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A MODEL OF SPECIES DENSITY IN SHORELINE VEGETATION[1]

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Abstract. Predicting the species density (number of species per unit area) of communities is a major goal of ecology. We present a regression model of species density on a local (0.25 m^2) scale for the vegetation of freshwater shorelines in southwestern Quebec, Canada. Two attributes of the vegetation, the amount of aboveground biomass (in grams) and the proportion of the vegetation composed of obligate perennial species, predicted 76% of the variation in species density. The success of the predictor variables suggests that competitive intensity, as reflected in biomass levels, and the time elapsed since the last disturbance event, as reflected in the proportion of the vegetation composed of obligate perennials, are important determinants of local variation in species density. The model was then tested against independent data from shoreline vegetation in southeastern Ontario, Canada. There were no significant differences in the two data sets in their response to the two independent variables in the full model. However, only 42% of the variance in species density was explained in the combined data set.

Key words: aboveground biomass; competition; disturbance; emergent macrophytes; functional classification; Ontario; perenniality; Quebec; shorelines; species density; species richness; wetlands.

INTRODUCTION

Explaining variation in species density (the number of species per unit area) is an important unsolved problem in theoretical community ecology (May 1986). This general area is also of practical importance. The maintenance of species richness on a local scale is often a priority in the management of nature reserves and its maintenance at the global scale is one of the three goals of the World Conservation Strategy (IUCN 1980).

Recent empirical studies concerning the determinants of tree species density at a continental scale (Currie and Paquin 1987, Adams and Woodward 1989) have shown that a large proportion of the variation could be explained by variables controlling primary production. The determinants of species density in herbaceous vegetation at scales relevant to individual plants are less well understood.

An important empirical observation, that species density of herbaceous vegetation on a local scale is a bitonic function, increasing to a maximum at intermediate levels of aboveground biomass and then decreasing at high levels of biomass, has been made in many vegetation types and geographical areas (e.g., Grime 1973, 1979, Al-Mufti et al. 1977, Wheeler and Giller 1982, Vermeer and Berendse 1983, Moore and Keddy 1989, Wisheu and Keddy 1989). Unfortunately, the qualitative nature of this generalization is difficult to test or use. Increases, decreases, or independence of species density with aboveground biomass can all be reconciled with the generalization since it does not specify how many species are to be expected at a given biomass level, or what the strength of the relationship should be (Wisheu and Keddy 1989). Wisheu and Keddy (1989) found that the biomass level at which maximum species density was observed varied considerably among nine studies. Furthermore, the strength of the relationship is variable and usually weak. For instance, Moore and Keddy (1989) found that only 34% of the variation in species density in the three Ontario wetlands included in that study could be explained by aboveground biomass, and that one could find anywhere from 2 to 20 species per 0.25 m^2 (the entire range of species densities observed in that study) at the biomass level that maximized species density. If predictive ability is an objective measure of "understanding" in science, then these results emphasize our rudimentary understanding of the determinants of species density at local scales.

Theoretical models suggest further variables that may improve the performance of the empirical biomass model. The effects of competition and disturbance on plant species density were first elaborated in a qualitative manner by Grime (1973), who used aboveground biomass and litter as an integrated measure of both productivity and disturbance. Huston's (1979) exploration of the nonequilibrium properties of systems of Lotka-Volterra competition equations showed that species density should be a bitonic function of the

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frequency of density-independent mortality (disturbance) and of the rate at which species are competitively displaced.

In this study we have used these suggestions to refine the biomass–species density model. Our choice of predictor variables, and their hypothesized relationship to Huston's (1979) model, are described next.

Aboveground biomass

Increasing amounts of aboveground biomass in shoreline vegetation can predict the intensity of depression of a species' growth rate due to competition in the field (Wilson and Keddy 1986), and interspecific variation in levels of biomass accumulation can accurately predict the degree of competitive depression produced by a species in common garden experiments (Gaudet and Keddy 1988). Thus, maximum yearly aboveground biomass levels may integrate some of the effects of competition referred to by Grime (1973) and by Huston (1979).

Proportional perenniality

Plant life history type may indicate past disturbance events (Harper 1977, Grime 1979). On fertile shorelines that are subject to frequent major disturbance events, such as ice scour in the spring, the vegetation is dominated by annual species. This observation was first published (to our knowledge) by Salisbury (1970), who observed that a recognizable pioneer flora ("mudflat annuals") was consistently found in fertile wetlands in Britain whenever the vegetation cover had been removed, but that this pioneer flora was quickly lost as perennials invaded and secondary succession proceeded. However, this phenomenon may not occur on shorelines with chronically infertile soils (Wilson and Keddy 1988, Wisheu and Keddy 1989). Brown and Southwood (1987) observed much the same phenomenon as did Salisbury in their study of secondary succession in old fields. Immediately following a large disturbance event species density was low and dominated by annuals. Species density reached a maximum in early- to midsuccessional fields that were composed of a mixture of annual, biennial, and perennial species, and then species density declined as the vegetation became dominated by perennial species. Peet (1978) found a similar pattern in his study of species density in the vegetation of the Colorado forests. Therefore, the proportion of the biomass composed of obligate perennials, as opposed to annuals or facultative annuals (perennials that are capable of setting seed their first year), may therefore explain some of the residual variation in the biomass model.

