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Species richness along multiple gradients: testing a general multivariate model in oak savannas

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A confirmatory structural equation model was built in order to test the generality of Grace and Pugesek's model of species richness. A main feature of their model was that light reaching the soil surface had the strongest effects on species richness, and that disturbance and biomass effects were largely indirect via effects on light. Their model was not confirmed for the understory vegetation of floodplain oak savannas and a new model had numerous fundamental differences. Disturbance history had the strongest direct effects on richness and these were independent of biomass effects. Richness was maximal at intermediate disturbance and biomass. Bivariate relationships between soil quality and species density were very weak because soil quality simultaneously had negative direct effects and positive indirect effects (through biomass), such that the total effect of soil was negligible. This provides an example of how structural modeling can provide insights that are not possible with other numerical methods. The complex effects of soils support recent findings that some soil components tend to increase richness via a species pool effect while other components tend to reduce richness via biotic interactions. The effects of light were not significant, but canopy trees had weak, positive effects, and this contradicts other structural models which have generally shown that shading reduces species richness. Here, species richness increases with shade presumably because of species pool effects, whereby the species pool increases by including prairie, savanna, and some woodland species and indirectly by reducing dominance by warm-season grasses. The results have implications for management because of the overall importance of disturbance history, however the majority of the variation in richness was left unexplained and this suggests other factors such as dispersal limitation, soil fungi, and historical effects may be of overriding importance in these oak savannas.

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Understanding and predicting diversity are fundamental themes and goals in ecology. The relationship between richness and biomass is commonly unimodal or monotonic (Grace 1999, Waide et al. 1999, Gross et al. 2000, Mittlebach et al. 2001). Most ecologists who have addressed this pattern have used a univariate approach, focusing directly on the effects of biomass (or some other measure of production) even though biomass itself may or may not be the direct causal factor affecting richness. In general, univariate methods tend to explain about half as much variation as do multivariate studies (Grace 1999).

Grace and Pugesek (1997) presented a structural equation model that addressed the multiple factors affecting species richness (species density). They found that species richness was most strongly affected by light reaching the soil surface and by abiotic stress related to soil quality. They also presented a general model for understanding how species richness varies in response to stress and disturbance. They proposed that the negative effects of biomass on species richness are both direct and indirect, by reducing light at the soil surface. Similarly, disturbance should tend to affect light levels both directly and indirectly via biomass.

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The concep- tual model was more fully described by Grace (1999).

The main goals of this paper are to (1) address the general model presented by Grace and Pugesek in order to test its generality in a system that is strongly structured by a soil quality gradient and a light availability – tree canopy gradient (Meisel et al. 2002) and (2) provide an alternative model, if necessary. Other structural models of species richness have been described (Grace and Julita 1999, Grace et al. 2000, Weiher et al. submitted), but none have explicitly tested the Grace and Pugesek model.

Methods

Ten remnant oak savannas located in the floodplain of the Chippewa River in western Wisconsin (USA) were randomly sampled along transects that traversed the variation in soils and shade. A total of 168 0.25 m^2 quadrats were sampled for understory (ground-layer) vascular plant composition. Above-ground biomass was collected from three 15 × 15 cm quadrats next to the corners of each quadrat and was dried at 70°C prior to weighing. Six 15 cm deep soil samples were collected from the perimeter of each quadrat and pooled. Soils were measured at the Univ. of Wisconsin Soils Testing Lab in Madison, WI. Tests included calcium, magnesium, nitrogen, phosphorus, potassium, zinc, cation exchange capacity, pH, percent organic matter, and soil texture. Light percent transmittance to the ground surface was measured with an AccuPAR-80 with an 80 cm integrating sensor (Decagon Devices, Pullman, WA). Percent tree canopy was measured with an LAI 2000 plant canopy analyzer (LI-COR, Lincoln, NE). Fire history was obtained from the Wisconsin Dept of Natural Resources and scored as years since burned and fire frequency (yr^{-1}) was calculated over the previous 12 years.

Community composition included open areas with poor soil which are similar to prairies and are dominated by *Andropogon gerardii* and *Sorghastrum nutans*. With increasing tree canopy shade (mostly by *Quercus macrocarpa*), the communities are increasingly dominated by forbs (*Solidago* sp. in particular), and with increasing soil quality shrubs (e.g. *Cornus racemosa*) become more dominant. With increasing shade, the communities grade into oak woodlands, with an abundant sedge understory (e.g. *Carex pennsylvanica*).

