate distinct preferences, an animal must not have moved into a vacated habitat, nor could a plant have grown better where it did not normally occur. Rather, each species must have performed best or remained in its original habitat, regardless of vacated habitats nearby. Because the responses of both species must be known to verify the occurrence of distinct preferences, reciprocal rather than simple removal experiments were needed to demonstrate distinct preference niche organization.

One-sided preferences were demonstrated when one species did as well or well in the second species' habitat, while the second species did not respond, or responded weakly to the removal of the first species. For example, two bee species were found to be normally distributed on flower types a and b respectively (Possingham 1992). When bee species 1 was removed, only a few individuals of species 2 went to the now vacant flower type a. However, when bee species 2 was removed, bee species 1 used flower types a and b in almost equal proportion, demonstrating one-sided preferences. As with distinct preference niche organization, one-sided preferences could only be demonstrated with reciprocal rather than simple removal experiments.

Centrifugal organization was demonstrated by first demonstrating a shared preference, and then demonstrating that secondary preferences were distinct. For example, Pennings and Callaway (1992) showed that in the absence of competition, two salt marsh plants both grew biggest in the middle marsh zones. In the waterlogged, frequently flooded low marsh, only one of the two species could persist, while in the saline, infrequently flooded high marsh, only the other species could persist. Both species preferred the middle marsh but had secondary preferences that were distinct. The determination of distinct secondary preferences required reciprocal rather than simple removal experiments.

To demonstrate optimal foraging, two species must be shown to have narrower niches when alone than when with a potential competitor. For example, two species of lizards were found to eat prey of different size (Pacala and Roughgarden 1985). The larger lizard ate large prey while the smaller lizard ate small prey. When alone however, the larger lizard did not expand its diet to include smaller prey. Rather, the lizard restricted its foraging to larger prey items. When along, the large lizard ate a narrower range of prey items than when with a potential competitor. Only one species needs to be removed for optimal foraging to be demonstrated.

In the researchers' statistical determinations of whether there were differences between the distributions of two species, statistical power favoured the detection of shared preferences, i.e., the acceptance of the null hypothesis of no difference in the distributions of two species. This statistical bias however, was offset by the biological responses required to determine a shared preference. A species must have responded to a removal experiment for a shared preference to be demonstrated, while failure to respond was consistent with distinct

preferences. The author is therefore confident that Type II errors have not unduly biased the numbers of demonstrated examples of shared versus distinct preferences in this survey.

All types of niche organization were 'indicated' when removal experiments were not performed, when removals were incomplete and possibly inadequate, or when removals were performed along a shorter segment of the resource gradient than where the pattern of partitioning occurred. Biomass was used as the indicator of a species' performance whenever possible.

Chi-square tests were used to determine whether the relative frequency of the different types of organization depended upon either characteristics of the study species or characteristics of the resource gradient. When expected frequencies were less than five, Fisher's exact probability tests were used. Tests were performed using Sigmastat Version 1.0 software (Jandel Scientific 1992-1994). When statistical analyses were performed, only studies with demonstrated examples were considered, unless otherwise stated.

RESULTS

In total, 2,132 articles were surveyed. There were 114 instances of resource partitioning that were accompanied by a discussion of niche organization. Among these, there were 47 occurrences of distinct preferences, 46 occurrences of shared preferences, 12 occurrences of one-sided preferences, 4 occurrences of centrifugal organization, and 5 examples consistent with optimal foraging theory (Table 1.1). Experimental demonstrations of how patterns of partitioning were generated accompanied 66 (or 58%) of the patterns,

with shared preferences being experimentally demonstrated more often than distinct preferences. Thirty-four examples of shared preferences were demonstrated versus 12 examples that were implied, and 17 examples of distinct preferences were demonstrated versus 30 examples that were implied ($x^2 = 11.9$, d.f. = 1, $p < .001$).

As expected, the literature survey did not yield sets of examples in proportions which are representative of nature, but the survey was expansive enough to contain examples from most major multicellular groups: terrestrial invertebrates (13), aquatic invertebrates (14), fish (19), amphibians (5), reptiles (6), mammals (10), birds (12), and plants (33, Table 1.1). Unicellular organisms were represented by only a single group of study species, the diatoms (Carney et al. 1988, Charles 1985).

Autotrophic organisms were partitioned through shared preferences more often than through distinct preferences (n = 17 and n = 2 respectively, $x^2 = 7.014$ for a goodness of fit test, d.f. = 1, p = 0.008). Among heterotrophic organisms, shared and distinct preferences occurred in equal frequency (n = 17 and n = 15 respectively, $x^2 = 5.55 \times 10^{-17}$ for a goodness of fit test, p = 1.000). When terrestrial and aquatic organisms were compared, how patterns of partitioning are formed was independent of habitat type. There were 6 examples each of shared and distinct preferences among terrestrial organisms. Among aquatic organisms, there were 9 examples of shared preferences and 7 examples of distinct preferences ($x^2 = 0.003$, d.f. = 1, p = 0.9564). However, when vertebrates were compared to invertebrates, the vertebrates did appear to be partitioned more frequently by shared preferences than by distinct. Among vertebrates, there were 14 examples of shared preferences and 6 examples of distinct preferences. Among invertebrates, there were 3

examples of shared preferences versus 9 examples of distinct preferences ($x^2 = 4.43$, d.f. = 1, p = 0.0354). This last result became nonsignificant however, when examples of "hosts" were removed from the data set (see below, p = 0.365).

Not all studies with demonstrated examples of niche organization were inter-species comparisons (Table 1.2). For example, resource partitioning also occurred among conspecifics of different age (n = 5) and of different sex (n = 1). In these situations, the organisms were always partitioning the gradient by way of shared preferences. The way in which heterotrophic organisms partition resources therefore seems dependant on whether inter- or intra-specific interactions are occurring (goodness of fit test, p = 0.055).

When organisms were described as being partitioned on different "host" foods or "host" carriers, rather than on different portions of a resource gradient, the form of niche organization was always that of distinct preferences (n = 5, Table 1.2). This was a significant association when compared to other heterotrophic organisms. Among heterotrophs, there were 6 examples of distinct preferences and 11 examples of shared preferences (p = 0.018). However, when the resource gradient itself was considered as a possible predictor for how organisms were partitioned, no significant trends were detected. Examples of shared and distinct preferences were not associated with either gradients of quantity or quality, nor were they associated with particular resources (e.g., food, water depth). Sample sizes might have been too small to allow Chi-square tests or Fisher's exact probability tests to detect associations between the different forms of niche organization and particular characteristics of the resource gradients.

DISCUSSION

Types of Niche Organization

In addition to shared and distinct preferences, three other types of niche organization were identified as giving rise to patterns of resource partitioning (Figure 1.3).

One-sided preferences

In 12 instances, the responses of organisms to removal experiments were intermediate between those consistent with distinct preferences and those consistent with shared preferences. One organism responded to the removal by expanding its niche, while the other organism either (a) did not respond, or (b) did not respond as strongly (Figure 1.3F, G). For example, in Bertness et al. (1992), when five salt marsh plant species were released from competition, two did better in less saline areas (shared preferences with the dominant species), while three others did as well in either salinity (one-sided preferences). Their responses were similar and differed only by degree. It seems likely therefore, that a gradient of responses exist, with distinct preferences and shared preferences (along with centrifugal organization) being extreme examples of the many types of niche organization that are possible.

Centrifugal organization

First described with rodent communities by Rosenzweig and Abramsky (1986), centrifugal organization is the situation in which both organisms express a primary preference for the same part of the resource gradient but have secondary preferences that are distinct. In this survey, there were four examples consistent with centrifugal organization, but the examples took two different forms. First, there were situations where one organism relinquished the preferred habitat to the other when competition occurred (Figure 1.3D, Kotler 1984, Smith 1990, Abramsky et al. 1990, 1991 and Kotler et al. 1991). This is the form consistent with previous discussions of centrifugal organization (Rosenzweig and Abramsky 1986, Keddy 1990, and Wisheu and Keddy 1992). Next, in two situations, increased competition created a standoff, and neither species occupied the preferred section of the habitat (Figure 1.3E, top right, Holbrook and Schmitt 1989, Schmitt and Holbrook 1990, and Pennings and Callaway 1992). This situation is previously undescribed but is consistent with centrifugal organization. Again, it appears that a gradient of situations exist, all generating the same patterns of partitioning.

Optimal foraging

In five situations, the fundamental niches of organisms contracted as a result of competitive release (Figure 1.3H). This is inconsistent with competition theory but is consistent with optimal foraging theory (Pyke et al. 1977). When given greater choice,

organisms specialized on particular resources, narrowing the range of resources they used. Not unexpectedly, all instances of optimal foraging occurred with animals, indicating that the removal experiments were inducing behavioral changes and were not demonstrating fundamental niches. These examples illustrate the caution required in determining an organism's fundamental niche.

Shared and distinct preferences

Among the surveyed articles, shared and distinct preferences were most frequently indicated (Table 1.1). Organisms with distinct preferences differed with respect to behaviour, physiology, and/or morphology, with the differences in one instance being parasite induced (Hechtel et al 1993). With shared preferences, the organism occupying the preferred habitat was usually the competitive dominant (n = 31), but there were also eleven examples of the preferred habitat being occupied by the organism most tolerant of predation or herbivory (Table 1.2). Competition therefore, should not be considered the only mode of interaction between organisms with shared preferences.

In the literature, shared preferences were demonstrated twice as often as were distinct preferences (Table 1.1). This may be because shared preferences occur more frequently in nature, or because shared preferences are unexpected and articles demonstrating them are readily published. The ratio of shared versus distinct preferences may also reflect the fact that distinct preferences are harder to demonstrate. Reciprocal removal experiments are needed to demonstrate distinct preferences, while one-way removals can demonstrate a

shared preference. There may also be fewer demonstrations of distinct preferences because manuscripts which imply but do not demonstrate distinct preferences may be submitted and accepted more readily since distinct preferences are well known and therefore expected by reviewers and editors. For example, there were ten articles in this survey that could be considered correlation studies. That is, authors identified patterns of partitioning, then assumed distinct preferences because morphological or physiological differences were related to the organisms' positioning along the environmental gradient. Such assumptions may not be valid since behavioural, morphological and/or physiological differences can be characteristics of species with shared preferences as well (Barnes 1985, Gliwicz and Lampert 1990, Berendse et al. 1992, Bertness et al. 1992, Tiebout 1993). Researchers do seem to make assumptions about their systems. In two instances, authors discussed one type of niche organization while their data supported another.

Predicting Occurrences of Shared and Distinct Preferences

Predictions can be made regarding how patterns of resource partitioning are being formed by considering characteristics of the organisms under study (Figure 1.4). Autotrophic organisms and conspecific heterotrophs of different age or gender are more likely to partition resources by way of shared preferences than by distinct preferences. This is consistent with the similar requirements that all autotrophs share (e.g., water, light, nutrients) and that conspecifics share. In contrast, organisms partitioning hosts are more likely to do so via distinct preferences. Distinct preferences would occur if organisms have

evolved specific adaptations for host compatibility. Further predictions based on other species characteristics or on characteristics of the resource gradient may become possible when larger surveys are undertaken. For example, Austin and Smith (1989) suggested that distinct preferences should occur along gradients that cannot be depleted (regulator gradients, e.g., temperature, pH), while shared preferences should occur along gradients that can be depleted (resource gradients, e.g., nutrients, light). More extensive surveys may verify this and may also enable other predictions to be made regarding the occurrences of the other types of niche organization. These initial results do demonstrate however, that alternative types of organization do exist and that predictions regarding their occurrences are possible.

Two cautions regarding the determination of niche organization should be made. First, patterns of partitioning that are determined experimentally may not occur in nature because of unforseen interactions. For example, fish in aquaria may show distinct preferences for different water depths, but the preference may not realized in nature. Instead, large predatory fish can force fish with distinct preferences into a common shallow water habitat (Mittelbach 1984, Fraser and Gilliam 1992). Predation or other mediating pressures can force organisms with distinct preferences into sharing the same section of the resource gradient, thereby preventing partitioning (see also Safina 1990, Suhonen 1993). Next, preferences expressed under experimental conditions may be impossible in nature. For example, with lepidopteran larvae, two species both preferred feeding on immature leaves in the lab, yet one species encounters only mature leaves in the field (Schroeder 1986). With sawflies, larvae in a lab fed on leaves upon which the adults did not oviposit (Roininen and Tahvanainen 1989).

Limitations to the Predictions

Predictions regarding the occurrences of the alternative types of niche organization can be made, but the following cautionary statements should be kept in mind. First, some organisms will express different preferences depending on the species with which they are interacting. For example, the preferences of the salamander *Desmognathus monticola* were shared with those of the larger *D. quadramaculatus* but were distinct from those of the smaller *D. ochrophaeus*. With *D. fuscus*, the response of *D. monticola* was consistent with optimal foraging (Southerland 1986a, b). Perhaps characteristics of the resources that the pairs of species use will one day help predict these different responses. Next, the same species may have different realized niches along different gradients (Mueller-Dombois and Ellenberg 1974) or have different realized niches along the same gradient but under different conditions (different weather, times of day, or seasons, Southerland 1986a, b, Hemphill 1991, Hill and Grossman 1993). Crested tits and willow tits for example, responded differently to experimental manipulations in spruce than in pine (Alatalo et al. 1987). Finally, different types of niche organization can be indicated depending on how performance is measured. For example, in Goldberg (1985), the use of measures of fitness other than biomass changed the type of niche organization from shared preferences to one-sided preferences. This is consistent with the suggestion that a gradient of preferences exists (Figure 1.3).

Speculation on Evolutionary Origins

If a gradient of preferences exists, then the evolutionary histories of shared and distinct preferences might be linked. A clue to a possible evolutionary relationship between the two types of organization can be found if we consider "specialists", those organisms with narrow realized niches. Within distinct preferences, a specialist is less widespread and inhabits an extreme habitat within the generalist's geographic range. Within shared preferences, a specialist is the subordinant or tolerant organism whose realized niche is the peripheral portion of its fundamental niche[2]. Paleontologists recognize that it is the short-ranging species (the specialists) of less abundant genera that evolve most rapidly (Boucot 1983). And it appears from statements made by authors of ecological studies that specialist species are often evolutionarily younger than generalists (e.g., Roininen and Tahvanainen 1989, Smith 1990, Ezcurra et al. 1991, but see Fellows and Heed 1972). Did some specialists begin with a tolerance of an extreme habitat, and then with time, lose the ability to occupy the preferred habitat? If so, then a possible pathway for the evolution of distinct preferences might be as depicted in Figure 1.5. Can distinct preferences evolve from shared preferences or are characteristics of the species or the environmental gradients the only factors determining niche organization? A consideration of these questions may not only help in predicting occurrences of the two types of organization, but may also help bridge the gap between ecology and evolutionary biology.

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[2] These same species can be called "generalists" if their fundamental niches are being considered (Morse 1974, Colwell and Fuentes 1975).

CONCLUSIONS

It is evident that there are still widespread misconceptions and confusion about how patterns of resource partitioning are formed. Some authors do not even question how the patterns are formed, while others make assumptions, ignoring what their data may indicate. It is important that researchers recognize that multiple types of niche organization do exist and that these types have different implications for how patterns of resource partitioning are generated. For example, the continuing debate on the importance of interspecific competition (Schoener 1983, Connell 1983, Goldberg and Barton 1992, Gurevitch et al. 1992) may not get resolved until it is recognized that the importance of competition in structuring communities will vary with whether the organisms have shared or distinct preferences.

In addition to documenting the frequency of shared and distinct preferences, this study found two forms of centrifugal organization, a gradient of situations consistent with one-sided preferences, and situations consistent with optimal foraging. Will future research uncover other types of niche organization? This study has shown that in some cases, it is possible to predict whether organisms have shared or distinct preferences. Can the more infrequent types of niche organization be predicted as well? By understanding the different types of niche organization that can create a pattern of resource partitioning, and by being able to predict their occurrences, we should now be able to clarify some of the remaining issues regarding resource partitioning. And the manner in which organisms partition resources is so central an idea to community ecology, that there is hardly an aspect of ecology that would not benefit by a clearer understanding of how patterns of resource partitioning are generated.

TABLE 1.1

Occurrences of the different types of niche organization. Numbers in bold are examples that were experimentally demonstrated while other examples were indicated.

	Distinct Preferences	Shared Preferences	One-sided Preferences	Centrifugal Organization	Optimal Foraging	Total	Grand Total
Terrestrial Invertebrates	**5** 6	**1** 0	**1** 0	**0** 0	**0** 0	**7** 6	13
Aquatic Invertebrates, microorganisms	**4** 3	**2** 3	**3** 1	**0** 0	**0** 0	**9** 7	16
Fish	**3** 2	**7** 4	**0** 0	**1** 0	**1** 1	**12** 7	19
Amphibians	**2** 0	**2** 0	**0** 0	**0** 0	**1** 0	**5** 0	5
Reptiles	**0** 4	**0** 0	**1** 0	**0** 0	**1** 0	**2** 4	6
Mammals	**1** 4	**2** 1	**0** 1	**1** 0	**0** 0	**4** 6	10
Birds	**0** 5	**3** 2	**0** 0	**1** 0	**0** 1	**4** 8	12
Plants	**2** 6	**17** 2	**3** 2	**1** 0	**0** 0	**23** 10	33
Total	**17** 30	**34** 12	**8** 4	**4** 0	**3** 2	**66** 48	114

TABLE 1.2

Studies containing examples of resource partitioning and niche organization. Examples in bold were experimentally demonstrated while other examples were indicated.

Organism	Gradient	Type of organization[1] and mode of interaction		Source
Terrestrial Invertebrates:				
Earthworms	food quantity, moisture, temp.	D	physiology	James 1988
Crickets	**moisture**	**D**	**behaviour**	**Howard and Harrison 1984a, b**
Bees	food quality	D	morphology	Harder 1985
Bees	**food quality**	**OS**	**exploitation competition**	**Possingham 1992, Inouye 1978**
Bees[2]	food quality	D	morphology	Johnson 1986
Spittlebugs	plant height, cover quality	D	morphology	McEvoy 1986
Sawflies	food quality (host species)	D	oviposition behaviour, physiology	Roininen and Tahvanainen 1989
Lepidopteran larvae	**food quality**	**S**		**Schroeder 1986**
Butterflies	food quality	D	morphology	May 1992
Aphids[2]	**food quality (host species)**	**D**		**Via 1991**
Aphids/beetles	**food quality (host age)**	**D**		**Kearsley and Whitham 1989**
Beetles	**food quality (host species)**	**D**	**oviposition behaviour**	**Siemens et al. 1991**
Mites[2]	**(host species)**	**D**	**behaviour, morphology**	**Brown and Wilson 1992**
Aquatic Invertebrates/Microorganisms:				
Diatoms	**nutrients, light, temperature**	**OS**	**exploitation competition, allelopathy**	**Carney et al. 1988**
Diatoms	pH	OS	competition	Charles 1985
Daphnia	**food quantity**	**S**	**feeding interference, predation**	**Gliwicz and Lampert 1990**
Daphnia[2]	salinity	S	competition	Weider and Hebert 1987, Wilson and Hebert 1992
Zooplankton	**food quantity**	**S**	**feeding interference**	**Kirk and Gilbert 1990, Kirk 1991**
Filter feeding insects	**food quantity**	**D**	**disturbance, predation**	**Hemphill 1991,**

				Hemphill and Cooper 1983
Predatory insects	water depth, temperature	D	physiology, oviposition behaviour	Streams 1987
Insects	nutrients	S	competition	Peterson et al. 1993
Isopods[5]	substrate characteristics	D	parasitism	Hechtel et al. 1993
Sea slugs[2]	food quality (host species)	D		Trowbridge 1991
Corals	light	OS	physiology	Stimson 1985
Shrimp[3]	water depth	S	predation	Kneib 1987
Turban snails	water depth	D	recruitment	Watanabe 1984
Limpets	substrate characteristics	D	predation	Mercurio et al. 1985
Limpets	substrate characteristics	OS	competition	Fletcher and Underwood 1987
Bivalves, gastropods	substrate characteristics	D	predation	Schmitt 1987
Fish:				
Sunfish	food quality	D	morphology	Mittelbach 1984
Sunfish[3]	food, water depth, veg. cover	S	predation	Werner and Hall 1988, Mittelbach 1984, Mittelbach and Osenberg 1993
Catfish[3]	water depth, food quantity	S	predation	Power 1984
Bass[3]	water depth	S	predation	Schlosser 1987
Minnows	water depth	D		Gorman 1988
Minnows	water depth	OF		Gorman 1988
Minnows[3]	water depth	S		Gorman 1988
Killifish[3]	water depth	S	predation	Kneib 1987
Surfperch	food quantity, substrate	CO	competition, behaviour	Holbrook and Schmitt 1989, Schmitt and Holbrook 1990
Surfperch[2]	food quality	S	interference competition	Holbrook and Schmitt 1992
Salmon[2]	depth, substrate characteristics	S	behaviour, interference competition	Gross 1991
Wrasses	food quality	D	morphology	Wainwright 1988
Subtidal cottids	substrate characteristics	OF	not competition	Norton 1991
Reef fish	substrate characteristics	S	interference competition	Robertson and Gaines 1986
Stream fish	water depth	S	predation	Schlosser 1987
Stream fish	velocity, depth, substrate charac.	D	morphology	Wikramanayake 1990
Stream fish	water velocity	S	competition	Hill and Grossman 1993
Sticklebacks	habitat	D	morphology	Schluter 1993
Lake fish	food quality	S	exploitation competition	Persson and Greenberg 1990

Amphibians:				
Salamanders	substrate characteristics	D		Southerland 1986a, b
Salamanders	substrate characteristics	OF	behaviour	Southerland 1986a
Salamanders	substrate characteristics	S	predation	Roudebush and Taylor 1987
Salamanders[3]	substrate characteristics	S	competition	Roudebush and Taylor 1987
Frog tadpoles	pH	D		Warner et al. 1993
Reptiles:				
Lizards	food quality, quantity	OF		Pacala and Roughgarden 1985
Lizards	perch position, food	OS	exploitation competition	Pacala and Roughgarden 1985, Rummel and Roughgarden 1985
Lizards	perch position	D		Salzburg 1984
Lizards	temperature	D	behaviour	Adolph 1990
Lizards	temperature	D	behaviour	Hertz 1992
Snakes	veg. cover, substrate charac.	D	physiology	Reinert 1984a,b
Mammals:				
Rodents	food quality, vegetation cover	S	interference competition	Linzey 1984
Rodents	vegetation cover	CO	competition, predation	Abramsky et al. 1990, 1991, Kotler et al. 1991
Rodents	food quantity, substrate charac.	D	morphology	Price and Waser 1985
Rodents	vegetation cover, food quantity	S	predation, competition	Kotler 1984
Rodents	vegetation cover	D	morphology	Harris 1984
Rodents	food quantity	OS	competition	Harris 1984
Rodents	nesting position	D		Dooley and Dueser 1990
Insectivores	food quality	S	interference competition	Dickman 1988
Bats	vegetation structure	D	morphology	Crome and Richards 1988
Bats	food quality, foraging height	D	morphology	Saunders and Barclay 1992
Birds:				
Penguins	temperature	D	behaviour	Trivelpiece et al. 1987
Phasianids	moisture	D	physiology	Kam et al. 1987

Hummingbirds	food quality	S	interference competition	Pimm et al. 1985
Hummingbirds	food quantity	S	interference competition, physiology	Tiebout 1991, Tiebout 1993
Hummingbirds	food quantity	S	interference competition	Kodric-Brown et al. 1984
Hummingbirds	food quality	D	morphology	Kodric-Brown et al. 1984
Corvids	habitat type	D		Andrén 1992
Chickadees[4]	foraging position	S	interference competition	Desrochers 1989
Tits	foraging position	S	interference, exploitation competition	Alatalo et al. 1987, Alatalo and Moreno 1987
Finches[2]	food quality	D	morphology	Price 1987
Finches[2]	food quality	CO	competition, morphology	Smith 1990
Sparrows	food quality	OF	morphology	Pulliam 1985
Plants:				
Sphagnum mosses	moisture	D	morphology, physiology	Titus and Wagner 1984
Amaranthus[2]	moisture	S	competition	Zangerl and Bazzaz 1984
Cattail	water depth	D		Grace 1985
Salt marsh spp.	water depth, exposure	S	competition	Bertness 1991a
Salt marsh spp.	water depth	OS	competition	Bertness 1991b
Salt marsh spp.	water depth, salinity	CO	competition	Pennings and Callaway 1992
Salt marsh spp.	salinity	S	competition, physiology	Bertness et al. 1992
Salt marsh spp.	salinity	OS	competition, physiology	Bertness et al. 1992
Lakeshore herbs	exposure, nutrients	S	competition	Wilson and Keddy 1986
Pool edge herbs	water depth	D	physiology	Bauder 1989
Coastal spp.	salinity	OS	competition	Sternberg and Swart 1987
Woody desert spp.	fertility, moisture	OS	competition, physiology	DeLucia et al. 1988, Schlesinger et al. 1989
Alpine annuals	temperature, moisture	D	physiology	Reynolds 1984
Tundra sedges	nutrients	S	competition	McGraw and Chapin 1989
Granite outcrop herbs	soil depth	OS	physiology, competition	Houle and Phillips 1989
Old field herbs	disturbance	S	competition	Turkington et al. 1993
Old field herbs	carbon dioxide	D	physiology	Wray and Strain 1987
Grassland herbs	nutrients	S	competition	Huenneke et al. 1990
Grasses	moisture	S	physiology, competition	Barnes 1985
Grasses	moisture	S	competition	Gurevitch 1986

Grasses	nutrient	S	competition	Tilman and Wedin 1991a, b
Grasses	nutrient, disturbance	S	competition	Campbell and Grime 1992
Grasses	nutrient, disturbance	S	morphology, competition	Berendse et al. 1992
Grasses	moisture, disturbance	D	physiology	Grulke and Bliss 1988
Shrubs	light	S		Denslow et al. 1990, Ellison et al. 1993
Shrubs	light	S		Greig 1993
Shrubs	exposure	D	morphology	Ezcurra et al. 1991
Shrubs	moisture, soil type	S	competition	Mustart and Cowling 1993
Trees	nutrients, pH	S	competition, seed predation	Goldberg 1985
Trees	light, nutrients	S	competition	Latham 1992
Trees	light	S		Bazzaz and Miao 1993
Trees[4]	moisture	D	physiology	Dawson and Ehleringer 1993
Aspen	soil depth	S	herbivory	Cantor and Whitham 1989

[1] D = distinct preferences, S = shared preferences, OS = one sided preferences, OF = optimal foraging, CO = centrifugal organization
[2] Same species, different "types" (genotypes, life history types, clones, morphs, etc).
[3] Same species, different age groups.
[4] Same species, different gender.
[5] Same species, with and without parasite.

