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The relationship between species richness and standing crop in wetlands: the importance of scale

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Abstract

One of the few important empirical generalizations regarding herbaceous plant systems has been the demonstration that species richness is related to standing crop with maximum richness occurring at moderate levels of standing crop. This relationship is normally demonstrated by comparing among vegetation types (i.e., vegetation with different dominants). We undertook this study to test whether the species richness-standing crop relationship was evident at a finer-grained level of organization, the within vegetation type level. Fifteen wetland sites were sampled in eastern Canada and species richness and standing crop determined in each of 224 0.25 m^2 quadrats. Each site was relatively homogeneous in terms of the dominant species present and were therefore categorized as single vegetation types. However, as a group, the sites comprised a wide range of vegetation types.

A second order polynomial regression indicated a significant bitonic relationship between species richness and standing crop at the among-vegetation types scale, that is, when all 15 sites were combined. At the within-vegetation type level, however, no significant relationships were observed ($p > 0.05$). The results indicate that the model of species richness proposed by Grime has predictive power at a coarse-grained level of organization, among vegetation types, but does not survive the transition to a finer-grained level of organization, the within vegetation type level. Therefore, the higher level processes which structure species richness patterns among vegetation types are not the same processes which determine richness patterns within a vegetation type.

Introduction

> *'By formalizing scale considerations we can unravel complexity'*
>
> Allen (1987)

In order for ecology to mature as a science we must make the transition from analyzing special cases to developing general models which allow us to make predictions concerning patterns and processes in nature (Austin 1985; Keddy 1987, 1989; Tilman 1987). A recent symposium on theory and models in vegetation science (see Vegetatio, vol. 69) suggests that for models to be testable and of broad generality the following must be explicitly stated: (1) the null hypothesis (Noy-Meir & van der Maarel 1987), (2) the dependent and independent variables which define the system of interest (Keddy 1987), and (3) the spatial and temporal scales for which the model is applicable (Allen & Starr 1982; Allen 1987; see also Holling 1986). Once the appropriate variables for describing the state of the system have been chosen, general models of pattern and process are possible. Part of developing general models is determining the scale wherein the models have maximum predictive power. Thus far, few models have demonstrated the potential to span between different levels of organization.

In this study, we consider the species richness-standing crop model proposed by Grime (1973, 1979) which predicts high species richness at moderate standing crop and low species richness at high and low standing crop (more recently, related models have been proposed by Connell (1978), Huston (1979) and Tilman (1982)). Grime's model of species richness is of considerable significance because it can be generalized to many vegetation systems (e.g., Al-Mufti *et al.* 1977; Willems 1980; Wheeler & Giller 1982; Bond 1983; Vermeer & Berendse 1983; Walker & Peet 1983; Day *et al.* 1988; Moore *et al.* in press; Wisheu & Keddy in press) and appears to be a general empirical relationship in plant ecology. Therefore, the model needs to be carefully scrutinized to determine the degree of generality which it achieves and to determine the scale in which accurate predictions can be made.

The studies of Grime's model of species richness cited above have each utilized systems with a variety of vegetation types. For instance, Al-Mufti *et al.* (1977) utilized a standing crop gradient which included such different vegetation types as grasslands and the herbaceous plant communities in forest understories. It is unclear whether a demonstrable species richness-standing crop relationship exists at finer levels of organization. In this study we consider Grime's species richness model at two levels of organization: (i) the 'among vegetation types' level which we define as being relatively heterogeneous (i.e., coarse-grained) with different areas having different dominant species, and (ii) the 'within vegetation type' level which we define as being a relatively homogeneous area (i.e., fine-grained) with the same dominant species throughout.

These two contrasting levels of organization need to be separated when considering patterns and processes in plant communities. For instance, models concerning zonation (e.g., Pielou & Routledge 1976; Pielou 1979; Keddy 1983; Wilson & Keddy 1985) or competition intensity gradients (e.g., Wilson & Keddy 1986) consider the among vegetation types level of organization while other models concerning population interactions (e.g., Aarssen *et al.* 1979; Grover 1988) consider the within vegetation type level of organization.