LISREL 8.3 (Scientific Software, Chicago, IL) was used for structural equation modeling (Jöreskog and Sörbom 1999). I generally followed the methods in Grace and Pugesek (1997) in order to maximize the likelihood of confirming their model. In order to transform the measured indicator (independent) variables and to maximize the amount of information gained, the indicators were transformed using Tablecurve (Jandel Scientific, San Rafael CA). The best fit line through the data was used to transform the data, with the limitation that the line must be third order or fewer and the line must be biologically reasonable. The transformed data, i.e. the predicted values, were then used as indicators. This was done to transform the data, not to test any specific hypothesis about the individual relationships (following Grace and Pugesek 1997). Only the six soil factors with highest r^2 were retained.

A confirmatory structural model was built following Grace and Pugesek's general model (Fig. 1). Because tree canopy cover can affect biomass and light, the tree canopy was included as a latent variable. In structural modeling, it is often customary to first build a measurement model that shows how well the measured indicator variables measure the latent conceptual variables of interest. Disturbance was measured by two indicator variables: fire frequency and years since burned. Soil was measured by organic matter, nitrogen, magnesium, moisture, sand, and silt. Once a satisfactory measurement model was built, a confirmatory structural model was tested.

Results

Disturbance and biomass had the strongest relationships with species richness, although all the relationships were weak (Fig. 2). Maximum species richness was found at intermediate amounts of disturbance, measured as both time since last burned or fire frequency, and at intermediate standing biomass. Maximum species richness was found at approximately 200 g m^{-2}. Species richness was not significantly related to either light reaching the soil or tree canopy cover. Soil factors appeared to have very weak relationships with species richness. Curvilinear regressions showed that soil effects were most pronounced at extreme values and the relationships tended to show maximum richness at intermediate values of soil quality.

When the transformed data were used in a stepwise (forward) multiple regression, disturbance frequency