FIGURES

Figure 1.1. Schimper (1903) proposed that although the distributions of terrestrial and aquatic halophytes are similar, they arose through different situations. He recognized that along a salinity gradient (x axis), halophytes are abundant on saline soils (shaded) while non-halophytic plants are abundant on fresh soils (unshaded, top). Abundances are along the y axis. Schimper suggested that terrestrial halophytes could occur on fresh soils but are restricted from growing there by competitively superior non-halophytic species (bottom right). Aquatic halophytes however, are physiologically restricted to growing in saline habitats and could not occupy non-saline areas even in the absence of non-halophytic plants (bottom left). A transplant experiment would confirm Schimper's proposal.

Figure 1.1

Distribution of Halophytes
Schimper 1903

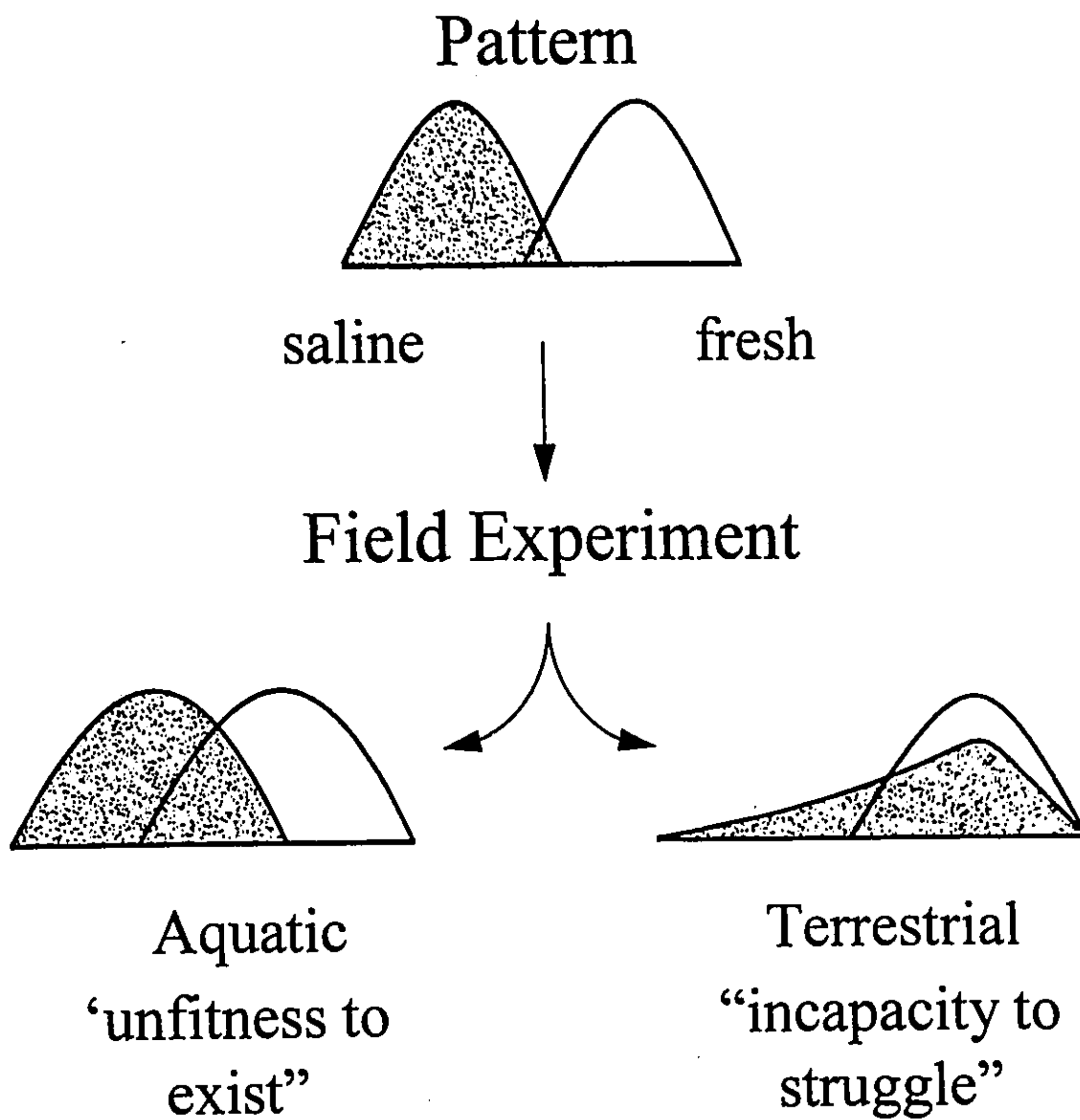
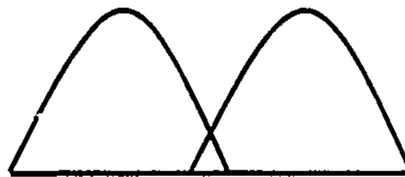


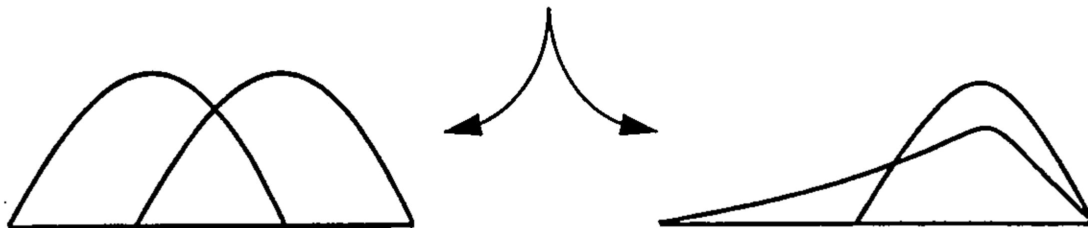
Figure 1.2. The same pattern of resource partitioning can arise through shared preference or through distinct preference niche organization. Two species are differentially distributed along a resource gradient (top). The abundances, or fitnesses of the two species are along the y axes while the resource gradient is the x axis. The actual distributions of the two species are their realized niches. The pattern of their distribution is the pattern of resource partitioning. Field experiments can reveal how the pattern of resource partitioning was formed. If removal experiments are made, and each species is allowed to occur along the gradient in the absence of potential competitors, then the fundamental niches of the species are identified (bottom). If both species do best or prefer different segments of the resource gradient, then the species have distinct preferences (bottom left). If both species do best or prefer the same segment of the resource gradient, then there will be competition. Only the competitive dominant will occupy the preferred site and the subordinant species will occur elsewhere (bottom right). This latter type of niche organization is called shared preferences.

Figure 1.2

Pattern
Resource Partitioning
(Realized Niches)



Field Experiment
(Fundamental Niches)



Distinct
Preferences

Shared
Preferences

Figure 1.3. The pattern of resource partitioning (A) can be formed by different types of niche organization. While (A) represents realized niches of species, (B-G) represent fundamental niches. With distinct preference niche organization (B), the two species differ physiologically, morphologically, or behaviourially, so fundamental niches approximate realized niches. Fundamental niches however, may be slightly wider than realized niches because competition that occurs where niches overlap may reduce realized niche widths. Distinct preferences are most commonly suggested as creating the pattern of resource partitioning. With shared preference niche organization (C), the fundamental niches of the two species overlap, with competition determining the realized niches. Shared preferences are seldom discussed but have been documented in the literature. Centrifugal organization (D, E) is a subset of shared preferences in that both species share a primary preference for the same segment of the resource gradient but have secondary preferences that are distinct. Competition again determines the species' realized distributions. One-sided preference organization (F, G) seems intermediary between shared and distinct preferences in that when competition is removed, one species expands its niche more than the other. In this instance, distributions are determined by competition and by physiological, morphological, and behaviourial attributes of the species. Optimal foraging (H) organization is inconsistent with competition theory in that when competition is removed, both

species narrow their niches. The two species restrict themselves to those segments of the resource gradient upon which they are most efficient, a reaction that is a behavioral response rather than a demonstration of a fundamental niche. The schematics for shared preferences and distinct preferences follow Keddy (1989), the rest have been sketched by the author.

Figure 1.3

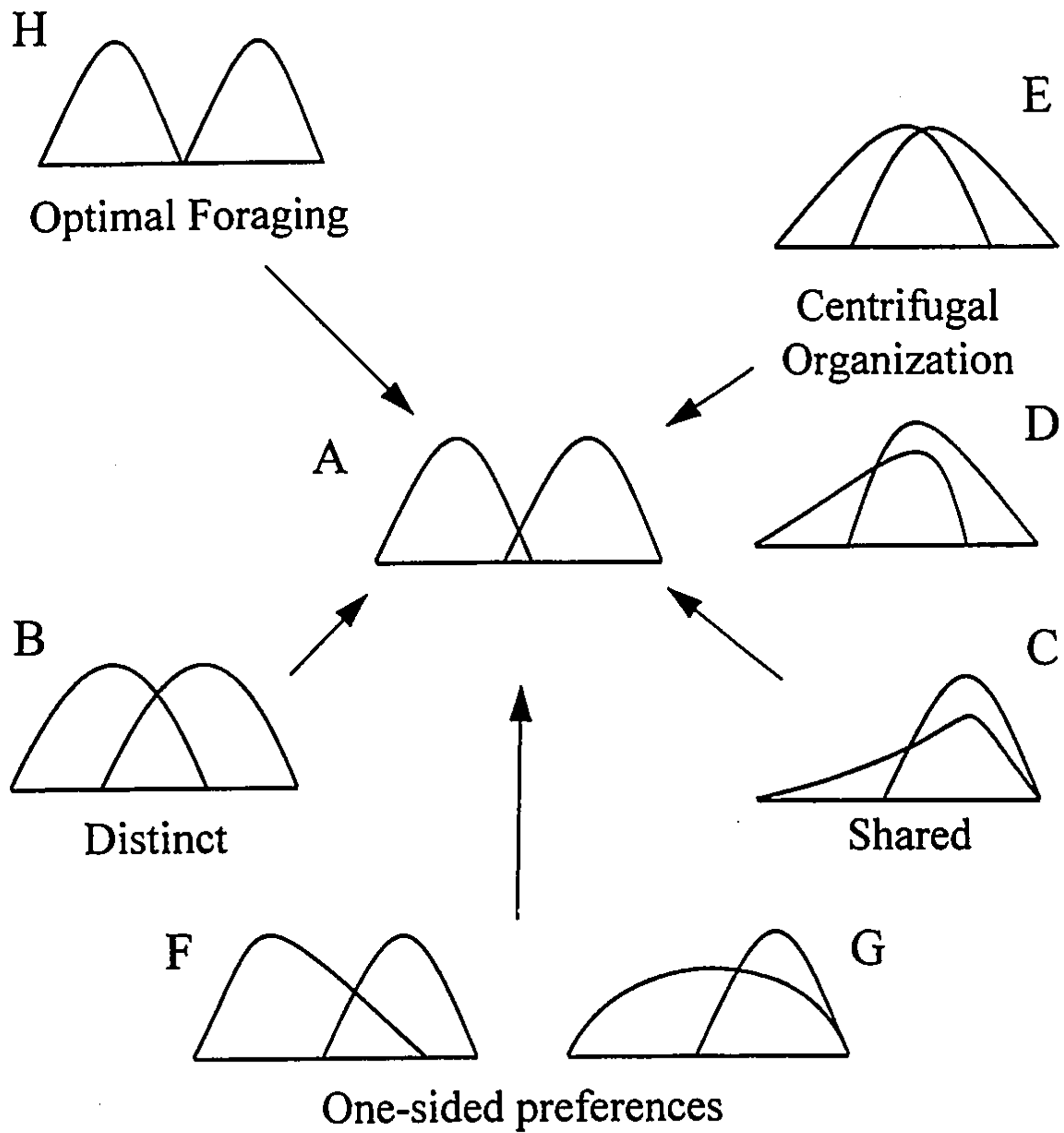


Figure 1.4. Predicting occurrences of shared and distinct preferences. If the study organisms are autotrophic, then there is a greater probability that shared rather than distinct preference niche organization is occurring. If the study organisms are heterotrophic, then there are equal chances of either shared or distinct preferences, unless the organisms are of the same species but of different sex. Then shared preference organization is predicted to occur. If the heterotrophic species are partitioned on hosts rather than along gradients, the prediction is for distinct preferences to be occurring. There are no known characteristics of the gradient that suggest either shared or distinct preference niche organization. The dashed line indicates significance at $\alpha = .055$ rather than $\alpha = .05$. The numbers in parentheses are observed frequencies.

Figure 1.4

Probabilities of Shared and Distinct Preferences

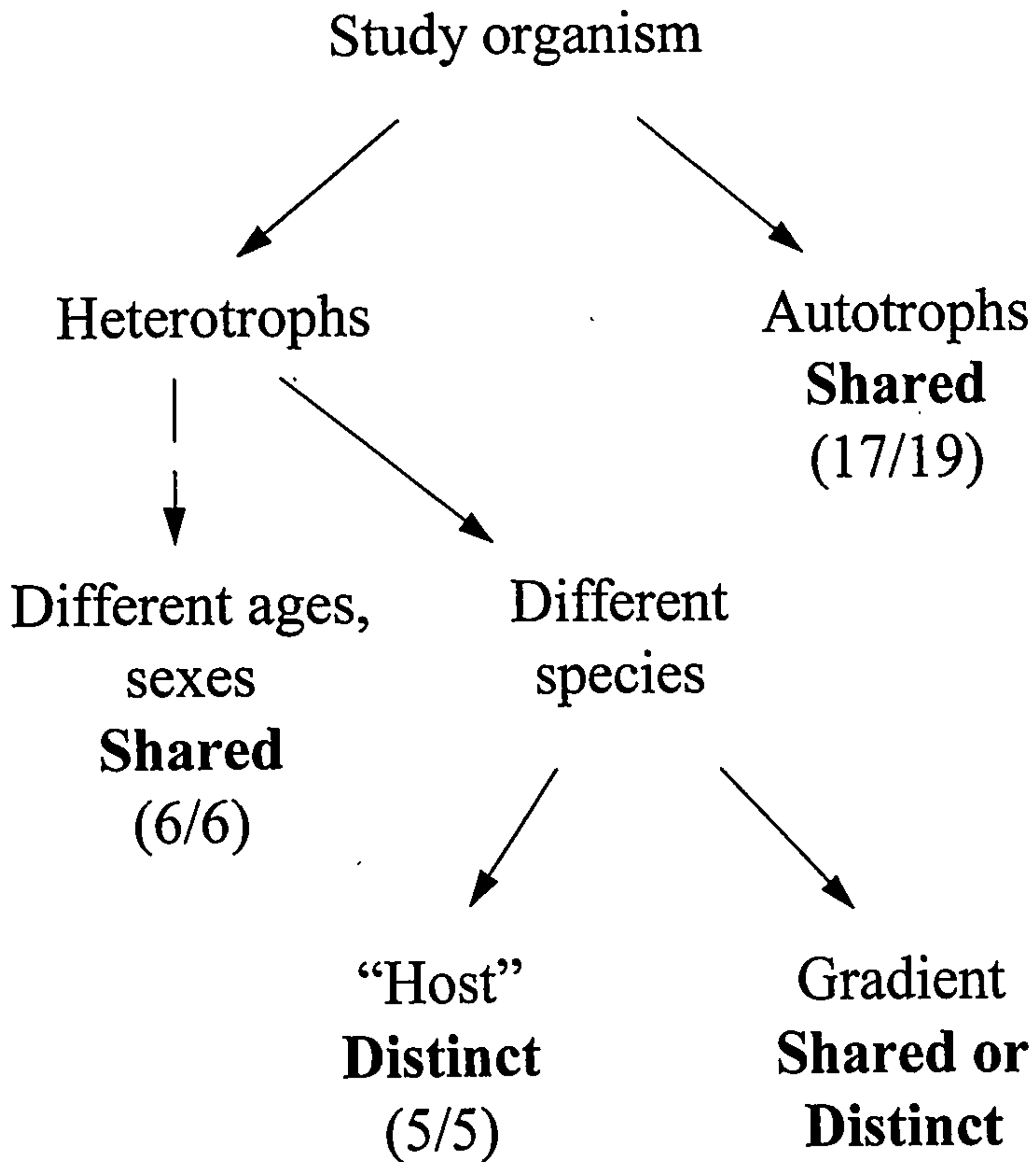
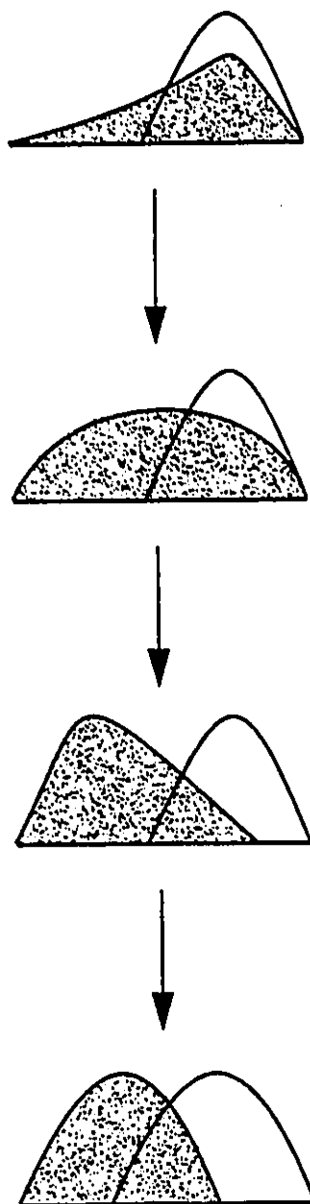


Figure 1.5. A possible pathway for the evolution of distinct preferences. Two genotypes begin by sharing a preference for the same segment of the resource gradient (top). Then, with time, the subordinant genotype (shaded) adapts to the less preferred habitat to which it has been relegated (middle). Finally, after being competitively excluded from the preferred habitat for a prolonged length of time, the 'subordinant' genotype is no longer able to occupy what was once its preferred habitat, even in the absence of the other genotype (bottom). There is now distinct preference organization. This scenario could occur between two species or between two genotypes with a new species evolving as a result of prolonged competition.

Figure 1.5



CHAPTER TWO

CENTRIFUGAL ORGANIZATION

ABSTRACT

Centrifugal organization integrates two of community ecology's main conceptual approaches: description of gradients and studies of process. Originally, centrifugal organization described the distributional patterns of two species along two resource gradients. This was later extended to multiple species or vegetation types and multiple resource gradients. The high resource ends of multiple gradients converge at a single preferred core habitat, while the low resource ends of the gradients diverge as dissimilar peripheral habitats where stresses and/or adversity are high. Weaker competitors are restricted to peripheral habitats as a result of a tradeoff between competitive ability and tolerance limits. In these habitats, species with specific adaptations to particular sources of adversity occur. Where resources are high, vegetation types have converged and domination by a single species occurs.

Experimental evidence supporting the validity of the centrifugal organization model to wetlands is reviewed. This evidence includes the determination that (1) plant species share a preference for regions where nutrients are in greatest supply, (2) that plant species differ with respect to their competitive abilities, (3) that plants inhabiting the preferred habitat are superior competitors, and (4) that there is a convergence of vegetation types in high resource regions, and a divergence where resources are low.

The centrifugal organization model can be used to describe and summarize large scale changes in life forms and vegetation types along multiple resource gradients. The centrifugal organization model also predicts how the size of species pools changes along a resource

gradient. Because of the greater variety of life forms and life history types in peripheral habitats, greatest pool size is expected where resources are low, a prediction that will be tested in Chapter Three.

INTRODUCTION

Despite the importance of spatial distributions along gradients to the study of ecology (Cowles 1899, Gleason 1926, Clements 1936), most studies are descriptive with little emphasis on how the distributional patterns are formed (e.g., Whittaker 1956, 1967). Models that integrate patterns and processes are few in number and of recent origin (e.g., Grubb 1977, Grime 1979, Tilman 1982, Rosenzweig and Abramsky 1986).

Grubb (1977) emphasized that patterns of coexistence are maintained by regeneration in different kinds of gaps, a model that is more appropriately applied to mosaic habitats than along gradients. Tilman (1982) proposed that with plants, competition organizes communities, with different species being limited by different resource ratios. There is controversy however, as to whether this model applies over broad ranges of resource levels (Keddy 1991). Grime (1979) proposed the intermediate diversity model, a model that recognizes changes in herbaceous vegetation along biomass gradients and which suggests that underlying stresses and disturbances reduce biomass and determine which ecological strategy is appropriate. Centrifugal organization (Rosenzweig and Abramsky 1986), is consistent with the intermediate diversity model but incorporates two rather than one resource gradients. Centrifugal organization was extended further by Keddy (1990) and corroborated by Wisheu and Keddy (1992) to multiple resource gradients and to a different community type.

In this chapter, I will begin by describing the original conception of the centrifugal organization model and the process behind it, shared preference niche organization. This will be followed by a presentation of how the model was extended. I will then present evidence

from the literature in support of the extended model and its application to wetland plant communities. As well, there are several predictions consistent with the centrifugal organization model, including a prediction of how species pools change along resource gradients.

THE CENTRIFUGAL ORGANIZATION MODEL

Two Species and a Single Gradient: Shared Preferences

Shared preference niche organization is when all species prefer or perform best at the same end of a resource gradient (Rosenzweig 1991). Plants, for example, all share a common requirement for a few basic resources; light, water and mineral nutrients. It therefore follows that most plants will grow their biggest, their fastest and will be most fecund where these basic resources are in greatest supply. Species vary however, in their competitive ability with some being competitively superior and others being subordinant. A trade-off is assumed here, between the ability to interfere competitively with neighbours, and the ability to tolerate low resource levels (either adversity *sensu* Southwood (1988) or stress *sensu* Grime (1979)). The outcome of different competitive abilities and different tolerance limits is that species become differentially distributed along the gradient, producing the pattern of resource partitioning (Figure 2.1).

Two Species, Two Gradients

When this basic pattern is extended to include two resource gradients, there is then the possibility of centrifugal organization (Figure 2.2). Both species share a preference for the same habitat but have secondary preferences that are distinct. As a result, when resources in the preferred habitat are disputed, the organisms can extend out in opposite directions into secondary habitats within which they are the strongest competitors. Having primary preferences that are shared and having secondary preferences that are distinct is the essence of centrifugal organization.

The basic pattern of centrifugal organization can take two forms (Chapter One). Either one species retreats from the disputed habitat (top right, Figure 2.2), or there is a standoff and both species retreat, with neither being the sole occupant of the preferred habitat (top left, Figure 2.2). In either situation, the same pattern of resource partitioning is produced.

Multiple Species, Multiple Gradients

Keddy (1990) proposed that centrifugal organization could be extended to many species and to multiple resource gradients. He proposed that centrifugal organization would occur along multiple resource gradients when the gradients radiate outwards from a single, central preferred habitat (Figure 2.3). The assumption is that the high resource end of multiple gradients are similar enough that they can be described as a "core" habitat which is

preferred by all species but that is dominated by one. As the one species prospers where resources are high, different species tolerate "peripheral" habitats, that is, habitats where resources are low. At the low resource end of each gradient, species with specific adaptations to particular sources of stress or adversity occur.

