Size-distance relationships reveal the importance, or lack thereof, of competition among understory plants in an old-growth deciduous forest

Marina S. Neytcheva

A thesis submitted to Saint Mary's University, Halifax, Nova Scotia
in partial fulfillment of the requirements for
the degree of Master of Science in Applied Science

April 2010, Halifax, Nova Scotia

© Marina S. Neytcheva, 2010

Approved: Dr. Jeff Houlahan, External Examiner
               Department of Biology, University of New Brunswick

Approved: Dr. Jeremy Lundholm, Senior Supervisor
               Department of Biology & Environmental Studies

Approved: Dr. Hugh Broders, Supervisory Committee Member
               Department of Biology

Approved: Dr. Cristian Suteanu, Supervisory Committee Member
               Department of Geography

Approved: Dr. Genlou Sun, Program Representative

Approved: Dr. Kevin Vessey, Dean of Graduate Studies

Date: April 12, 2010

NOTICE:

AVIS:

Canada

ABSTRACT

**Size-distance relationships reveal the importance, or lack thereof, of competition
among understory plants in an old-growth deciduous forest**

Marina S. Neytcheva

In this study, I applied the little-used method of size-distance relationships to the
ecological problem of species coexistence by investigating competitive interactions in an
old-growth deciduous forest understory community, with the specific objectives to (1)
explore and critically assess the method and (2) test the predictions of niche and neutral
theory regarding the intensity of intra- versus interspecific competition. No fatal flaws
were detected in the method, but the mechanisms of species coexistence in this
community remain unclear, as the finding that intraspecific competition is less intense
than interspecific competition was inconsistent with the predictions of both niche and
neutral theory. More importantly, though, size-distance relationships revealed that
competition is less important than expected, which suggests that asking what enables
species coexistence may have been an inappropriate line of inquiry to begin with, given
that the coexistence question itself is based on assumptions about competition that were
not justified in this community. I, therefore, advise ecologists to reassess the approach to
the study of natural diversity by rethinking both the questions posed and the methods
used.

April 26, 2010

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

"The literature on competition is as vast and diverse as beetles in the biosphere" (Keddy 2001, p. ix) reads the opening page of a volume entirely dedicated to competition. The many books (e.g. Grace and Tilman 1990, Sommer and Worm 2002) and countless papers written on the subject are a testimony to the extent to which competition has captivated the attention of ecologists since the beginning of ecology. This extraordinary interest and investment in competition may have originated with an intuitive belief in its significance, but the ongoing academic pursuit of the competitive process is grounded in field experimental data pointing towards its presence and importance in nature (Connell 1983, Schoener 1983, Aarssen and Epp 1990, Goldberg and Barton 1992, Gurevitch et al. 1992).

Yet, while competition—defined as "an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned" (Begon et al. 1996, p. 214)—has become the conceptual backbone of community ecology, it can be elusive and exceedingly difficult to study in natural communities subject to variability in both space and time (Wiens 1977, Pianka 1981, Peters 1991, Tokeshi 1999). Experimental manipulations remain a popular approach to the empirical study of competition (Freckleton and Watkinson 2001, Keddy 2001), yet nonexperimental methods, albeit less popular, may greatly contribute to a better understanding of the competitive process and warrant further examination. I, thus, turn to one particular nonmanipulative technique.

1

Size-distance relationships, whose development spans several decades and multiple authors, are a pattern-based approach to the identification and assessment of competition in plant communities. The method was introduced by Pielou (1960, 1961) and consists of an analysis of the relationship between two variables: the distance between a pair of neighbouring plants (distance being a simple measure of density) and the sum of their sizes. If larger plants are farther apart than smaller plants—an observation consistent with competition-induced density-dependent effects on individual plant size and survivorship—the resulting positive correlation between distance and sum of sizes provides evidence for competitive interference, whereas no relationship between these variables indicates absence of competition (Pielou 1960, 1961). Furthermore, Welden and Slauson (1986) suggested that, after fitting a regression line to the data, size-distance relationships can be used not only to identify the occurrence of competition in natural communities, but also to quantify its intensity and importance. Competition intensity can be defined as the degree to which competition negatively affects an organism (the greater the reduction in growth, survival, and/or reproduction, the more intense the competitive interactions), and when sum of sizes is displayed on the x-axis and distance on the y-axis, the slope of the regression line is a direct measure of competition intensity. In other words, a steeper slope indicates a greater negative effect of competition on plant growth because, at a given inter-plant distance, a steeper slope is associated with a smaller combined size of neighbours than a shallower slope (Welden and Slauson 1986). On the other hand, the coefficient of determination (r^2) of the regression measures the importance of competition among neighbouring plants relative to

all other factors that influence the size and spatial arrangement of individuals (Welden and Slauson 1986).

So, the combined efforts of Pielou (1960, 1961), Welden and Slauson (1986) furnished ecologists with a new method for the detection and quantification of plant competition in nature, but though capable of addressing a range of questions related to the competitive process, size-distance relationships have not been widely embraced. Why have ecologists passed by a method that seems to have so much potential? Previous users of size-distance relationships have not questioned their validity (Yeaton and Cody 1976, Yeaton et al. 1977, Gutierrez and Fuentes 1979, Fuentes and Gutierrez 1981, Nobel 1981, Philips and MacMahon 1981, Taylor and Aarssen 1989, Briones et al. 1996, Carrick 2003, Larrea-Alcazar and Soriano 2006, Meyer et al. 2008), although some suggestions for improvement have been made (Welden et al. 1988, Wilson 1991, Shackleton 2002) and the approach has generally been poorly explored. It is possible that the method is fatally flawed, but it is also possible that it has simply been forgotten. While the reason for the scarce use of size-distance relationships in ecological investigations may not be easily ascertained, I was intrigued by this phenomenon and set out to explore the method by applying it to the equally intriguing question of species coexistence.

Plant community ecologists devote much time and effort to understanding species coexistence, the 'problem' of coexistence stemming from the general consensus that interspecific competition, which poses a risk of competitive exclusion, is both common and fundamentally important in natural vegetation (Bengtsson et al. 1994, Silvertown 2004, Berger et al. 2008). So, as coexistence has essentially been defined as the absence

3

of competitive exclusion (Aarssen 1983, Tokeshi 1999, Keddy 2001), ecologists fascinated with the observed diversity of competing species in nature have been trying to determine what prevents competitive exclusion and allows coexistence. According to long-standing niche models, species avoid competitive exclusion through niche differentiation, as a reduction or elimination of niche overlap effectively eliminates competition for common limiting resources (Aarssen 1983, Giller 1984). Alternatively, more recent neutral models (Bell 2000, 2001, Hubbell 2001) have lead to the explanation that coexistence ensues, despite intense competition, from ecological equivalence, as no single species is competitively superior to any other species.

Although it is now recognized that both niche and neutral mechanisms likely shape community structure (Alonso et al. 2006), the relative contribution of each is still largely unknown but can be discerned by empirically testing theoretical predictions. Since niche theory predicts that niche differentiation reduces the intensity of interspecific competition relative to intraspecific competition (Chesson 2000), while no difference between interspecific and intraspecific competition intensity is expected under the neutral model (Hubbell 2001), a comparison of intraspecific and interspecific competition intensity would test predictions of both coexistence theories and yield support for either a niche or neutral explanation of community diversity. The intensity of competition can, in turn, be quantified by size-distance relationships, so the method provides an excellent opportunity to determine whether coexistence is enabled by niches or neutrality.

In the current study, therefore, the method of size-distance relationships was applied to the ecological problem of coexistence by investigating competitive interactions in an old-growth deciduous forest understory community. My objectives were two-fold:

(1) to analytically explore and critically assess the method of size-distance relationships and (2) to test the predictions of niche and neutral theory regarding the intensity of intra- versus interspecific competition. I aimed to first optimize the method by carrying out improvements at both the sampling and analytical stages, subsequent to which size-distance relationships were explored by addressing the question of species coexistence from both a community-wide (global) and species-specific perspective and carefully evaluating the findings of the two analytical approaches.

METHODS

Study system

This research was conducted in the Grande Anse river valley of Cape Breton Highlands National Park, Nova Scotia, Canada (46.80°N, 60.73°W). The valley covers an area of approximately 1,619 ha and is characterized by mature old-growth deciduous forest stands dominated by *Acer saccharum* (sugar maple). Although old-growth forests comprise only 0.6% of the forest area in Nova Scotia (Lynds and LeDuc 1995), much insight about ecological processes can be gained from these systems, generally free from human disturbance (McCarthy 2003), whose community patterns and species composition reflect long-term community dynamics.

In particular, the investigation centred on the understory layer of the forest, which was defined as all vascular plant species, including the seedlings and saplings of woody species, one metre or less in height. The understory stratum has received relatively little

scientific attention, as most studies of forest dynamics have elected to focus on the dominant forest vegetation, i.e. trees (McCarthy 2003, Gilliam 2007). The forest understory, though, provides an ideal opportunity to investigate the coexistence of competing species not only because it boasts the highest level of species diversity among all forest strata in most eastern North American hardwood forests (McCarthy 2003, Gilliam 2007), but also because in temperate deciduous forests with intact canopies, less than 3% of the incident photosynthetically active solar radiation reaches the forest floor (Neufeld and Young 2003), so members of the understory community are expected to compete at least for light resources.

Sampling design and neighbourhood data collection

The sampling unit in this study was a plant neighbourhood, consisting of a target plant and its ten nearest neighbours. Six hundred neighbourhoods, distributed over the entire spatial extent of the study site, were randomly selected and sampled between June and August 2008. While, to the best of my knowledge, all previous users of size-distance relationships, except Meyer et al. (2008), have restricted their sampling to nearest-neighbour pairs only, I agree with Welden et al. (1988) and Shackleton (2002) that extending the analysis to include plants beyond the first nearest neighbour would provide a more meaningful assessment of competitive interactions, so my first attempt to optimize the method consisted of sampling ten nearest neighbours. In addition to measuring the distance between the rooting centres of the target plant and each of its nearest neighbours, data collection at each neighbourhood entailed taxonomically

6

identifying (to the species level) all individuals in the neighbourhood and measuring their size. Plant size can be quantified using a variety of indices, but the chosen measure of plant size must be consistent with the rationale behind interpreting a positive correlation between distance and sum of sizes as evidence of competition, which is as follows.