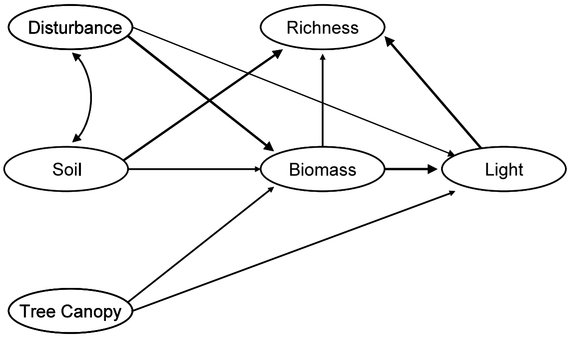
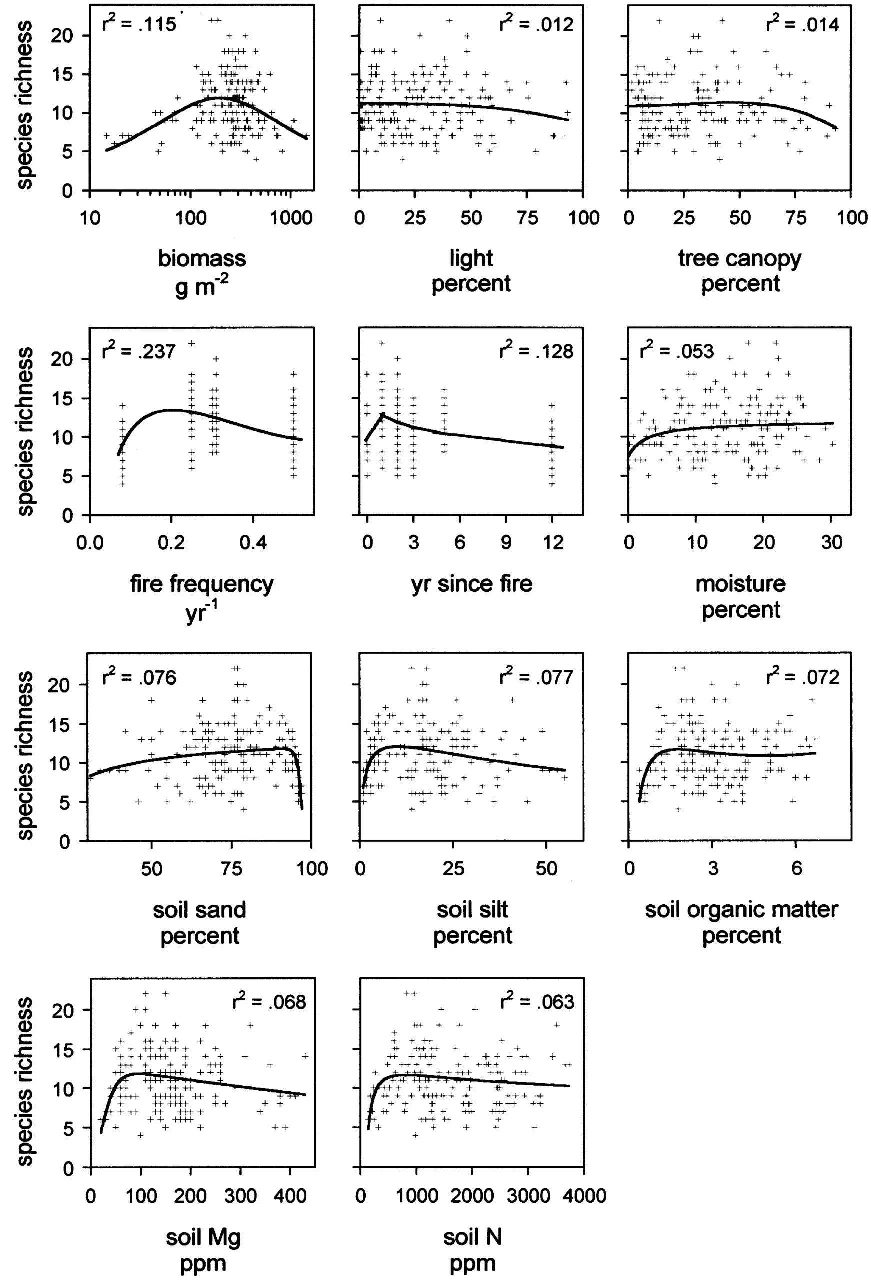


Fig. 1. The hypothetical model, based on Grace and Pugesek's (1997) general model for species richness, with canopy tree effects added. Strong effects are shown as bold arrows.

Fig. 2. Bivariate plots and curvilinear regressions.



and biomass explained 27.3% of the variation in species richness (Table 1). No other factors were significant.

The final measurement model fit the data well (Fig. 3, $\chi^2 = 18.57$, df = 13, p = 0.137, GFI = 0.954, where goodness of fit index values over 0.90 indicate good model fit). Note that the lack of significance indicates the covariance structure of the data does not significantly differ from that predicted by the model. Soil quality was strongly correlated with a suite of soil factors, and the strongest relationships were with soil nitrogen, magnesium and percent organic matter. Disturbance was strongly associated with years since burning and fire frequency. In addition, soil moisture was related to disturbance. This was apparently an artifact of sampling caused by the lack of moist, undisturbed sites (as these are no longer savannas, but have undergone succession to forest or woodland).

A confirmatory structural model showed significant differences between the model and the data ($\chi^2 = 70.83$, df = 39, $p < 0.001$). Therefore, Grace and Pugesek's model was not confirmed in the oak savannas studied here. The confirmatory model showed that several of

Table 1. Stepwise (forward) multiple regression results.

	Standardized coefficient	p	Partial correlation	Cumulative adjusted r^2
Fire frequency (yr^{-1})	0.425	<0.0001	0.435	0.231
Biomass ($g\ m^{-2}$)	0.224	0.0013	0.247	0.273

the hypothesized paths were not significant. Light had no significant effect on species richness, disturbance had no significant effect on biomass, and tree canopy had no effect on light or biomass.