Example I

The term centrifugal organization was first used by Rosenzweig and Abramsky (1986) while studying the spatial distributions of two species of desert gerbils. The two species shared a preference for the same habitat (regions with adequate seed supplies and moderate vegetation cover) which both occupied at low population densities (Figure 2.4). As densities increased however, the gerbil species expanded their ranges in different directions towards alternate habitats within which they were the best competitors. One species selected regions with higher vegetation densities, tolerating smaller abundances of seeds. The other species required more seed and could deal with a lack of shelter. The key feature of this distribution is that both species shared a preference for the core habitat but had secondary preferences that were distinct. Enclosure experiments, during which gerbil populations were varied, have verified the role of competition in forming this distribution (Abramsky et al. 1990).

Example II

Pennings and Callaway (1992) described resource use by salt marsh plants in

southern California. Two species both grew best in a middle marsh zone, where salinity was moderate and where infrequent flooding occurred (Figure 2.5). At the low marsh zone, frequent flooding left soils waterlogged and within the high marsh zone, high salinity lowered plant water potentials. The two species were evenly matched competitors however, so neither species was the sole occupant of the preferred habitat. Instead, an abrupt border in the middle of the preferred habitat separated populations of the two species.

Interpreting patterns of resource use as examples of centrifugal organization is often difficult since removal experiments, which would test for shared preferences and would verify the role of competition in structuring the community, are not always performed (Chapter One). Thus, the existence of centrifugal organization is often indicated rather than demonstrated experimentally. Nevertheless, demonstrated examples of centrifugal organization can be found in the literature (e.g., Culver 1970, Holbrook and Schmitt 1989, Schmitt and Holbrook 1990, Smith 1990).

Example III

Keddy (1990) proposed that the centrifugal organization model should also be applicable to wetlands. In wetlands, the core habitat has low disturbance and high fertility, and is dominated by large leafy species capable of forming dense canopies (Figure 2.6). In eastern North America, *Typha* creates a light-stressed environment for subordinate species. Beyond the core, different constraints create peripheral habitats within which different groups of species and vegetation types occur (Figure 2.3). Along a soil phosphorus gradient for

example, that is highest in a fertile embayment and lowest at a sandy shore, the community composition changes from a high biomass *Typha* dominated wetland to a sparsely vegetated shoreline with species like *Drosera intermedia* (Figure 2.6). *Drosera* is an insectivorous species and indicates infertile conditions (Givnish 1988).

Gradients of nutrient concentrations however, are only some of the many gradients that occur in wetlands. Different kinds of disturbances occur and the species found along these gradients differ from those found along gradients of fertility. *Typha* again occupies fertile, protected areas, but where ice scour occurs, *Eleocharis* is found (Figure 2.6). The reed *Eleocharis* has deeply buried rhizomes that are protected from severe ice scour (Day et al. 1988). Where the disturbance is frequent flooding accompanied by mud deposition, only fast growing annuals like *Bidens* can set seed and reappear after mud deposition (Grubb 1985). Peripheral habitats that are formed by different kinds and combinations of infertility and disturbance support distinctive floras that reflect differing environmental conditions (e.g., shoreline fens (Charlton and Hilts 1988), interdunal swales and sand spits (Reznicek and Catling 1989), coastal plain wetlands (Wisheu and Keddy 1989a, 1994, Wisheu et al. 1994), and river banks (Brunton and Di Labio 1989, Nilsson et al. 1989).

EVIDENCE FOR SHARED PREFERENCES IN WETLANDS

If the centrifugal organization model is applicable to wetland communities, then shared preferences should occur. That is, species should perform best at the same end of the resource gradient, species should differ in their competitive abilities, and competition should

be most intense within the preferred habitat.

Experiment I: Testing for shared preferences

To test for the presence of shared preferences, Wilson and Keddy (1985) grew twelve different wetland species by themselves in ten different substrates of increasing organic content. Although the species occurred at different points along the fertility gradient in the field, when moved into experimental conditions where there was no competition, eleven of the twelve grew larger in more fertile soil. There was a shared preference for the organic end of the soil gradient.

Experiment II: Differing competitive abilities

Gaudet (1993) and Gaudet and Keddy (1988) investigated whether (1) species differ in their competitive abilities and if so, (2) whether strong competitors occupy preferred habitats. They measured and compared the competitive abilities of 44 different wetland species grown in organic soil. Each of the 44 target species was grown in a pot with a phytometer, one species whose reduction in growth quantifies the competitive abilities of target plants (Clements and Goldsmith 1924). Both the target species and the phytometer were harvested at the end of the growing season. The target species was a weak competitor when the phytometer with which it grew was the same size as the phytometers that grew alone. On the other hand, the target plant was a strong competitor when the phytometer's growth was

suppressed.

Wetland species did differ in their competitive abilities. The superior competitors were large wetland plants that can shade subordinate species (Gaudet and Keddy 1988, Gaudet 1993). Also, the top five competitors, *Lythrum salicaria*, *Bidens cernua*, *Phalaris arundinacea*, *Stachys palustris*, and then *Typha latifolia*, did occupy fertile, undisturbed core habitat (see also Figure 3.14 in Chapter Three). Wilson and Keddy (1986) had similar results when, by measuring each species competitive ability, they were able to predict field distributions along an environmental gradient. Again, the better competitors occupied the fertile end of the resource gradient.

In the core habitat there is a convergence towards a similar morphology; tall, fast growing competitive dominants, species which may be competitively equivalent (e.g., Agren and Fagerström 1984, Aarssen 1989). In peripheral habitats, there are a variety of habitat types and a vast array of life forms and plant morphologies. Once the constraints of intense competition are released, a wide array of life forms become possible in response to the wide array of environmental conditions. For example, a variety of annuals occupy sites experiencing disturbance while a diverse group of stress tolerant species are typical of nutrient stressed sites (Grubb 1985, Boston and Adams 1987, Givnish 1988, Wisheu and Keddy 1989b).

Experiment III: Competitive interactions

Grace (1987) constructed an experimental pond and grew six month old specimens of

Typha latifolia and *T. domingensis* in monoculture and in mixture along a water depth gradient. Two years later, the relative yield of each of the two species was calculated by dividing the biomass of the species in mixture by its biomass in monoculture. Relative yield values were used as indicators of competitive ability. When greater than 0.5, relative yield values indicated competitive superiority since the species grew better in the presence of a different species than it did in monoculture. Values less than 0.5 indicated that the species was competitively suppressed, while .5 indicated that a species grew equally well with either the same or a different species. *T. latifolia* seems competitively superior to *T. domingensis* in that its relative yield values were consistently at or above 0.5 (Figure 2.7). *T. latifolia* was however, unable to survive in the deepest water treatments, so the deep water habitat was where *T. domingensis* could apparently escape competitive domination.

Experiment IV: Competitive interactions

A similar experiment using *Typha orientalis* and *Juncus kraussii* was performed by Zedler et al. (1990) along a salinity gradient: either fresh, brackish, saline, or hypersaline. Four ramets of the two species were transplanted into either monoculture and mixed-species pots with different salinities. When grown in mixed-species pots in the fresh, brackish and saline treatments, *Typha* outgrew *Juncus* (Figure 2.8). The relative yields of *Typha* were greater than 0.5, indicating that the mean total biomass of two *Typha* ramets in the mixed pots was more than half the biomass of four *Typha* ramets in monoculture. *Juncus*, with relative yields less than 0.5, was suppressed. Adult plants of *Typha* however, were unable to

survive in the hypersaline treatment, while specimens of *Juncus* could. The hypersaline treatment exceeded the tolerance limits of *Typha* and provided a peripheral habitat where *Juncus* was no longer dominated by *Typha*. Niche widths of the two species vary, so the subordinate species finds refuge in the peripheral stressed habitat.

EVIDENCE FOR CENTRIFUGAL ORGANIZATION IN WETLANDS

Although there is evidence for shared preferences in wetlands, tests are needed to determine whether vegetation gradients do converge in core habitats. One approach would be to test whether vegetation similarity increases with resource levels. Resource levels are highly correlated with biomass in wetlands (Wisheu et al. 1991), so similarity could be measured along a biomass gradient. If wetlands are centrifugally arranged, then the species composition of different high biomass sites should be more similar than the species composition of different low biomass sites. Moore (1990) did such a test, and has found such patterns.

Moore (1990) used data collected from 15 sites representing a wide array of biomass and vegetation types. Within each site, 15 .25 m^2 quadrats were randomly placed, species frequencies were measured, and above ground biomass was harvested. The resulting 225 quadrats were then ranked in order of standing crop, and mean dissimilarity of each quadrat to the ten nearest neighbours (nearest in measured biomass, not spatial location) was calculated. Quadrat similarity was positively correlated with biomass indicating convergence of vegetation types in high biomass habitats and divergence where biomass is low. Similar

patterns of convergence have been reported in artificial wetlands (Weiher and Keddy 1995) and in aquatic bryophyte communities (Muotka and Virtanen 1995).

UTILITY OF THE MODEL

By expanding the centrifugal organization model to many organisms and to multiple resource gradients, large scale changes in life forms and community structure can now be described. Allusions to patterns consistent to centrifugal organization appeared in the literature as long ago as 1905 (Oksanen 1991) and more recently in 1977 (Orians and Solbrig 1977). These observations can now to summarized and described using the model.

The centrifugal organization model can also be used predictively. The model is consistent with the intermediate diversity model (Grime 1979) in that the centrifugal organization can be considered an expansion of the intermediate diversity model from a single gradient to multiple resource gradients. Predictions made by the intermediate diversity model are therefore common to both models. These predictions include the following. (1) Alpha diversity (the number of species in a sample of uniform habitat, Whittaker 1975) will be highest at intermediate levels of biomass. (2) Particular kinds of organisms such as competitive dominants and rare species, will be distributed along resource gradients in a specific pattern. (3) Communities will respond to eutrophication with shifts in life form and species composition towards those forms and species associated with core habitats.

A prediction unique to the centrifugal organization model is presented in Figure 2.9. An assumption of centrifugal organization is that the number of vegetation types and the

number of life forms and life history types increases towards the peripheral end of resource gradients. It therefore follows that the species pool (the total number of species that inhabit a certain section of a resource gradient) should also increase towards the periphery. As more peripheral habitats are considered, and a greater variety of life forms and life history types are represented, the pattern of greater pool size in peripheral habitats will intensify. This prediction will be tested in chapter three.

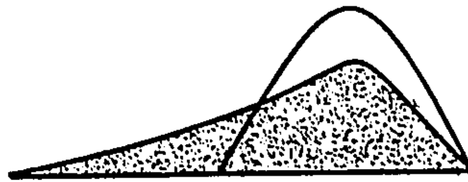
FIGURES

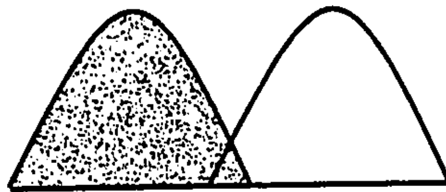
Figure 2.1. Along a single resource gradient, shared preferences can produce the pattern of resource partitioning. Two species share a preference for the same section of the resource gradient (top). The species differ however, in their competitive abilities. One is competitively superior, while the other (shaded) is subordinant but tolerant of low resource levels. The two species will therefore be differentially distributed along the resource gradient, with the dominant species occupying the high resource end, and with the subordinant occurring where resources are low (bottom).

Figure 2.1

Single Gradient, Two Species

Shared Preferences





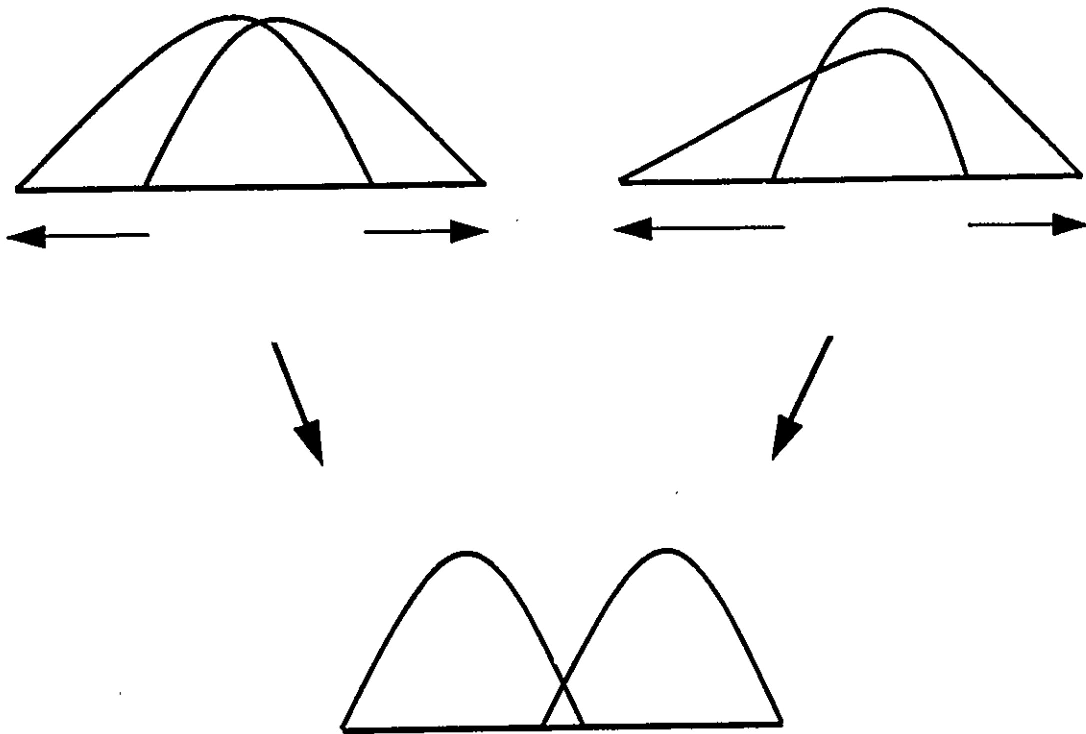
Pattern of
Resource Partitioning

Figure 2.2. There are two forms of centrifugal organization that can produce the pattern of resource partitioning. Centrifugal organization is when both species share a primary preference for the same habitat but have secondary preferences that are distinct (top). The shared habitat is where resources are in greatest supply. The species' secondary preferences are along gradients along which each species is the best competitor. Arrows indicate the direction of the secondary preferences. Competition occurs within the preferred habitat, so only the dominant species occupies the preferred habitat (top right) or the species are evenly matched competitively and neither is the sole occupant of the preferred habitat (top left). Either scenario gives rise to the pattern of resource partitioning (bottom).

Figure 2.2

Two Gradients, Two Species

Centrifugal Organization



Pattern of
Resource Partitioning

Figure 2.3. Centrifugal organization along multiple resource gradients and with multiple species. Centrifugal organization assumes that the high resource end of gradients are similar enough that they can be described as the same habitat, the core habitat. However, while there is convergence to a similar habitat type where resources are high, there is divergence where resources are low. A variety of different peripheral habitats exist at the low resource end of gradients.

Figure 2.3

Multiple Gradients,
Multiple Species

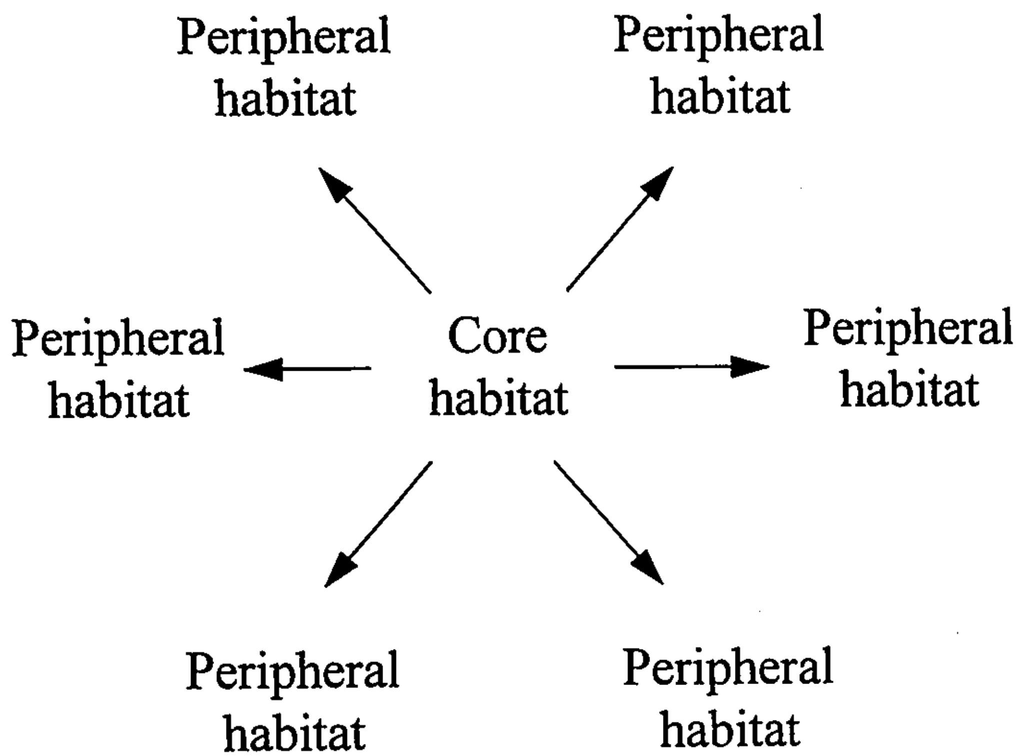


Figure 2.4. Centrifugal organization of two species of *Gerbillus*. The primary preference of both species is for regions with moderate seed abundance and moderate vegetation cover. However, the two species differ with respect to their secondary preferences. *G. allenbyi* (shaded) requires denser vegetation than *G. pyramidum*, but can tolerate sparser seed supplies. *G. allenbyi* can be excluded from the preferred habitat by *G. pyramidum*. (From a description by Rosenzweig and Abramsky 1986.)

Figure 2.4

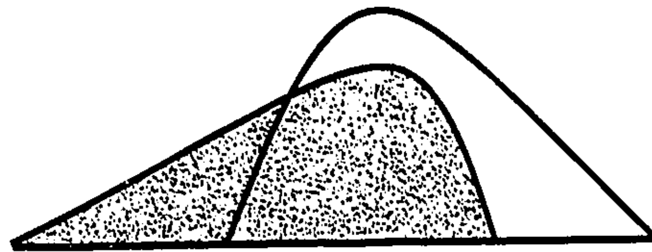
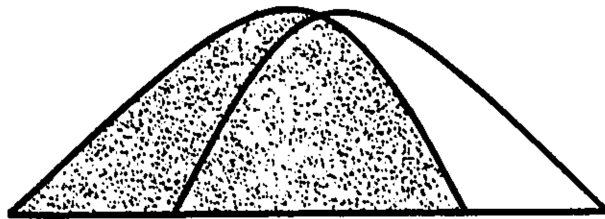


Figure 2.5. Centrifugal organization of marsh plants. Both species have a primary preference for the middle marsh zone but have secondary preferences that are distinct. *Salicornia virginica* (shaded) can tolerate waterlogging that frequent flooding causes, while *Arthrocnemum subterminalis* can tolerate high salinity. Neither species can exclude the other from the preferred habitat. Rather, the preferred habitat is split, with each occupying the portion in which it is the superior competitor. (From a description by Pennings and Callaway 1992).

Figure 2.5



Salinity →

Flooding frequency

Figure 2.6. Centrifugal organization in wetlands. Large, leafy dominants such as *Typha* occupy the core habitat while peripheral habitats are occupied by a variety of species and vegetation types. Arrows indicate gradients along which nutrient levels and disturbances change, with each peripheral habitat being a unique combination of stress and/or disturbance. First (bottom left), along gravel lakeshores, severe wave wash restricts the community to species capable of vegetative propagation and tolerant of infertile conditions (e.g., *Coreopsis*, *Sabatia*). Next (clockwise), along sandy lakeshores, moderate wave wash allows regeneration from the seed bank to occur, but species must still be tolerant of infertility (e.g., *Rhexia*). Then, in severely ice scoured wetlands, sand and clay habitats are fertile while river banks are infertile. Along riverbanks that are sandy and lightly scoured, plants must tolerate infertility (e.g., *Drosera*). In infertile interdunal swale areas, flooding is infrequent as compared to beaver pond wetlands where frequent flooding and frequent depositions of mud promote the occurrence of annuals (e.g., *Bidens*). (After Moore et al. 1989.)

Figure 2.6

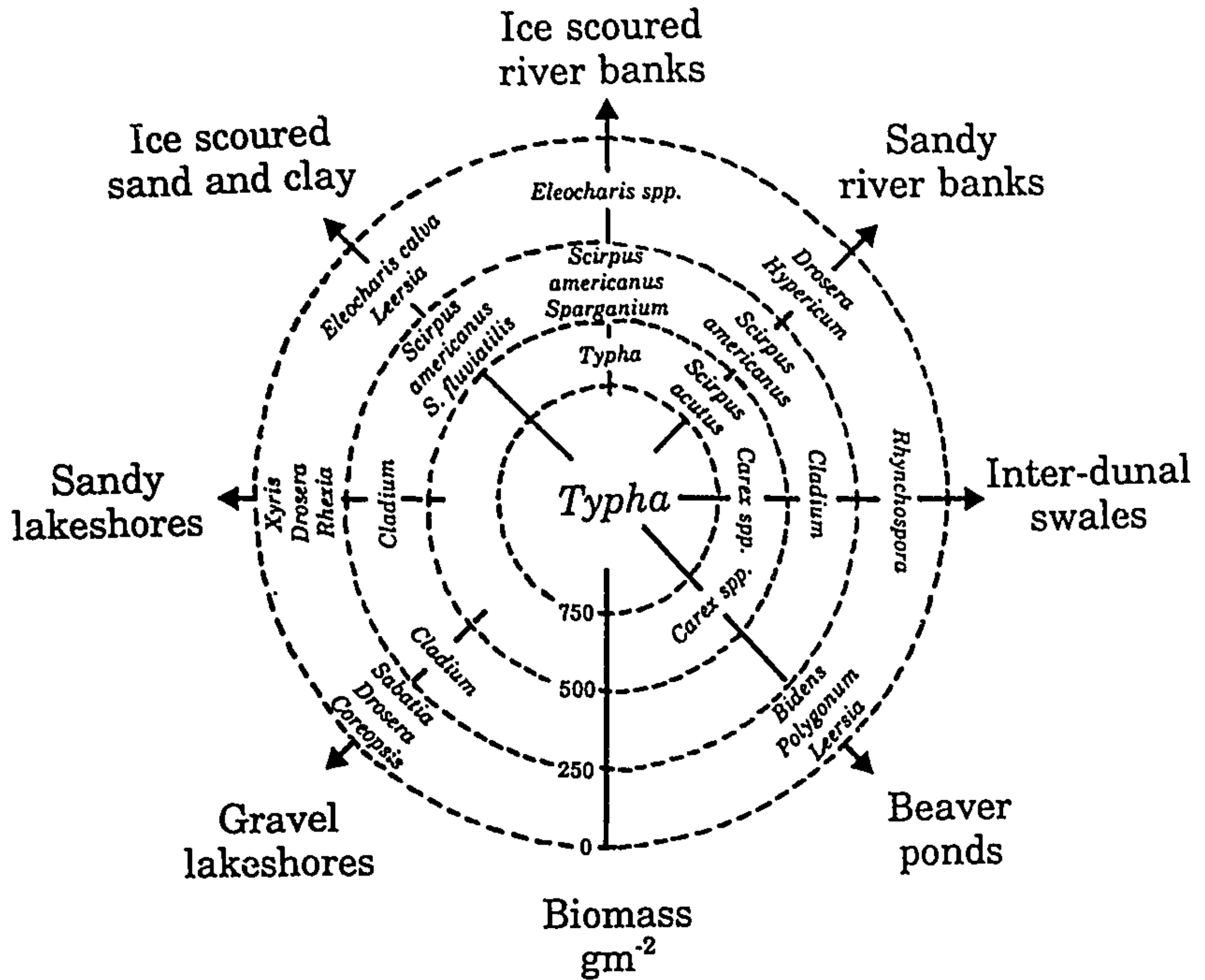


Figure 2.7. Distributions and competitive abilities of *Typha latifolia* (closed circle) and *T. domingensis* (open circle) along a water depth gradient. Relative yield values are calculated as the biomass of a species when growing in mixture divided by its biomass when growing in monoculture. The values indicate competitive ability. The horizontal dashed line indicates that a species grows equally well with conspecifics as with heterospecifics. *T. latifolia* is competitively dominant but cannot survive the deep water treatment. *T. domingensis* has wider tolerance limits and can therefore escape competitive domination by occurring where water is deep. (After Grace 1987.)