When plants compete for a limited amount of shared resources, individuals, by definition, adversely affect each other during the process of resource acquisition (Tokeshi 1999). Restricted size and mortality are common consequences of competition because plant growth (during which resources are converted into biomass) and survival depend on an individual's ability to meet its resource needs, which diminishes with the onset of competitive interactions. In addition, the closer plants are to each other (i.e. the higher the density of neighbours), the more likely they are to compete and experience the adverse effects of competition, such as size suppression. Consequently, a pattern of larger plants being farther apart than smaller plants can be plausibly explained by the process of resource competition, i.e. plants in high density neighbourhoods that are close together are small because competition prevented them from acquiring the resources necessary to attain a larger size. The inference of competition from a positive correlation between distance and sum of sizes, though, relies on the assumption that the measure of size is proportional to resource acquisition.

Plant biomass, therefore, being most representative of resource uptake, as resources are converted into biomass, is the ideal measure of plant size to use in size-distance relationships. Nevertheless, measuring plant biomass requires destructive sampling and greatly magnifies the sampling effort, so I used a proxy of biomass instead. The height, length (maximum canopy diameter), and width (canopy diameter

7

perpendicular to the maximum canopy diameter) of individual plants were measured and used to calculate a rectangular index of above-ground plant volume. Although this index does not represent actual plant volume, such a three-dimensional measure of size has been shown to explain between 60 and 99% of the variation in plant biomass in over 100 species (Huenneke et al. 2001). So, while biomass may be the best measure of plant size, obtaining a direct measure of plant biomass was logistically impractical; the rectangular index of plant volume, though, should provide an adequate measure of size, due to its strong relationship with biomass.

Statistical analysis

Slope of size-distance relationships.—Within the framework of size-distance relationships, an aim of detecting the presence (or absence) of competition in a given community can be achieved by analyzing the relationship between distance and sum of sizes using correlation analysis. However, when the aim is to evaluate competition intensity, a line, whose slope is a measure of intensity, must be fitted to the data. Unfortunately, previous users of size-distance relationships have not given much consideration to the line-fitting method employed and have opted for traditional linear regression. Unlike others, though, in my attempt to optimize the method of size-distance relationships, I examined the properties and assumptions of several line-fitting methods and argue that linear regression is not appropriate for estimating the slope of size-distance relationships, as more accurate slope estimates can be obtained via alternative line-fitting techniques.

Linear regression produces a fitted line that minimizes the sum of squared vertical distances from each observation to the line, but most importantly, it assumes that the X variable is fixed or measured without error. The violation of this assumption is of little consequence when a line is fitted for prediction purposes, but it has serious implications if the goal of line-fitting is to accurately estimate the mutual slope of two random variables, since if there is any error associated with X, linear regression produces a biased slope (Warton et al. 2006). In addition, linear regression is marked by asymmetry in the sense that a dependent (Y) and independent (X) variable must be selected. Yet, size-distance relationships are symmetric relationships: either distance or sum of sizes can be the dependent or independent variable, as either variable can be the biological cause of the other, i.e. plant size may depend on the 'initial' spacing among individuals, but size may equally likely affect plant spacing, as large plants suppress the growth and survivorship of neighbouring individuals (Welden et al. 1988). In such cases, when it is difficult or impossible to decide which of two variables to regress on the other, the regression of X on Y is an equally valid alternative to the regression of Y on X, but, unless the correlation coefficient between X and Y is ± 1, the two lines do not converge (Ricker 1973).

Overall, size-distance relationships are not predictive models but rather relationships of interdependence or covariation between two continuous random variables. An estimate of the slope, then, requires a line-fitting method that describes the relationship between the variables without having to specify one as dependent on the other; in essence, the method should allow for error in both variables and retain the position of the line upon axes reversal. Linear regression, as outlined above, does not

9

meet these criteria, but major axis (MA) and standardized major axis (SMA) estimation, sometimes collectively referred to as Model II regression (Quinn and Keough 2002), can be appropriate methods of bivariate line-fitting under particular circumstances. The major axis is the line that minimizes the sum of squared perpendicular distances from each observation to the fitted line (Quinn and Keough 2002), while the standardized major axis is the major axis calculated on standardized data (Warton et al. 2006)—the line minimizing the sum of triangular areas formed by vertical and horizontal lines from each observation to the fitted line (Quinn and Keough 2002). Neither MA nor SMA assumes an error-free independent variable and both produce a line whose position does not vary with rotation of the coordinate axes, but simulation work by Warton et al. (2006) has shown that SMA lines are estimated with greater precision (smaller standard error of the slope) than MA lines. Therefore, I chose SMA estimation to summarize the relationship between distance and sum of sizes. Because the null hypothesis that the slope of the SMA line equals zero cannot be formally tested (Quinn and Keough 2002), though, SMA lines were fitted to the data only if significant correlations were found between the variables (testing the null hypothesis that the population correlation coefficient equals zero essentially provides the same evidence for a significant non-zero slope as testing the null hypothesis that the slope of the line equals zero (Quinn and Keough 2002)).

Neighbourhood extent of competition.—Before size-distance relationships could be constructed to characterize intraspecific and interspecific competition, it was first necessary to determine how many neighbours to include in the analysis. It is conceivable and highly probable that a given plant simultaneously interacts with several individuals

10

rather than its first nearest neighbour only, so I sampled ten nearest neighbours, but competitive interactions may not extend as far as the tenth neighbour. To avoid underestimating neighbourhood competition and further optimize the method, I aimed to analytically determine the neighbourhood extent of competition (i.e. identify how many of the ten sampled nearest neighbours interfere with the target) and only include neighbours that show evidence for competitive interference in subsequent analyses.

The neighbourhood extent of both intraspecific and interspecific competition was investigated using Pearson product-moment correlations, performed separately for each of the ten neighbours in the neighbourhood (variables were logarithmically transformed to ensure bivariate normality). For any given neighbour rank, competitive interactions between the target and the given neighbour were inferred from a positive correlation between sum of volumes (the sum of the volumes of the target and the given neighbour) and distance (the distance between the target and the given neighbour). For example, to determine whether intraspecific competition occurs between third nearest-neighbours and target plants, a correlation analysis between ln(distance) and ln(sum of volumes) was performed based on all neighbourhoods in which the third nearest-neighbour was the same species as the target. Alternatively, to determine if tenth nearest-neighbours engage in interspecific competition with target plants, a correlation analysis between ln(distance) and ln(sum of volumes) was performed based on all neighbourhoods in which the tenth nearest-neighbour was a different species than the target. In total, ten intra- and ten interspecific correlation analyses were performed, all of which indicated significant positive correlations between ln(distance) and ln(sum of volumes) (Table 1), suggesting that, overall, each of the ten neighbours in a neighbourhood engages in either intra- or

interspecific competition with the target. As a result, all sampled neighbours were included in all further analyses.

Global comparison of intraspecific and interspecific competition intensity.—The question of species coexistence was first approached from a global perspective: all sampled neighbourhoods were used to test the predictions of niche and neutral theory by calculating and comparing the slopes of intra- and interspecific size-distance relationships. The vast majority of sampled neighbourhoods contained both intra- and interspecific neighbours, so theoretically, a measure of both intra- and interspecific competition intensity could be obtained from the same set of neighbourhoods. This, however, would produce intra- and interspecific slopes that are not statistically independent, thus violating the assumption of independence in the test for differences between slopes. To ensure the independence of slopes, I divided the dataset into two groups, so intra- and interspecific competition intensity were estimated from two different sets of neighbourhoods. Neighbourhoods consisting of only intra- or interspecific neighbours were assigned to the intra- and interspecific groups, respectively, but all remaining neighbourhoods comprised of both intra- and interspecific neighbours were randomly assigned to one of the two groups.

The intraspecific neighbourhood set was used to construct an intraspecific size-distance relationship, with distance on the y-axis and sum of volumes on the x-axis. Each point represents a single neighbourhood and was obtained by calculating distance, as the average distance of all intraspecific (same species as the target) neighbours from the target, and sum of volumes, as the sum of the target's volume and the average volume of all intraspecific neighbours. The covariation between distance and sum of volumes was

12

assessed using the Pearson product-moment correlation coefficient, after logarithmically transforming the variables to ensure bivariate normality. If the variables were significantly positively correlated, a line summarizing the relationship between ln(distance) and ln(sum of volumes) was fitted to the data in accordance with SMA estimation procedures. The slope of the fitted line was calculated using (S)MATR (version 2), a software application provided by Warton and colleagues (Warton et al. 2006). An interspecific size-distance relationship was similarly constructed from the interspecific neighbourhood set, but naturally, the computations were based on interspecific (different species than the target) rather than intraspecific neighbours. Finally, to compare the intensity of intra- and interspecific competition, the slopes of the intra- and interspecific size-distance relationships were tested for statistical differences using (S)MATR (version 2), but this test was only performed if significant positive correlations between ln(distance) and ln(sum of volumes) were obtained for both the intra- and interspecific groups.

Species-specific comparison of intraspecific and interspecific competition intensity.—An alternative approach to testing niche and neutral theory globally is to compare intra- and interspecific competition intensity for each species separately. In fact, while a global analysis can yield useful general information, the comparison of intra- and interspecific competition intensity is most biologically relevant when conducted at the species level, since competition occurs among individual plants belonging to different species. The most meaningful question, therefore, is whether individuals of a given species compete more intensely with conspecific or heterospecific individuals, and this question can be best addressed by performing separate analyses for every single species

in the community. Unfortunately, most species in the community were not sufficiently abundant to be examined separately. Prohibitively small sample sizes, thus, restricted the species-specific comparison of intraspecific and interspecific competition intensity to the three most abundant species in the community—*Acer saccharum*, *Oxalis acetosella*, and *Maianthemum canadense* (refer to Table 2 for species abundance information). Analytically, the procedures here were identical to those performed in the global analysis, but the analyses were performed for each of the three species separately.

