REPORT

Species–energy relationships and habitat complexity in bird communities

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Abstract

Species–energy theory is a commonly invoked theory predicting a positive relationship between species richness and available energy. The More Individuals Hypothesis (MIH) attempts to explain this pattern, and assumes that areas with greater food resources support more individuals, and that communities with more individuals include more species. Using a large dataset for North American birds, I tested these predictions of the MIH, and also examined the effect of habitat complexity on community structure. I found qualitative support for the relationships predicted by the MIH, however, the MIH alone was inadequate for fully explaining richness patterns. Communities in more productive sites had more individuals, but they also had more even relative abundance distributions such that a given number of individuals yielded a greater number of species. Richness and evenness were also higher in structurally complex forests compared to structurally more simple grasslands when controlling for available energy.

Keywords

Abundance, birds, community structure, evenness, habitat heterogeneity, productivity, rarefaction, species richness, species–energy theory.

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INTRODUCTION

Understanding the factors that regulate the richness of biological communities is a fundamental problem in contemporary ecology. Primary productivity, a measure of the energy entering an ecosystem, has been a focus of richness studies, however the exact form of the productivity–richness relationship has been debated (e.g. Ricklefs & Schluter 1993; Mittelbach *et al.* 2001; Chase & Leibold 2002; Whittaker & Heegaard 2003). Species–energy theory is a commonly invoked theory that predicts a positive relationship between species richness and available energy (Brown 1981; Wright 1983; Wright *et al.* 1993). Species richness of a variety of taxa has been shown to increase with various resource-based estimates of available energy including potential and actual evapotranspiration (Wright 1983; Currie & Paquin 1987; Currie 1991; Francis & Currie 2003), net primary productivity (Wright 1983; Guegan *et al.* 1998; Kaspari *et al.* 2000) and precipitation (Brown & Davidson 1977). The most commonly suggested explanation for this general pattern was dubbed the More Individuals Hypothesis (MIH) by Srivastava & Lawton (1998), and assumes that (1) areas with greater food resources should support more individuals, and (2) communities with more individuals are

able to support more species populations above some minimum viable size. Although not all populations in a community exist at this critical size, the implicit assumption here is that the relative abundance distribution remains essentially constant (e.g. log normal), such that an increase in total abundance will result in the addition of a predictable number of species.

Most large-scale richness studies lack data on abundance to test the above assumptions, and the few studies that have sufficient data report mixed results. While a positive relationship between energy and abundance has been shown for ants across a natural productivity gradient (Kaspari *et al.* 2000), such a relationship was not found for aquatic tree hole communities where productivity was experimentally manipulated (Srivastava & Lawton 1998). Ant assemblages (Kaspari *et al.* 2000) and herbaceous plant communities (Stevens & Carson 1999) show a strong relationship between density and species richness, while tree density is essentially invariant over a broad range of richness values (Enquist & Niklas 2001). These conflicting results suggest that other factors may have an impact on the relationship between environmental productivity and species richness.

One problem that all correlation-based analyses of richness patterns face is co-variation with other, often

unconsidered, variables. Across continental gradients of productivity, animal communities are generally sampled in habitats ranging from deserts and grasslands to forests. Clearly, habitat structure is a major covariate of productivity at this broad scale, as three-dimensional vegetational complexity tends to increase in conjunction with available energy. Even in the experimental manipulation of Srivastava & Lawton (1998), augmenting productivity via the addition of leaf litter simultaneously increased the habitat complexity of their aquatic microcosms. While many authors have demonstrated the importance of environmental heterogeneity in influencing richness patterns (e.g. MacArthur 1964; Kerr & Packer 1997; Rahbek & Graves 2001), I am not aware of any that have suggested that heterogeneity might play a role in producing observed species–energy patterns.

In this paper, my objective is twofold. First, I test the main predictions and assumptions of the MIH using a large dataset for North American birds and a remotely sensed index of environmental production. Second, I attempt to disentangle the effects of available energy and habitat structure on the relations among energy supply, abundance, and richness. I do this by comparing bird communities within and between structurally simple grasslands and vertically more complex deciduous forests.