Figure 2.7

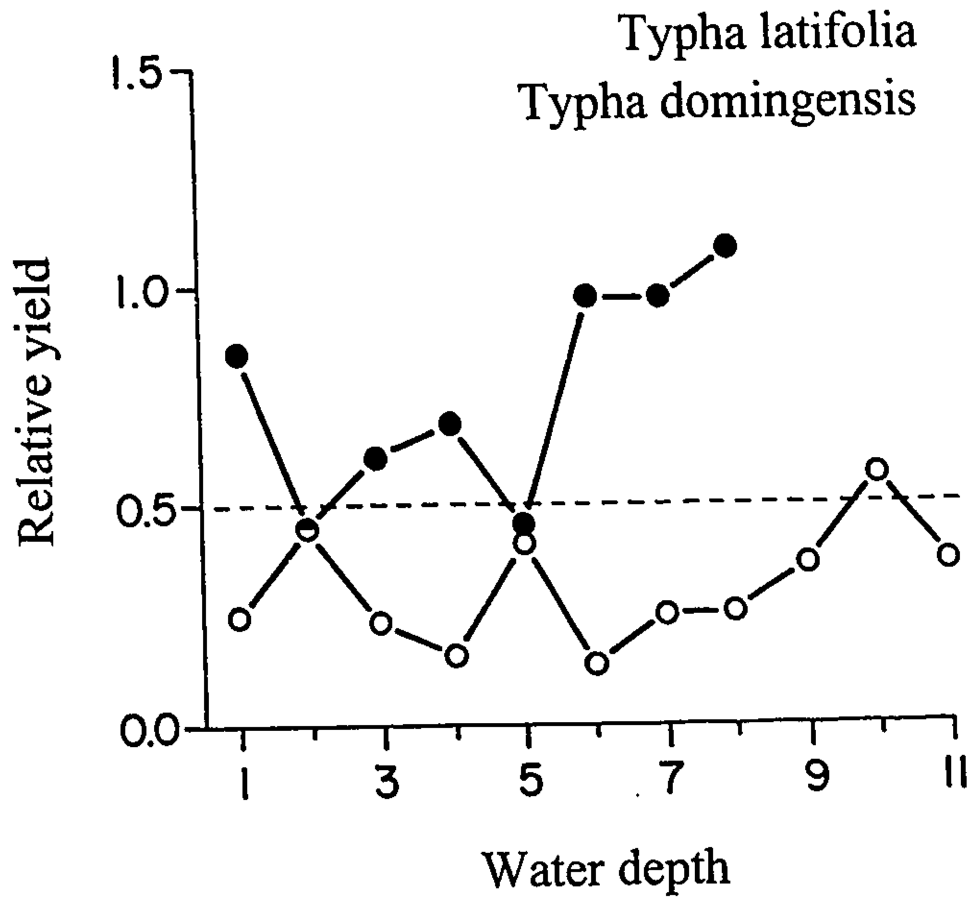


Figure 2.8. Distributions and competitive abilities of *Typha orientalis* (closed circle) and *Juncus kraussii* (open circle) along a salinity gradient. Relative yield values are calculated as the biomass of a species growing in mixture divided by its biomass when growing in monoculture. The values indicate competitive ability. The horizontal dashed line indicates that a species grows equally well with conspecifics as with heterospecifics. *Typha* dominates in the fresh, brackish and saline habitats, but cannot occur in hypersaline water (40 ppt). *Juncus* can tolerate hypersaline water and can therefore escape competitive domination in this habitat type. (After Zedler et al. 1990).

Figure 2.8

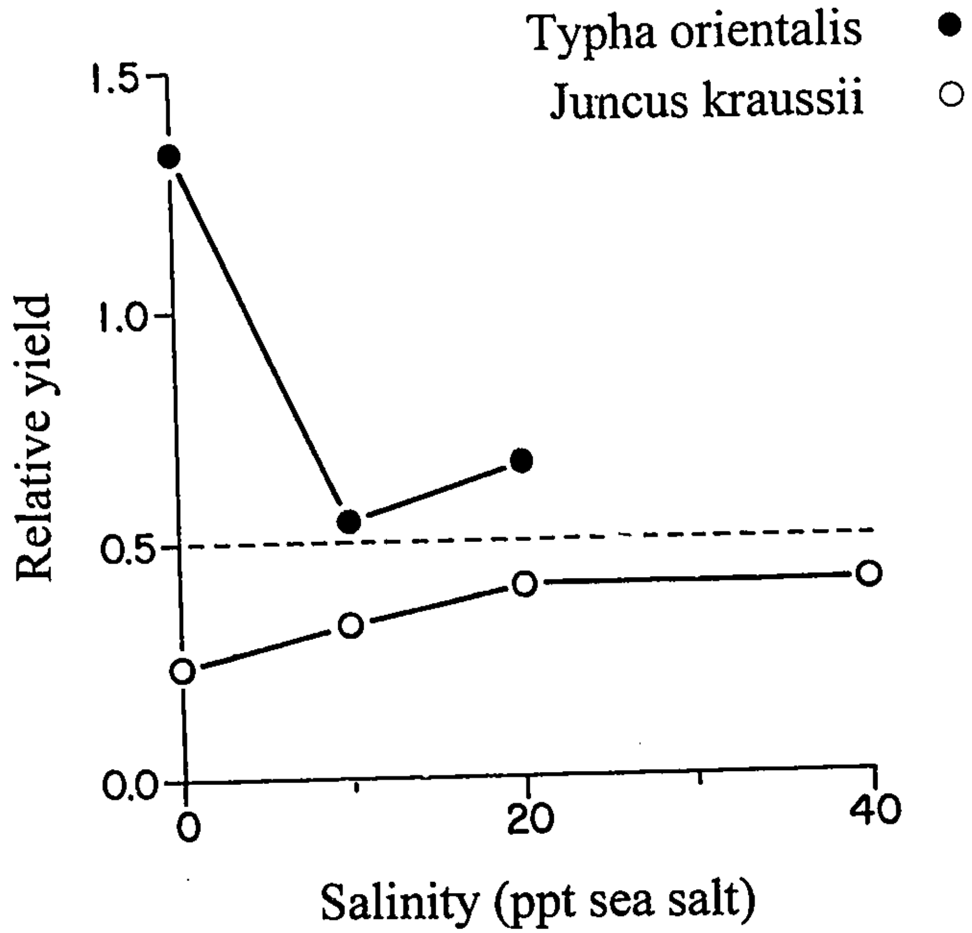
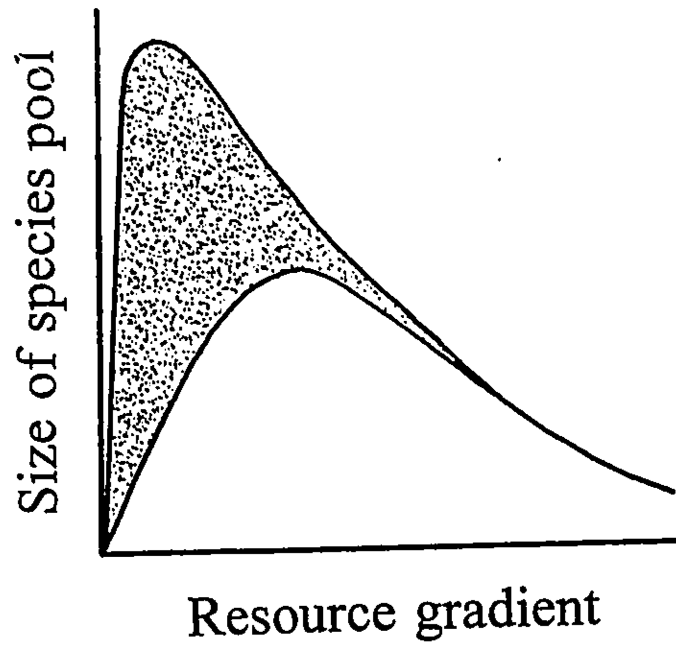


Figure 2.9. Predicted changes in the size of the species pool along a resource gradient. The species pool is the pool of species available to colonize a given habitat. Shading indicates the zone in which pool size is expected to occur. Centrifugal organization assumes that the number of vegetation types and number of life form and life history types increases at the low end of resources gradients. If so, then the size of the species pool should also increase where resources are low. However, pool size will decline to zero where resources are no longer available.

Figure 2.9

Centrifugal Organization



CHAPTER THREE

THREE COMPETING MODELS FOR PREDICTING THE SIZE OF SPECIES POOLS: A TEST USING EASTERN NORTH AMERICAN WETLANDS

ABSTRACT

With growing emphasis on protecting diversity, there is an increasing need for models that can predict the size of species pools in different habitats. Three models make predictions of how the species pool should change along environmental gradients. First, the productivity model predicts that the largest species pools will occur at high productivity (or at high biomass in herbaceous systems). Next, the species pool model predicts that the largest species pools will occur at the same biomass level as highest alpha diversity (the number of species in a small sample of uniform habitat). Finally, centrifugal organization predicts that species pools will be largest where biomass is low. I tested the three models to determine which was most appropriate using biomass / species composition data from 33 eastern North American wetlands. The resulting 640 quadrats produced a pattern of pool size consistent with the species pool model. Both alpha diversity and the species pool were maximum at intermediate biomass levels. This suggests that (1) the processes of stress tolerance, disturbance tolerance, and competition that are associated with changes in alpha diversity may also influence the species pool, and (2) the more easily measured alpha diversity values can be used to predict where large species pools might occur.

INTRODUCTION

Patterns of diversity are considered central to both the study of ecology and to the development of applications for biological conservation (May 1986). As befitting the importance of the subject, several recent books have focused on the subject (e.g., Ricklefs and Schluter 1993, Huston 1994, Rosenzweig 1995). These books highlight how many factors are associated with diversity and how many models have been proposed to account for variation in diversity along gradients. Several established models focus on predicting changes in alpha diversity, the diversity in small samples of uniform habitat (sensu Whittaker 1975). For example, models by Grime (1973, 1979), Connell (1978) and Huston (1979) all predict that alpha diversity will be highest at intermediate biomass, where productivity and disturbances are moderate. This relationship between biomass and alpha diversity has been demonstrated repeatedly (e.g., Al-Mufti et al. 1977, Willems 1980, Wheeler and Giller 1982, Bond 1983, Vermeer and Berendse 1983, Walker and Peet 1983, Wisheu and Keddy 1989b, Shipley et al. 1991, Rejmanko et al. 1995, Muotka and Virtanen 1995). However, a new and more pressing challenge is to predict changes in biodiversity.

Biodiversity is the pool of species available to colonize a given habitat. The size of the species pool is determined by speciation and extinction rates (Wiens 1983) and by historical processes governing migration (Zobel 1992). It has therefore been suggested that extant species richness should be viewed as an artifact of past biogeographical and historical events rather than as a product of ecological opportunities (Cornell and Lawton 1992, Li and Adair 1994). However, there are few opportunities to test this view. Many of the questions

regarding the species pool can only be addressed at the landscape scale, and few data sets exist at this scale. Nevertheless, models that make predictions of how species pools change along environmental gradients have been proposed.

There are at least three competing models in the literature that predict where large species pools will occur in relation to habitat biomass. The oldest model, the productivity model, states that there will be greater numbers of species with increasing productivity (Figure 3.1, Connell and Orias 1964, see also Southwood 1977, 1988). With increasing productivity, larger populations are supported and the populations tend to be sedentary. Since these larger populations also promote more frequent interspecific associations and contain greater genetic variability, speciation is favoured. Species diversity is therefore related to productivity in a non-decreasing relationship (Figure 3.1). In wetlands, this prediction can be translated as larger species pools with increasing biomass. Wetlands are herbaceous systems that are subjected to winter die back, so above ground biomass is a measure of productivity.

Next, the species pool model (Taylor et al. 1990) predicts that the largest species pools will occur at lower biomass than the preceding model. The species pool should reach maximum size at the same biomass as the maximum of alpha diversity (Figure 3.2). Like the productivity model, this newer model also relates the size of the species pool to opportunities for speciation. The species pool model states that larger pools are a consequence of greater area and/or geological age of habitats (see also Eriksson 1993). However, by itself, this explanation is insufficient to explain why maximum alpha diversity and pool size should coincide. It is therefore implicit in the model that alpha diversity is a

constant subset of the species pool. This idea is reminiscent of Preston's sampling hypothesis (Preston 1948, Cornell and Lawton 1992), which suggests that species assemblages are random samples drawn from a pool of potential colonists. The second model to be tested in this study is therefore a combination of Taylor et al. (1990) and Preston (1948), but will be referred to as the species pool model. The species pool model has not been previously tested (but see Pärtel et al. in press).

Finally, the centrifugal organization model (Keddy 1990, Wisheu and Keddy 1992, see also Chapter Two) predicts that the species pool will be highest near the low end of the biomass gradient (Figure 3.3). Pool size is viewed as an artifact of habitat diversity, with there being more different kinds of low biomass habitats than high biomass habitats. As the number of habitats used to generate measurements of the species pool is increased, the size of the species pool will rise, primarily in low biomass habitats. Maximum pool size will not not be coincident with maximum alpha diversity. To test among the three models predicting changes in the size of the species pool, I therefore needed to construct and then compare patterns of alpha diversity and pool size along a biomass gradient.

METHODS

To construct patterns of alpha diversity, counts are made of the numbers of species in samples of habitat. However, to construct patterns of pool size, species must be identified and data should come from geographically diverse habitats. There are therefore few opportunities to compare alpha diversity values with measurements of the species pool. An

occasion does exist however, to make such comparisons with wetland plants. I participated in a 7 year exercise to document alpha diversity patterns in eastern North American wetlands. Standardized sampling initiated in 1983 has resulted in a large volume of data having been collected in a variety of geographically diverse wetlands.

Sampling Procedure

Species composition was recorded and biomass measurements were made in wetlands in Ontario, Quebec, and Nova Scotia. Sampling occurred between July 23 and October 1, intermittently from 1983 to 1990. The wetlands were in seven different geographic areas, areas defined on the basis of ecoclimatic region and drainage basin (Figure 3.4, Table 3.1). Low biomass wetlands, such as those at Wilsons Lake and in the Georgian Bay area (Figures 3.5, 3.6) were included in the sampling, as were wetlands with moderate levels of biomass, such as sites at Matchedash Bay and along the Tusket River (Figures 3.7, 3.8). High biomass wetlands that were sampled included sites such as an Ottawa River shoreline and a cattail stand at Matchedash Bay (Figures 3.9, 3.10). Since I required that each geographic area be represented by low, medium, and high biomass wetlands, supplemental sampling in geographic areas 1, 4, and 6 was undertaken from August 26 to September 5, 1992. In total, information from 640 quadrats was assembled, with 184 (or 28.8 %) of the quadrats having been collected by the author. SYSTAT cluster analyses (SYSTAT 1990) were used to identify the wetlands as 33 distinct sites (Appendix 2).

In each wetland, 0.25 m^2 quadrats were positioned within the zone of emergent marsh or wet meadow vegetation, below the shrub zone and above aquatic macrophytes. The plant species present in this zone and included in quadrats are listed in Appendix 3. Quadrats were positioned so as to represent the full range of biomass values present at the wetlands, with no fewer than 10 quadrats at each wetland site. Species area curves indicated that at least 10 quadrats should be used to represent each site (Figure 3.11). From within each quadrat, all rooted vascular plant species were identified and all aboveground standing crop was harvested, dried for at least 24 hrs at 60° C in a forced-air convection oven, and weighed to the nearest 0.01 g. Sample results are given in Appendix 4.

Given that the data collection spanned 7 years and 6 participants, the data's accuracy and usefulness towards generating values of alpha diversity and pool size needed to be verified. All data sets were therefore proofed by comparing the assembled data sets to the original field notes, which were still available in all but one instance. Herbarium specimens were consulted as required. Also, the quadrats containing plants that were not identified to species were eliminated unless no other members of the genus had occurred (e.g., *Veronica*, Appendix 3). Nomenclature was standardized to Gleason and Cronquist (1963) with the addition of *Typha glauca* Godr. Portions of the data set assembled for this study have been used by the following: Wisheu (1987), Day et al. (1988), Moore and Keddy (1989), Wisheu and Keddy (1989a, b), Moore (1990), Lee (1993), Gaudet (1993), Keddy and Sharp (1994), and Gaudet and Keddy (1995).

Analysis

To calculate the size of a species pool, quadrats need to be grouped together in a set, and then the total number of species in the set can be counted. For example, in two quadrats with 5 species each, alpha diversity values would be 5 in each. But the species pool for the combined quadrats would range from 5 (if both quadrats had identical species) to 10 (if none of the species in the two quadrats were the same). That is,

$$P_{min} = \alpha_{max} \quad \text{and} \qquad P_{max} = \Sigma^n \alpha$$

where P denotes pool size and n is the number of quadrats grouped together in a set. Generating patterns of how the species pool changes along a biomass gradient therefore required that quadrats be grouped. The grouping method will be described in some detail because there have been only a few attempts to relate species pool and alpha diversity measurements (Cornell 1985, Cornell and Lawton 1992, Kohn and Walsh 1994, but see Cresswell and Vidal-Martinez 1995) and this is the first attempt to describe how these measurements change along a gradient.

All quadrats from the wetlands were ranked from lowest to highest biomass. Then, taking sets of 100 quadrats at a time (e.g., 100 with the lowest biomass), subsets of 50 quadrats were randomly drawn without replacement. Fifty quadrats were randomly drawn from the initial set of 100 quadrats so that the 50 quadrats represented exactly 9 different wetland sites from 6 of the 7 geographic areas. This ensured that greater geographic

diversity within some groups of quadrats would not artificially inflate the size of the species pool (Figure 3.12). Fifty quadrats were drawn because this number was the maximum number of quadrats that could represent exactly 9 sites and 6 geographic areas. If fewer quadrats had been drawn, they would have represented fewer sites and would have decreased the scale at which the species pool was being measured.

Once 50 quadrats had been drawn, pool size was calculated, as well as average biomass and average alpha diversity. Next, from the same initial set of 100 quadrats, a second subset of 50 quadrats was randomly selected, and then the size of the pool, average biomass, and average alpha diversity values were re-calculated. Subsampling was repeated a total of 5 times, to estimate mean values of pool size and average alpha diversity for values of average biomass. This procedure generated a single point in each of the two graphs in Figure 3.16. Finally, the whole procedure was repeated for other sets of 100 quadrats, shifted 20 quadrats up the biomass gradient each time.

Data was managed using Excel 4.0 (Microsoft Corporation 1992), graphics were designed using Sigmaplot 2.0 (Jandel Scientific 1986-1994), and statistics were performed with Sigmastat 1.0 (Jandel Scientific 1992-1994) and SYSTAT 5.0 (SYSTAT 1990).

RESULTS

Alpha Diversity

Alpha diversity in wetland habitats was greatest at intermediate levels of biomass.

The range of standing crop values extended from 0.37 to 1219 g per 0.25 m^2 and the range of alpha diversity values were from 1 to 24 species per quadrat (Figure 3.13). Maximum alpha diversity occurred in the biomass range of 5 to 60 g / .25 m^2, results consistent with predictions of intermediate diversity (Grime 1973, 1979, Huston 1979). This range of biomass values is also consistent with the range reported to support maximum alpha richness in other eastern North American wetlands (Wilson and Keddy 1988, Shipley et al 1991).

One of the intermediate diversity models makes predictions of how some plant functional types will be distributed (Grime (1979). Plant functional types are groups of plants that are not taxonomically related but that share a common growth form or life history characteristic. A number of functional types can be identified in wetlands (Hutchinson 1975, Boutin and Keddy 1993). Grime's model states that maximum alpha diversity will occur at intermediate biomass, that competition between species will be most intense at high biomass, and that species occurring where biomass is low will be either stress tolerant or disturbance tolerant plants (Grime 1979). As predicted, plant species that have been identified as being competitive dominants were most abundant within high biomass habitats (Figure 3.14), while stress tolerant isoetid species were most abundant at low biomass and did not occur where biomass was high (Figure 3.15). Isoetids are small, slow growing plant species that often grow as rosettes or are evergreen. They have been identified as stress tolerators by Boston and Adams (1987). The abundances of isoetids and competitive dominants therefore indicate that at high biomass, competition limits alpha diversity, while in low biomass communities, environmental stresses limit the numbers of species that can occur.

Size of the Species Pool

As predicted by the species pool hypothesis (Taylor et al. 1990), maximum pool size occurred at the same point along the biomass gradient as did maximum average alpha diversity (Figure 3.16). At low to intermediate biomass (36 g/.25 m^2), fifty quadrats produced a species pool of, on average, 132 species. This contrasts with the lowest biomass levels (4 g/.25m^2), where fifty quadrats had an average species pool of 87 different species and at the highest biomass levels (316 g/.25m^2) where an average of only 47 species occurred in fifty quadrats. At all points along the biomass gradient, measurements of alpha diversity and pool size were very tightly correlated[3] ($r = .97$, $p < 0.05$), with alpha diversity representing a nearly constant fraction of the species pool (Figure 3.17).

Consistency of the alpha diversity / pool size ratio

In Figure 3.17, alpha diversity is consistently 7-10% of the species pool. That is, each quadrat contains on average, 7-10% of the species pool. To test whether this percentage changed when species pools are generated using different numbers of quadrats (n not equal to 50), I repeated the procedure of calculating the size of the species pool using n = 30 and n = 10. When fewer than 50 quadrats were used to calculate measures of pool

[3] Since the data points in Figure 3.16 represent a running mean, there is autocorrelation between adjacent values. To address this issue, the correlation was repeated on a reduced data set where values would be independent. Only every fifth value was used (n = 6). The new correlation coefficient was .99, $p < 0.05$.

diversity, the size of the pool decreased (Figure 3.18) but maximum pool size occurred at the same point along the biomass gradient. Each quadrat contained a greater fraction of the species pool, but the fraction remained constant regardless of the biomass levels of the wetlands used to make the calculations (Figure 3.19).

A further test of the consistency of the alpha diversity / species pool ratio was performed using quadrats that represented different numbers of sites. I explored the consequences of altering the number of sites from which a constant number of quadrats were drawn. When three rather than nine sites were grouped for calculating the size of the species pool, pool size decreased, but the species pool hypothesis was still supported (Figure 3.20). Again, alpha diversity was a constant albeit larger fraction of the species pool (Figure 3.21). Regardless of the number of quadrats used or the number of sites being represented, (1) alpha diversity remained a constant subset of the species pool, and (2) maximum pool size occurred coincident with maximum alpha diversity.

DISCUSSION

The patterns I observed are inconsistent with both the first model (productivity model) and the third model (centrifugal organization). Instead, the tight relationship between alpha diversity and pool size is consistent with the species pool model (Taylor et al. 1990, Preston 1948) which suggests that species assemblages are random samples drawn from a pool of potential colonists.

The Species Pool Model

This study supports the species pool model but the mechanism of the model remains unclear. In the original explanation of the species pool model (Taylor et al. 1990), it was explicitly proposed that greater pool size is determined by greater opportunities for speciation, a function of greater geological age and/or global area. With this scenario, the well-known peak in alpha diversity at intermediate biomass is actually caused by the peak in pool size in this habitat type. This implies that alpha diversity is controlled through evolution rather than through ecological interactions.

An alternative (or complimentary) view is that the species pool may itself be controlled, in part, by the very mechanisms (e.g., stress tolerance, disturbance tolerance, and competition) that have been proposed as controls on diversity within a quadrat (Connell 1978, Grime 1973, 1979, Huston 1979). These mechanisms may be operating at the evolutionary and biogeographic scales as well as at the quadrat scale. The distributions of stress-tolerant isoetids (Boston and Adams 1987) and competitive dominants (Gaudet and Keddy 1988) within the species pool indicate that competition and stress tolerance may be mechanisms operating within the species pool (Figure 3.14).

While the mechanisms of tolerance and competition may play a role in determining the species pool, these mechanisms continue to be forces within communities. There are proportionally more isoetids in low biomass quadrats and more competitive dominants in high biomass quadrats than a random subsample of the pool would dictate (Figure 3.23). These two groups of species are therefore responding to the environment, indicating that community

composition is not solely an artifact of random sampling. As species colonize, some species appear to be favoured by the environment and are therefore more frequent in the community. Other species may colonize but occur infrequently. Alpha diversity remains a constant fraction of the species pool, so environmental factors apparently influence which species are chosen from the species pool.

There are important conservation implications to the species pool model. First, because there is a constant relationship between alpha diversity and pool size, the more easily measured alpha diversity value can be used to estimate the size of the species pool. Second, it is now possible to predict how species pools will change from one habitat to the next. For example, the preservation of low biomass wetlands will protect a larger species pool than the preservation of high biomass wetlands.

Alternative Models

The centrifugal organization model did not predict how the size of species pools change along the biomass gradient. It is therefore inappropriate to use the model. It is possible however, that the centrifugal organization model represents a limiting case and is applicable to other systems. Centrifugal organization may occur where competitive dominants successfully exclude subordinants to peripheral low biomass habitats (Chapter Two, see also Ellenberg 1988). If the process of competitive exclusion is less than complete or weak, then subordinants could invade into higher biomass sites with sufficient frequency to regularly occur in species pools well away from peripheral habitats. If subordinants do

invade into intermediate biomass sites, then peaks in pool size would occur in intermediate biomass habitats such as was found in this study.