RESULTS

The global analysis, including all neighbourhoods and all species, revealed significant positive correlations between ln(distance) and ln(sum of volumes) for both intraspecific (Fig. 1a) and interspecific (Fig. 1b) neighbourhood interactions. Regression lines were, therefore, fitted to the data, and the slopes of the intraspecific and interspecific lines were compared but were not found to be significantly different ((S)MATR test statistic = 0.117, P = 0.696; Fig. 1c).

On the other hand, when the analyses were performed separately for *Acer saccharum*, *Oxalis acetosella*, and *Maianthemum canadense*, no significant correlations between ln(distance) and ln(sum of volumes) were found for any of the three species when intraspecific neighbourhood interactions were examined (Fig. 2a, c, e). Interspecifically, a significant positive correlation between ln(distance) and ln(sum of volumes) was found for *Acer saccharum* (Fig. 2b) but not for *Oxalis acetosella* (Fig. 2d) or *Maianthemum canadense* (Fig. 2f).

14

The lack of significant correlations in the species-specific analysis (Fig. 2) can be interpreted in two ways—lack of competition or insufficient statistical power to detect a significant relationship, even if competition is occurring in the statistical population at large. To address potential power concerns, the analyses were repeated with all the available neighbourhoods (i.e. neighbourhoods in which *Acer saccharum* was the target species, for example, were not randomly assigned to an intra- and interspecific group, but intra- and interspecific competition were rather assessed from an overlapping set of neighbourhoods), which, while eliminating the possibility of performing a slope comparison test, nearly doubled the sample size. Nevertheless, even after increasing the statistical power of the tests by increasing the sample size, none of the species displayed a significant positive correlation between ln(distance) and ln(sum of volumes) intraspecifically (Fig. 3a, c, e). Interspecifically, a significant positive correlation between ln(distance) and ln(sum of volumes) was found for *Acer saccharum* (Fig. 3b) and *Maianthemum canadense* (Fig. 3f) but not for *Oxalis acetosella* (Fig. 3d).

So, even after a substantial increase in power, intraspecific competition was not detected among individuals of the three most abundant species in the community (Fig. 3). Yet, considering that these species comprise over 400 of the 600 sampled neighbourhoods, how can these results be reconciled with the significant global positive intraspecific correlation between ln(distance) and ln(sum of volumes) (Fig. 1a), which points towards the presence of intraspecific competition in the community overall?

The answer to this question was obtained by acknowledging and investigating species differences. Unarguably, species differ in their mean above-ground size, but species in this community were also found to differ in their mean inter-individual

distances, contributing to a significant positive between-species correlation in mean ln(distance) and mean ln(sum of volumes), both intraspecifically (Fig. 4a) and interspecifically (Fig. 4b). These species-specific differences, however, were not accounted for in the original global analysis, so in order to focus the analysis on the within-species relationship between ln(distance) and ln(sum of volumes) by removing mean differences in ln(distance) and ln(sum of volumes) among species, the variables were standardized and the global analysis was repeated. Standardizations were performed by dividing each ln(distance) and ln(sum of volumes) value belonging to a given species by the mean ln(distance) and mean ln(sum of volumes), respectively, of that species, resulting in standardized variables with a mean of 1 for every species (Wilson 1991). For example, distance in any given intraspecific sugar maple neighbourhood (i.e. a neighbourhood with a sugar maple target plant and one or more sugar maple neighbours) was standardized by dividing the ln(distance) value in that neighbourhood by the mean ln(distance) of all intraspecific sugar maple neighbourhoods; similarly, sum of volumes was standardized by dividing the ln(sum of volumes) value in that neighbourhood by the mean ln(sum of volumes) of all intraspecific sugar maple neighbourhoods. After this standardization, the global analysis no longer yielded a significant correlation between ln(distance) and ln(sum of volumes) intraspecifically (Fig. 5a), but a significant positive correlation between ln(distance) and ln(sum of volumes) was still obtained interspecifically (Fig. 5b).

Overall, after standardizing the variables in the global analysis, intraspecific competition was no longer detected in the community (Fig. 5)—the global results now consistent with the species-specific results (Fig. 3)—but the evidence for interspecific

competition was retained. Yet, it is possible that intraspecific competition occurs over shorter distances than interspecific competition and so remains undetected when all ten neighbours are used in the analysis. This issue was addressed earlier by investigating the neighbourhood extent of both intraspecific and interspecific competition and showing that each of the ten neighbours individually interacts with the target (Table 1). However, these analyses were conducted on the raw data, which have now been shown to yield spurious positive correlations intraspecifically. So, I repeated the intraspecific analyses after standardizing the variables and found that none of the neighbours displayed significant positive correlations between ln(distance) and ln(sum of volumes) (Table 3), suggesting that even short-range intraspecific competitive interactions may not occur in this community.

In summary, the analytical exploration of the method, including the process of reconciling the results of the global and species-specific analyses, has yielded two important insights—regarding statistical power and standardizations—into the method of size-distance relationships. Competition-wise, the results point towards present interspecific but weak or absent intraspecific competitive interactions.

DISCUSSION

Despite an intensive, nearly century-long research effort, species coexistence has remained an unresolved 'problem' that community ecologists are still grappling with. I, like others before me, have undertaken the current investigation in an attempt to gain an understanding of coexistence. Yet, I, unlike others, am also largely motivated by a desire

17

to explore the strengths and limitations of a seldom-used method, in order to evaluate its utility in addressing ecological questions. Guided by this goal and the knowledge that my ability to shed light on the mechanisms of coexistence depends on the integrity of the method, I begin with an assessment of the rigor and validity of size-distance relationships.

First of all, the analysis has revealed that nonsignificant size-distance relationships can be difficult to interpret because a nonsignificant result can be associated with either an absence of competition for limiting resources, or an inability to detect competitive interactions due to low statistical power. The power of a statistical test refers to the probability of detecting (with a sample) a given effect that occurs in the statistical population, and power depends on the sample size and effect size, among other factors (Quinn and Keough 2002). In terms of the correlation analysis necessitated by size-distance relationships, a small sample size and/or small effect size (i.e. low r, and therefore low competition importance) may lead to insufficient statistical power for the detection of competitive interactions. From a biological standpoint this means that the ability of size-distance relationships to accurately quantify the intensity of competition may be comprised by relatively unimportant competition, since even strong competitive interactions may be masked by other factors (e.g. predation, dispersal, environmental heterogeneity) that influence the sizes and spatial arrangement of plants. Low power, therefore, poses a problem for the detection and quantification of competition, but maximizing the sample size of the analysis should allow investigators to detect even relatively unimportant competition.

Accordingly, the global analysis initially performed (Fig. 1) was largely

motivated by a desire to maximize statistical power (while examining intra- and

interspecific competition intensity for individual species is ideal, it is not statistically

realistic because most species in any given community are rare, resulting in small sample

sizes and attendant analytical challenges). A global analysis, utilizing all available data

seemed to be a reasonable approach to obtaining a general understanding of intra- and

interspecific competitive interactions in the community overall; yet, in this case, it proved

misleading due to unanticipated differences among species in average sum of sizes and

inter-individual distances (Fig. 4). Since removing mean differences among species by

standardizing the variables (see Results for details on the standardization procedure)

effectively eliminated the intraspecific correlation between them (Fig. 5a), the global

positive intraspecific correlation based on raw data (Fig. 1a) stemmed from a positive

between-species correlation of mean ln(distance) and mean ln(sum of volumes) (Fig. 4a).

A positive between-species correlation of distance and sum of sizes, though, does not

necessarily indicate competitive interference among individuals of the constituent

species, whereas a positive within-species correlation is indicative of competition, further

supporting my proposition that size-distance relationships should ideally be analyzed at

the within-species level. So, while a global analysis of raw data may not be

representative of the within-species relationship between distance and sum of sizes,

potentially leading to incorrect conclusions about the occurrence of competition, a global

analysis of standardized data is advantageous in that it both preserves within-species

relationships and maximizes statistical power. On the whole, although the idea of

standardizing the variables in a size-distance relationship was first introduced by Wilson

19

(1991) in the context of comparing competition intensity among sites of differing fertility, the analytical exploration of the method has revealed that, depending on the nature of the data, standardizations can be equally important to the accurate detection of competition in multi-species communities.

Moreover, a main allegation against size-distance relationships that did not transpire from the current analysis but warrants attention nonetheless is the possibility that mechanisms other than resource competition can give rise to a positive correlation between distance and sum of sizes. This possibility exists, but while the sizes and spatial arrangement of plants can be independently influenced by a variety of factors—age, genetics, environmental heterogeneity, herbivory, disease, competition, seed predation, disturbance, allelopathy, dispersal, chance, measurement error, etc. (Weiner and Thomas 1986, Welden et al. 1988)—few processes can plausibly explain a pattern in which larger plants are farther apart than smaller plants. Competition for resources, as already discussed (see Methods) is a prime candidate, but allelopathy, a type of negative interaction marked by the release of toxic compounds in the environment (van Andel 2005), may also produce this pattern, if the following conditions are met: (1) all individuals of all species, from newly germinated seedlings to mature adult plants, produce and release allelochemicals in proportion to their size; (2) released allelochemicals persist in the environment in a zone immediately surrounding and proportional to the size of the 'donor' plant; and (3) released allelochemicals negatively affect the growth, survival, and establishment of all neighbouring individuals, regardless of species identity. While ecologists' current knowledge of allelopathy is fairly basic, direct evidence for allelopathy in the field is elusive (Royo and Carson 2006), and the

20

interaction is considered largely one-sided, i.e. one species releases toxins that harm another (van Andel 2005), so it is highly unlikely that all of the above conditions are routinely met in natural communities. In contrast, ecologists do know that individuals of all plant species require the same set of resources, compete for them when resource supply is limited relative to demand, and suffer the negative consequences of competition, so the conditions necessary for resource competition to produce a positive correlation between distance and sum of sizes are in place in natural vegetation. Of course, the causal role of competition cannot be confirmed without experimentation (Welden and Slauson 1986), but unlikely hypotheses can be eliminated based on empirical observations and logical reasoning that follows the principle of parsimony (Schurr et al. 2004). Therefore, while size-distance relationships provide only circumstantial evidence for competition, in the current study I favour resource competition as the most plausible and most parsimonious explanation of the observed spatial pattern and so retain it as the working hypothesis, interpreting the results accordingly.