This study evaluates the usefulness of both aboveground biomass and the proportion of the vegetation composed of obligate perennials ("proportional perenniality") as predictors of plant species density on freshwater shorelines in southwestern Quebec, Canada. The resulting model is then tested using a previously published data set of plant species density of freshwater shorelines in southeastern Ontario, Canada.

METHODS

Study sites

Five freshwater shorelines in southwestern Quebec, Canada, were sampled during the period of peak aboveground biomass (September and October) in 1988. Included were two sites from the St. Lawrence River (Baie du Febvre, 46°10′ N, 72°40′ W, and Fort St. François, 46°17′ N, 72°35′ W), and one each from the Rivière Des Prairies (45°45′ N, 73°35′ W), the Rivière des Cerises (45°16′ N, 72°11′ W), and Lac d'Argent (45°19′ N, 72°16′ W). Sites were chosen to span the widest range of biomass levels found on freshwater shorelines in this geographical area. This data set will be called the "Quebec" data set. Voucher specimens were collected for all plants that could not be confidently identified and the taxonomic status of these specimens was verified by a taxonomist of wetland vascular plants (Dr. P. Catling) of the Biosystematic Research Institute of Agriculture Canada. Species nomenclature follows Marie-Victorin (1964) throughout this report.

The first site along the St. Lawrence River, Port Saint François, was exposed to incoming waves and consequently had a sandy substrate. The vegetation was dominated by annuals (*Bidens cernua, Chenopodium polyspermum, Cyperus aristatis, Eragrostis pectinacea, Gnaphalium uliginosum, Juncus bufonius, Lindernia dubia, Polygonum lapathifolium*), facultative annuals (*Leersia oryzoides, Lythrum salicaria, Plantago major*) and an obligate perennial (*Scirpus americanus*).

The second site along the St. Lawrence River, Baie du Febvre, was a large, gently sloping shoreline marsh with organic soil. Dominant species included only one annual (*Panicum capillare*), relatively more facultative annuals (*Agrostis stolonifera, Lythrum salicaria, Leersia oryzoides, Mimulus ringens, Penthorum sedoides*) and relatively more obligate perennials (*Eleocharis smallii, Scirpus americanus, Scirpus fluviatilus, Scirpus validus, Sium suave, Typha angustifolia*).

The site along the Rivière des Prairies contained a number of different habitats. The lower, exposed shores had sandy substrate, and the vegetation was dominated by annuals (*Chenopodium album, Echinocloa crus-galli, Polygonum lapathifolium*) and facultative annuals (*Leersia oryzoides*), as well as two fast-growing perennials (*Eleocharis erythropoda, Scirpus validus*). The lower undisturbed shores were dominated by perennials (*Sagittaria latifolia, Sparganium eurycarpum, Typha angustifolia*). The higher undisturbed shores were dominated by perennials (*Convolvulus sepium, Phalaris arundinacea*).

Lac d'Argent is a small oligotrophic lake with steep sandy shorelines, and its shoreline vegetation was dom-

TABLE 1. Summary of the southwestern Quebec and southeastern Ontario data sets.

Site	Quadrats N* (number)	Species S† (no./quadrat)	Biomass B‡ (g/quadrat)	Obligate perennials P‖ (proportion)
Quebec data set				
Rivière des Prairies	13	3–15	51–265	0.3–1.0
Baie du Febvre	8	6–18	57–197	0.5–0.9
Port St. François	12	4–24	9–306	0.1–0.6
Rivière des Cerises	5	5–6	114–299	0.9–1.0
Lac d'Argent	10	1–4	3–22	1.0
Ontario data set				
Luskville	75	2–19	13–344	0.4–1.0
Westmeath	74	2–24	1–433	0.6–1.0
Presqu'ile	75	2–13	13–652	0.2–1.0

* N is the number of 0.25-m^2 quadrats.
† S is the range in the number of vascular plant species per quadrat.
‡ B is the range in the dry mass (grams) of living aboveground biomass per quadrat.
‖ P is the range in the proportion of the biomass composed of obligate perennial species per quadrat.

inated by *Eleocharis smallii, Eriocaulon septangulare,* and *Lobelia dortmanna.*

The site along the Rivière des Cerises is a large, gently sloping marsh at the mouth of the Rivière des Cerises as it empties into Lake Memphramagog. The soil is very organic, and the vegetation is dominated by *Typha latifolia.*

Sampling procedure

Sampling followed the methods of Moore and Keddy (1989). Quadrats (50 × 50 cm) were randomly placed along the shoreline in the emergent zone at each site using a random number table, with the restriction that the full range of aboveground biomass within a site be included. Areas within a site having different amounts of aboveground biomass were visually assessed before sampling began and before the taxonomic identity of the species composing the vegetation was known, as in Wisheu and Keddy (1989).