The purpose of this study was to test whether Grime's model can make effective predictions of species richness along within vegetation type standing crop gradients in wetlands. Therefore, the null hypothesis tested was that there was no relationship between species richness and standing crop at the within vegetation type level of organization. This test had two steps: (1) constructing a species richness-standing crop curve from a polynomial regression which included data from a wide array of vegetation types, and (2) testing whether the correlation between species richness and standing crop predicted from the among vegetation types data could be detected within each vegetation type.

Methods

Study areas

Three study areas were chosen to represent a wide variety of wetland vegetation types in eastern Ontario (Presqu'ile and Westmeath) and western Quebec (Luskville), Canada and a total of 15 sites were sampled. Each site was relatively homogeneous as determined by the most common species present (Table 1) and each was therefore treated as a single vegetation type. Together, the sites comprised a variety of vegetation types as can be seen by comparing the dominant species found at each site (Table 1). The Presqu'ile study area (44°0′N, 77°43′W) is a peninsula located on the north Lake Ontario shoreline within Presqu'ile Provincial Park. The sites surveyed included infertile wet meadows, a fen, a *Carex* marsh and a *Typha* marsh. The Westmeath study area (45°47′N, 76°50′W) is a riverine shoreline located on the Ottawa River 22 km southwest of the City of Pembroke. At this location, we surveyed open beach wetlands and sheltered marshes located in Bellows Bay. A *Typha* marsh located 15 km south of Westmeath was also surveyed. The Luskville study area (45°31′N, 76°6′W) is also a riverine shoreline located 5 km west of Luskville, Quebec on the Ottawa River. The survey included open beach wetlands, sheltered riverine marshes, and a *Typha* marsh.

Table 1. The most common species[1] found in each of the 15 wetland sites sampled in this study. Mean frequency (±95% C.I.) was calculated by summing the number of subquadrats each species was recorded in (9 subquadrats/quadrat) and dividing by the total number of quadrats sampled in each wetland (15 quadrats/wetland). Only those species with greater than 50% mean frequency are included. The number of quadrats/wetland each species was found in is also shown.

Location	Species	Mean abundance ±95% C.I.	#Quadrats/15
Luskville			
Site 1	*Leersia oryzoides*	8.73±1.27	15
2	*Eleocharis erythropoda*	9.00±0.00	15
	Leersia oryzoides	6.33±5.36	15
3	*Eleocharis erythropoda*	4.87±7.76	13
	Eleocharis palustris	8.67±1.76	15
	Lythrum salicaria	5.80±4.68	15
	Scirpus americanus	8.93±0.56	15
4	*Agrostis stolonifera*	8.73±0.99	15
	Scirpus fluviatilis	6.87±2.42	15
	Sparganium eurycarpum	5.60±4.35	15
5	*Typha angustifolia*	6.47±2.42	15
Presqu'ile			
Site 1	*Dichanthelium acuminatum*	7.87±4.03	15
	Rhynchospora capillacea	6.27±8.24	12
	Scleria verticillata	9.00±0.00	15
2	*Cladium mariscoides*	9.00±0.00	15
	Equisetum variegatum	7.13±3.97	15
	Potentilla anserina	8.20±3.05	15
3	*Calamagrostis canadensis*	4.60±4.85	14
	Scirpus americanus	7.40±4.78	15
4	*Carex aquatilis*	5.67±5.94	14
	Carex lanuginosa	7.80±3.73	15
5	*Typha latifolia*	7.20±3.65	15
Westmeath			
Site 1	*Scirpus americanus*	4.93±4.95	15
2	*Fimbristylis autumnalis*	4.80±6.28	12
	Hypericum boreale	6.20±6.28	15
	Scirpus americanus	8.93±0.56	15
3	*Scirpus acutus*	8.20±2.70	15
4	*Carex vesicaria*	6.27±5.28	14
	Lemna minor	5.20±3.73	15
5	*Lemna minor*	8.00±1.99	15
	Typha angustifolia	7.00±6.11	15

[1] Nomenclature as in Gleason & Cronquist (1963) except *C. lanuginosa* Michx. and *D. acuminatum* (Swartz) Gould & Clark.