Upon assessing the findings of the present inquest into size-distance relationships, I readily admit that the method is not without imperfections and should be used with caution. Despite my attempts for optimization, the measure of plant size used in this study was adequate, but not ideal, and even after sampling as many as ten nearest neighbours, neighbourhood interactions may have still been underestimated. Moreover, a limitation of the current analysis is that the average distance to intra- and interspecific neighbours did not fully reflect the density of conspecific and heterospecific plants, respectively, because different neighbourhoods were characterized by different numbers

21

of conspecific and heterospecific neighbours (i.e. the analysis did not account for differential competitive effects of one versus two or more neighbours). Nevertheless, the error introduced by this analytical approach should apply equally to the intraspecific and interspecific results, given that the number of neighbourhoods containing one, two, three, etc. intraspecific neighbours is approximately the same as the number of neighbourhoods containing one, two, three, etc. interspecific neighbours. Future studies, though, can benefit from further improvements in the measure of plant biomass, assessment of neighbourhood competition, and estimation of competitive effects (i.e. a better approach to the analysis would be to quantify sum of sizes as the sum of the target plant's size and the sum of sizes, rather than the average, of all intra- or interspecific neighbours). In addition, low statistical power presents a challenge for the interpretation of nonsignificant results, and a global analysis based on raw, or unstandardized, data may yield misleading results. While investigators should always aim to maximize statistical power, standardizations may not always be required, but the nature of the data and the specific approaches to its analysis should always be carefully considered prior to constructing size-distance relationships. Furthermore, caution should be exercised when interpreting a positive correlation between distance and sum of sizes as evidence of competition, since there may be circumstances under which competition is not the most plausible and parsimonious explanation of this pattern. Overall, the method seems versatile, but it may not be equally suitable for all questions and investigations of competition, so I advise against the uncritical use of size-distance relationships and urge investigators to not only carefully think about and optimize the method to the questions and system at hand, but to also exercise caution in the analysis and interpretation of the data.

Nevertheless, notwithstanding potential limitations, size-distance relationships possess numerous strengths. Large amounts of data replicated over large spatial scales can be collected relatively quickly with little logistical difficulties. In addition, in quantifying natural patterns shaped by long-term interactions among community members, the method operates over ecologically relevant time scales, which not only contributes to its generality and realism (Welden et al. 1988), but also enables it to detect weak, long-lasting competition, whose effects can remain undetected by field experiments of limited duration (Welden et al. 1988, Tokeshi 1999), especially in communities with slow demographic processes (Meyer et al. 2008). Finally, one of the greatest strengths of size-distance relationships is their capacity to distinguish between and quantify both the intensity and, most importantly, the importance of competition—a research imperative that has been greatly emphasized by plant ecologists in recent years (Freckleton and Watkinson 2001, Brooker et al. 2005, Brooker and Kikvidze 2008, Freckleton et al. 2009, Lamb et al. 2009, Mitchell et al. 2009).

All in all, while, admittedly, size-distance relationships are not perfect and should be used cautiously, the same can be said about any other tool ecologists employ in the study of competition, so the mystery of their seldom use in ecological investigations remains unresolved. Barring consequences of careless application, the method, to the best of my knowledge, is free of inherently fatal flaws, but given the strong historical emphasis on experimental approaches, it may have been dismissed by virtue of its nonexperimental nature. Alternatively, the method may have been forgotten. Despite their lack of popularity, though, I conclude that size-distance relationships can be a

23

powerful tool in the study of competition, so having no reason to doubt the validity of the results, I now turn to the coexistence findings.

Testing the predictions of niche and neutral theory requires the quantification of intra- and interspecific competition intensity, but while a significant positive correlation between ln(distance) and ln(sum of volumes), with an associated line fitted through the data, were obtained interspecifically (Fig. 5b), the intensity of intraspecific competition was more difficult to assess. The nonsignificant intraspecific relationships obtained in the species-specific analysis (Fig. 3), the standardized global analysis (Fig. 5), and the reassessment of the neighbourhood extent of competition using standardized data (Table 3) all suggest that intraspecific competition is either entirely absent (i.e. resources are not scarce and limiting) or relatively unimportant, such that a significant positive correlation between distance and sum of sizes cannot be detected. Low competition importance can be attributed to factors other than competition, such as facilitation, that influence the sizes and/or spatial arrangement of plants. Since the same processes that affect the sizes and/or distances of conspecific neighbours, though, likely influence the sizes and/or distances of heterospecific neighbours, the importance of intra- and interspecific competition is expected to be similar. This suggests that intraspecific competition is less intense, if present, than interspecific competition (if intraspecific competition was as intense as or more intense than interspecific competition, intraspecific competitive interactions should have been detected with the current method). Consistent with this interpretation are the findings that, in neighbourhoods containing both intra- and interspecific neighbours, intraspecific neighbours were, on average, significantly closer to the target than interspecific neighbours ($t=-2.178$, $P=0.029$, $df=5008$) but were also significantly smaller

24

than interspecific neighbours (t=-3.250, P=0.001, df=5008). So, intraspecific competition intensity, in this case, may be greatly reduced by a small individual plant size, i.e. at the given neighbourhood density, plants are too small to interfere with each other's ability to acquire sufficient resources.

The weaker intensity of intraspecific competition compared to interspecific competition, though, does not support the predictions of either niche or neutral theory. Coexistence via resource partitioning seems unlikely, since competition intensity appears to depend more on plant size than on species identity. In fact, further support for the influence of plant size on competitive interactions in this community comes from the finding that interspecific competition was not detected in neighbourhoods in which interspecific neighbours are smaller than intraspecific neighbours (Fig. 6). This result was obtained by splitting the set of neighbourhoods containing both intra- and interspecific neighbours into two groups—one in which interspecific neighbours are smaller, on average, than intraspecific neighbours (Group I) and one in which they are bigger (Group II). Intraspecific and interspecific relationships between ln(distance) and ln(sum of volumes) were then investigated for both groups using standardized data, but the only significant correlation between these variables was obtained for the interspecific analysis of Group II (Fig. 6). These results suggest that intraspecific competition between target plants and neighbours is weak or absent, regardless of whether these neighbours are larger (Fig. 6a) or smaller (Fig. 6c) than heterospecific neighbours. Most importantly, though, the current results also suggest that interspecific competition is not ubiquitous, as it was only detected in neighbourhoods in which interspecific neighbours are larger than intraspecific neighbours (Fig. 6d) but was not detected in neighbourhoods

25

in which interspecific neighbours are smaller than intraspecific neighbours (Fig. 6b). Overall, it seems that weak or absent intra- and interspecific competition in this community can be attributed to small plant stature at the given neighbourhood density, so species-specific size differences, rather than species identity alone, appear to influence inter-individual interactions. While these results do not provide support for niche theory, they are also not in line with predictions of neutral theory, so the mechanisms that facilitate coexistence remain unclear.

Asking what enables species coexistence, though, may have been an inappropriate line of inquiry to begin with. The question itself is based on the assumption that competition is a potent force in nature (Walter 1988, Keddy 2001), yet competition in this old-growth forest understory community was not important enough to be detected among conspecific neighbours in all sampled neighbourhoods and heterospecific neighbours in nearly 40% of the neighbourhoods; moreover, even when detected among heterospecifics, it seemed quantitatively unimportant (r^2=0.082). I must acknowledge that the results of this study suggest that competition is relatively unimportant to plant size and distance, exclusively, but if competitive interactions do not result in a detectable effect on growth, competition is unlikely to be important to survival, or reproduction, and ultimately individual fitness. Overall, then, a low importance of the competitive process has profound implications for the question of coexistence because if interspecific competition is not prevalent and important enough in natural communities to even pose a risk of competitive exclusion, as appears to be the case in this community, species coexistence need not be a competition-induced 'problem' that requires solutions. Hence,

the question I now turn my attention to is whether potent competitive interactions really are 'the norm' in plant communities, as has been generally alleged.

The relative unimportance, and perhaps absence, of intra- and even interspecific competition in the community under investigation was surprising but not anomalous, as competition, while detected in some, has not been found in other understory communities. Interspecific competition between ferns and tree seedlings in the understory has been previously reported (Horsley 1993, George and Bazzaz 1999, Royo and Carson 2008), and in contrast to this study, intraspecific competition among sugar maple mast year seedlings has also been detected (Taylor and Aarssen 1989). On the other hand, there has been mixed evidence for intraspecific competition in forest populations of violets (Waller 1981) and no evidence for competition among forest understory plants in both tropical (Wright 2002, 2007, Paine et al. 2008) and temperate (Ricard et al. 2003) contexts. While this is not a comprehensive survey of the literature, it is apparent that competition is not ubiquitous in forest understories. Understory plants may compete in certain communities, under certain circumstances, such as increased plant densities, following masting events (Taylor and Aarssen 1989), or increased growth rates due to an improved light environment in canopy gaps (Waller 1981, Marks and Gardescu 1998, Gilliam 2007). Also likely, though, are conditions not conducive to competitive interactions, such as low natural densities (Waller 1981, Wright 2007, Paine et al. 2008), small plant stature, and low growth rates typical of shade-tolerant understory plants (Neufeld and Young 2003). So, if competition is transient in both time and space, even in communities such as forest understories, where at least competition for light is

expected to be prominent due to a limited light environment, how prevalent and important is it in natural communities overall?