METHODS

Environmental data

I used a remotely sensed vegetation index from the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer satellite to estimate environmental productivity during the breeding season. The normalized difference vegetation index (NDVI) is a measure of greenness, calculated from reflectance in the near infrared and red portions of the electromagnetic spectrum. While the index has certain limitations (Box et al. 1989; Huete 1989), it has been shown to be correlated with total green biomass and net primary productivity (Goward & Dye 1987; Chong et al. 1993; Paruelo et al. 1997). Using an atmospherically corrected 1-km resolution composite image for the month of June 1992, I calculated the mean value of NDVI within a radius of 39-km from the starting coordinates of each Breeding Bird Survey (BBS) route. Previous work has shown that an estimate of productivity during the breeding season is more appropriate than an annual estimate for birds, which migrate in response to seasonal variation in available energy (Hurlbert & Haskell 2003). The use of a monthly composite image eliminated the effects of occasional cloud cover, and the spatial neighbourhood of 39-km radius ensured that the entire survey route fell within the area being characterized. I assume that June NDVI is positively correlated with the total amount of plant and animal food available to birds in the breeding season.

Bird data

Data on the abundance and species richness of birds were compiled from the North American BBS (Bystrak 1981) for the year 2000. I examined a total of 658 survey routes occurring in grassland or desert and 1184 routes occurring in deciduous forest. Each BBS route is a standardized roadside survey consisting of 50 points separated at 800 m intervals, and at each point a single-observer records all birds seen or heard within 400 m and over a 3-min period. Surveys are conducted on a single morning in May or June. I used only routes that met BBS data quality standards, and species that were considered to be primarily marine or aquatic were excluded from analyses.

Although each point count along a BBS survey route ideally records a sample of the birds present within a 400 m radius, the effective survey radius will actually vary from route to route depending on characteristics of both the local habitat and the species composition. I expect that the effective radius of surveys in grassland habitats is close to the intended 400 m, while the effective survey radius in forest habitats with thick understory might be as short as 50–100 m. In such extreme examples, a forest survey might actually sample <5% of the area sampled in a grassland. In addition, within a given habitat type, the effective survey radius might also be expected to decay with increasing NDVI, assuming that sites with higher NDVI have a greater volume or density of foliage that might obscure the aural or visual detection of birds. Again, this effect will likely be more pronounced in forests than in grasslands.

Rarefaction

The existence of a survey area bias poses problems for comparing raw richness values, particularly across habitat types. For this reason, I use rarefaction to calculate the expected species richness of a route for a given number of individuals observed (Hurlbert 1971; Brewer & Williamson 1994). Rarefaction curves also provide additional insight into features of community structure across sites. While the height of a rarefaction curve provides a comparative estimate of richness controlling for the number of individuals, the initial rate of increase is mathematically equivalent to Hurlbert's (1971) probability of interspecific encounter, an unbiased measure of evenness (Olszewski 2004). Furthermore, rarefaction curves offer a novel way of evaluating whether the difference in richness between high- and low-energy environments is purely due to an individual-based sampling effect as suggested by the MIH. If such were the case, then both rarefaction curves would overlap each

other with identical trajectories. Alternatively, if energy availability influences the manner in which energy is partitioned among species in addition to limiting the total number of individuals, then the difference in relative abundance distributions would be evident in the divergence of low- and high-energy rarefaction curves.

Survey bias in abundance

While there is no way to calculate unbiased abundance values with these data, I can assess how the potential survey bias might distort the underlying relationship between abundance and NDVI. If the bias is independent of NDVI and varies only with habitat type, then the true NDVI-abundance relationship for forest habitats should have the same slope but a higher intercept than the observed regressions. If the effective survey radius decays with NDVI and the decay rate is higher in forests than in grasslands as seems to be the case (Schieck 1997), then the unbiased trend should have a higher intercept and a more positive slope than the observed pattern, with these effects more pronounced in forests. In addition, if the decay rate is sufficiently high, it can create the impression that total bird abundance decreases with NDVI even if the unbiased relationship is actually positive (see Appendix A). If strong positive relationships are observed, they exist in spite of this bias, not because of it.

Statistical analyses

The relationship between NDVI and the expected species richness of a sample of 200 individuals was evaluated by fitting linear, quadratic, and power functions using ordinary least squares regression. Abundance values were log-transformed in order to normalize residuals. Spatial autocorrelation is necessarily present in these geographic data, and some believe that it leads to inflated estimates of the number of degrees of freedom in significance tests. However, the statistically significant relationships presented in this study would remain significant at $P < 0.01$ if only 1% of the observations were statistically independent. Thus, the probability of an increased type I error rate due to spatial autocorrelation appears to be negligible for the relationships reported here.