An alternative structural model showed good model fit to the data (Fig. 4, $\chi^2 = 45.40$, df = 33, p = 0.072, GFI = 0.922). The direct, indirect, and total effects of latent variables are shown in Table 2. The measured factors explained 34% of the variation in species richness and nearly 50% of the variation in biomass. Disturbance had the strongest effect on species richness, and the effect was direct. The positive sign of the relationship should be interpreted as showing that intermediate disturbance causes maximal species richness because disturbance data were transformed. Biomass also had significant direct effects, with a similar interpretation of the positive effects. Soil quality had two independent effects on richness. There was a weak indirect effect of soil, mediated through biomass, and there was an opposing direct effect of nearly equal magnitude. The sum of these effects was close to zero (Table 2), and this explains the weak bi-variate relationships between soil factors and species richness. There was also a weak, positive effect of tree canopy cover.

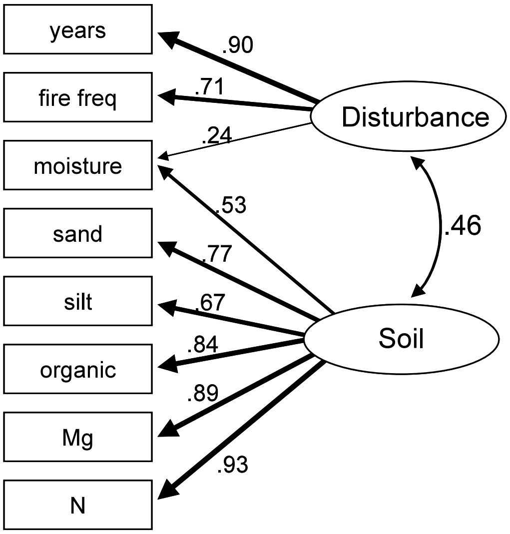


Fig. 3. The final measurement model. Straight arrows show the degree of correlation between the latent (conceptual) variables (in ellipses) and the measured indicator variables (in boxes). Curved, double-headed arrow between latent variables also shows correlation.

Discussion

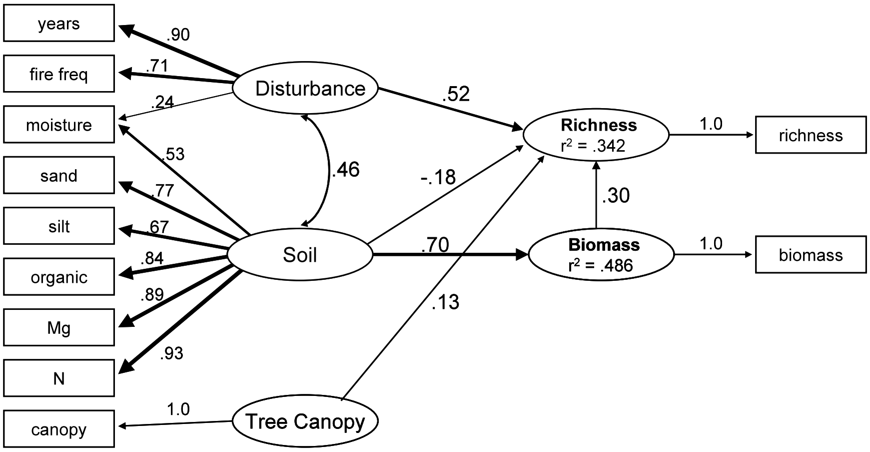
Disturbance and biomass had the strongest effects on species richness and Grace and Pugesek's (1997) general model was not confirmed. While Grace and Pugesek probably did not intend their model to be applied to every plant community, as the only multivariate model that has been examined both empirically and theoretically (Grace 1999, 2001a), it is an important starting place to seek confirmation and generality. The main differences between the final structural model found here and the hypothetical model are a lack of strong light effects and a direct effect of disturbance, rather than an indirect effect.

The lack of a strong effect of light was most likely due to the presence of scattered canopy trees. In both herbaceous marshes (Grace and Pugesek 1997) and blackland prairies succeeding into cedar woodlands (Weiher et al. submitted), more homogeneous canopies result in decreasing richness with reduced light. In oak savannas, the presence of canopy trees produces a heterogeneous light environment, both spatially and temporally. In addition, at the latitude of this study (~44°43′N), the summer sun has a relatively low angle during most of each day. This means much of the light is coming from the sides of an assemblage, rather than from directly overhead, and this decreases the importance of fine-scale standing biomass.