The question has been raised before, but a general acceptance of the pervasiveness of competitive interactions in nature ensued from the findings of Connell (1983), Schoener (1983), Aarssen and Epp (1991), Goldberg and Barton (1992), and Gurevitch et al. (1992), who after surveying the literature of field experiments on interspecific competition concluded that competition is both present and important in natural communities. Yet, while the consensus that competition occurs (Tokeshi 1999) is not unreasonable, the assumption that it is 'the norm' (Austin 1990) is, perhaps, debatable. The question regarding the prevalence and importance of interspecific competition in ecological communities may have been prematurely and unwisely put to rest, as several authors have pointed out that the true frequency of competition in nature cannot be accurately estimated from survey data, given that the literature, subject to both a reluctance of researchers to initiate experimental tests of competition if its absence is suspected and an underreporting of negative results, is not necessarily representative of nature (Peters 1991, Tokeshi 1999, Keddy 2001). Negative results, though, both in terms of the occurrence, as outlined above, and relative importance (Mitchell et al. 2009) of competition in natural communities are appearing in the literature, so competition may not be as ubiquitous as generally assumed and accepted.

While few modern ecologists, if any, will explicitly argue that competition is ever-present and all-important in nature, most acknowledging the role of other processes, including predation, parasitism and mutualism, in community structure (Chase and Leibold 2003), all community ecologists studying species coexistence implicitly assume

that competition is present enough and important enough to pose a threat to coexistence (Walter 1988). In light of the accumulating evidence that competition is not as pervasive as usually assumed, though, species in natural communities may not face a threat of competitive exclusion to any significant extent, so the study of species coexistence, which strives to identify the factors that prevent competitive exclusion, may be a misguided pursuit (Walter 1988). I do not imply that competition is never present and always unimportant in natural communities, but until our collective knowledge of the importance of competitive interactions in nature substantially improves, I caution against questions rooted in potentially unjustifiable assumptions.

Abandoning the concept of coexistence may, therefore, be a practical and productive enterprise, not because I advocate for community ecologists to terminate their quest for understanding natural diversity, but because it would be beneficial to start thinking about the diversity of nature outside the context of competition. Coexistence is indeed a *concept* inseparable from the process of competition, rather than a *pattern* observed in nature. Instead of focusing on the concept of coexistence, though, community ecology would be better served by an effort to understand patterns, such as species richness gradients, relative abundance distributions, and temporal species turnover. Similarly, instead of focusing exclusively on competition, patterns of species diversity may be more effectively elucidated by embracing the multitude of processes that are well acknowledged to occur in nature. Nothing can be lost by adopting a holistic approach to the study of community structure, as competition can continue to be investigated under this framework, but much can be gained by viewing community diversity through a multi-process lens, rather than competition-only spectacles.

Similarly, community ecology can benefit from the adoption of more varied methodological approaches to the empirical investigation of abundance, distribution, and diversity. Controlled field experiments are popular in ecology (Keddy 2001), but while they are powerful tools for inferring causal relationships (Connor and Simberloff 1986, Keddy 2001), experiments lack generality (Diamond 1986, Keddy 2001) and are difficult and sometimes impossible to perform (Connor and Simberloff 1986, McIntire and Fajardo 2009). Nevertheless, experimental manipulations have been emphasized over nonexperimental approaches, whose evidence has been viewed with scepticism (Connor and Simberloff 1986). Descriptive studies have been criticized for indulging in free-form data collection, due to lack of well-justified questions (Keddy 2001), but this may be a problem of the past, as modern nonexperimental analyses are question-driven, grounded in *a priori* hypotheses and ecological theory and/or knowledge (Schurr et al. 2004, McIntire and Fajardo 2009). Yet, the mere description of nature is also valuable, as understanding natural complexity must begin with an account of natural patterns (Fortin and Dale 2005). Granted, nonexperimental evidence can sometimes be difficult to evaluate (Connor and Simberloff 1986), but interpretation need not always be problematic (Freckleton and Watkinson 2001), and if used carefully, nonmanipulative approaches can effectively overcome some of the drawbacks of experiments. Ultimately, neither experimental nor nonexperimental approaches are without limitations, so both are equally necessary in the quest to gain meaningful insights into the workings of natural communities (Freckleton and Watkinson 2001). Historically, ecologists have not made use of the complete arsenal of appropriate methodology (Diamond 1986), but if we limit ourselves to experimental approaches, we also limit the scope of the questions we can

30

address (Connor and Simberloff 1986, Chase and Leibold 2003) and, thus, impoverish our ability to acquire knowledge about natural systems. A research strategy, though, that acknowledges the value of and integrates a diversity of approaches can further the goals of community ecology, as more complete understanding can be achieved by complementary methodologies (Diamond 1986).

To conclude, I remind the audience that what ecologists think and know about natural patterns and processes depends on the methods they use to study nature. The choice of methodology is critically important to the research outcome, as the validity of the ensuing knowledge depends on the integrity and rigor of the methodological approach. The value of a method, though, may not always be apparent, and popularity, or lack thereof, may not always reflect worth, as evidenced by the current study in which a little-used method lacking fundamental flaws has lead to important insights about competition in an old-growth forest understory community. Ecologists' fascination with competition has inspired innumerable studies of the process, yet our current knowledge of competition seems insufficient to justify long-held assumptions about its primacy in nature. Therefore, for community ecology, the way forward may lie not only in discarding the competition-based view of life, but also in conceding that patterns of diversity are likely shaped by a diversity of processes, which would be best examined using a diversity of methodological approaches.

LITERATURE CITED

Aarssen, L. W. 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. American Naturalist 122:707-731.

Aarssen, L. W., and G. A. Epp. 1990. Neighbor manipulations in natural vegetation: a review. Journal of Vegetation Science 1:13-30.

Alonso, D., R. S. Etienne, and A. J. McKane. 2006. The merits of neutral theory. Trends in Ecology and Evolution 21:451-457.

Austin, M. P. 1990. Community theory and competition in vegetation. Pages 215-238 *in* J. B. Grace and D. Tilman, editors. Perspectives on plant competition. Academic Press, San Diego.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: individuals, populations, and communities. Blackwell Science, Oxford.

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

Bell, G. 2001. Neutral macroecology. Science 293:2413-2418.

Bengtsson, J., T. Fagerstrom, and H. Rydin. 1994. Competition and coexistence in plant communities. Trends in Ecology and Evolution 9:246-250.

Berger, U., C. Piou, K. Schiffers, and V. Grimm. 2008. Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. Perspectives in Plant Ecology, Evolution and Systematics 9:121-135.

Briones, O., C. Montana, and E. Ezcurra. 1996. Competition between three Chihahuan desert species: evidence from plant size-distance relations and root distribution. Journal of Vegetation Science 7:453-460.

Brooker, R., Z. Kikvidze, F. I. Pugnaire, R. M. Callaway, P. Choler, C. J. Lortie, and R. Michalet. 2005. The importance of importance. Oikos 109:63-70.

Brooker, R. W., and Z. Kikvidze. 2008. Importance: an overlooked concept in plant interaction research. Journal of Ecology 96:703-708.

Carrick, P. J. 2003. Competitive and facilitative relationships among three shrub species, and the role of browsing intensity and rooting depth in the Succulent Karoo, South Africa. Journal of Vegetation Science 14:761-772.

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

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

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist 122:661-696.

Connor, E. F., and D. Simberloff. 1986. Competition, scientific method, and null models in ecology. American Scientist 74:155-162.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3-22 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper & Row, New York.

Fortin, M. J., and M. R. T. Dale. 2005. Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge.

Freckleton, R. P., and A. R. Watkinson. 2001. Nonmanipulative determination of plant

    community dynamics. Trends in Ecology and Evolution 16:301-307.

Freckleton, R. P., A. R. Watkinson, and M. Rees. 2009. Measuring the importance of

    competition in plant communities. Journal of Ecology 97:379-384.

Fuentes, E. R., and J. R. Gutierrez. 1981. Intraspecific and interspecific competition

    between matorral shrubs. Acta Oecologica-Oecologia Plantarum 2:283-289.

George, L. O., and F. A. Bazzaz. 1999. The fern understory as an ecological filter:

    growth and survival of canopy-tree seedlings. Ecology 80:846-856.

Giller, P. S. 1984. Community structure and the niche. Chapman and Hall, London.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate

    forest ecosystems. BioScience 57:845-858.

Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific

    competition in natural communities: a review of field experiments with plants.

    American Naturalist 139:771-801.

Grace, J. B., and D. Tilman, editors. 1990. Perspectives on plant competition. Academic

    Press, San Diego.

Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A metaanalysis of

    competition in field experiments. American Naturalist 140:539-572.

Gutierrez, J. R., and E. R. Fuentes. 1979. Evidence for intraspecific competition in the

    Acacia caven (leguminosae) savanna of Chile. Oecologia Plantarum 14:151-158.

Horsley, S. B. 1993. Mechanisms of interference between hay-scented fern and black

    cherry. Canadian Journal of Forest Research 23:2059-2069.

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

Huenneke, L. F., D. Clason, and E. Muldavin. 2001. Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. Journal of Arid Environments 47:257-270.

Keddy, P. A. 2001. Competition. Kluwer Academic Publishers, Dordrecht.

Lamb, E. G., S. W. Kembel, and J. F. Cahill. 2009. Shoot, but not root, competition reduces community diversity in experimental mesocosms. Journal of Ecology 97:155-163.

Larrea-Alcazar, D. M., and P. J. Soriano. 2006. Spatial associations, size-distance relationships and population structure of two dominant life forms in a semiarid enclave of the Venezuelan Alps. Plant Ecology 186:137-149.

Lynds, J. A., and J. LeDuc. 1995. Old forests of Nova Scotia. Nova Scotia Department of Natural Resources, Parks and Recreation Division. Occasional Papers No. 1.

Marks, P. L., and S. Gardescu. 1998. A case study of sugar maple (*Acer saccharum*) as a forest seedling bank species. Journal of the Torrey Botanical Society 125:287-296.