RESULTS

Consistent with the prediction of species–energy theory, expected species richness increased with increasing NDVI, with no evidence of a unimodal relationship (quadratic term: $P = 0.83$ in grassland, $P = 0.58$ in forest). The NDVI-expected richness relationship was well fit by both linear and power functions, explaining 45–49% of the variation in

richness across both habitat types (Fig. 1a). Regardless of model, the increase in expected richness was stronger across deciduous forest survey routes ($S = 50.1(NDVI) + 15.6$, $R^2 = 0.30$) than across grassland routes ($S = 29.1(NDVI) + 21.2$, $R^2 = 0.16$; ANCOVA, difference in slopes, $F_{1,1809} = 39.37$, $P < 0.0001$). This difference in slope remained even when analyses were restricted to the range of NDVI common to both forests and grasslands
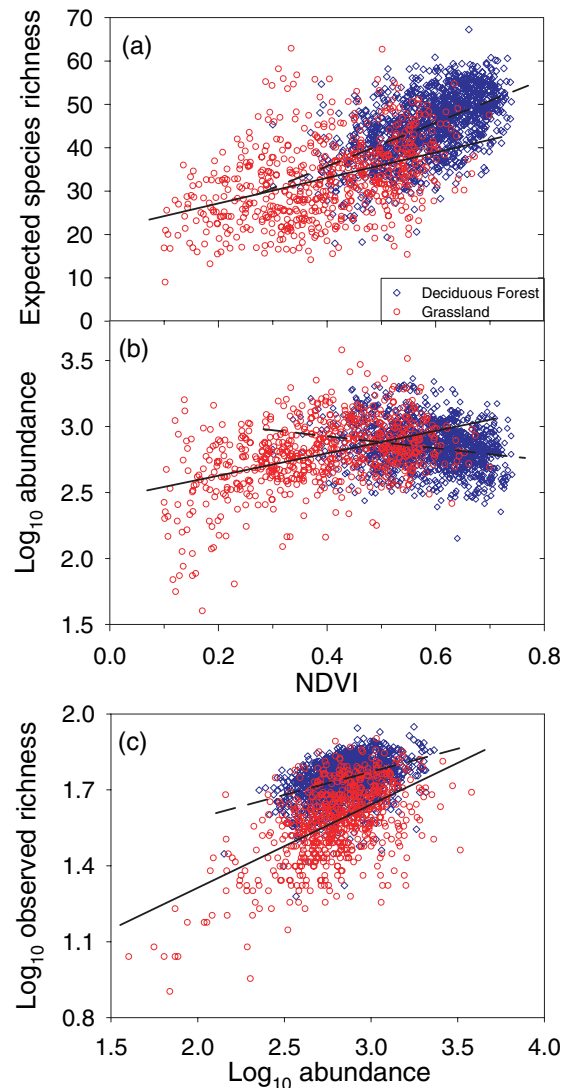

Figure 1 Relationships among the normalized difference vegetation index (NDVI), species richness and abundance for bird communities in deciduous forest (blue diamonds, dashed line) and grassland (red circles, solid line). (a) The expected species richness for a sample of 200 individuals vs. NDVI. (b) The total number of individuals observed over the survey vs. NDVI. (c) The uncorrected species richness observed on a survey as a function of the total number of individuals observed.

$(F_{1,1581} = 18.06, P < 0.0001)$. Observed abundance increased with NDVI in grasslands (Fig. 1b, $\log N = 0.84$ $(NDVI) + 2.46, R^2 = 0.18$), and exhibited a weakly negative relationship with NDVI in forests. Finally, observed richness also increased as a power function with observed abundance (Fig. 1c) in both forests ($\log S = 0.18(\log N) + 1.21, R^2 = 0.15$) and grasslands ($\log S = 0.33(\log N) + 0.66, R^2 = 0.31$).

The rarefaction curves depicted in Fig. 2 reflect the richness and relative abundance distributions of bird communities of different habitat types and energy regimes. Controlling for habitat type, the average rarefaction curve for high NDVI environments tends to lie above those for lower NDVI environments (Fig. 2a, b). In addition, the average rarefaction curve for forests lies above that for grasslands (Fig. 2c) in any given NDVI band. Thus, controlling for abundance, richness tends to increase with both available energy and habitat complexity.

Finally, I examined the relative abundance of the most abundant species (dominance) as a function of NDVI and habitat type. Dominance decreased with NDVI at a similar rate in both habitat types (ANCOVA, difference in slopes, $F_{1,1838} = 0.49, P = 0.48$), and the intercept was significantly lower in forest vs. grassland habitats (ANCOVA, effect of habitat: $F_{1,1839} = 46.84, P < 0.0001$, Fig. 3).