In order to estimate the proportion of the vegetation composed of obligate perennials in each quadrat, it was divided into nine equal subquadrats. In each quadrat the vegetation was identified to species, the number of species was recorded, and an estimate of abundance of each species was obtained by scoring the presence or absence of each species in each of the nine subquadrats. The relative frequency of each species in the quadrat was calculated by dividing the number of scores recorded for a species (maximum of nine) by the total number of scores for all species in that quadrat. All aboveground parts of living vascular plants were harvested and dried to a constant mass at 80°C. Each species was then classified as being either an obligate perennial (i.e., requiring more than one growing season to produce seeds), or as an "annual." This second category included both annuals and facultative annuals (i.e., perennial species capable of setting seed their first growing season). Facultative annuals were: *Agrostis stolonifera, Epilobium ciliatum, Erucustrum gallicum, Eupatorium perfoliatum, Lycopus americanus, Leersia oryzoides, Lythrum salicaria, Mimulus ringens, Penthorum sedoides, Plantago major, Rorippa palustris,* and *Verbena hastata.*

The data of Moore and Keddy (1989) (the "Ontario" data set) were used to provide an independent test of the model developed from the Quebec data set. The Moore and Keddy (1989) data consisted of 224 quadrats collected from three sites, two from the Ottawa River (Luskville [45°31′ N, 76°6′ W] and Westmeath [45°47′ N, 76°50′ W]) and one site from Lake Ontario (Presqu'ile [44°0′ N, 77°43′ W]) during 1986 and 1987. See Moore and Keddy (1989) and Day et al. (1988) for information concerning species composition and site characteristics.

Since these two data sets were collected in different years, were composed of sites in a different geographical area, and were obtained with an equivalent methodology, they should represent a strong test of the model. Table 1 summarizes these two data sets.

Statistical analyses

Predictive relationships were obtained using least squares regression. Before performing the regression analyses, species density was transformed to its natural logarithm to better approximate a normal distribution and to stabilize its variance. When bivariate plots of ln(species density) against the predictor variables showed evidence of nonlinear responses, transformations of the predictor variables were sought to best approximate quadratic functions. All statistical analyses were performed using SYSTAT (Wilkinson 1988*a*). Contour plots were obtained using the distance-weighted least squares algorithm of SYGRAPH (Wilkinson 1988*b*), with a tension parameter of 0.1.

RESULTS

Development of the model: the Quebec data set

Fig. 1A and B show bivariate plots of species density as a function of aboveground biomass (in grams per

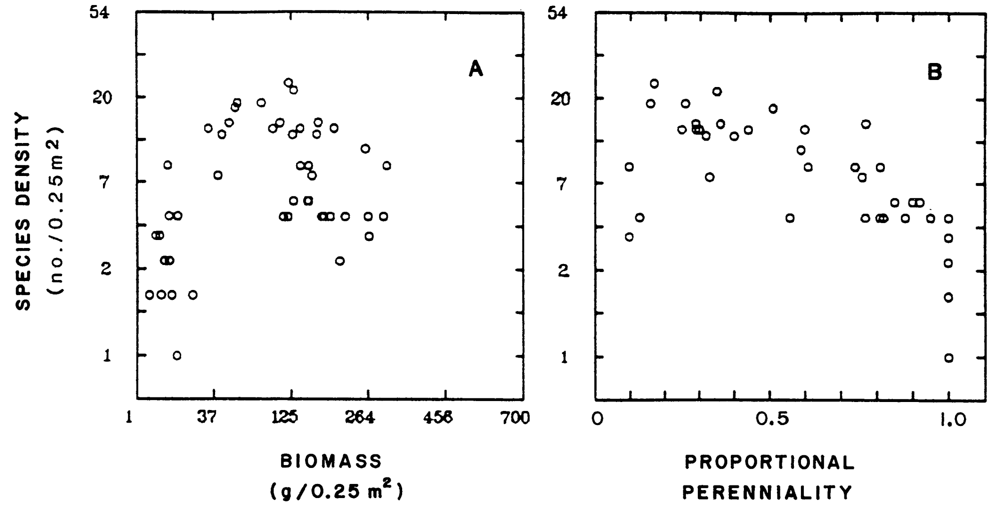

FIG. 1. Bivariate plots of species density per 0.25 m^2 of shoreline plants in southwestern Quebec, Canada, as a function of (A) the amount of aboveground biomass (g/0.25 m^2) and (B) the proportion of the vegetation consisting of obligate perennial species. Note the transformed scales for biomass and density.

0.25 m^2) and of the proportion of the vegetation consisting of obligate perennial species, respectively, for the Quebec data set. Both predictor variables showed evidence of bitonic relationships to species density but with substantial scatter.

Table 2 summarizes the results of the regression analyses. Both standing crop and obligate perenniality had a quadratic relationship with species density. Only moderate amounts of the variance in ln(species density) were accounted for by the quadratic regression involving ln(biomass) (37%, Eq. 1a, Table 2) or the square root of biomass (41%, Eq. 1b), but the quadratic regression involving proportional perenniality accounted for 69% of the variance (Eq. 1c).

When quadratic terms involving both biomass and perenniality were included, the model became more accurate. The resulting predictor equation was found to be sensitive to the transformation used for biomass; if a square root transformation instead of a logarithmic transformation was used, there were significant quadratic responses to both biomass and proportional perenniality, and 76% of the total variance in ln(species density) was explained (Eq. 1e). If a logarithmic transformation was used, there was no significant quadratic response to biomass, and slightly less (73%) of the total variance was explained (Eq. 1d). Despite the different functional forms of Eqs. 1d and e, the predicted values were very similar. Interactions between the predictor variables were tested but did not significantly improve the fit. The R^2 value of observed and predicted values of Eqs. 1d and e of Table 2, when species density was back transformed to an arithmetic scale and corrected for bias (Baskerville 1972), was 0.75 and 0.66, respectively. Therefore, even on an arithmetic scale 75% of the variance could be explained. Using Eq. 1e of Table 2, we would predict a maximum species density at 100 g/0.25 m^2, or 400 g/m^2 of aboveground biomass and at a proportional perenniality of 0.37 in the shoreline vegetation of southwestern Quebec. Fig. 2 shows the response surface of Eq. 1e in Table 2, back transformed to an arithmetic scale, after correcting for bias (Baskerville 1972). The equation generating the response surface is:

$$S = 3.59e^{0.20\sqrt{B} - 0.01B + 2.29P - 3.07P^2},$$

where S = species density, B = aboveground biomass, and P = proportional perenniality.