McCarthy, B. C. 2003. The herbaceous layer of eastern old-growth deciduous forests. Pages 163-176 *in* F. S. Gilliam and M. R. Roberts, editors. The herbaceous layer in forests of eastern North America. Oxford University Press, Oxford.

McIntire, E. J. B., and A. Fajardo. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. Ecology 90:46-56.

Meyer, K. M., D. Ward, K. Wiegand, and A. Moustakas. 2008. Multi-proxy evidence for competition between savanna woody species. Perspectives in Plant Ecology, Evolution and Systematics 10:63-72.

Mitchell, M. G. E., J. F. Cahill, and D. S. Hik. 2009. Plant interactions are unimportant in a subarctic-alpine plant community. Ecology 90:2360-2367.

Neufeld, H. S., and D. R. Young. 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests. Pages 38-90 *in* F. S. Gilliam and M. R. Roberts, editors. The herbaceous layer in forests of eastern North America. Oxford University Press, Oxford.

Nobel, P. S. 1981. Spacing and transpiration of various sized clumps of a desert grass, *Hilaria rigida*. Journal of Ecology 69:735-742.

Paine, C. E. T., K. E. Harms, S. A. Schnitzer, and W. P. Carson. 2008. Weak competition among tropical tree seedlings: implications for species coexistence. Biotropica 40:432-440.

Peters, R. H. 1991. A critique for ecology. Cambridge University Press, Cambridge.

Philips, D. L., and J. A. MacMahon. 1981. Competition and spacing patterns in desert shrubs. Journal of Ecology 69:97-117.

Pianka, E. R. 1981. Competition and niche theory. Pages 167-196 *in* R. M. May, editor. Theoretical ecology: principles and applications. Sinauer Associates, Sunderland.

Pielou, E. C. 1960. A single mechanism to account for regular, random and aggregated populations. Journal of Ecology 48:575-584.

Pielou, E. C. 1961. Segregation and symmetry in two-species populations as studied by nearest-neighbour relationships. Journal of Ecology 49:255-269.

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

Ricard, J. P., C. Messier, S. Delagrange, and M. Beaudet. 2003. Do understory sapling respond to both light and below-ground competition?: a field experiment in a north-eastern American hardwood forest and a literature review. Annals of Forest Science 60:749-756.

Ricker, W. E. 1973. Linear regressions in fishery research. Journal of the Fisheries Research Board of Canada 30:409-434.

Royo, A. A., and W. P. Carson. 2006. On the formation of dense understory layers in forest worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Canadian Journal of Forest Research 36:1345-1362.

Royo, A. A., and W. P. Carson. 2008. Direct and indirect effects of a dense understory on tree seedling recruitment in temperate forests: habitat-mediated predation versus competition. Canadian Journal of Forest Research 38:1634-1645.

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

Schurr, F. M., O. Bossdorf, S. J. Milton, and J. Schumacher. 2004. Spatial pattern formation in semi-arid shrubland: a priori predicted versus observed pattern characteristics. Plant Ecology 173:271-282.

Shackleton, C. 2002. Nearest-neighbour analysis and the prevalence of woody plant competition in South African savannas. Plant Ecology 158:65-76.

Silvertown, J. 2004. Plant coexistence and the niche. Trends in Ecology and Evolution 19:605-611.

Sommer, U., and B. Worm, editors. 2002. Competition and coexistence. Springer, Berlin.

Taylor, D. R., and L. W. Aarssen. 1989. Neighbour effects in mast year seedlings of *Acer saccharum*. American Journal of Botany 76:546-554.

Tokeshi, M. 1999. Species coexistence: ecological and evolutionary perspectives. Blackwell Science, Oxford.

van Andel, J. 2005. Species interactions structuring plant communities. Pages 238-264 *in* E. van der Maarel, editor. Vegetation Ecology. Blackwell Science Ltd., Oxford.

Waller, D. M. 1981. Neighborhood competition in several violet populations. Oecologia 51:116-122.

Walter, G. H. 1988. Competitive exclusion, coexistence and community structure. Acta Biotheoretica 37:281-313.

Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. Bivariate line-fitting methods for allometry. Biological Reviews 81:259-291.

Weiner, J., P. Stoll, H. Muller-Landau, and A. Jasentuliyana. 2001. The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. American Naturalist 158:438-450.

Weiner, J., and S. C. Thomas. 1986. Size variability and competition in plant monocultures. Oikos 47:211-222.

Welden, C. W., and W. L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Quarterly Review of Biology 61:23-44.

Welden, C. W., W. L. Slauson, and R. T. Ward. 1988. Competition and abiotic stress among trees and shrubs in northwest Colorado. Ecology 69:1566-1577.

Wiens, J. A. 1977. Competition and variable environments. American Scientist 65:590-597.

Wilson, S. D. 1991. Variation in competion in Eucalypt forests: the importance of standardization in pattern analysis. Journal of Vegetation Science 2:577-586.

Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130:1-14.

Wright, S. J. 2007. Plant diversity in tropical forests. Pages 351-367 *in* F. I. Pugnaire and F. Valladares, editors. Functional Plant Ecology: Second Edition. CRC Press, Boca Raton.

Yeaton, R. I., and M. L. Cody. 1976. Competition and spacing in plant communities: the northern Mohave Desert. Journal of Ecology 64:689-696.

Yeaton, R. I., J. Travis, and E. Gilinsky. 1977. Competition and spacing in plant communities: the Arizona Upland Association. Journal of Ecology 65:587-595.

Zinck, M., editor. 1998. Roland's flora of Nova Scotia. Nimbus Publishing, Halifax.

Table 1. Results from analyses of Pearson product-moment correlations between ln(distance) and ln(sum of volumes).

Neighbour rank	(a) Intraspecific			(b) Interspecific		
	r	P	n	r	P	n
1	0.110	0.049	320	0.181	0.002	280
2	0.114	0.042	319	0.259	1.06×10^{-5}	281
3	0.155	0.007	303	0.277	1.30×10^{-6}	297
4	0.197	7.32×10^{-4}	291	0.257	4.78×10^{-6}	309
5	0.178	0.002	301	0.219	1.35×10^{-4}	299
6	0.262	3.83×10^{-6}	303	0.372	3.68×10^{-11}	297
7	0.225	7.95×10^{-5}	303	0.325	9.95×10^{-9}	297
8	0.239	5.05×10^{-5}	283	0.271	9.89×10^{-7}	317
9	0.235	9.50×10^{-5}	270	0.257	2.15×10^{-6}	330
10	0.274	3.26×10^{-6}	280	0.295	7.65×10^{-8}	320

Notes: Neighbours were either the same (intraspecific) or different (interspecific) species as the target plant, and separate correlation analyses were performed for each of the ten neighbours in the sampled neighbourhoods.

Table 2. An estimate of species abundance based on the number of neighbourhoods in which a given species is the target plant.

Species	Code	Target in no. neighbourhoods	
		Intraspecific	Interspecific
Acer saccharum	*Asa*	307	262
Oxalis acetosella	*Oa*	56	64
Maianthemum canadense	*Mc*	56	59
Gymnocarpium dryopteris	*Gd*	25	25
Thelyptersis noveboracensis	*Tn*	21	21
Phegopteris connectilis	*Pc*	19	18
Dryopteris intermedia	*Di*	14	17
Acer pensylvanicum	*Ap*	7	17
Dennstaedtia punctilobula	*Dp*	13	14
Trientalis borealis	*Tb*	5	6
Deparia acrostichoides	*Da*	5	5
Viola blanda	*Vb*	3	4
Polystichum acrostichoides	*Pa*	3	3
Aralia nudicaulis	*An*	2	3
Athyrium felix-femina	*Af*	2	3
Rubus pubescens	*Rp*	2	3
Streptopus roseus	*Sro*	0	3

Huperzia lucidula	Hl	2	2
Listera convallarioides	Lco	2	2
Acer rubrum	Ar	1	2
Dryopteris campyloptera	Dc	1	2
Matteucia struthiopteris	Ms	1	2
Acer spicatum	Asp	0	2
Aster acuminatus	Aa	1	1
Coptis trifolia	Ct	1	1
Lonicera canadensis	Lca	1	1
Mitchella repens	Mr	1	1
Smilacina racemosa	Sra	1	1
Solidago flexicaulis	Sf	1	1
Viola macloskeyi	Vm	1	1
Cornus alternifolia	Ca	0	1

Notes: Neighbourhoods are classified as intraspecific if they contain plants that are the same species as the target and interspecific if they contain plants that are different species than the target. For example, *Acer saccharum* was the target plant in 307 neighbourhoods that contained other *Acer saccharum* individuals and was also the target in 262 neighbourhoods that contained neighbours of different species. In total, 554 intraspecific and 547 interspecific neighbourhoods were sampled. The abbreviated species names (code) appear in Fig. 4. Nomenclature follows Zinck (1998).

Table 3. Results from analyses of Pearson product-moment correlations between standardized ln(distance) and standardized ln(sum of volumes).

Neighbour rank	r	P	n
1	-0.096	0.086	320
2	-0.072	0.199	319
3	-0.034	0.560	303
4	-0.023	0.702	291
5	-0.020	0.727	301
6	-0.031	0.596	303
7	-0.079	0.168	303
8	-0.006	0.916	283
9	-0.149	0.014	270
10	-0.069	0.252	280

Notes: Separate correlation analyses were performed for each of the ten neighbours in the sampled neighbourhoods, but only intraspecific (same species as the target) neighbours were analyzed.

FIGURE LEGENDS

Figure 1. Variation of ln(distance) with ln(sum of volumes) for (a) intraspecific and (b) interspecific neighbourhood interactions. P and r^2 values reflect results from Pearson product-moment correlations between ln(distance) and ln(sum of volumes). Distance was calculated as the average distance of all intraspecific (or interspecific) neighbours from the target and sum of volumes as the sum of the target's volume and the average volume of all intraspecific (or interspecific) neighbours. Regression lines were fitted using the standardized major axis (SMA) estimation method. Both the intraspecific and interspecific relationships are presented in (c) to facilitate the visual comparison of slopes.