However, the limiting case scenario described above may rarely happen. Subordinants may rarely be successfully restricted to peripheral habitats since only the most dominant species appears capable of suppressing subordinants (M. L. Rosenzweig pers. comm.). Subordinant species would then occur just beyond the region where dominant species have their influence, at intermediate and not low biomass levels. Unless subordinant species are restricted to peripheral habitats, then maximum pool size will not occur at low biomass levels as predicted by the centrifugal organization model (Chapter Two). Unless limiting case scenarios are identified and the applicability of the centrifugal organization model can be confirmed, then centrifugal niche organization appears limited to two rather than to multiple resource gradients (Chapter Two).

The productivity model also failed to predict patterns in the sizes of species pools in eastern North American wetlands, yet this model has previously proven successful using North American trees (Currie and Paquin 1987). I can only speculate that the differing results may be due to (1) the consideration of an entire flora versus a dominant growth form, (2) the lengths of the productivity gradients and the ensuing effects of scale (Wright et al 1993), i.e., an east-west array of wetland sites versus a longer north-south gradient of tree diversity, or (3), the nature of the productivity gradients. My wetland gradient is probably a gradient of nutrient or light availability (a resource gradient sensu Austin and Smith 1989). The gradient in Currie and Paquin (1987) is a gradient of actual evapo-transpiration, probably related to temperature (a regulator gradient, Austin and Smith 1989). When species

are distributed along resource gradients such as nutrient or light availability, competition will occur and some species will be excluded, even if (or especially when) some resources are in high supply. When species are distributed along regulator gradients such as temperature, competition for the resource (e.g., heat) will probably not occur and a greater number of species may coexist (Austin and Smith 1989). Further testing of both the species pool model and the productivity model may determine when each of the two models is appropriate.

CONCLUSION

There is still much to be resolved regarding patterns of diversity but we now have one more tool for predicting where centres of high diversity might occur. By using the species pool model and the intermediate diversity models (Grime 1973, 1979, Connell 1978, Huston 1979), we can now predict how alpha diversity and the species pool will change along biomass gradients. Since patterns of alpha diversity and pool size parallel each other, at least in this case, the more easily measured alpha diversity value can be used to predict maximum biodiversity. While the applicability of this relationship in other systems remains to be explored, we now know that for wetlands in eastern North America, protecting the low - intermediate biomass wetlands with high alpha diversity will protect large species pools as well.

TABLE 3.1

The location and description of biomass levels within each of ten sampled geographic areas. Ecoclimatic regional codes and drainage basin names follow Environment Canada (1989) and Energy, Mines and Resources Canada (1985) respectively. Dominant species are those that occurred most frequently in the quadrats.

Area	Ecoclimatic Region	Drainage Basin	Site	No. of quadrats	Biomass ($gm/.25m^2$) min.	max.	Dominant species
1	HCTa	Seaboard	Tusket River	15	7.8	325.6	*Calamagrostis canadensis, Carex stricta*
			Wilsons North	76	.9	141.9	*Cladium mariscoides, Solidago galetorum*
			Wilsons South	56	1.1	62.0	*Gratiola aurea, Dulicheum arundinaceum*
2	HMTh	Lake Erie	Long Point	20	7.8	33.7	*Rhynchospora capillacea, Scleria verticillata*
			Rondeau	19	28.9	155.9	*Calamagrostis canadensis, Leersia oryzoides*
3	MCTh	Lake Ontario	Oshawa	18	83.4	324.6	*Phalaris arundinacea, Calamagrostis canadensis*
			Presqu'ile A	15	12.8	27.0	*Scleria verticillata, Panicum lanuginosum*
			Presqu'ile B	14	48.6	128.0	*Scirpus americanus, Calamagrostis canadensis*
			Presqu'ile C	15	111.0	290.3	*Carex lasiocarpa, Carex aquatilis*
			Presqu'ile D	15	207.9	651.5	*Typha latifolia, Leersia oryzoides*
			Presqu'ile E	20	6.2	100.1	*Cladium mariscoides, Potentilla anserina*
			P. E. Point	10	37.3	125.1	*Carex stricta, Calamagrostis canadensis*
			Sandbanks	13	5.2	43.2	*Eleocharis pauciflora, Cladium mariscoides*
4		Lake Huron	Matchedash A	15	99.3	193.4	*Calamagrostis canadensis, Carex lacustris*
			Matchedash B	10	68.0	1219.1	*Sparganium eurycarpum, Typha latifolia*
			Oliphant	17	2.2	25.3	*Scleria verticillata, Tofieldia glutinosa*
5		Ottawa River	Capital region	30	2.0	296.1	*Typha latifolia, Lythrum salicaria*
			Constance Bay	10	39.5	119.4	*Eleocharis palustris, Scirpus acutus*

			Lucerne Blvd.	23	13.5	335.7	*Typha latifolia, Eleocharis palustris*
			Luskville A	15	13.0	57.1	*Lindernia dubia, Eleocharis erythropoda*
			Luskville B	15	18.4	63.2	*Eleocharis erythropoda, Leersia oryzoides*
			Luskville C	13	64.2	126.2	*Scirpus americanus, Eleocharis palustris*
			Luskville D	15	66.4	176.9	*Agrostis stolonifera, Scirpus fluviatilis*
			Luskville E	15	190.7	343.9	*Typha angustifolia, Rumex verticillata*
6	HCTh	Lake Huron	Aspdin	13	67.5	340.2	*Calamagrostis canadensis, Carex lasiocarpa*
			Georgian	43	.4	388.2	*Eriocaulon septangulare, Rhexia virginica*
			Sparrow	10	23.3	765.4	*Pontederia cordata, Sparganium americanum*
7		Ottawa River	Westmeath A	15	1.0	178.0	*Scirpus americanus, Carex lenticularis*
			Westmeath B	15	26.8	120.5	*Scirpus americanus, Hypericum boreale*
			Westmeath C	15	114.4	212.6	*Scirpus acutus, Potentilla palustris*
			Westmeath D	14	50.8	215.3	*Carex vesicaria, Scirpus cyperinus*
			Westmeath E	15	194.4	432.9	*Typha glauca, Sium suave*
			Westmeath F	16	5.8	123.3	*Eleocharis palustris, Scirpus acutus*

FIGURES

Figure 3.1. The productivity modei states that the species pool will increase with productivity (Connell and Orias 1964). Shading indicates the region within which measurements of the species pool are expected to occur. Since productivity can be approximated with measurements as biomass in herbaceous communities subjected to winter die back, then in herbaceous communities, the productivity model predicts increasing pool size with increasing biomass.

Figure 3.1

Productivity Model

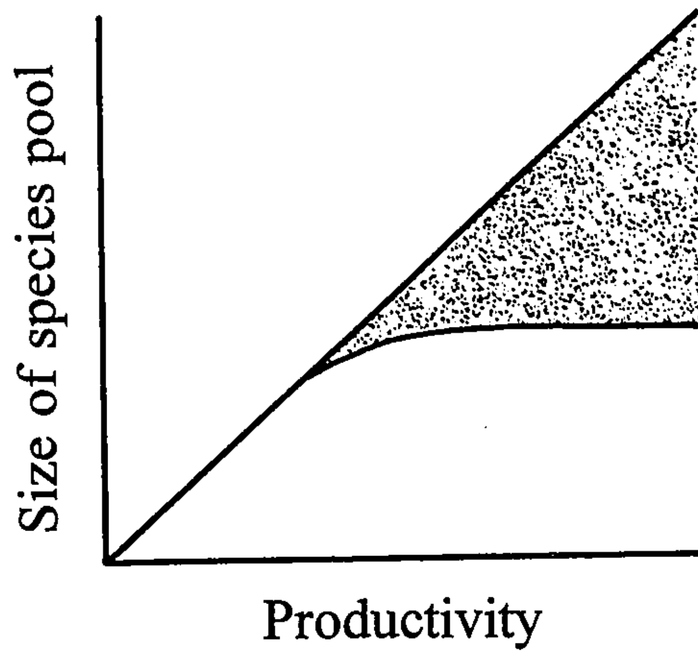


Figure 3.2. The species pool model states that the species pool will be largest where alpha diversity is greatest (Taylor et al. 1990). This is because species assemblages are random samples drawn from the species pool (Preston 1948). The peak in alpha diversity is therefore caused by the peak in pool size. Species pools are largest at intermediate biomass as a consequence of greater area and/or geological age of intermediate biomass habitats.

Figure 3.2

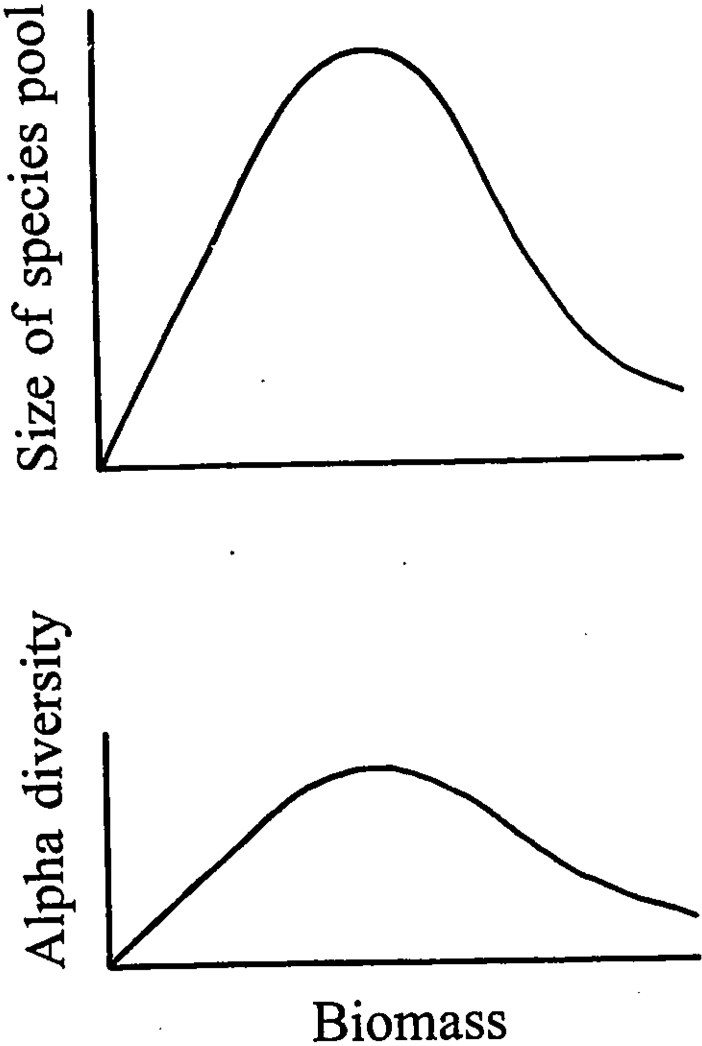


Figure 3.3 The centrifugal organization model predicts that the species pool will be largest at biomass levels below where alpha diversity is greatest (see Chapter Two). This is because there is a greater variety of low biomass habitats as compared to high biomass habitats. Also, a greater variety of species are restricted to low rather than to high biomass habitats. Shading indicates the region within which measurements of the species pool are expected to occur.

Figure 3.3

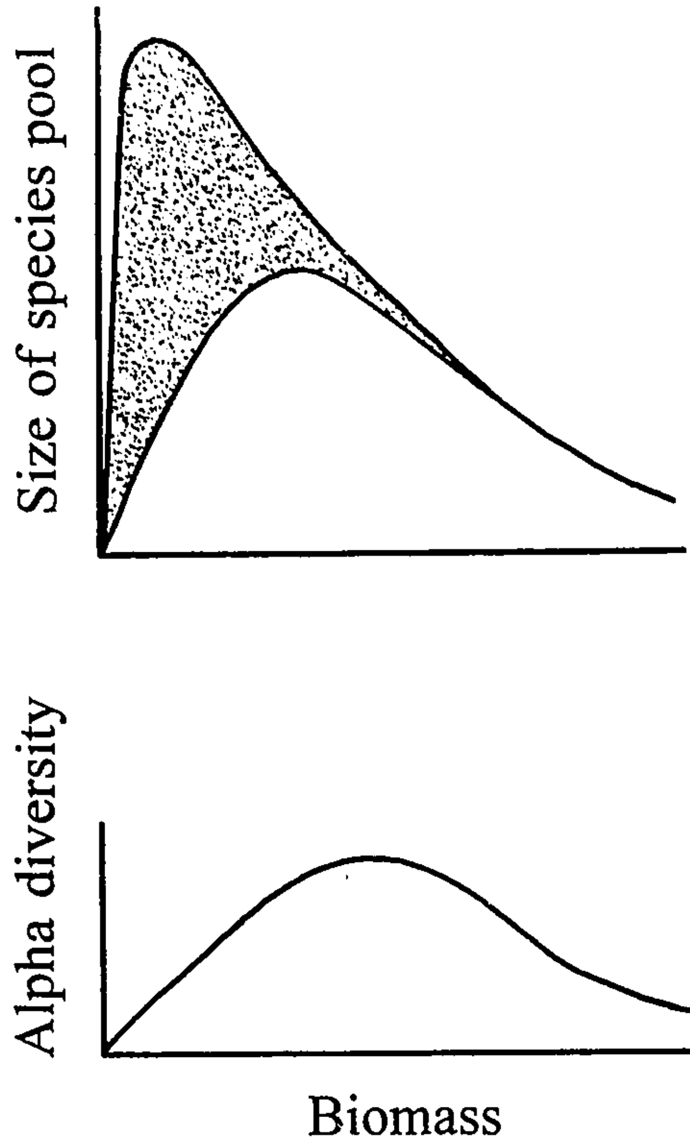


Figure 3.4. Locations of data collection within Ontario, Quebec, and Nova Scotia. Numbers identify the 7 different geographic areas within which wetlands were located. The divisions were defined on the basis of ecoclimatic region and drainage basin. Thick dashed lines indicate different ecoclimatic regions, while thin dashed lines denote drainage basins. The ecoclimatic regions and the drainage basins are identified in Table 3.1. Small dots indicate the location of 1 wetland site, medium dots indicate the location of 2 or 3 wetland sites, and large dots indicate the location of 5 or 6 wetland sites.

Figure 3.4

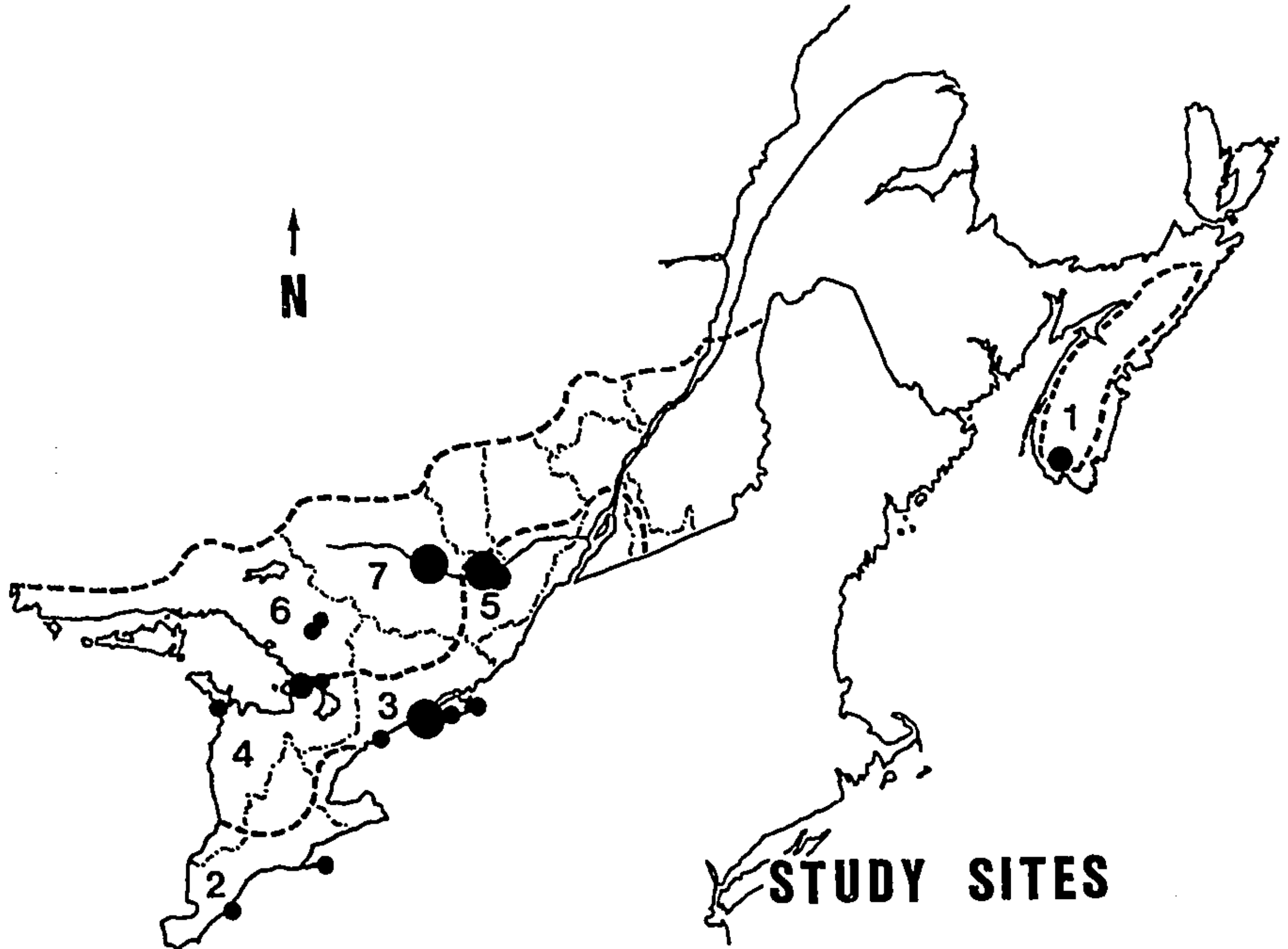


Figure 3.5. The low biomass shorelines of Wilsons Lake, Nova Scotia. Wilsons Lake North (A) is an infertile cobble shoreline subjected to strong wave wash and frequent ice scouring (Wisheu and Keddy 1989b). Severe flooding can also occur several times in a growing season. Because of this unusual flooding regime and the infertile nature of the substrate, large populations of nationally significant species occur along this shore, including one globally imperilled species (*Scirpus longii*), two nationally endangered species (*Coreopsis rosea* and *Hydrocotyle umbellata*), one nationally threatened species (*Sabatia kennedyana*) and four species that are nationally rare (*Rhexia virginica*, *Habenaria flava*, *Solidago galetorum*, *Panicum longifolium*). These species find refuge from competition by occurring on shorelines with conditions that other wetland plants cannot tolerate (Wisheu and Keddy 1994). At Wilsons Lake South (B), boulder shorelines occur and fewer rare species can be found. (Photos by I. C. Wisheu.)

Figure 3.5

Figure 3.6. A low biomass shore at Axe Lake, one of many sandy lakes in the Georgian Bay area of Ontario. This lake and others in the region are on a remnant of the former shoreline of post-glacial Lake Algonquin (Keddy 1982). Conditions here are similar to the conditions at Wilsons Lake North (Figure 3.5) in that there is an infertile substrate and severe wave wash. The two sites have many species in common but while regeneration occurs from the seedbank at Axe Lake, vegetative propagation occurs at Wilsons Lake (Wisheu and Keddy 1991). (Photo by P. A. Keddy.)

Figure 3.6

Figure 3.7. A quadrat of intermediate biomass being sampled at Matchedash Bay, Ontario. Monocots dominated this eutrophic wetland. *Sparganium* and *Rhynchospora* occurred within intermediate biomass areas (foreground), while *Typha* dominated where vegetation was more lush (background). (Photo by I. C. Wisheu.)

Figure 3.7

Figure 3.8. A wet meadow of intermediate biomass along the Tusket River, Nova Scotia. Different sedges dominated this site. There were several kinds of *Carex* and *Rhynchospora*, and a few specimens of the globally imperilled sedge, *Scirpus longii*. (Photo by N. M. Hill.)

Figure 3.8

Figure 3.9. A high biomass meadow along the Ottawa River, Quebec. Monocots dominate but the European exotic, *Lythrum salicaria* has begun to invade. (Photographer unknown.)

Figure 3.9

Figure 3.10. A high biomass cattail stand at Matchedash Bay, Ontario. At this site, *Typha latifolia* formed a near monoculture, with only a few specimens of other species co-occurring. Few species can tolerate the low light levels produced by the tall, fast growing clonal dominant. (Photo by I. C. Wisheu.)

Figure 3.10

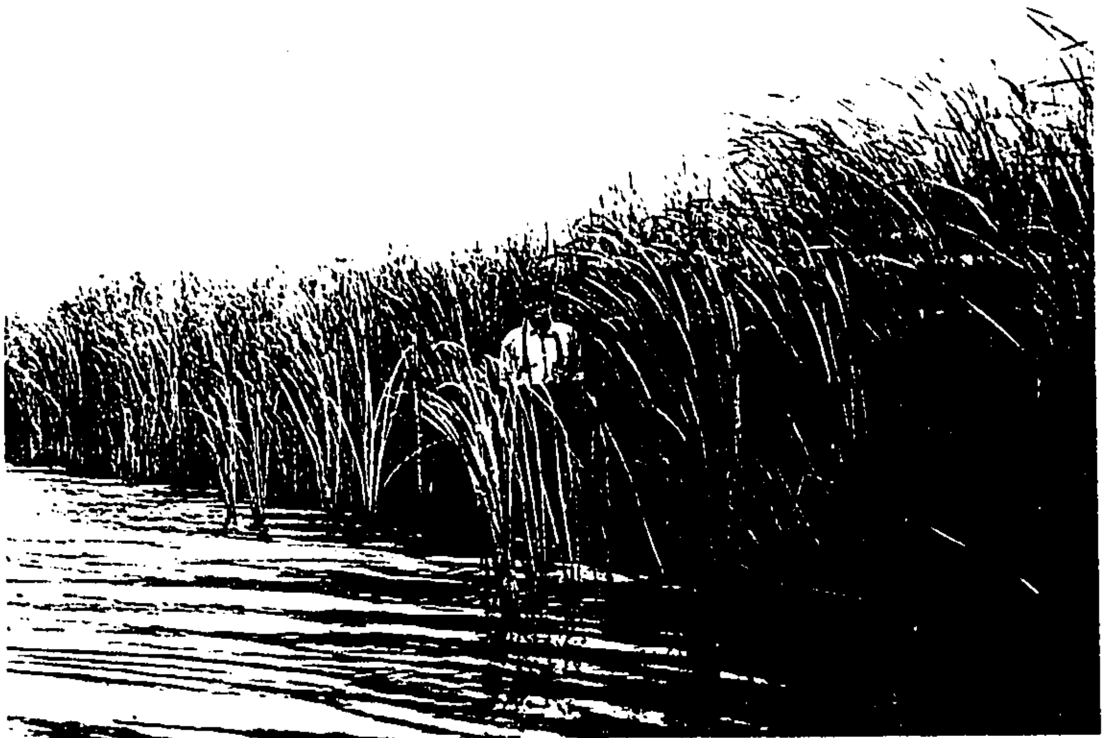


Figure 3.11. Species area curves. During the period of standardized sampling, some wetland sites were represented by fewer than ten quadrats. However, these wetlands were not used in this study since species area curves revealed that at least ten quadrats were needed for detecting the majority of species in a site. The wetland sites represented in the Figure are, in ascending order, Westmeath E, Presqu'ile E, Westmeath A, Presqu'ile A, Luskville A, and Wilsons North.