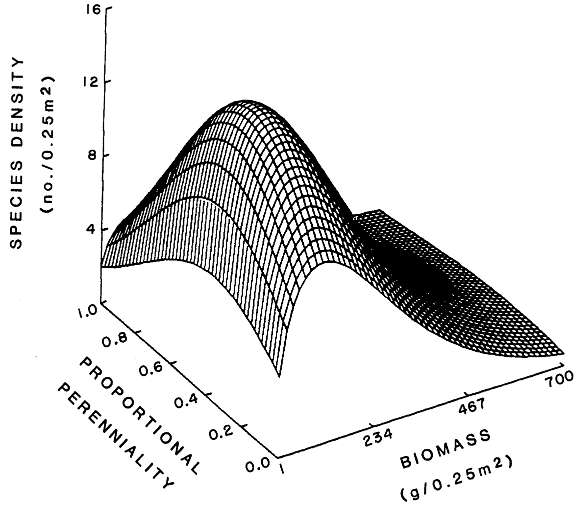

FIG. 2. Response surface of the regression predicting species density per 0.25 m^2 of shoreline plants in southwestern Quebec, Canada, as a function of the amount of aboveground biomass (g/0.25 m^2) and the proportion of the vegetation consisting of obligate perennial species.

TABLE 2. Summary of the regression analyses used to predict species density. In all cases the response variable is the natural logarithm of the number of plant species per 0.25 m^2. Predictor variables are the natural logarithm (LNB) or the square root (SQRB) of maximum annual aboveground biomass (B, g/0.25 m^2) and the proportion of the biomass composed of obligate perennials (P). Values in brackets are the standard errors of the coefficients. Only variables, including intercepts, that were significant at $P < .05$ are included.

Model	R_{adj}^2*	SE_{est}†
1. Quebec data		
a) $-1.81 + 1.94\mathrm{LNB} - 0.23\mathrm{LNB}^2$ (0.80) (0.49) (0.07)	0.37	0.60
b) $0.44\mathrm{SQRB} - 0.02B$ (0.08) (0.00)	0.41	0.58
c) $1.88 + 3.72P - 4.51P^2$ (0.27) (1.07) (0.88)	0.69	0.42
d) $1.40 + 0.13\mathrm{LNB} + 3.17P - 3.94P^2$ (0.31) (0.05) (1.03) (0.85)	0.73	0.39
e) $1.21 + 0.20\mathrm{SQRB} - 0.01B + 2.29P - 3.07P^2$ (0.30) (0.06) (0.00) (1.05) (0.09)	0.76	0.37
2. Moore and Keddy (1989) data		
a) $1.20 + 0.77\mathrm{LNB} - 0.13\mathrm{LNB}^2$ (0.18) (0.09) (0.01)	0.38	0.48
b) $2.49 - 0.002B$ (0.13) (0.0005)	0.25	0.53
c) $1.15 + 3.81P - 3.33P^2$ (0.48) (1.39) (0.95)	0.15	0.56
d) $0.78\mathrm{LNB} - 0.12\mathrm{LNB}^2 + 4.30P - 3.37P^2$ (0.09) (0.01) (1.12) (0.76)	0.45	0.45
e) $1.34 - 0.002B + 3.72P - 3.08P^2$ (0.43) (0.0005) (1.23) (0.84)	0.33	0.50
3. Moore and Keddy (1989) and Quebec data combined		
a) $0.82 + 0.86\mathrm{LNB} - 0.13\mathrm{LNB}^2$ (0.19) (0.10) (0.01)	0.25	0.55
b) $1.77 + 0.08\mathrm{SQRB} - 0.005B$ (0.13) (0.03) (0.001)	0.18	0.58
c) $1.95 + 1.96P - 2.34P^2$ (0.27) (0.84) (0.62)	0.23	0.56
d) $1.04\mathrm{LNB} - 0.14\mathrm{LNB}^2 + 1.96P - 2.19P^2$ (0.12) (0.02) (0.73) (0.53)	0.42	0.48
e) $1.64 + 0.10\mathrm{SQRB} - 0.006B + 1.90P - 2.21P^2$ (0.27) (0.02) (0.001) (0.77) (0.56)	0.35	0.51

* R_{adj}^2 is the fraction of the variance accounted for by the model, adjusted for the number of independent variables.
† SE_{est} is the standard error of the predicted number of species.

Fig. 3 shows the interpolated contours of species density. This contour map generally accords well with the regression surface of Fig. 2; areas of disagreement are seen to be areas of the plane with few data points. For instance, the contour surface in Fig. 3 shows no decrease in species density at very low proportions of obligate perennial vegetation when biomass is between 75 and 200 g, while the regression surface (Fig. 2) does show such a decrease. However, Fig. 3 also shows that there were no data points in this area of the plane.