One effect of a heterogeneous tree canopy is an increased abundance of partially shade tolerant savanna and woodland forbs (Leach and Givnish 1999, Meisel et al. 2002). Thus the partial tree canopy tends to increase the size of the fundamental species pool (sensu Weiher 1999, Grace 2001b). At the same time, dominance by warm season (C4) grasses decreases with tree canopy cover (Meisel et al. 2002), thereby also releasing some species from competitive effects. Oak trees apparently have weakly positive effects on a variety of species when their canopy cover is moderate. At larger spatial scales (1023 m^2), species richness is maximal when the tree canopy is around 40% (Weiher and Howe 2003).

In the oak savannas studied here, fire was the main indicator of disturbance, while in Grace and Pugesek's study, herbivory was the indicator of disturbance. It is reasonable to consider disturbance as a latent variable, but we should be aware of qualitative differences in disturbance type when making comparisons among ecosystems. Grime's (1979) definition of disturbance as something that removes biomass is still a good general

Fig. 4. The final structural equation model. Arrows between latent variables (in ellipses) show completely standardized regression coefficients and these can be interpreted as the degree of independent correlation.



definition, but we should not try to equalize disturbance effects without referencing the type or quality of disturbance. For instance, fire and mowing can have dramatically different effects on prairie diversity (Collins et al. 1998). The importance of disturbance quality may be one reason why Mackey and Currie (2001) did not find support for a simple, general effect of disturbance on richness.

The results presented here tend to support the 'dynamic equilibrium model' (Huston 1994) that places emphasis on both disturbance and productivity in affecting species richness. Because most of the variation was left unexplained, the results also agree with Mackey and Currie's (2001) conclusion that disturbance does not tend to explain the majority of the variation in species richness. Disturbance did however have much stronger independent effects than the other measured variables, and it is precisely this comparative framework that makes structural modeling valuable. When one can assess the independent effects of multiple conceptual variables and compare them, then our understanding of the relative importance of these conceptual drivers is enriched.

The emergence of soil effects also shows the strength of structural equation modeling. Using both correlations and multiple regression, soil factors appeared to have very weak, if any, effect on species richness. However, the structural model showed that soil quality has an indirect effect on species richness and an opposing direct effect and these effects were of similar magnitude. While this kind of result seems at first counter intuitive, other structural models which have deconstructed soil quality into two components have shown that the two soil components can have opposing effects on richness (Grace et al. 2000, Weiher et al. submitted). These effects can be explained as being caused by a positive effect on the fundamental species pool and by a negative effect of biotic interactions. In this study, these two opposing effects tend to offset each other and this produces a very weak total effect of soils and weak bi-variate relationships between soils and richness. Structural equation modeling has the capacity to reveal these hidden relationships.

Table 2. Standardized total, direct, and indirect effects of the latent predictor variables on species richness.

	Total effect	Direct effect	Indirect effect via biomass
Disturbance	0.52	0.52	n.s.
Soil	0.03	−0.18	0.21
Tree Canopy	0.13	0.13	n.s.
Biomass	0.30	0.30	–

The results have implications for the management of oak savannas in that many savannas have less than ideal burning regimes for maximizing plant species richness. However, there are two important caveats. First, patterns of species richness in small quadrats does not scale up to larger-scale patches in these oak savannas (Weiher and Howe 2003). Second, over 60% of the variation in species richness was not accounted for. Some of this lack of fit may be due to the problem of fitting curves through data which should probably be described by upper-limit functions. Other factors, besides those studied here, are also likely to be of importance. Soil fungi can have negative effects on species richness in prairies (Hartnett and Wilson 1999) and the composition of vegetation in turn can affect fungal composition (Eom et al. 2000). Dispersal limitation (sensu Hubbell 2001) may also be important as an additional factor that could affect both species richness and the local species pools. Long-term historical effects could also be playing a significant role (Drake 1991, Pärtel and Zobel 1999). It seems that one or more of these factors likely have strong effects on oak savanna diversity.

Is there a general model for species richness? The results found here suggest the generality of a model will certainly be limited by the type of disturbance one is dealing with, and that oak savannas do not behave in accordance with Grace's model. There are still far too few examples to reject or accept Grace's general model. The next step may be to address under what conditions does such a model hold true and when does it not.

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