Wetland surveys

The descriptive surveys described below were done at Presqu'ile (September 12–14, 1986), Westmeath (August 25–26, 1987) and Luskville (August 18–19, 1987). At each study area, five sites of varying standing crop were selected. In each site, fifteen quadrats were randomly chosen and the vegetation sampled using a 0.5 m×0.5 m quadrat with nine equivalent subquadrats. The presence of each species in each subquadrat was recorded and the vegetation clipped to ground level, dried to constant biomass at 60 °C, and weighed. Voucher specimens of all species encountered were deposited at the Agriculture Canada herbarium (DAO) and/or the University of Ottawa herbarium (OTT).

Data analysis

Among vegetation types

The data from the 15 sites were combined for a total of 224 quadrats (one sample was lost before weighing) and a second order polynomial regression was performed between species richness (#sp/0.25 m^2) and standing crop (g/0.25 m^2) using the SPSSX statistical package.

Within vegetation type

Each of the 15 sites was then analyzed separately to test for a linear relationship between richness and standing crop within each site. Low standing crop sites (<26 g/0.25 m^2; as empirically derived from the second order polynomial regression performed on all 224 quadrats) were tested for a significant positive linear regression and high standing crop sites (>26 g/0.25 m^2) were tested for a significant negative linear regression. All analyses were performed using the SPSSX statistical package.

Results

Among vegetation types

Fig. 1 indicates that species richness was initially low (3–13 species) at very low standing crop (<15 g/0.25 m^2), rapidly increased to maximum species richness (3–24 species) at moderate standing crop (15–125 g/0.25 m^2), after which species richness declined gradually to eventually reach a constant low level (2–5 species) at very high standing crop (>375 g/0.25 m^2). The second order polynomial regression equation,

$$y = -0.91+16.52(\log_{10}(x+1)) - 5.81(\log_{10}(x+1)^2) \qquad (1)$$

where x is standing crop (g/0.25 m^2) and y is species richness (#sp/0.25 m^2), was found to be highly significant (multiple $r=0.59$, $r^2=0.34$, $p<0.0001$).

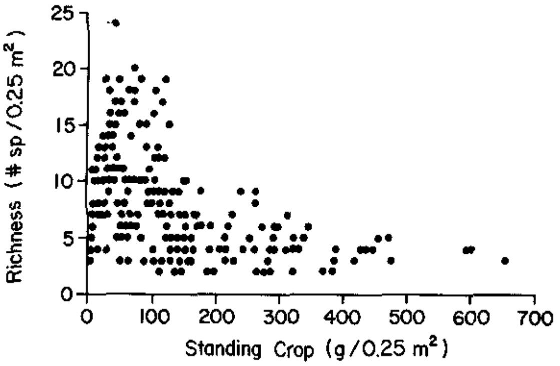

Fig. 1. Species richness plotted against standing crop in a broad range of wetland vegetation types located in Ontario (Presqu'ile and Westmeath) and Quebec (Luskville) (n=224 0.25 m^2 quadrats). The second order polynomial regression, $y=-0.91+16.52(\log_{10}(x+1)) - 5.81(\log_{10}(x+1)^2)$ where x is standing crop (g/0.25 m^2) and y is species richness (#sp/0.25 m^2), was found to be highly significant (multiple $r=0.59$, $r^2=0.34$, $p<0.0001$).

Both the first and second order variables contributed significantly to the regression equation ($p<0.0001$) indicating that there was a significant bitonic relationship between species richness and standing crop when the data from all 15 sites were included.