Figure 2. Variation of ln(distance) with ln(sum of volumes) for intraspecific and interspecific neighbourhood interactions for *Acer saccharum*, *Oxalis acetosella*, and *Maianthemum canadense*. P and r^2 values reflect results from Pearson product-moment correlations between ln(distance) and ln(sum of volumes). Distance was calculated as the average distance of all intraspecific (or interspecific) neighbours from the target and sum of volumes as the sum of the target's volume and the average volume of all intraspecific (or interspecific) neighbours. Regression lines were fitted using the standardized major axis (SMA) estimation method, provided that a significant correlation between the variables was first detected.

Figure 3. Variation of ln(distance) with ln(sum of volumes) for intraspecific and interspecific neighbourhood interactions for *Acer saccharum*, *Oxalis acetosella*, and *Maianthemum canadense*. *P* and r^2 values reflect results from Pearson product-moment correlations between ln(distance) and ln(sum of volumes). Distance was calculated as the average distance of all intraspecific (or interspecific) neighbours from the target and sum of volumes as the sum of the target's volume and the average volume of all intraspecific (or interspecific) neighbours. Regression lines were fitted using the standardized major axis (SMA) estimation method, provided that a significant correlation between the variables was first detected. Note the increased sample sizes compared to Fig. 2.

Figure 4. Between-species relationship of mean ln(distance) and mean ln(sum of volumes) for (a) intraspecific and (b) interspecific neighbourhood interactions. *P* and r values reflect results from Pearson product-moment correlations between mean ln(distance) and mean ln(sum of volumes). Distance was calculated as the average distance of all intraspecific (or interspecific) neighbours from the target and sum of volumes as the sum of the target's volume and the average volume of all intraspecific (or interspecific) neighbours; ln(distance) and ln(sum of volumes) here represent the average species value of these variables. Abbreviated species names distinguish different species. Full species names corresponding to the abbreviated codes can be found in Table 2.

Figure 5. Variation of ln(distance) with ln(sum of volumes) for (a) intraspecific and (b) interspecific neighbourhood interactions, based on standardized data. *P* and r^2 values reflect results from Pearson product-moment correlations between ln(distance) and

ln(sum of volumes). Distance was calculated as the average distance of all intraspecific (or interspecific) neighbours from the target and sum of volumes as the sum of the target's volume and the average volume of all intraspecific (or interspecific) neighbours. The variables were standardized by dividing each ln(distance) and ln(sum of volumes) value of a given species by the mean ln(distance) and mean ln(sum of volumes), respectively, of that species. Regression lines were fitted using the standardized major axis (SMA) estimation method, provided that a significant correlation between the variables was first detected.