Figure 3.11

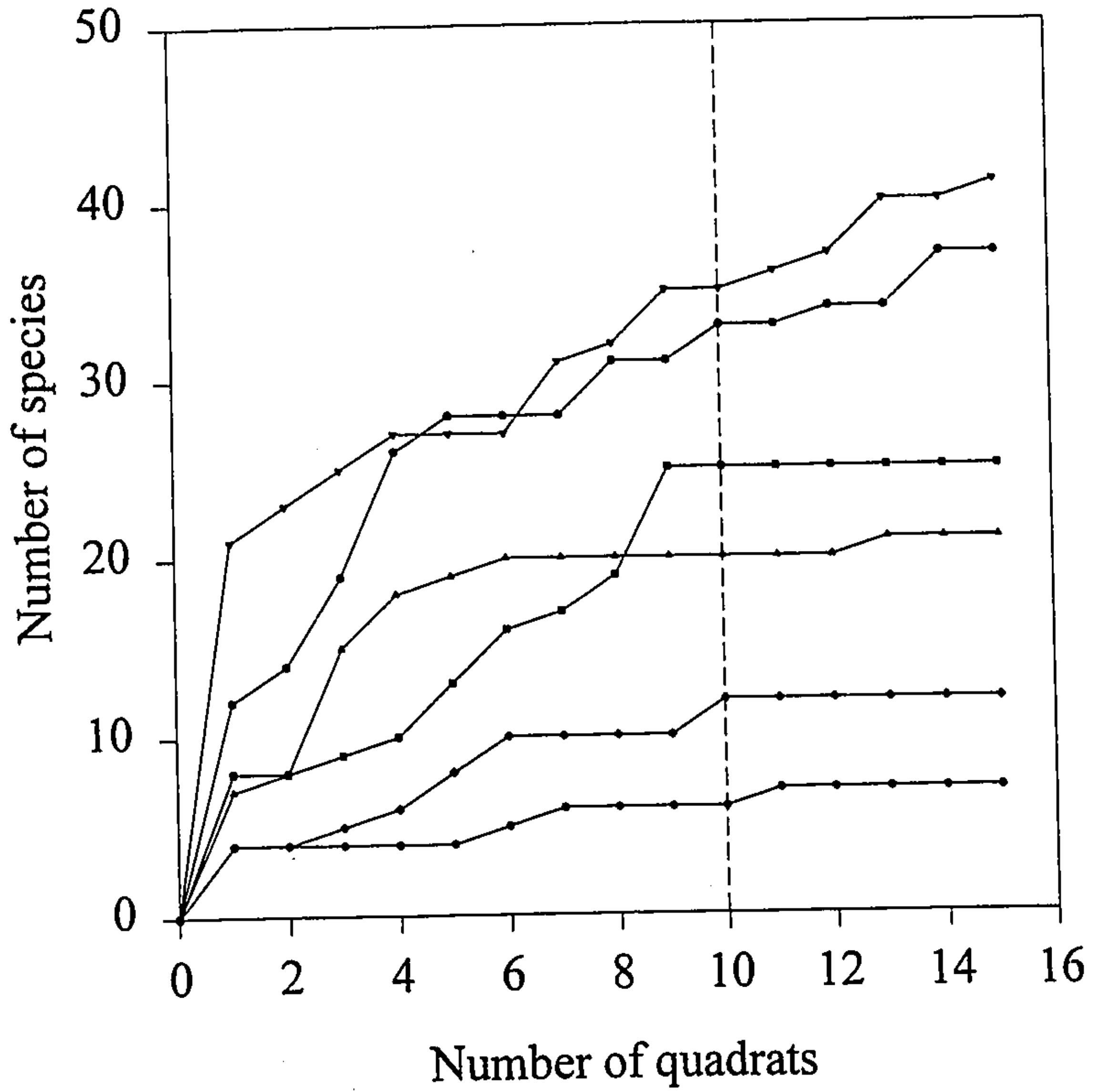


Figure 3.12. Numbers of sampled sites (circles) and sampled geographic areas (squares) along the biomass gradient. When the wetlands were sampled, it was recognized that each geographic area should be represented by low, intermediate, and high biomass wetlands. In this way, 100 quadrats with the lowest most values of biomass would be from the same number of geographic areas as 100 quadrats of highest biomass. This would prevent greater geographic variation in one set of quadrats from influencing calculations of the species pool. However, while each set of 100 quadrats did come from an almost identical number of geographic areas, there was enormous variation in the number of sites that each set of quadrats represented. For example, 100 quadrats with an average biomass of 81 gm/.25 m^2 represented 23 different wetland sites, while an identical number of quadrats with an average of 4 gm/.25 m^2 came from only 9 different sites. Before meaningful measurements of the species pool could be made, sets of quadrats had to represent identical numbers of geographic areas and wetland sites.

Figure 3.12

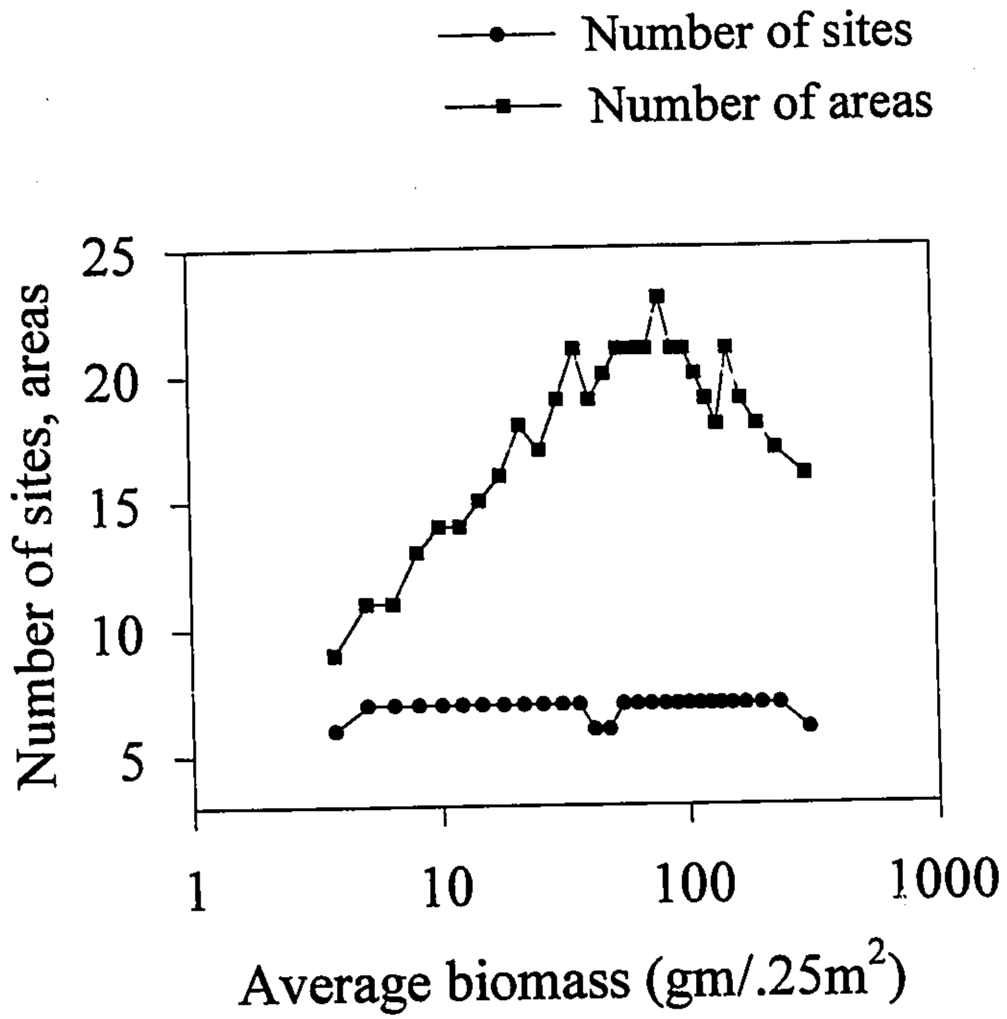


Figure 3.13. Alpha diversity in wetland habitats was greatest at intermediate levels of biomass. A quadratic regression line is superimposed on the 640 data points.

Figure 3.13

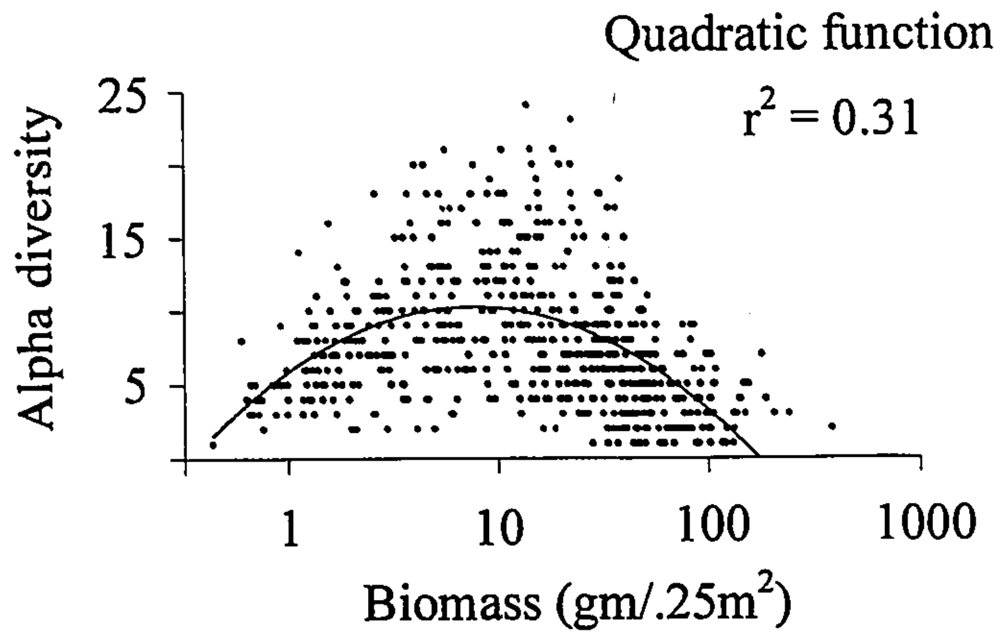


Figure 3.14. Competitive dominants expressed as proportions of quadrats and plotted against the biomass of wetland habitats. The five competitive dominants are those identified by Gaudet and Keddy (1988) as having the highest competitive abilities of 44 wetland species. They were most abundant within high biomass wetlands.

Figure 3.14

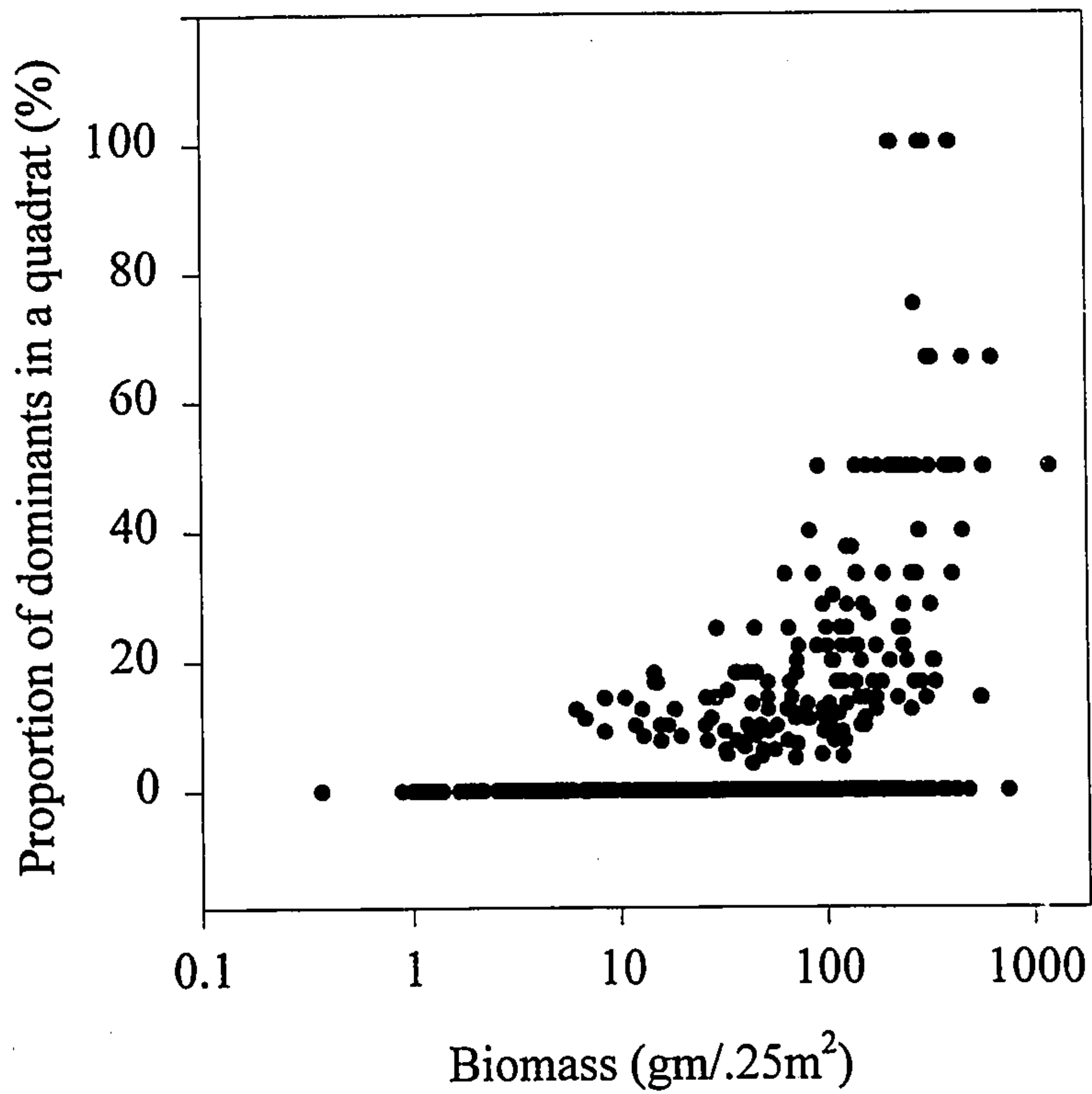


Figure 3.15. Stress-tolerant isoetids expressed as proportions of quadrats and plotted against the biomass of wetland habitats. The ten isoetid species are from a list by Boston and Adams (1987). Isoetid species did not occur within high biomass wetlands.

Figure 3.15

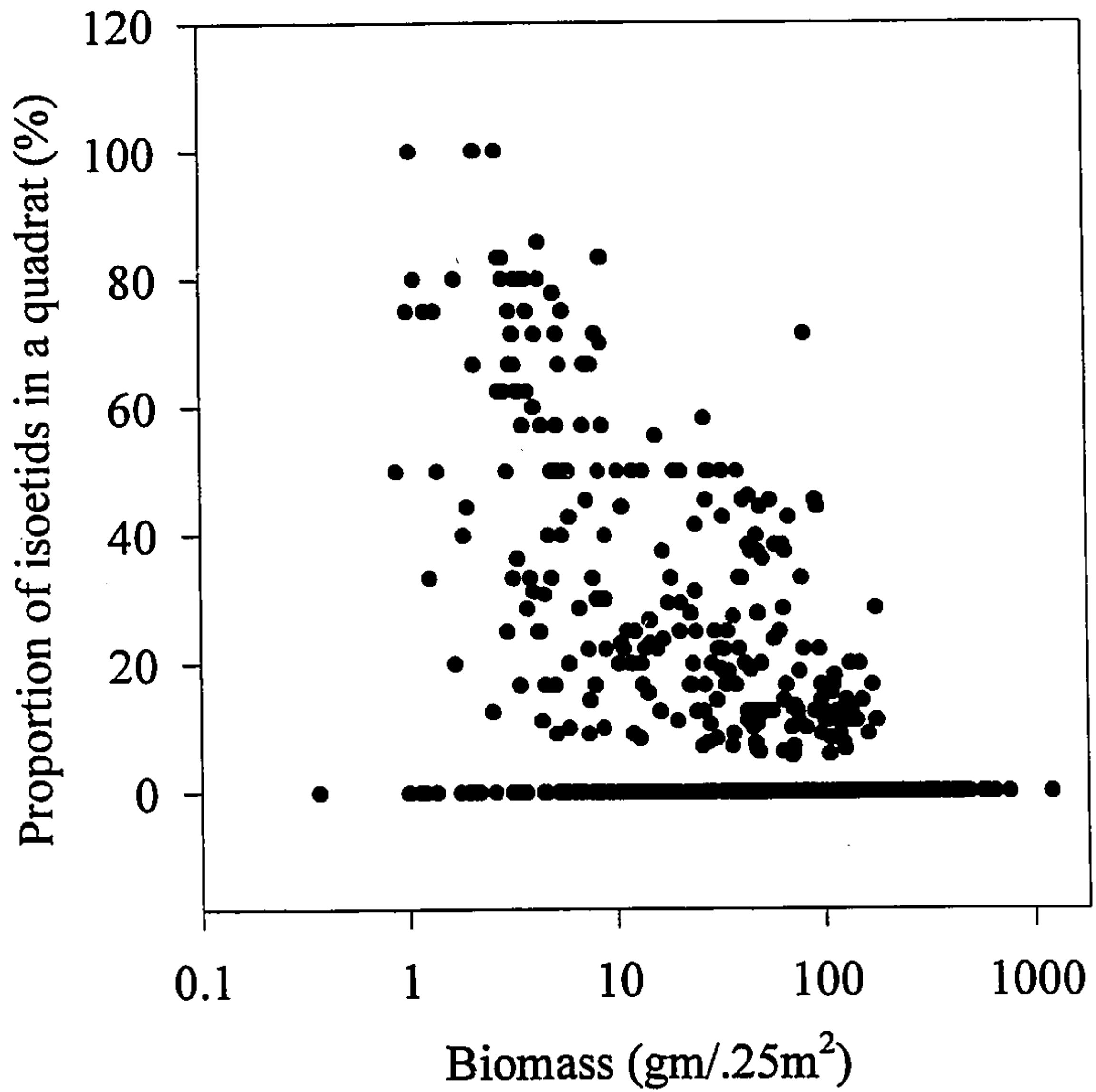
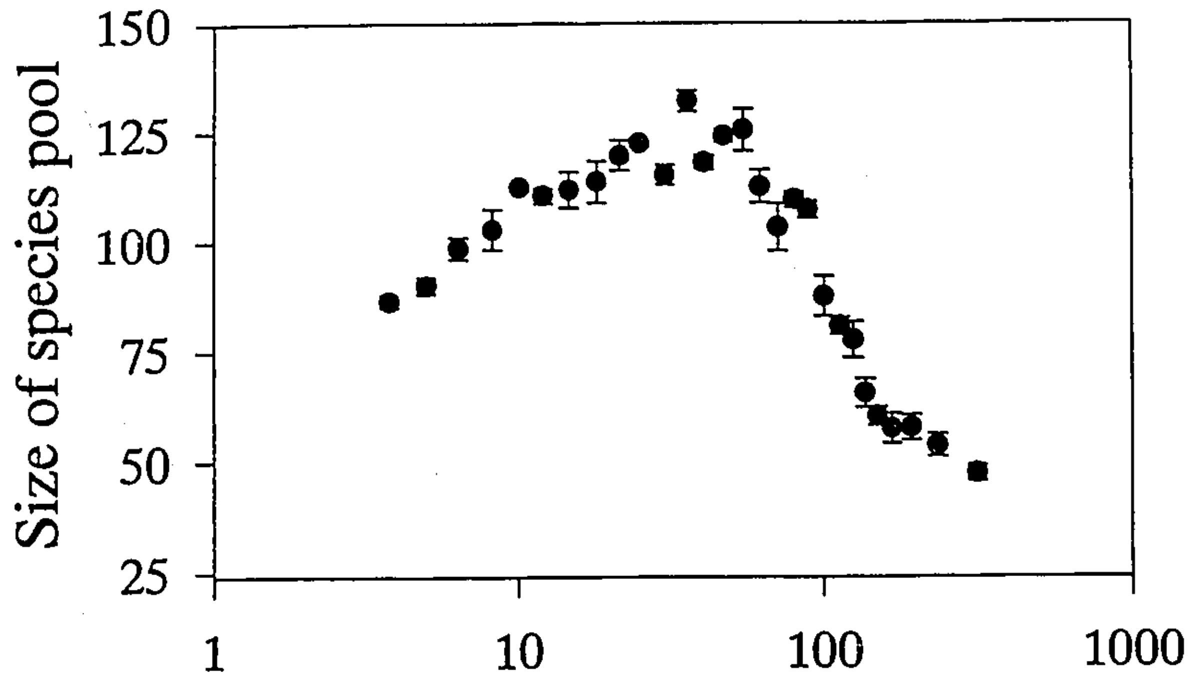


Figure 3.16. The size of species pools (top) and average alpha diversity (bottom) plotted against the average biomass of wetland habitats. As predicted by the species pool model, maximum pool size occurred at the same point of the biomass gradient as maximum alpha diversity. Each dot represents mean values calculated from five randomly selected sets of 50 quadrats each. The 50 quadrats were drawn without replacement from sets of 100 quadrats. Groups of 100 quadrats represented segments of the biomass gradient, shifted 20 quadrats each time. For example, 100 quadrats of lower most biomass (quadrats 1 - 100), 100 quadrats of next lowest biomass (quadrats 21-120), another set of 100 quadrats (quadrats 41-140), etc. Bars represent the standard errors of the means.

Figure 3.16



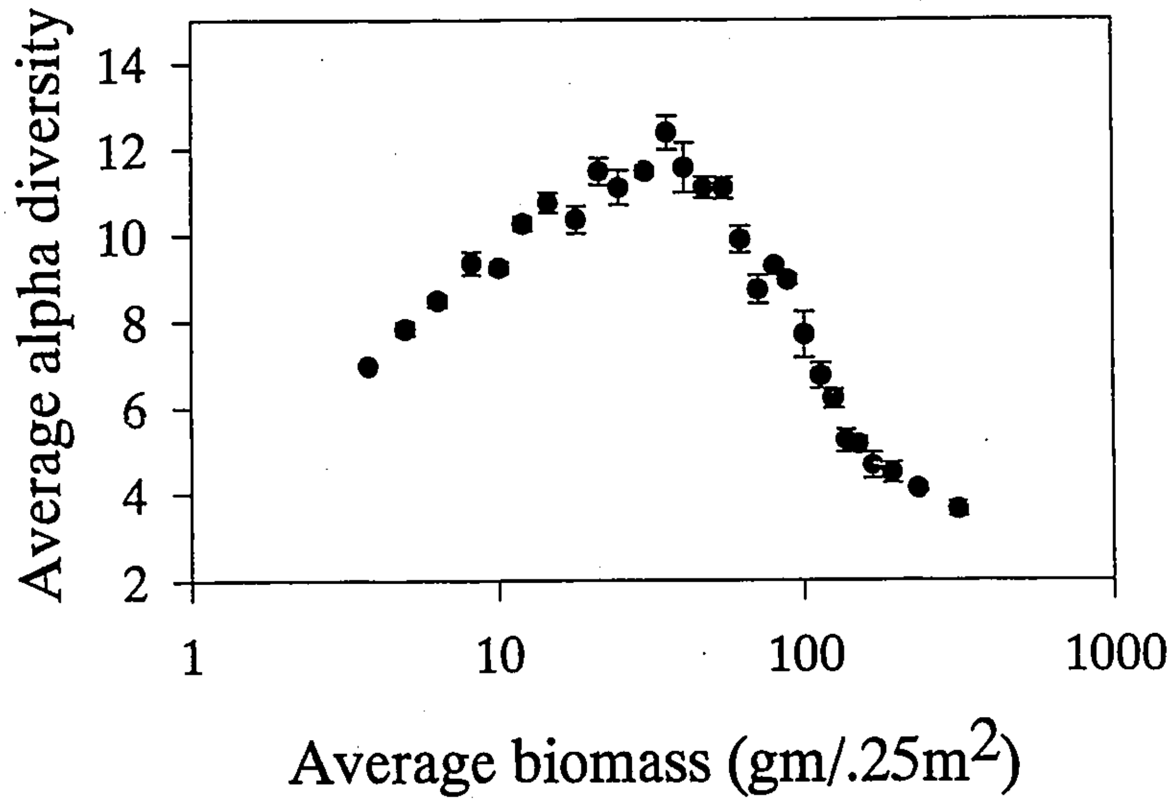
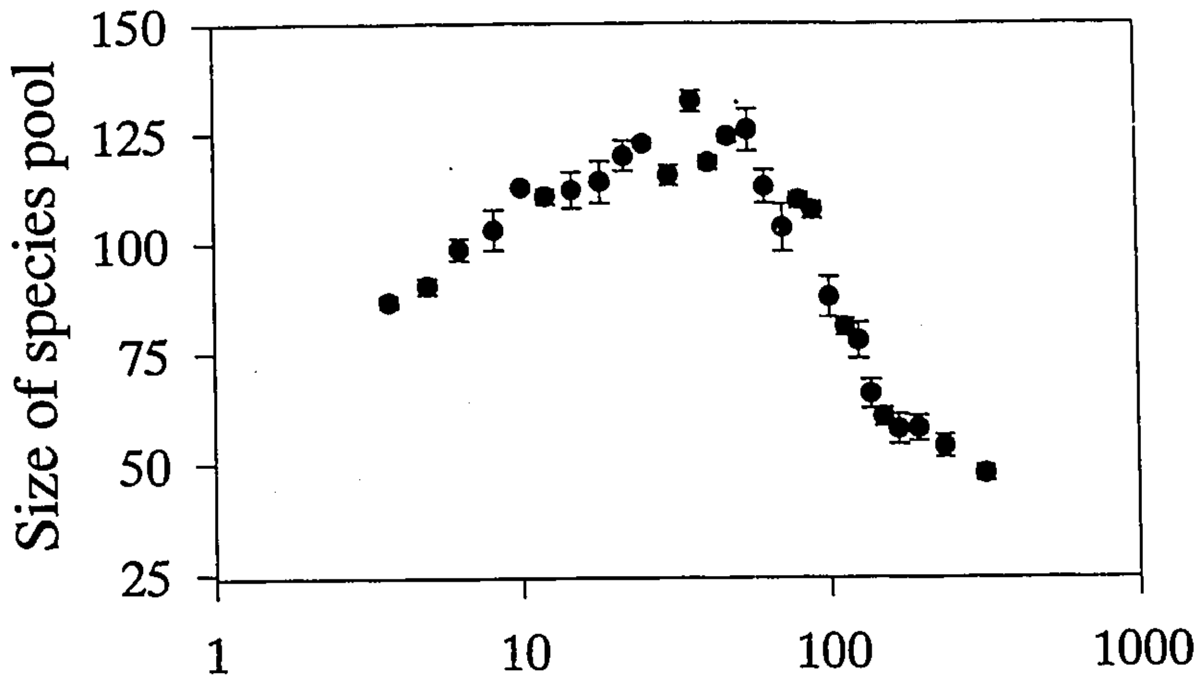