Within vegetation type

Fig. 2 shows that within each vegetation type, species richness does not appear to have a predictable relationship with standing crop. As shown in Table 2, none of the linear regressions for the 15 sites were significant at p=0.05. (Based on the among vegetation types model, sites with less than 26 g/0.25 m^2 were tested for a positive slope and sites with greater than 26 g/0.25 m^2 were tested for a negative slope.) Of the two cases where r was greater than 0.4, the slope of one was opposite the predicted direction (Presqu'ile, Site 4).

Alternative tests using equivalent sample sizes

One difficulty in interpreting these results is that the sample size ($n=224$) is much greater in the among

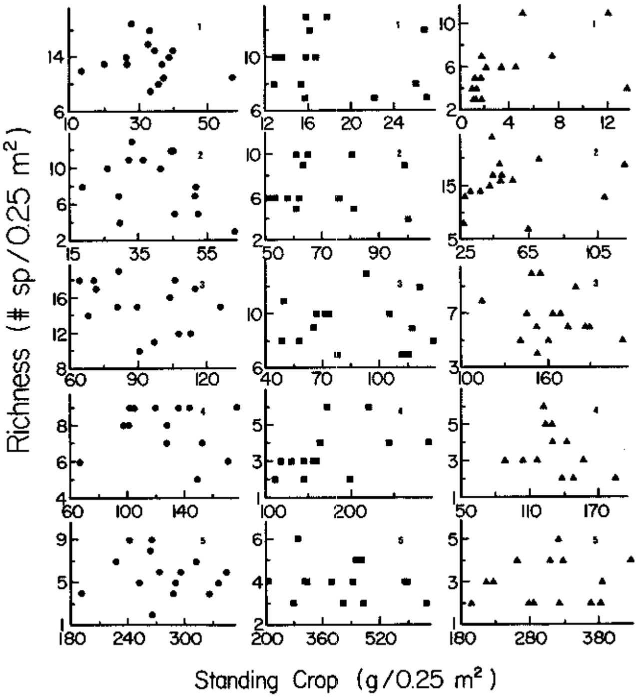

Fig. 2. Species richness versus standing crop at the within vegetation type level in each of 15 sites located in Quebec (● = Luskville, sites 1–5) and Ontario (■ = Presqu'ile, sites 1–5; ▲ = Westmeath, sites 1–5). Linear regressions performed for each site were all found to be non-significant ($p > 0.05$).

Table 2. The location and mean standing crop (g/0.25 m^2) for each of the 15 wetland sites sampled in this study. We predicted that low standing crop sites (<26 g/0.25 m^2) would have a positive species richness-standing crop relationship whereas high standing crop sites (>26 g/0.25 m^2) would have a negative relationship. The slope (r) and significance level of r are indicated.

Location	Mean S.C.	r	p
Luskville			
Site 1	32.7	−0.16	0.58
2	40.0	−0.34	0.22
3	92.3	−0.30	0.27
4	124.6	−0.06	0.82
5	277.7	−0.11	0.69
Presqu'ile			
Site 1	17.8	−0.18	0.52
2	67.0	−0.18	0.51
3	86.8	−0.06	0.84
4	173.1	0.42	0.12
5	421.6	−0.20	0.47
Westmeath			
Site 1	4.0	0.47	0.08
2	54.5	0.17	0.55
3	163.0	−0.25	0.37
4	131.9	−0.06	0.84
5	315.8	0.23	0.40

vegetation types regression than in the within vegetation type regressions ($n = 15$). Therefore, the significant relationship between species richness and standing crop among vegetation types, but not within, may simply be a consequence of differences in sample sizes.

We tried two techniques to eliminate the possible effects of sample size (see Heads & Lawton 1983). The first was to equate sample sizes by randomly selecting 15 samples from the among vegetation types data set. Even with the much reduced sample sizes, 10 of 15 draws gave significant second order polynomial regressions ($p < 0.05$) between species richness and standing crop (Fig. 3). This is in sharp contrast with the previous section where none of the 15 within vegetation type regressions were significant even though sample sizes were equivalent to the regressions derived from the random draws.