DISCUSSION

The MIH predicts that species richness increases with productivity via an increase in the total number of individuals that can be supported in an area. While I found support for the relationships predicted by the MIH, I found strong evidence that other mechanisms must also be involved in the determination of species richness and community structure. First of all, the nature of the productivity-richness and abundance-richness relationships varied between habitat types, suggesting an important effect of habitat structure. Expected species richness increased at a faster rate in deciduous forests than in grasslands along the NDVI gradient. Also, contrary to expectations, abundance decreased with NDVI in forests. It is possible, and I would contend probable, that the observed decrease is due primarily to smaller effective survey areas at high NDVI, and that the underlying pattern is actually similar to the positive relationship observed in grasslands (see Appendix A). However, I cannot entirely dismiss the possibility that the different trends in forests and grasslands indicate real differences in the way bird communities respond to increasing productivity in these distinct environments.

The most striking results emerge from comparisons of the average rarefaction curves for habitats differing in habitat complexity and energy availability. The MIH predicts that available energy acts on richness via abundance,
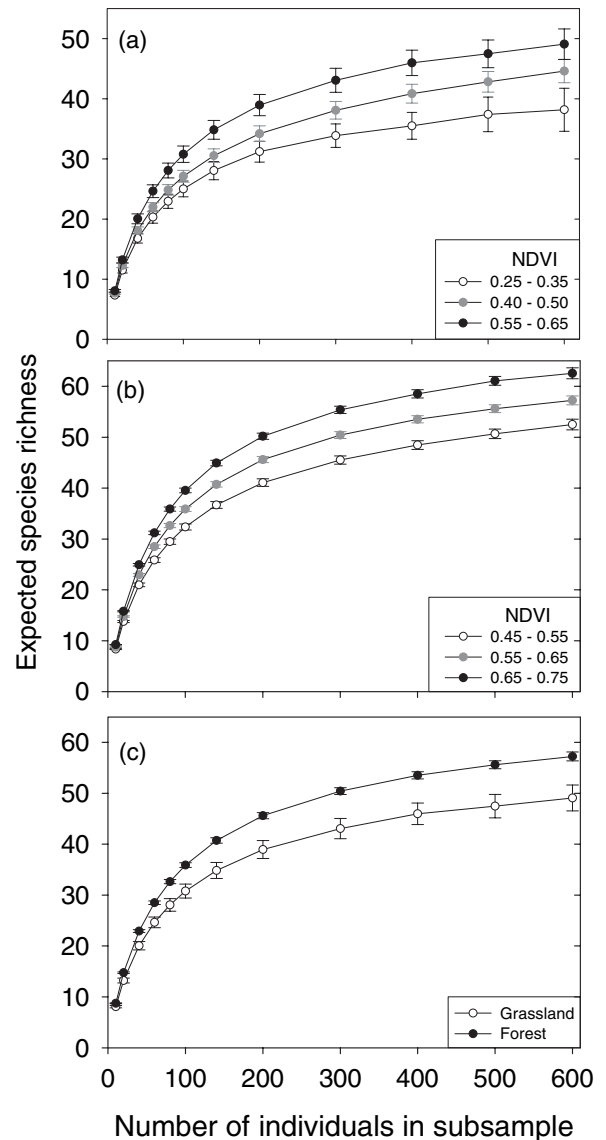

Figure 2 Average rarefaction curves showing the number of species expected in a subsample of a given size. Rarefaction curves were calculated for each survey route separately, and values represents the mean expected richness of a survey of a given habitat-NDVI class with bars indicating ± 2 SE. Rarefaction curves vary with NDVI for both (a) grassland and (b) deciduous forest. (c) For bird surveys with $0.55 < NDVI < 0.65$, the forest curve lies above the grassland curve. Similar results are obtained for other bands of NDVI as well.

suggesting that as energy increases, richness will increase by sliding along the rarefaction curve to the right. The curves in Fig. 2a, b indicate that the MIH alone cannot explain the increase in richness along the energy gradient. In communities with higher NDVI, the same number of individuals is partitioned into a greater number of species
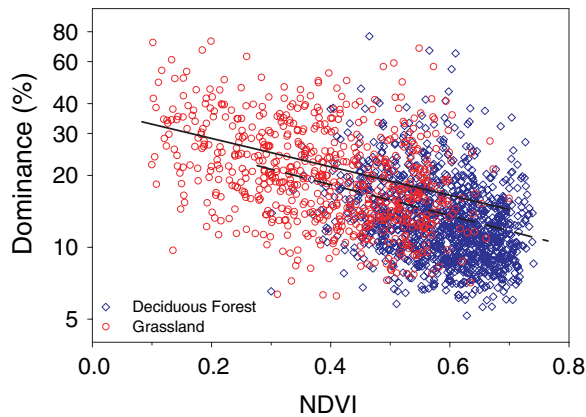
Figure 3 Relative abundance of the most abundant species in a community as a function of NDVI and habitat type. Log(*Dominance*) = (−0.58NDVI)−0.47−(0.08*H*), where *H* = 0 in grassland and *H* = 1 in forests, R^2 = 0.29. Deciduous forest are represented by blue diamonds, dashed line; grassland are represented by red circles, solid line.

with a more even relative abundance distribution. I expect that restricting the analyses to single habitat types controls for most of the variation in vegetational complexity, however, it should be noted that variation in NDVI within a habitat type still reflects changes in habitat structure (e.g. tall vs. short grass prairie) in addition to differences in available energy.