Testing the model

Ontario data.—Fig. 4 plots species density against aboveground biomass and proportional perenniality in the Ontario data of Moore and Keddy (1989). The model developed from the Quebec data predicted a significant proportion of the variation in species density of the Ontario data ($P < .001$), and there was no evidence of a systematic bias (Fig. 5).

We repeated the regression analysis for the data of Moore and Keddy (1989). There was again evidence for a quadratic response to the percentage of obligate perennials (Eq. 2c, Table 2), as well as a quadratic response to ln(biomass) (Eq. 2a). Although the models involving the quadratic ln(biomass) term accounted for almost the same amount of the variance in the Ontario (Eq. 2a) and Quebec data (Eq. 1a), the quadratic term involving proportional perennially accounted for much less of the variance (15 vs. 69%) in the Ontario set (Eq. 2c). As in the Quebec data, the significance of a quadratic response to biomass in the Ontario data was sensitive to the type of transformation used. A square root transformation of biomass removed any bitonic trend in ln(species density). When both quadratic terms of ln(biomass) and proportional perenniality were included, all were significant, although the resulting regression accounted for only 45% of the total variance. No quadratic biomass term existed when the square root transformation of aboveground biomass was used, and only 34% of the variance was explained. Interactions between the predictor variables were tested but did not significantly improve the fit. Using Eq. 2d of

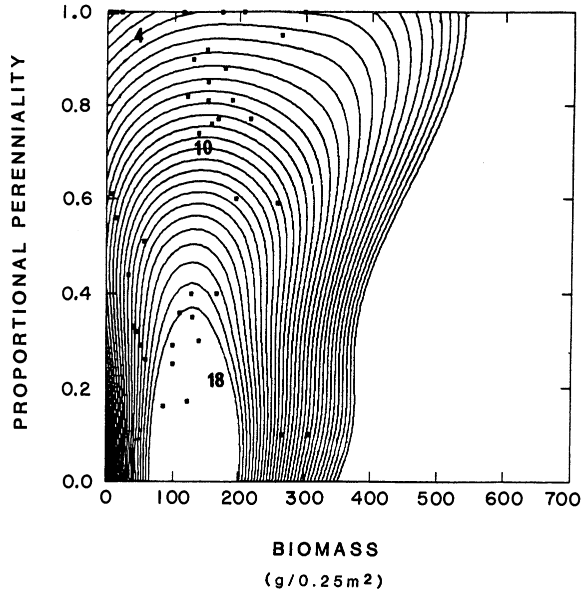

FIG. 3. Contour plot of species density per 0.25 m^2 of shoreline plants in southwestern Quebec, Canada, as a function of the amount of aboveground biomass (g/0.25 m^2) and the proportion of the vegetation consisting of obligate perennial species. The contours were determined using a locally weighted least squares algorithm. The squares represent the actual data points.

Table 2, we would predict a maximum species density of the shoreline vegetation in southeastern Ontario at 26 g/0.25 m^2, or 104 g/m^2 of aboveground biomass and a proportional perenniality of 0.64. Fig. 6 shows the response surface of Eq. 2d, back transformed to an arithmetic scale, after correcting for bias (Baskerville 1972). The equation generating this surface is:

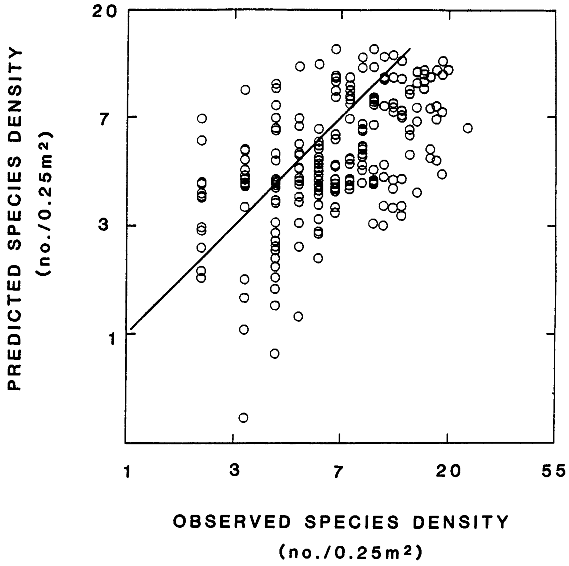

FIG. 5. The predicted density of species per 0.25 m^2 in the southeastern Ontario data, based on the regression from the southwestern Quebec data, is plotted against the observed values. Note the transformed scales.

$$S = 1.11e^{0.78\ln(B) - 0.12(\ln(B))^2 + 4.30P - 3.37P^2}.$$

Fig. 7 shows the contour graph of species density for the Ontario data. Again, there was a good general agreement between the contour surface and the regression response surface. Areas of disagreement are also areas with few data points, for instance, at very high biomass levels (>500 g) with intermediate levels of proportional perenniality.