Figure 6. Variation of ln(distance) with ln(sum of volumes) for two groups of intraspecific and interspecific neighbourhood interactions, based on standardized data. Group I consists of neighbourhoods in which interspecific neighbours are smaller than intraspecific neighbours, on average, while Group II is comprised of neighbourhoods in which interspecific neighbours are larger than intraspecific neighbours, on average. P and r^2 values reflect results from Pearson product-moment correlations between ln(distance) and ln(sum of volumes). Distance was calculated as the average distance of all intraspecific (or interspecific) neighbours from the target and sum of volumes as the sum of the target's volume and the average volume of all intraspecific (or interspecific) neighbours. The variables were standardized by dividing each ln(distance) and ln(sum of volumes) value of a given species by the mean ln(distance) and mean ln(sum of volumes), respectively, of that species. Regression lines were fitted using the standardized major axis (SMA) estimation method, provided that a significant correlation between the variables was first detected.
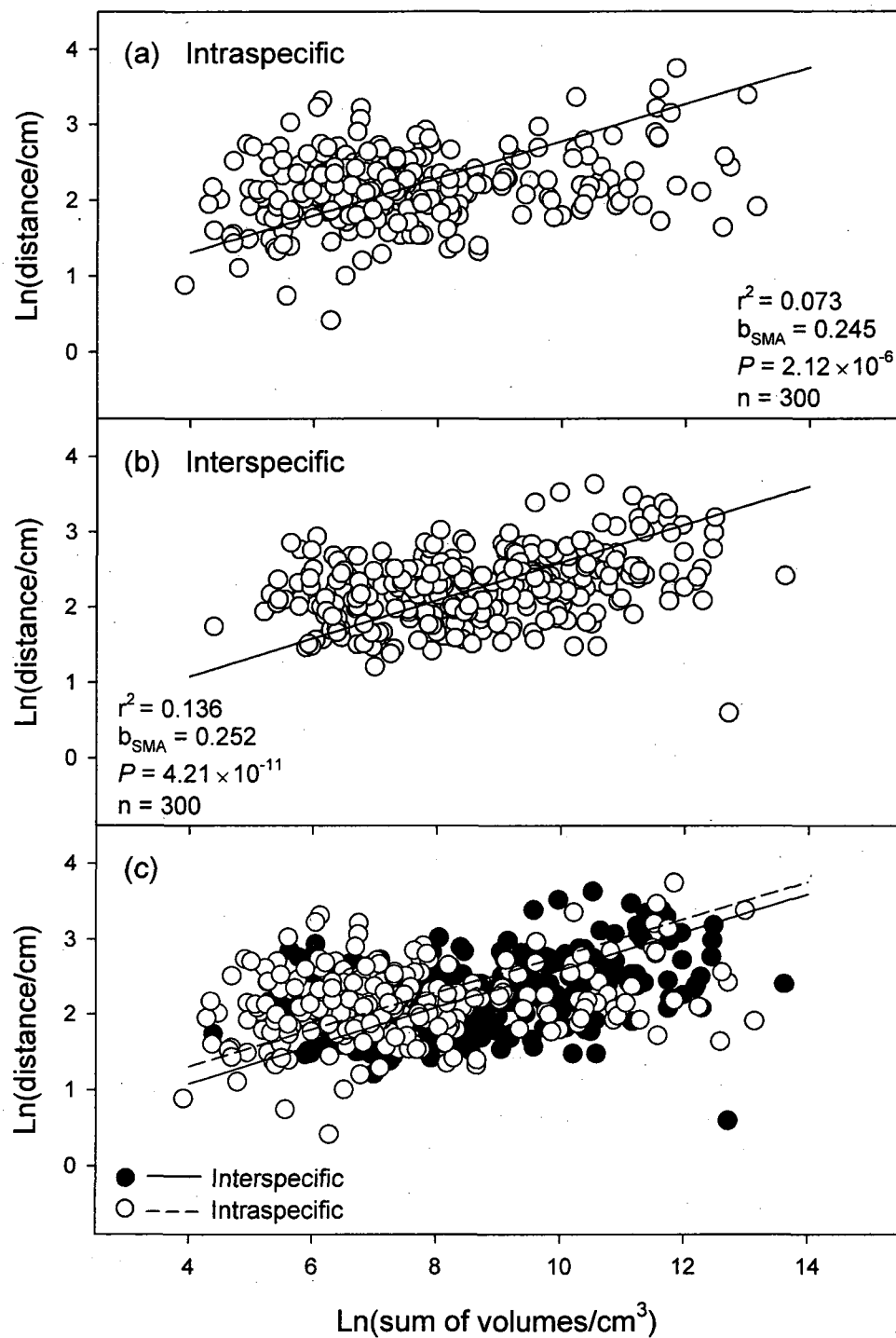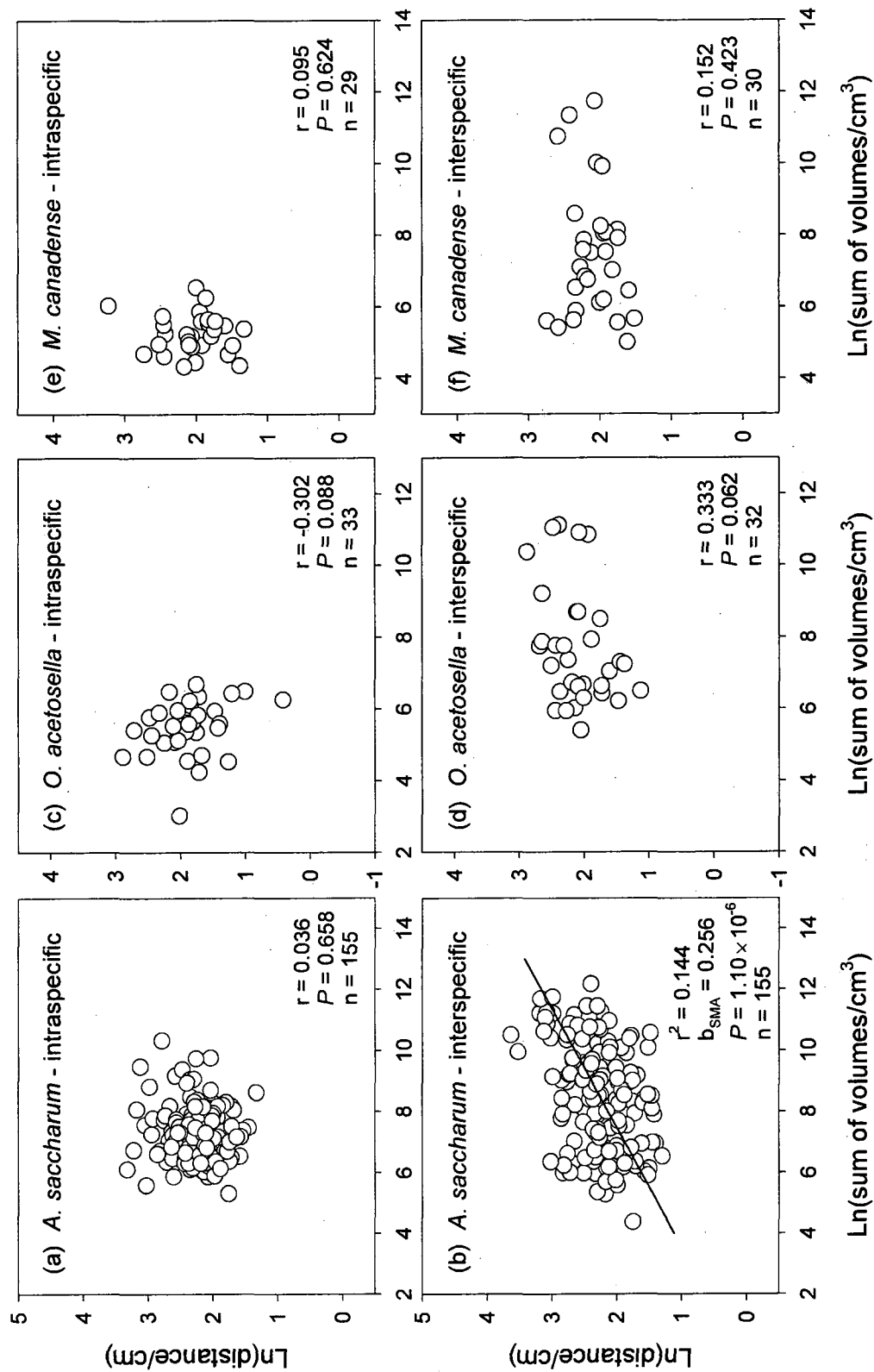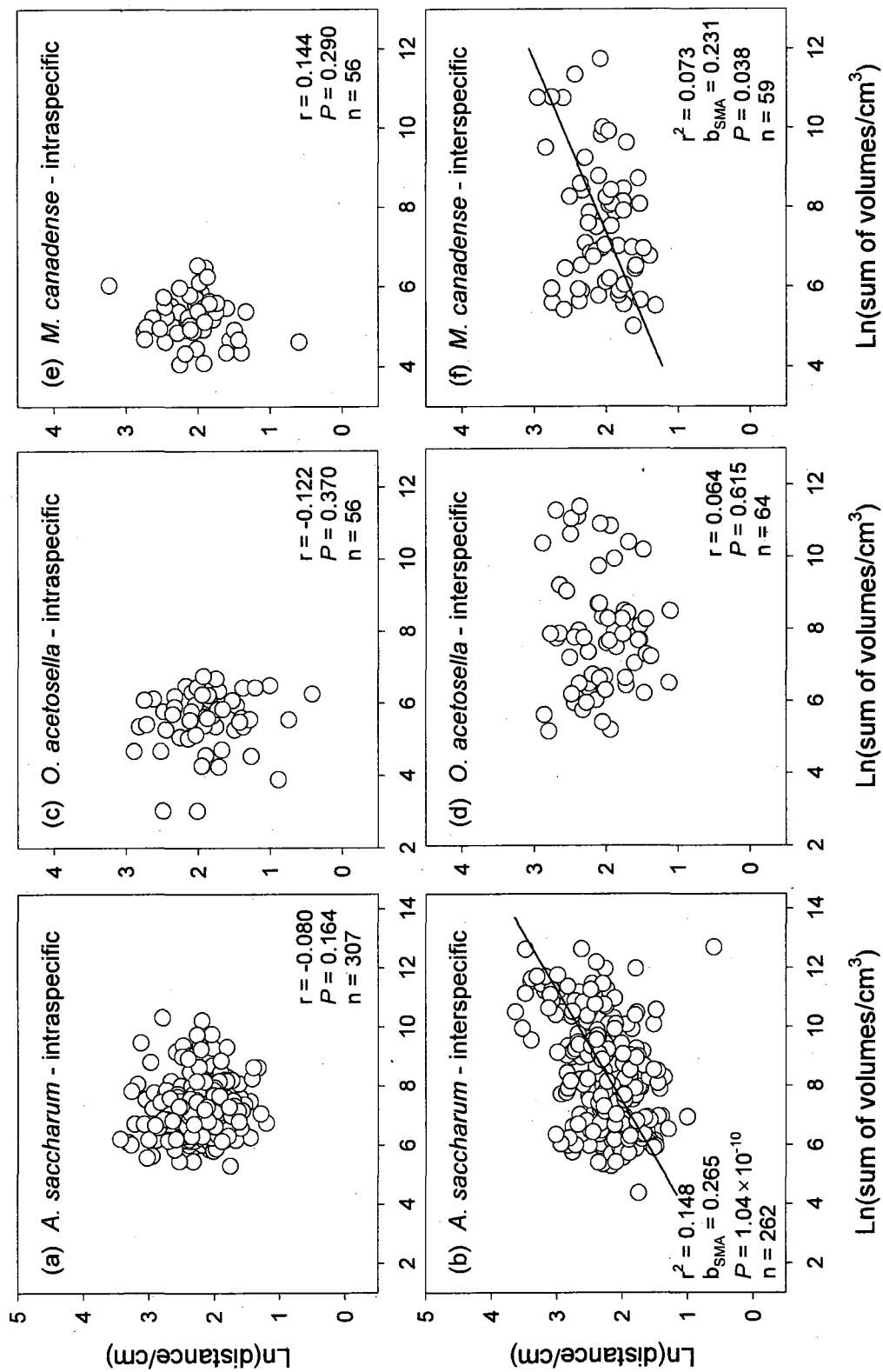
(a) Intraspecific
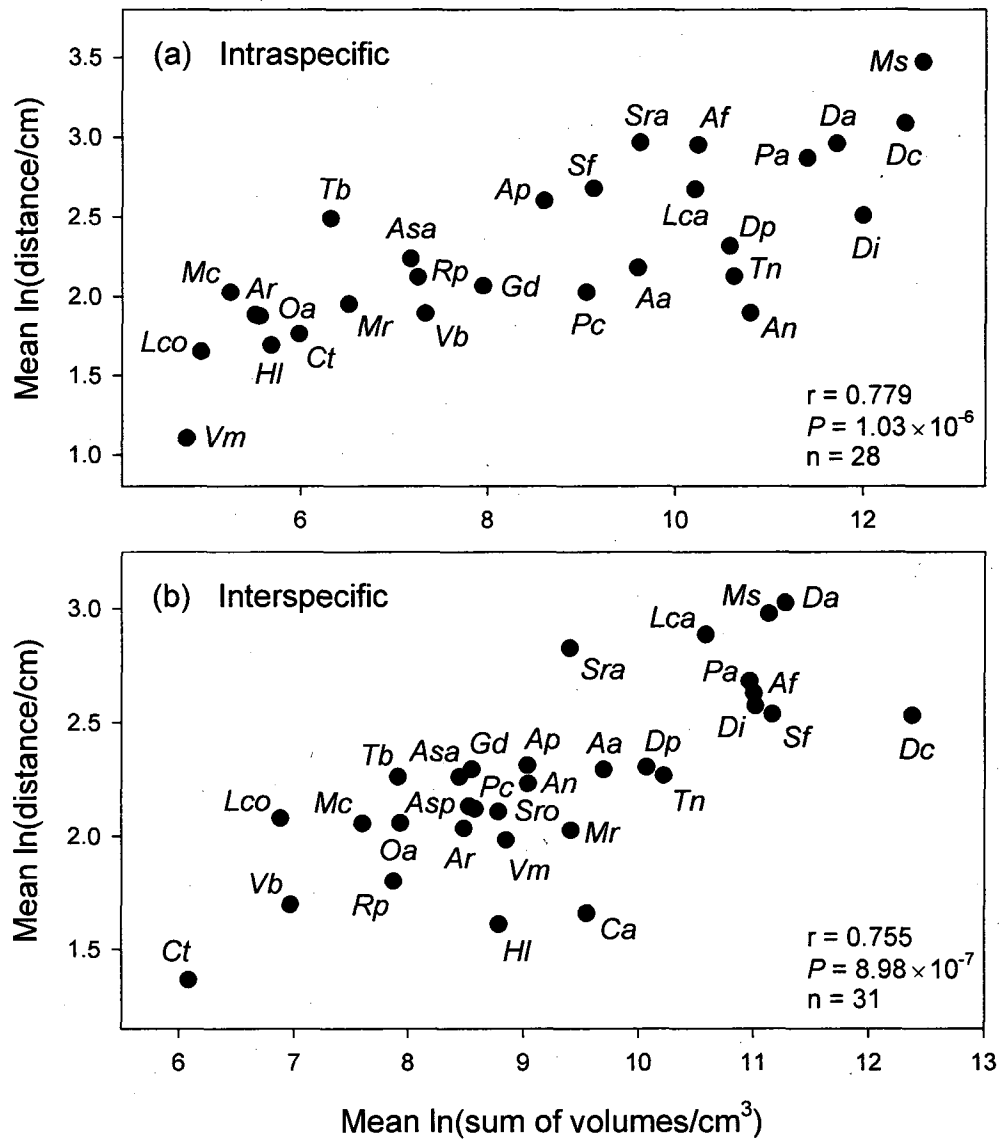
Ln(distance/cm)

$r^2 = 0.073$
$b_{SMA} = 0.245$
$P = 2.12 \times 10^{-6}$
$n = 300$

(b) Interspecific

Ln(distance/cm)

$r^2 = 0.136$
$b_{SMA} = 0.252$
$P = 4.21 \times 10^{-11}$
$n = 300$

(c)

Ln(distance/cm)

● —— Interspecific
○ - - - Intraspecific

Ln(sum of volumes/cm^3)

Fig. 1

47

Fig. 2

48

Fig. 3

49

Fig. 4

Fig. 5

51

(a) Intraspecific I

$r = -0.012$
$P = 0.870$
$n = 182$

(b) Interspecific I

$r = -0.027$
$P = 0.718$
$n = 182$

(c) Intraspecific II

$r = 0.015$
$P = 0.793$
$n = 319$

(d) Interspecific II

$r^2 = 0.082$
$b_{SMA} = 1.105$
$P = 2.03 \times 10^{-7}$
$n = 319$

Standardized ln(distance/cm)

Standardized ln(sum of volumes/cm^3)

52

Fig. 6