Figure 3.16



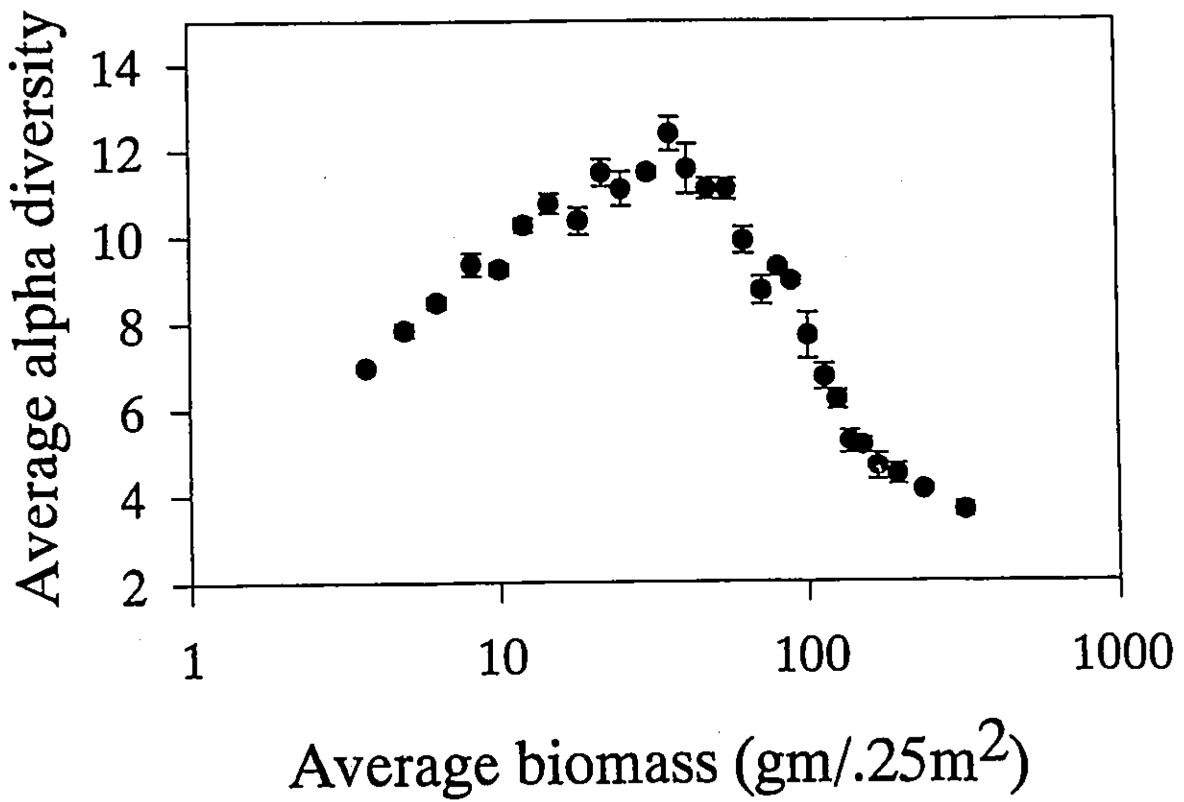


Figure 3.17. The ratio of average alpha diversity to pool size plotted against the average biomass of wetland habitats. Each quadrat is a constant subset of the species pool. The shaded region is where values cannot occur when n = 50 (see Appendix 5).

Figure 3.17

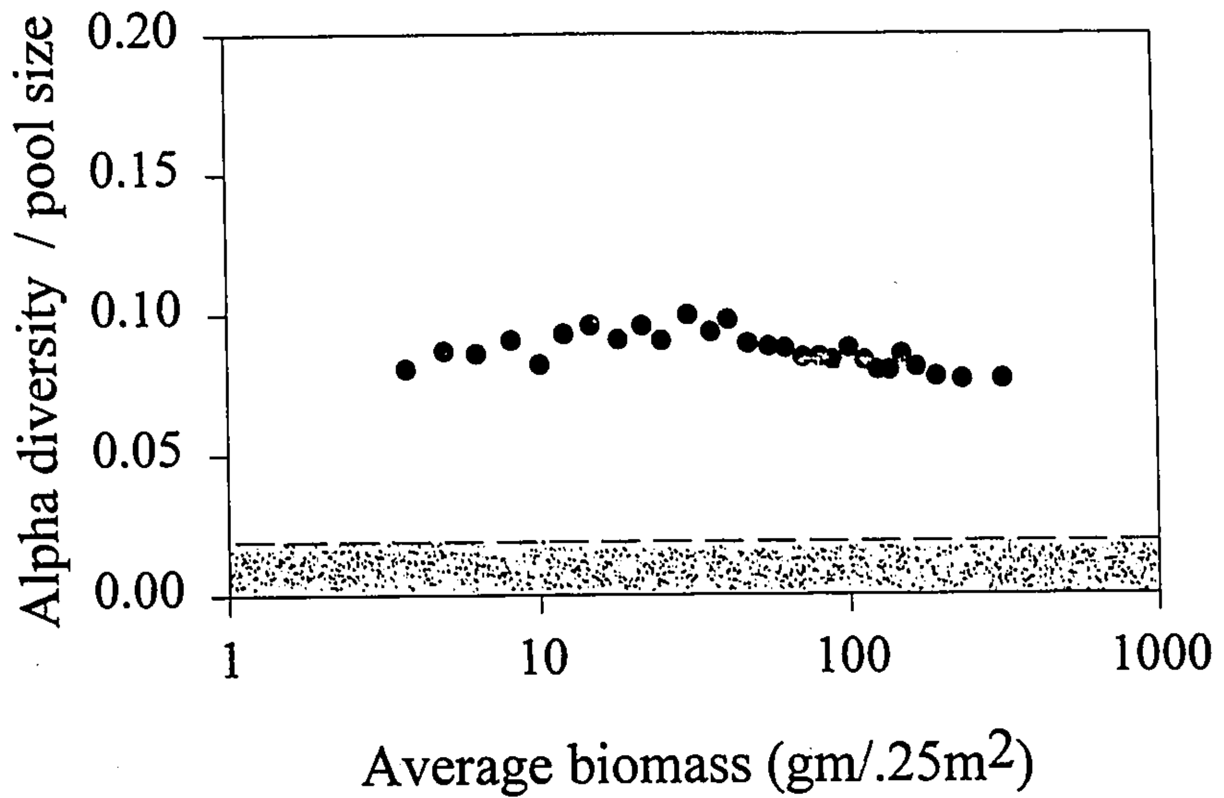


Figure 3.18. The size of species pools plotted against the average biomass of wetland habitats. Maximum pool size occurred at the same point along the biomass gradient regardless of how many quadrats were used to calculate species pool values. Each symbol represents mean values calculated from randomly selected sets of 10, 30, and 50 quadrats each. Because each set of quadrats had to represent exactly 9 sites and 6 geographic areas, greater numbers of quadrats could not be selected. Two sets of 10 quadrats, 1 set of 30 quadrats, and 5 sets of 50 quadrats were selected.

Figure 3.18

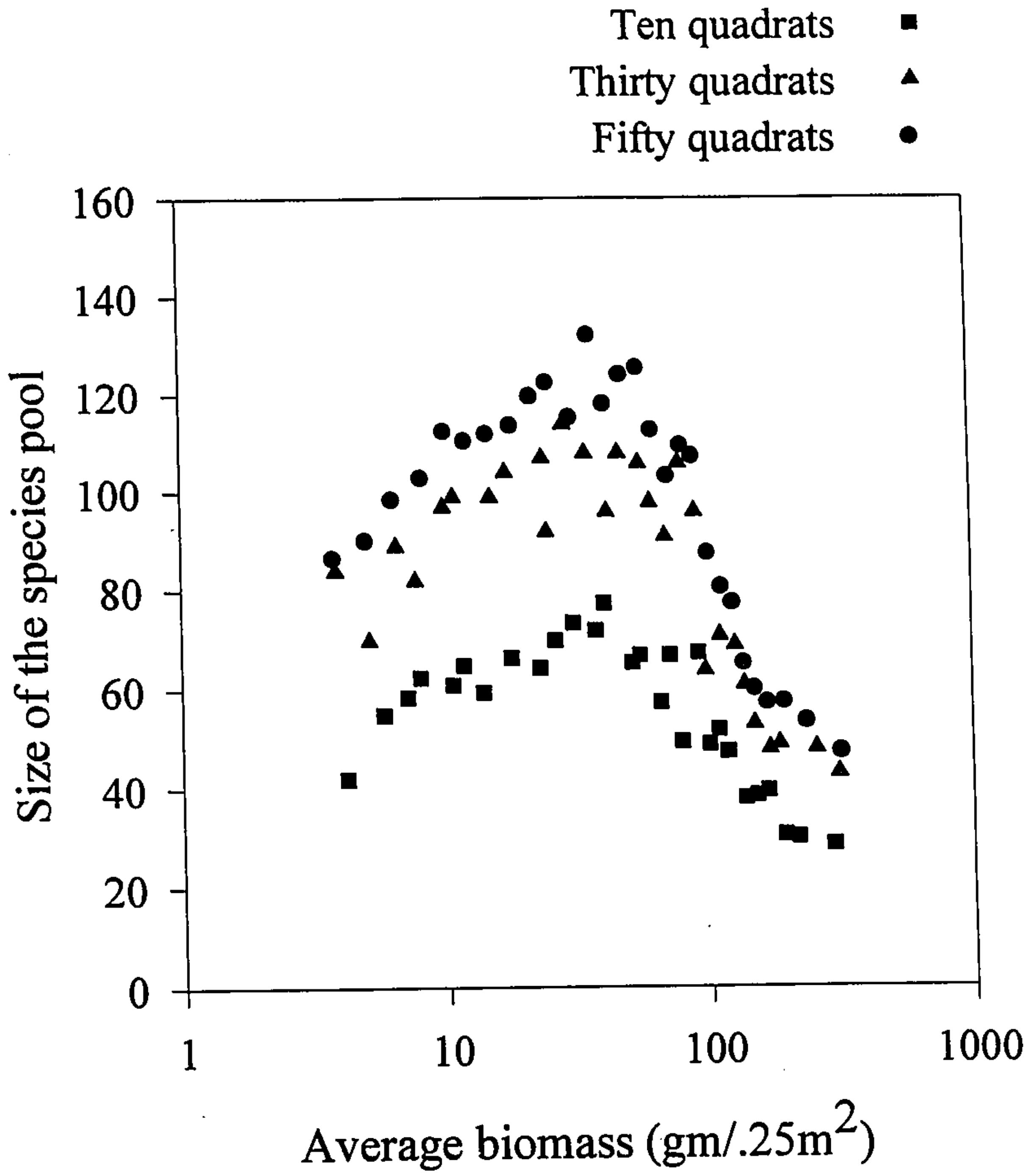


Figure 3.19. The ratio of average alpha diversity to pool size plotted against the average biomass of wetland habitats. Each quadrat is a constant subset of the species pool regardless of how many quadrats were used to calculate pool size. The size of species pools was calculated using 10, 30, or 50 quadrats. Two sets of 10 quadrats, 1 set of 30 quadrats, and 5 sets of 50 quadrats were selected.

Figure 3.19

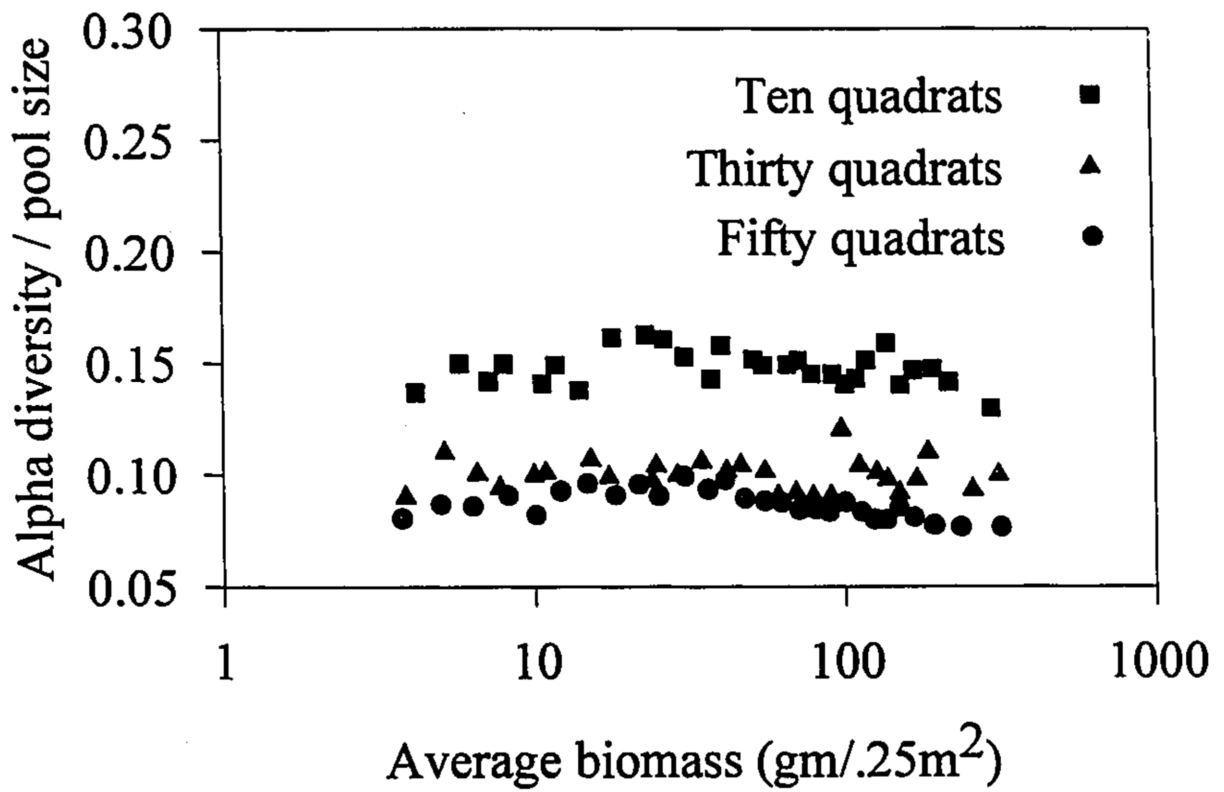


Figure 3.20. The size of species pools plotted against the average biomass of wetland habitats. Maximum pool size occurred at the same point along the biomass gradient regardless of how many sites were represented by each set of quadrats used to calculate species pool values. Each symbol represents mean values calculated from five randomly selected sets of 30 quadrats each, representing either 3 or 9 wetland sites. Thirty quadrats were selected each time instead of 50 because 50 quadrats could not represent exactly 3 or 9 sites. Two sets of quadrats representing 3 sites, and 1 set of quadrats representing 9 sites were selected.

Figure 3.20

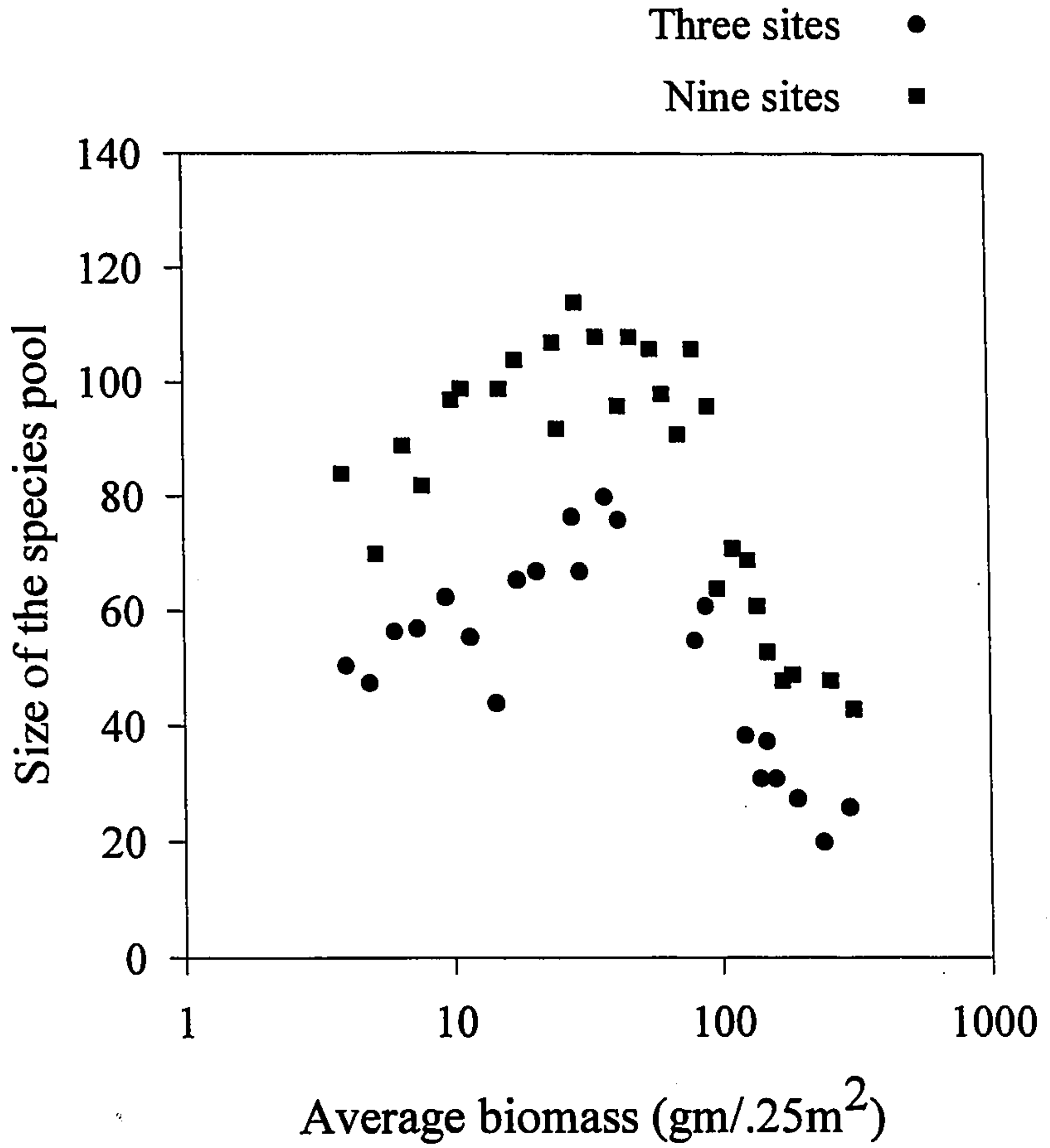


Figure 3.21. The ratio of average alpha diversity to pool size plotted against the average biomass of wetland habitats. Each quadrat is a constant subset of the species pool regardless of how many sites were represented by each set of quadrats used to calculate pool size. The size of species pools were calculated using 30 quadrats representing either 3 or 9 sites. Two sets of quadrats representing 3 sites, and 1 set of quadrats representing 9 sites were selected.

Figure 3.21

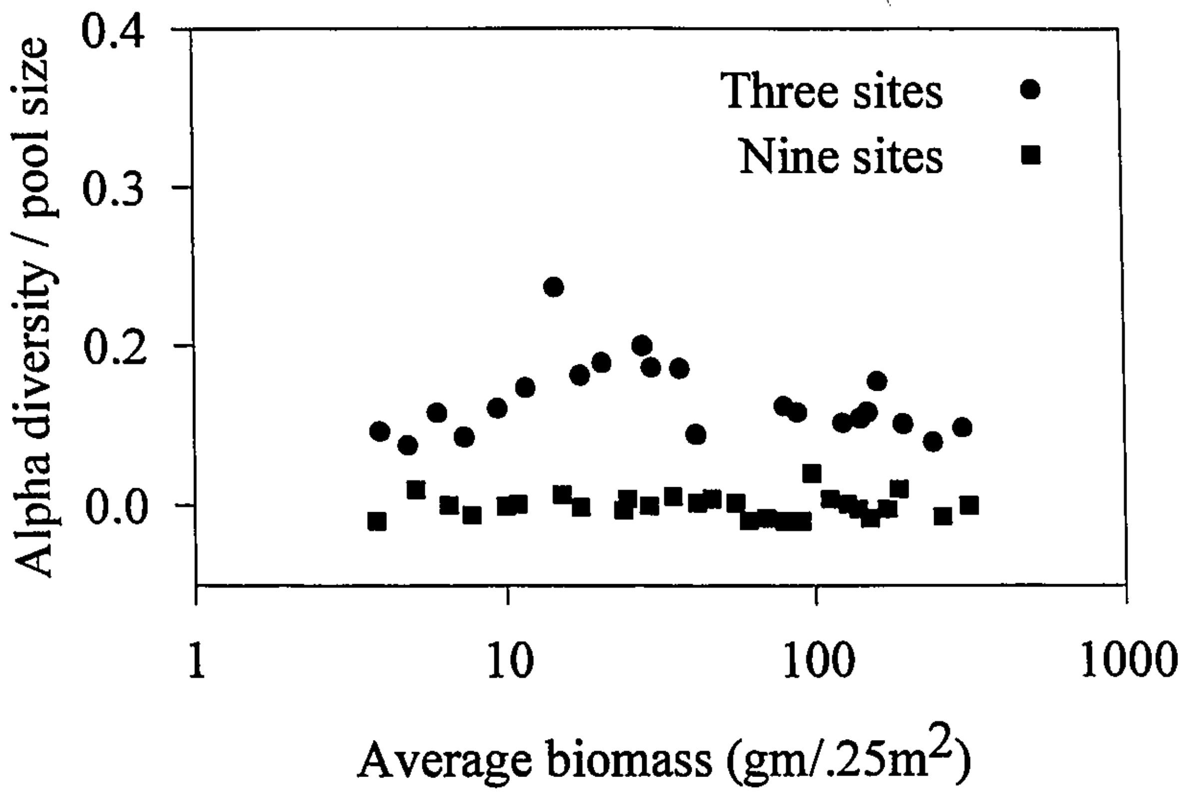


Figure 3.22. Stress-tolerant isoetids (circles) and competitive dominants (squares) expressed as proportions of the species pool and plotted against the average biomass of wetland habitats. There are proportionally more isoetids in species pools of low biomass wetlands and proportionally more competitive dominants in the species pools of high biomass wetlands. The species are as described in Figures 3.14 and 3.15. Species pools were generated using 100 quadrats at a time.