Combined data.—The differences in the regressions from the Quebec and the Ontario data sets may reflect

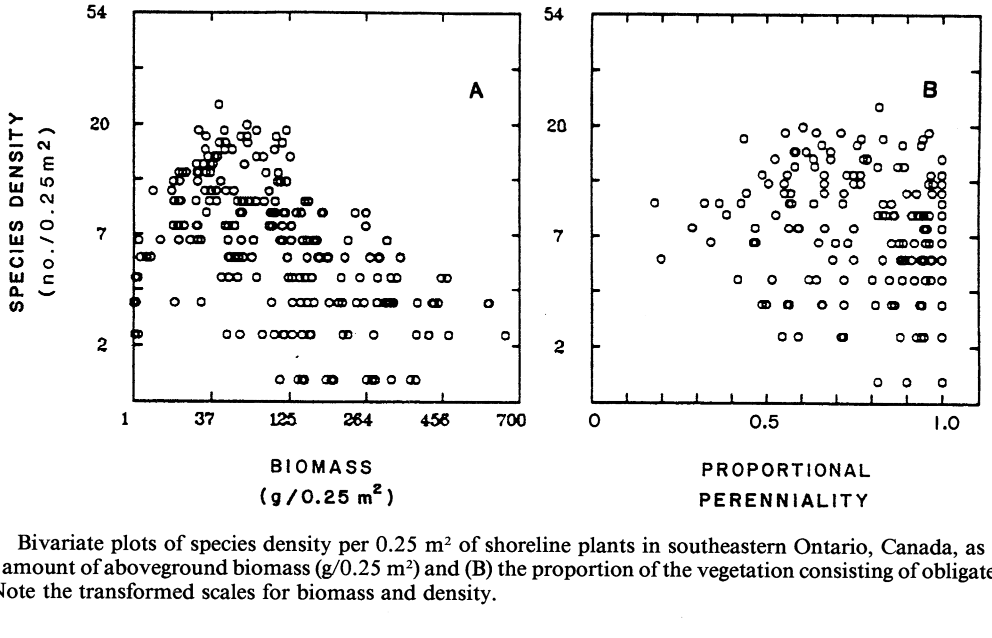

FIG. 4. Bivariate plots of species density per 0.25 m^2 of shoreline plants in southeastern Ontario, Canada, as a function of (A) the amount of aboveground biomass (g/0.25 m^2) and (B) the proportion of the vegetation consisting of obligate perennial species. Note the transformed scales for biomass and density.

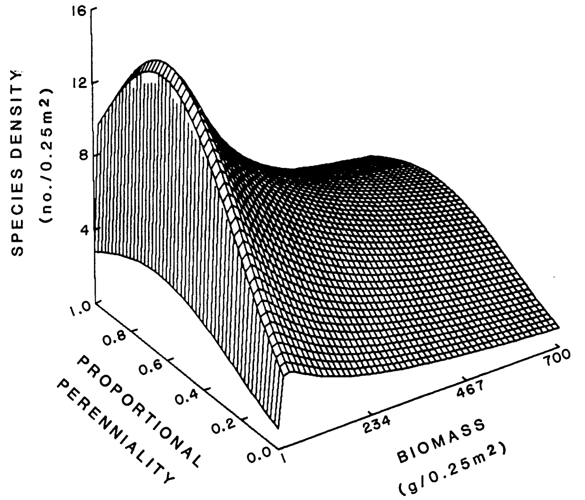

FIG. 6. Response surface of the regression predicting species density per 0.25 m^2 of shoreline plants in southeastern Ontario, Canada, as a function of the amount of aboveground biomass (g/0.25 m^2) and the proportion of the vegetation consisting of obligate perennial species.

differences in the observed combinations of aboveground biomass and proportional perenniality. The data sets were therefore combined. The inclusion of a categorical variable, indicating to which data set the data belong, did not significantly improve the fit of either the quadratic biomass model ($P < .87$) or of the quadratic model involving proportional perenniality ($P < .28$). The quadratic terms for both ln(biomass) and proportional perenniality significantly improved the fit of the model, and 42% of the variance in this combined data set was explained by the resulting regression. The same result was found using the square root transformation of biomass, but only 35% of the variance was explained. The categorical variable, indicating to which data set the data belong, was introduced into the model involving both biomass and proportional perenniality but was not significant ($P < .28$) in equations using either biomass transformation. Therefore, there was no evidence for any systematic differences between the two data sets beyond those involving the predictor variables. The response surface of Eq. 3d of Table 2, after back transforming to an arithmetic scale, is shown in Fig. 8. The equation generating the response surface, after correcting for bias (Baskerville 1972) is:

$$S = 1.12e^{1.04\ln(B) - 0.14(\ln(B))^2 + 1.96P - 2.19P^2}.$$

The contours of species density are shown in Fig. 9.

DISCUSSION

Seventy-six percent of the variance in species density on shorelines up to 150 km apart in the Quebec data set could be predicted using only two easily measured vegetational attributes. This level of predictive ability is noteworthy given the crude estimates of relative abundance used in the calculation of proportional perenniality. Similar results were obtained from the Moore and Keddy (1989) data set although the relationship was weaker. This indicates that a model that is both accurate and general has not yet been obtained. On the other hand, the inclusion of proportional perenniality always improved the accuracy of the predictions over those obtained using only biomass. Our models are therefore improvements over models using only biomass as a predictor variable.

Moore and Keddy's (1989) study found that species density exhibited systematic trends with biomass only when a wide range of biomass values was included in the analyses (from 4 to 2600 g/m^2). When the more restricted ranges of biomass levels that normally occur within a vegetation type were used, no systematic trends were found. They hypothesized that variables associated with disturbance and seedling regeneration would be more useful in areas with more restricted ranges of biomass. Wisheu and Keddy (1989) found that the species density–biomass relationship was quite variable even within a single lake, and speculated that the inclusion of plant growth forms would improve the model.