The comparison of rarefaction curves between habitat types while controlling for NDVI suggests that an increase in habitat complexity also facilitates the division of resources among different species. Willson (1974) found that as foliage height diversity and vegetation volume increased, avian richness increased due to the addition of new foraging guilds rather than to the expansion of guilds already present. These observations are consistent with the Resource Specialization Hypothesis, an alternative explanation for positive species–energy patterns, which suggests that as productivity increases, the number of resource types that can support specialist species increases (Abrams 1995; Srivastava & Lawton 1998; Pianka 2000). In the case of birds, as productivity increases and habitats shift toward more three-dimensional environments, resources become divided more equitably among a greater variety of foraging habitats. Niche apportionment models typically assume that the distribution and availability of niches in a habitat then determine the relative abundances of the species filling those niches (e.g. Tokeshi 1999; Sugihara *et al.* 2003).

Controlling for habitat structure, I have shown that avian species richness increases along an energy gradient as a result of at least two separate factors. First, in grasslands, and probably in forests as well, more productive sites tend to have more individuals. Second, in more productive sites a given number of individuals yields a greater number of species. This shift toward more even relative abundance distributions with less dominance by the most abundant species has been observed in comparisons of rank-abundance curves across latitudinal and energetic gradients (Hubbell 2001), but is not explicitly considered by most empirical studies attempting to explain richness patterns. I have shown that a similar shift in the relative abundance distribution and increase in richness also results from an increase in habitat complexity. This observed dependence of the relative abundance distribution on environmental factors is an area of research that merits much more attention. The development of a mechanistic theory of species richness depends critically on understanding the rules that govern resource partitioning among species and how those rules change with energy and habitat heterogeneity.

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APPENDIX A

Here I present a simple model showing how the existence of a survey area bias weakens the observed relationship between abundance and normalized difference vegetation index (NDVI), and potentially even makes an underlying positive relationship appear negative. Assume that the purpose of the survey is to count all birds within a radius R of the observer. However, the average effective survey radius, r, is expected to decay with increasing NDVI, and the rate of decay is expected to be dependent on habitat structure. As such, r is given by

$$r = R\exp(-c\text{NDVI}), \quad c > 0 \tag{A1}$$

where c is a habitat-specific constant that is higher in forests than in grasslands. The fraction of area actually sampled will vary as a function of NDVI and the habitat type such that

$$\frac{r^2}{R^2} = \exp(-2c\text{NDVI}) \tag{A2}$$

If the total number of birds present over the survey area of radius R is given by N, and if they are distributed at random over the survey area, then the expected number of individuals observed as a function of NDVI and habitat type is

$$E(N) = N\exp(-2c\text{NDVI}) \tag{A3}$$

Now assume that the underlying relationship between abundance and NDVI is a positive monotonic function. For convenience and to be consistent with Fig. 1b, I use the logarithmic relationship,

$$\ln N = k\text{NDVI} + A, \quad k > 0 \tag{A4}$$

but the results are qualitatively similar for any other increasing function.

Solving for N in Eq. (A3) and substituting this expression into Eq. (A4) gives the observed relationship between abundance and NDVI given the survey area bias assumed in Eq. (A1).

$$\ln[E(N)\exp(2c\text{NDVI})] = k\text{NDVI} + A \tag{A5}$$

$$\ln E(N) = (k - 2c)\text{NDVI} + A \tag{A6}$$

Thus, the existence of a survey bias ($c > 0$) will reduce the slope of the relationship between observed abundance and

NDVI, and when $c > 0.5k$ the slope will appear negative despite an underlying positive relationship. A conservative empirical estimate of $k = 1.93$ is based on the linear regression of ln $E(N)$ on NDVI for grasslands, where the bias is expected to be minimal. If survey bias alone were driving the observed negative relationship between ln $E(N)$ and NDVI in forests (observed slope $k - 2c = -1.04$), then c would be approximately 1.5. This corresponds to a $\sim$50% reduction in effective survey radius in the densest forest (NDVI = 0.8) compared with the most open forest (NDVI = 0.3), which does not seem implausible.