Another technique of equating sample sizes was to divide the among vegetation types data set into 15 approximately equal standing crop classes on a logarithmic scale. For each class we calculated mean species richness and mean standing crop. As before,

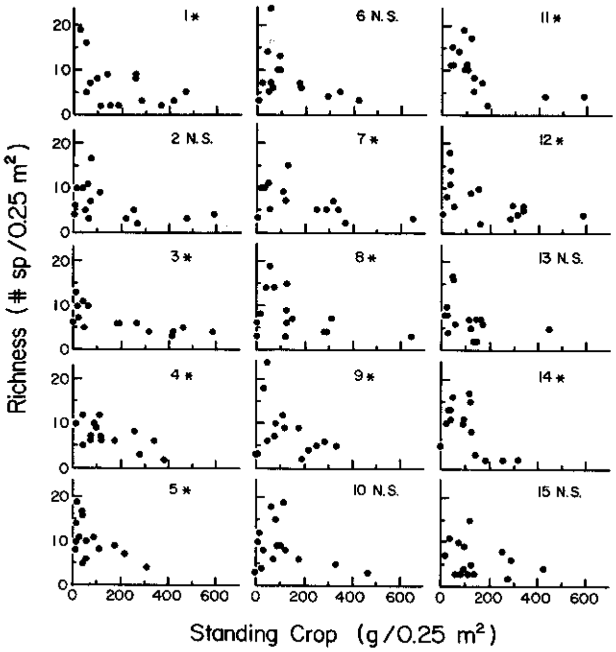

Fig. 3. Species richness plotted against standing crop in each of 15 random draws (n = 15 quadrats) from the total data set ($n = 224$). * indicates a significant ($p < 0.05$) second order polynomial regression between species richness and standing crop. N.S. indicates a non-significant polynomial regression.

the second order polynomial regression was highly significant (multiple $r=0.90$; $r^2=0.81$; $p<0.0001$) (Fig. 4). Together these results are strong evidence that lack of a significant relationship between species richness and standing crop in the 15 within-vegetation type comparisons was not due to reduced sample sizes but is an inherent attribute of the within-vegetation type level of organization.

Discussion

When comparing among vegetation types, the data indicate that as standing crop increased, species richness initially increased to reach a maximum at moderate standing crop, after which richness gradually declined (Fig. 1). This relationship between species richness and standing crop has also been found in many other wetland systems (Wheeler & Giller 1982; Vermeer & Berendse 1983; Day *et al.* 1988; Moore *et al.* in press; Wisheu & Keddy in press) and is likely a general trend in herbaceous plant systems (Grime 1973, 1979; Tilman 1982; but see Vermeer & Verhoeven 1987). However, the data presented here demonstrate that patterns found at this level of organization may not be found at another (Fig. 2).

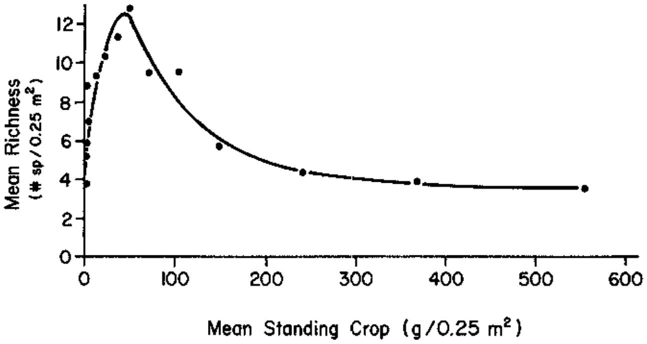

Fig. 4. Mean species richness plotted against mean standing crop for 15 equivalent standing crop classes as calculated on a logarithmic scale. In each class we calculated mean species richness and standing crop and tested for a significant second order polynomial regression. The polynomial regression, $y=-1.10+15.54(\log_{10}(x+1)) - 5.23(\log_{10}(x+1)^2)$ where x is mean standing crop (g/0.25 m^2) and y is mean species richness (#sp/0.25 m^2), was found to be highly significant (multiple $r=0.90$, $r^2=0.81$, $p<0.0001$)

The importance of scale

We have shown that Grime's model describes among vegetation types, but not within vegetation type, variation in species richness. This result illustrates Allen & Starr's (1982) point about choosing the appropriate scale for ecological models. It also suggests the potential for sterile debates when one school of thought operates on the among vegetation types scale, while another operates on the within vegetation type scale (Fig. 5).