In this study we found that the inclusion of one such plant attribute associated with disturbance, the proportion of the aboveground biomass composed of obligate perennials (Harper 1977, Grime 1979), successfully accounted for part of the residual variation in the species density–biomass relationship. When the veg-

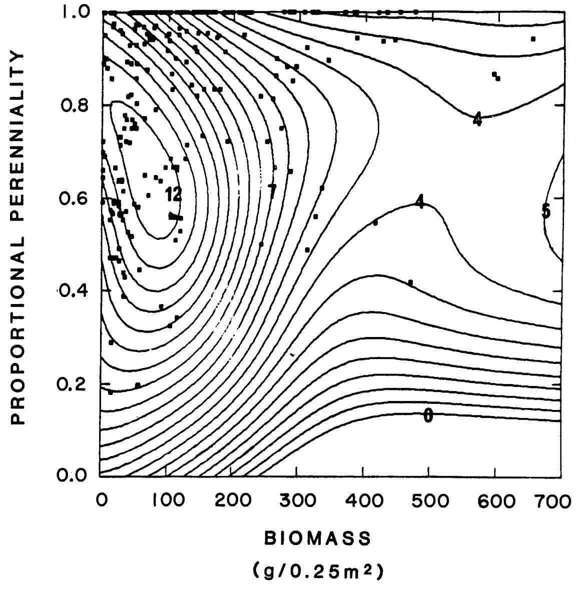

FIG. 7. Contour plot of species density per 0.25 m^2 of shoreline plants in southeastern Ontario, Canada, as a function of the amount of aboveground biomass (g/0.25 m^2) and the proportion of the vegetation consisting of obligate perennial species. The contours were determined using a locally weighted least squares algorithm. The squares represent the actual data points.

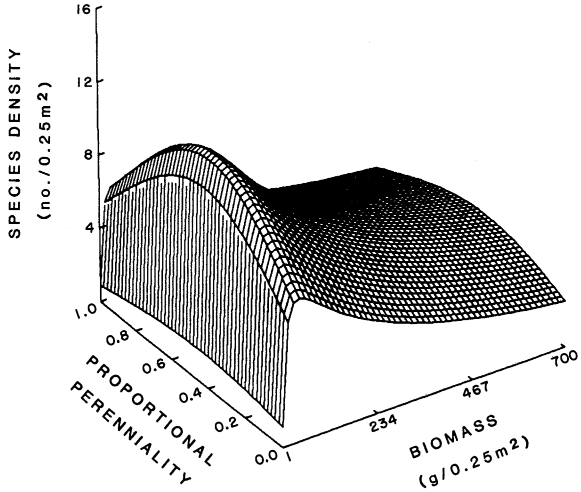

FIG. 8. Response surface of the regression predicting species density per 0.25 m^2 of shoreline plants in both southeastern Ontario and southwestern Quebec, Canada, as a function of the amount of aboveground biomass (g/0.25 m^2) and the proportion of the vegetation consisting of obligate perennial species.

etation was composed primarily of either obligate perennials, or of annuals and facultative annuals, species density was decreased independent of biomass levels. This result is similar to the observation of Brown and Southwood (1987) concerning changes in species density during secondary succession in old-field vegetation.

Interpretation of the pattern

Bitonic responses of species density to the rate of competitive exclusion and frequency of disturbance are logical consequences of Lotka-Volterra dynamics in nonequilibrium systems (Huston 1979). Yodzis (1978) further showed that this pattern would be especially pronounced when "species" could be arranged in a competitive hierarchy. These theoretical studies can be used to interpret our empirical results.

Wilson and Keddy's (1986) field experiments demonstrated that the degree to which the growth of test plants was reduced due to competition increased with increasing levels of aboveground biomass. This conclusion was supported by the common garden experiments of Gaudet and Keddy (1989). Keddy and Shipley (1989) showed that competitive hierarchies are found in many types of vegetation, including wetland vegetation. Therefore, the vegetation of sites with high levels of aboveground biomass can be expected to experience strong competitive pressures and a more rapid rate of competitive exclusion, conditions which Huston (1979) and Yodzis (1978) have shown would reduce species density independent of the frequency of disturbance. The amount of aboveground biomass at a site may therefore reflect the first of Huston's (1979) two variables: the rate of competitive exclusion.

The vegetation of freshwater shorelines in temperate regions experiences episodes of density-independent mortality of varying intensities and frequencies. One documented agent of disturbance is ice scour (Keddy 1982, Nilsson et al. 1989), which can vary greatly in intensity even within a single site (Wisheu and Keddy 1989). We have observed some riverine shorelines, dominated by annual species, in which all aboveground vegetation is removed each spring and a layer of sand up to 10 cm in depth is deposited. Logically, vegetation that is completely destroyed each year can only consist of annuals or perennials that can set seed in a single year, i.e., facultative annuals. In sites in which the effects of ice scour are less intense one finds patches of bare substrate. One would then expect a mosaic of vegetation patches in various stages of secondary succession, consisting of a mixture of annuals and obligate perennials. In areas where ice scour is minimal, vegetation consisting primarily of large perennials such as *Typha* spp., *Phalaris arundinacea,* or *Phragmites communis* are found (Keddy 1989). Therefore, the proportion of the vegetation composed of obligate perennials may approximate the second of Huston's (1979) two variables: the degree of density-independent mortality.