Figure 3.22

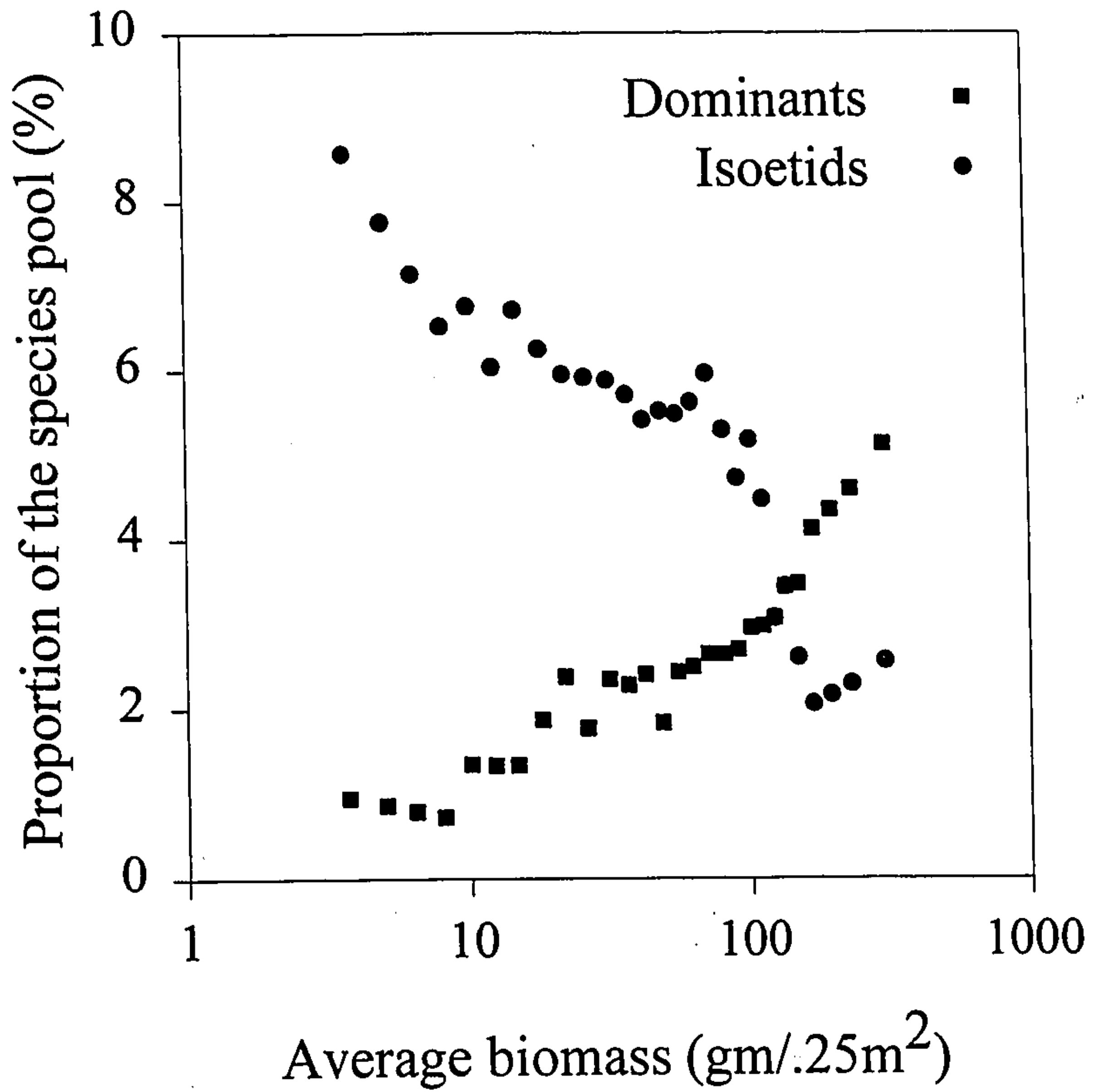
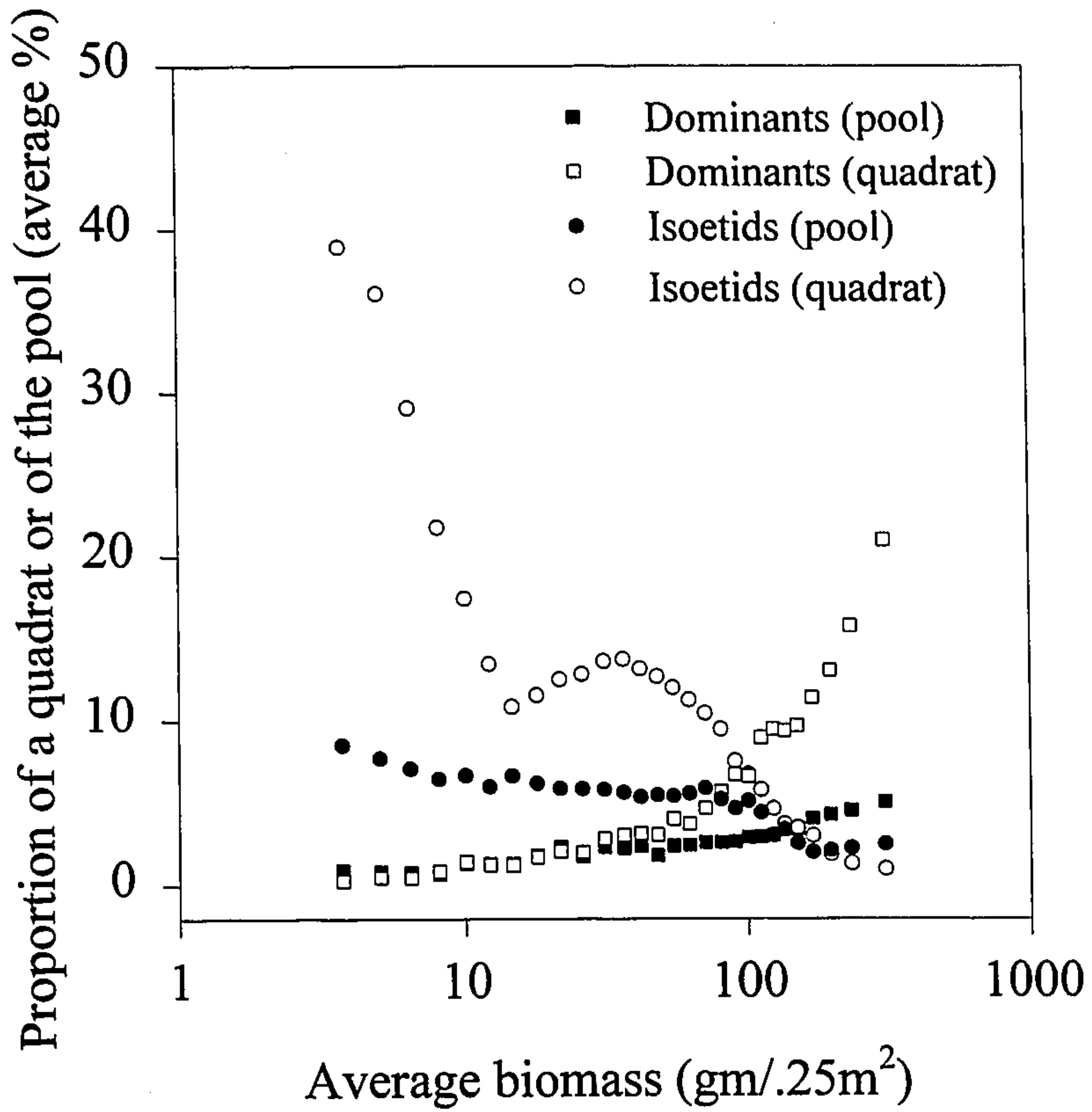


Figure 3.23. Stress-tolerant isoetids (circles) and competitive dominants (squares) expressed as proportions of either quadrats or the species pool and plotted against the average biomass of wetland habitats. The species are as described in Figures 3.14 and 3.15. Light symbols are averages of 100 quadrats. Dark symbols were calculated using 100 quadrats at a time. If the content of a quadrat is simply a random subset of the species pool, then proportions of isoetids and dominants within quadrats should be identical to proportions in the species pool.

Figure 3.23



APPENDIX 2

To determine how many distinct wetland sites had been sampled, average linkage clustering was used (Jongman et al. 1987, SYSTAT 1990) with clustering based on the presence or absence of species in quadrats. A minimum euclidean distance value below which sites should be combined, was established by comparing two 'sites' considered to be identical. The resulting euclidean distance value was 1.493, and so all pairs of 'sites' with distance values below this value were combined. Pairs of 'sites' with distance values slightly above this value were also combined (e.g., 1.574, 1.551) since these were also in close physical proximity. The results of average linkage clustering were consistent with centroid linkage, complete linkage, single linkage, median, and ward's minimum variance clustering.

APPENDIX 3

The 262 species encountered during sampling. Species names follow Gleason and Cronquist (1963) with the addition of *Typha glauca* Godr.

Acorus calamus L.

Adiantum pedatum L.

Agrostis hyemalis (Walt.) BSP.

Agrostis perennans (Walt.) Tuckerm.

Agrostis stolonifera L.

Alisma plantago-aquatica L.

Anacharis canadensis (Michx.) Rich.

Andropogon scoparius Michx.

Anemone canadensis L.

Aristida longespica Poir.

Artemisia campestris L.

Asclepias incarnata L.

Aster junciformis Rydb.

Aster lateriflorus (L.) Britt.

Aster nemoralis Ait.

Aster novae-angliae L.

Aster pilosus Willd.

Aster ptarmicoides (Nees) T. & G.

Aster puniceus L.

Aster simplex Willd.

Aster tradescanti L.

Bartonia paniculata (Michx.) Muhl.

Bidens beckii Torr.

Bidens cernua L.

Bidens frondosa L.

Boehmeria cylindrica (L.) Sw.

Calamagrostis canadensis (Michx.) Beauv.

Calamagrostis lacustris (Kearn.) Nash.

Calamagrostis neglecta (Ehrh.) Gaertn.

Callitriche deflexa A. Br.

Campanula aparinoides Pursh.

Carex aquatilis Wahl.

Carex atherodes Spreng.

Carex aurea Nutt.

Carex bullata Schk.

Carex comosa Boott.

Carex crawei Dewey.

Carex hystericina Muhl.

Carex lacustris Willd.

Carex lasiocarpa Ehrh.

Carex lenticularis Michx.

Carex limosa L. and/or *Carex paupercula* Michx.

Carex lurida Wahl.

Carex oligosperma Michx.

Carex pairaei F. Schultz.

Carex projecta Mackenzie.

Carex rostrata Stokes.

Carex stricta Lam.

Carex tribuloides Wahl.

Carex vesicaria L.

Carex viridula Michx.

Chenopodium glaucum L.

Cicuta bulbifera L.

Cirsium vulgare (Savi) Tenore.

Cladium mariscoides (Muhl.) Torr.

Convolvulus sepium L.

Coreopsis rosea Nutt.

Cornus amomum Mill.

Cornus rugosa Lam.

Cornus stolonifera Michx.

Cyperus aristatus Rottb.

Cyperus dentatus Torr.

Cyperus engelmanni Steud.

Cyperus esculentus L.

Cyperus rivularis Kunth.

Danthonia spicata (L.) Beauv.

Deschampsia cespitosa (L.) Beauv.

Drosera intermedia Hayne.

Drosera rotundifolia L.

Dulichium arundinaceum (L.) Britt.

Echinochloa crusgalli (L.) Beauv.

Echinocyctis lobata (Michx.) T. & G.

Elatine minima (Nutt.) Fisch. & Mey.

Eleocharis acicularis (L.) R. & S.

Eleocharis erythropoda Steud.

Eleocharis flavescens (Poir.) Urban.

Eleocharis ovata (Roth) R. & S.

Eleocharis palustris (L.) R. & S.

Eleocharis pauciflora (Lightf.) Link.

Eleocharis robbinsii Oakes.

Eleocharis tenuis (Willd.) Schult.

Epilobium ciliatum Raf.

Equisetum arvense L.

Equisetum fluviatile L.

Equisetum variegatum Schleich.

Eriocaulon septangulare With.

Erucastrum gallicum (Willd.) O. E. Schulz.

Eupatorium maculatum L.

Eupatorium perfoliatum L.

Fimbristylis autumnalis (L.) R. & S.

Galium obtusum Bigel.

Galium palustre L.

Galium trifidum L.

Gentiana procera Holm.

Gerardia purpurea L.

Glyceria borealis (Nash) Batchelder.

Glyceria canadensis (Michx.) Trin.

Glyceria grandis S. Wats.

Glyceria obtusa (Muhl.) Trin.

Gnaphalium uliginosum L.

Gratiola aurea Pursh.

Habenaria clavellata (Michx.) Spreng.

Habenaria flava (L.) R. Br.

Helenium autumnale L.

Houstonia canadensis Willd.

Hydrocotyle umbellata L.

Hypericum boreale (Britt.) Bickn.

Hypericum ellipticum Hook.

Hypericum kalmianum L.

Hypericum majus (Gray) Britt.

Ilex verticillata (L.) Gray.

Impatiens biflora Walt.

Iris versicolor L.

Isoetes echinospora Durieu.

Isoetes macrospora Durieu.

Juncus alpinus Vill.

Juncus balticus Willd.

Juncus brachycephalus (Engelm.) Buch.

Juncus brevicaudatus (Engelm.) Fern.

Juncus bufonius L.

Juncus canadensis J.Gay.

Juncus effusus L.

Juncus filiformis L.

Juncus militaris Bigel.

Juncus nodosus L.

Juncus pelocarpus E. Meyer.

Juncus subtilis E. Meyer.

Juniperus horizontalis Moench.

Lathyrus palustris L.

Leersia oryzoides (L.) Sw.

Lindernia dubia (L.) Pennell.

Linum medium (Planch.) Britt.

Liparis loeselii (L.) Rich.

Lobelia dortmanna L.

Lobelia kalmii L.

Ludwigia palustris (L.) Ell.

Lycopodium inundatum L.

Lycopus americanus Muhl.

Lycopus europaeus L.

Lycopus uniflorus Michx.

Lycopus virginicus L.

Lysimachia nummularia L.

Lysimachia terrestris (L.) BSP.

Lysimachia thyrsiflora L.

Lythrum salicaria L.

Medicago lupulina L.

Mentha arvensis L.

Mimulus ringens L.

Mollugo verticillata L.

Muhlenbergia uniflora (Muhl.) Fern.

Myrica gale L.

Myriophyllum spicatum L.

Myriophyllum tenellum L.

Myriophyllum verticillatum L.

Najas flexilis (Willd.) Rostk. & Schmidt.

Nuphar variegatum Engelm.

Nymphaea odorata Ait.

Nymphoides cordata (Ell.) Fern.

Onoclea sensibilis L.

Osmunda regalis L.

Panicum capillare L.

Panicum flexile (Gatt.) Scribn.

Panicum lanuginosum Ell.

Panicum longifolium Torr.

Panicum philadelphicum Bernh.

Panicum virgatum L.

Parnassia glauca Raf.

Parthenocissus quinquefolia (L.) Planch.

Penthorum sedoides L.

Phalaris arundinacea L.

Physostegia virginiana (L.) Benth.

Pilea pumila (L.) Gray.

Plantago major L.

Pogonia ophioglossoides (L.) Ker.

Polygonum hydropiperoides Michx.

Polygonum hydropiper L.

Polygonum lapathifolium L.

Polygonum natans Eat.

Polygonum persicaria L.

Pontederia cordata L.

Potamogeton gramineus L.

Potamogeton natans L.

Potamogeton oakesianus Robbins.

Potamogeton perfoliatus L.

Potamogeton robbinsii Oakes.

Potamogeton spirillus Tuckerm.

Potamogeton zosteriformis Fern.

Potentilla anserina L.

Potentilla fruticosa L.

Potentilla palustris (L.) Scop.

Prenanthes racemosa Michx. (probably)

Primula mistassinica Michx.

Prunella vulgaris L.

Ranunculus aquatilis L.

Ranunculus flammula L.

Rhexia virginica L.

Rhynchospora capillacea Torr.

Rhynchospora capitellata (Michx.) Vahl.

Rhynchospora fusca (L.) Ait. f.

Rorippa islandica (Oeder) Borbas.

Rumex verticillatus L.

Sabatia kennedyana Fern.

Sagittaria cuneata Sheldon.

Sagittaria graminea Michx.

Sagittaria lancifolia L.

Sagittaria latifolia Willd.

Sagittaria rigida Pursh.

Salix interior Rowlee.

Salix lucida Muhl.

Sarracenia purpurea L.

Satureja glabella (Michx.) Briquet.

Scirpus acutus Muhl.

Scirpus americanus Pers.

Scirpus cyperinus (L.) Kunth.

Scirpus fluviatilis (Torr.) Gray.

Scirpus longii Fern.

Scirpus subterminalis Torr.

Scirpus torreyi Olney.

Scirpus validus Vahl.

Scleria verticillata Much.

Scutellaria galericulata L.

Scutellaria lateriflora L.

Selaginella apoda (L.) Spring.

Selaginella selaginoides (L.) Link.

Senecio pauperculus Michx.

Setaria glauca (L.) Beauv.

Sisyrinchium montanum Greene.

Sium suave Walt.

Solanum dulcamara L.

Solidago canadensis L.

Solidago galetorum (Greene) Friesn.

Solidago graminifolia (L.) Salisb.

Solidago ohioensis Riddell. (probably)

Solidago uliginosa Nutt.

Sonchus uliginosus Bieb.

Sorghastrum nutans (L.) Nash.

Sparganium americanum Nutt.

Sparganium eurycarpum Engelm.

Spartina pectinata Link.

Spiraea latifolia (Ait.) Borkh.

Spiranthes cernua (L.) Rich.

Spiranthes romanzoffiana Cham.

Sporobolus cryptandrus (Torr.) Gray.

Sporobolus vaginiflorus (Torr.) Wood.

Stachys palustris L. (probably)

Taraxacum officinale Weber.

Thelypteris palustris Schott.

Thuja occidentalis L.

Tofieldia glutinosa (Michx.) Pers.

Triadenum fraseri (Spach) Gl.

Triglochin maritima L.

Typha angustifolia L.

Typha glauca Godr.

Typha latifolia L.

Urtica dioica L.

Utricularia cornuta Michx.

Utricularia resupinata B. D. Greene.

Utricularia subulata L.

Vaccinium macrocarpon Ait.

Vallisneria americana Michx.

Verbena hastata L.

Veronica sp.

Vicia cracca L.

Viola lanceolata L.

Viola nephrophylla Greene.

Xanthium strumarium L.

Xyris caroliniana Walt.

Zizania aquatica L.

Zosterella dubia (Jacq.) Small.

APPENDIX 4

Sample results. Site, geographic area, and quadrat identification numbers are followed by descriptions of the quadrat (biomass in gm/.25m^2, alpha diversity) and presence/absence data for 262 species. Genus and species names are abbreviated to four letters each.

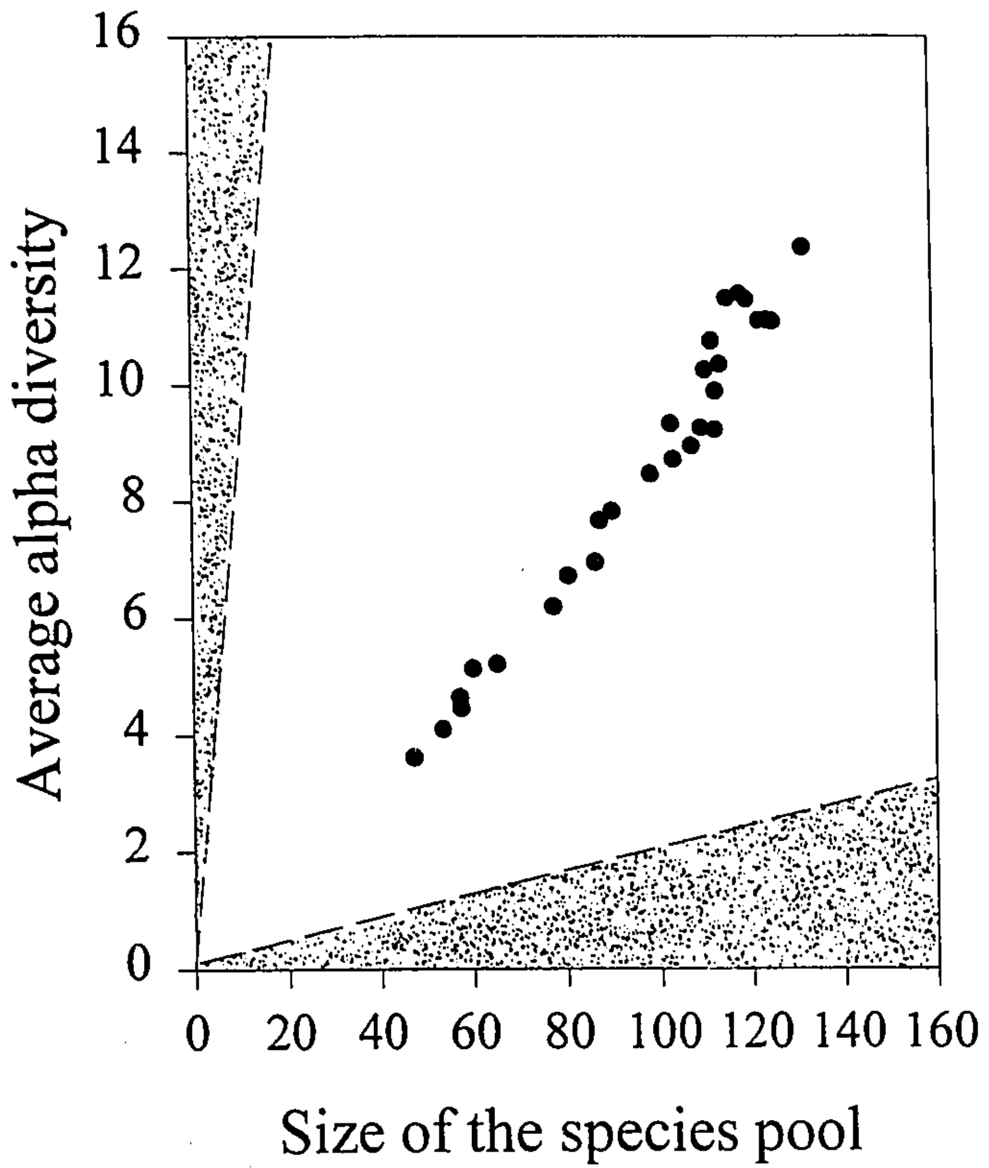
Appendix 4

site	area	quadrat	biomass	alpha	acorcala	adiapeda	agrohyem	agropere
26	6	44	0.37	1	0	0	0	0
2	1	10	0.89	8	0	0	0	0
28	7	2	1	4	0	0	0	0
2	1	11	1.01	4	0	0	0	0
3	1	35	1.06	3	0	0	0	0
3	1	91	1.1	5	0	0	0	0
28	7	15	1.14	3	0	0	0	0
28	7	12	1.2	5	0	0	0	0
3	1	78	1.23	4	0	0	0	0
28	7	10	1.28	3	0	0	0	0
28	7	8	1.36	4	0	0	0	0
3	1	80	1.37	4	0	0	0	0
3	1	25	1.4	2	0	0	0	0
28	7	13	1.68	5	0	0	0	0
2	1	65	1.72	5	0	0	0	0
28	7	9	1.77	3	0	0	0	0
26	6	14	1.86	5	0	0	0	0
26	6	21	1.94	9	0	0	0	0
17	5	35	1.96	5	0	0	0	0
3	1	84	2.12	6	0	0	0	0
28	7	5	2.13	6	0	0	0	0
3	1	23	2.15	5	0	0	0	0
26	6	37	2.16	3	0	0	0	0
3	1	77	2.18	4	0	0	0	0
16	4	20	2.2	13	0	0	0	0
3	1	2	2.54	8	0	0	0	0
16	4	19	2.6	18	0	0	0	0
2	1	67	2.74	3	0	0	0	0
3	1	86	2.75	4	0	0	0	0
2	1	4	2.76	8	0	0	0	0
2	1	9	2.81	6	0	0	0	0
2	1	66	2.91	5	0	0	0	0
2	1	69	2.93	6	0	0	0	0
3	1	41	2.95	8	0	0	0	0
3	1	34	3	4	0	0	0	0
2	1	12	3.01	10	0	0	0	0
2	1	72	3.13	4	0	0	0	0
2	1	68	3.14	6	0	0	0	0
26	6	11	3.16	9	0	0	0	0
26	6	6	3.22	3	0	0	0	0
2	1	64	3.24	7	0	0	0	0
3	1	45	3.3	9	0	0	0	0
2	1	71	3.32	5	0	0	0	0
2	1	18	3.36	8	0	0	0	0
2	1	98	3.37	11	0	0	0	1

APPENDIX 5

The average alpha diversity / pool size relationship. Since both measures of diversity are calculated from the same data, the measurements are not independent. There are therefore regions within which values cannot occur (indicated by shading).

Appendix 5



GENERAL CONCLUSIONS

Since Hutchinson's early definition of pattern (1953), ecology has proceeded from the recognition of repeatable patterns to the combining of pattern with process (e.g., Kikkawa and Anderson 1986). In Chapter One, I addressed the question of how patterns of resource partitioning are formed. This exploration of patterns of partitioning included an examination of processes and went to the next crucial step for ecology, that of prediction (Peters 1991). Using examples from the literature, I was able to (1) quantify shared preference niche organization as frequent and widespread, (2) identify alternative mechanisms and possible variability, and (3) begin the establishment of guidelines for predicting the occurrences of shared versus distinct preferences.

The centrifugal organization model was explored in Chapter Two. One element, the predicted pattern in pool size, was tested in Chapter Three. I documented how the size of species pools changes along a biomass gradient. The resulting pattern was inconsistent with centrifugal organization but was consistent with a previously published (but untested) model, the species pool model. This model states that the pattern of pool size will be the same as the pattern of alpha diversity along a biomass gradient. That is, alpha diversity is a random subset of the species pool, an idea first presented by Preston (1948), and now supported empirically by my results.

Since alpha diversity and the species pool produced similar patterns, then the processes governing alpha diversity and pool size might be the same. This means that (1) ecological processes such as stress tolerance, disturbance tolerance, and competition might be

infuencing the species pool, and/or (2) alpha diversity could be viewed as an artifact of past biogeographical and historical events rather than as a product of ecological opportunities (Cornell and Lawton 1992, Li and Adair 1994). This possibility and the consequences have already been considered. For example, Lawton (1991) proposed the following.

> "If the number of bird species coexisting in a 5 ha plot of forest is determined by the number of species in the regional pool, which in turn is determined by biogeography and evolutionary history (as well might be the case), knowing the direct and indirect interactions between five species of warblers, revealed by exquisite experiments would be no more than an amusing footnote to the dominant processes that really determine the size of the local assemblage."

Does the "key to community structure" really "lie in extrinsic biogeography rather than in intrinsic local processes" (Cornell and Lawton 1992)? How important are biogeographical and historical events in determining alpha diversity? How important are ecological processes in determining the size of species pools? These are important questions to consider if we wish to understand community assembly.

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