The data presented here dealt only with patterns between two variables. It is also probable that processes are fundamentally different at these two scales. Shipley & Keddy (1987) have explored the confusion which can arise by inferring process from pattern. Nonetheless, some comments on process are necessary.

At the among-vegetation types level, Grime postulated that stress, disturbance and dominance control species richness. Recent experimental studies of wet-

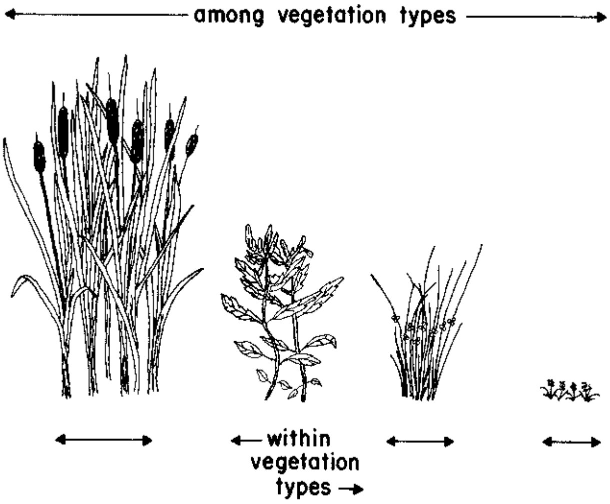

Fig. 5. Different patterns and processes are found at different levels of organization. For instance, zonation patterns along environmental gradients are concerned with the among vegetation types level of organization while patterns of recruitment in gaps are concerned with the within vegetation type level of organization. Similarly, important processes vary between the among vegetation types (e.g., competition intensity gradients, stress gradients) and the within vegetation type (e.g., recruitment, competitive hierarchies) levels of organization. Sterile debates may erupt when groups studying different scales interact without first specifying the level of organization they are exploring.

land communities have shown that competition intensity does vary predictably among vegetation types with different standing crop (Wilson & Keddy 1986), and that competitive ability is strongly correlated with plant size (Gaudet & Keddy 1988). These processes are likely less important at the within vegetation type level where there is less variation in standing crop and morphology. At the within vegetation type level, variables associated with lower level processes are likely to be more useful. The most promising of these would likely be those variables associated with processes creating patchiness. Examples include temporal variation in perturbation and gap regeneration (Grubb 1977), spatial variability in seed predation (Janzen 1970) and dispersal (Grubb 1977), localized herbivory (Lubchenco 1978), and microsite variation (Harner & Harper 1976).

Another example may further illustrate the difficulty in extrapolating from processes occurring at one level of organization to those occurring at another. Kimmerer (1978) (cited in Allen & Starr 1982) described the bryophyte communities on the cliffs of the Kickapoo River. The low frequency, higher level process constraining lower level processes is disturbance frequency which creates the observed bryophyte zonation patterns (among vegetation types). However, within each zone (within vegetation type) there are distinct patches whose patterns bears no relationship to disturbance frequency but rather is a function of a lower level process – location of most recent disturbance. Therefore, this study clearly demonstrates that lower level patterns are not predictable from knowledge of higher level processes.

We conclude that general models in plant ecology, like other general models, will have scale limitations. Some of the criticisms levelled at general models (e.g., Harper 1982; Grubb 1985) can be viewed as misunderstandings of these inherent constraints of models. Such criticisms could be rephrased to become valuable contributions to general theory if they were presented as attempts to define the scale where a general model does not apply rather than simple rejections of the model entirely. Then we could construct a nested hierarchy of models, with specific sub models incorporated within more general models (Keddy 1989). Determining the appropriate scale for different models is a process as important as developing general models for plant ecology.

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