The resulting response surfaces and contour maps, incorporating quadratic terms of biomass and obligate perenniality, are strikingly similar to Huston's (1979)

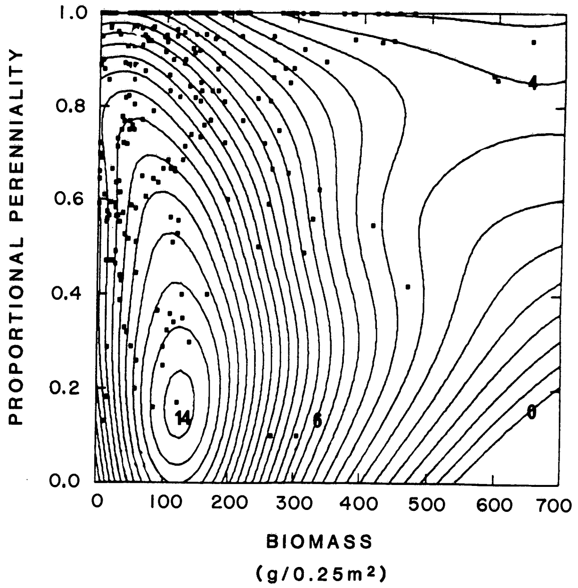

FIG. 9. Contour plot of species density per 0.25 m^2 of shoreline plants in both southeastern Ontario and southwestern Quebec, Canada, as a function of the amount of aboveground biomass (g/0.25 m^2) and the proportion of the vegetation consisting of obligate perennial species. The contours were determined using a locally weighted least squares algorithm. The squares represent the actual data points.

hypothesized relationship. Such a concordance should not be considered strong evidence for the presumed mechanisms underlying Huston's (1979) model, because Huston's (1979) explanatory variables, the rate of competitive exclusion and disturbance, were not directly measured by us, but our results do further increase their plausibility. Only field experiments can reasonably determine whether the relationship between the model predictions and the observed patterns will be robust to perturbation and therefore whether the mechanistic interpretation is correct.

Such field experiments would likely manipulate soil nutrient levels and gap sizes. Such control variables are reasonable for small-scale studies and useful because they are easily manipulated. These two variables are neither reasonable nor useful for large-scale predictive relationships, such as obtained in this study, because both variables are relatively difficult to measure in natural herbaceous vegetation (especially gap sizes). Further, the limiting nutrients are likely to change from site to site and even from season to season. This is particularly true of shorelines that are inundated for different lengths of the growing season and with year-to-year fluctuations in water levels. The best strategy is likely to include field experiments that manipulate nutrient levels and gap size, but with aboveground biomass and proportional perenniality measured as covariates.

If the mechanistic interpretation of our results is correct, then the model should break down when "obligate perenniality" is not inversely associated with disturbance, or when aboveground biomass is not correlated with competitive intensity. The first condition may occur in the vegetation of unproductive shorelines, which is often dominated by obligate perennials even though substantial ice scouring occurs (Wilson and Keddy 1988, Wisheu and Keddy 1989). Such shorelines represent an important test of the model and its mechanistic interpretation. Wilson and Keddy (1988) showed that species density of shoreline vegetation in an infertile lake was a function of aboveground biomass. Species density was low (0–4 species/0.25 m^2) at very low biomass levels (0.25–2.0 g/0.25 m^2), increased rapidly to an average of seven species at biomass levels of between 5 and 150 g/0.25 m^2 and then decreased slightly to an average of five species at $\approx$200 g/0.25 m^2, the highest biomass level encountered. Using Eq. 3d of Table 2, and assuming that none of the species were facultative annuals (there were no annuals), our model predicts two species at 2 g/0.25 m^2. At 100 g/0.25 m^2, our model predicts six species. At 200 g/0.25 m^2 our model predicts four species. Thus, it appears that our model can predict species density even in this site. On the other hand, Wisheu and Keddy (1989) found an average of $\approx$ 16 species per 0.25 m^2 at biomass levels of $\approx$30 g in an infertile lake in Nova Scotia, Canada. According to our model, such species densities would only occur in vegetation containing 30–40% obligate perennials (Fig. 3), yet there were no annuals at the site and only a few facultative annuals (e.g., *Juncus filiformis*). Whether the data set of Wisheu and Keddy (1989) really represents an exception would require estimates of relative abundance obtained with the same methodology as used in this paper.

One possible explanation for such exceptions, if they occur, is that "annualness" is associated not only with disturbance, but with disturbance in *productive* habitats (Grime 1979). The vegetation of infertile shorelines, such as the ones studied by Wilson and Keddy (1988) and Wisheu and Keddy (1989) are dominated by perennials with a characteristic growth form called "isoetids" (Hutchinson 1975, Boston 1986, Boston and Adams 1987). Such plants have very low maximum relative growth rates (Shipley and Peters 1990) and stiff evergreen leaves, all traits related to what Grime (1979) calls "stress tolerators." Thus, the inclusion of the proportion of the vegetation consisting of isoetids, or perhaps of evergreen species, may further improve the model.

The fact that a single model can describe local-scale species density over a substantial geographical area, and can explain up to 76% of its variation, suggests that the study of species density can progress from a speculative to a predictive level. The fact that the predictor variables used in the model can be linked to population-level processes (competition, disturbance, stress) suggests that eventually a model that is both predictive and explanatory can be obtained. This remains to be demonstrated.

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