PRIMARY PRODUCTIVITY AND MACRO-INVERTEBRATE DIVERSITY IN FOUR TROPICAL FORESTS

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Abstract: The current high rate of ecosystem degradation necessitates an effort to understand ecosystem functioning. Biodiversity may influence ecosystem function, and productivity has been suggested as a driving factor of biodiversity. We studied the relationship between biodiversity and productivity in tropical forests. Biodiversity is a complex concept, and multiple metrics are required to define it. We used a standard sampling method to compare diversity of the macro-invertebrate communities in four different tropical forests. Depending on the spatial scale that was considered, both evenness and diversity, but not richness, increased with increasing productivity. However, results varied at different scales, indicating that patterns of biodiversity are scale-dependent.

Key words: alpha diversity, evenness, gamma diversity, heterogeneity, invertebrates, productivity-diversity curves, richness, scale

INTRODUCTION

In recent years, biodiversity has gained the attention of ecologists and the public as an important factor in ecosystem functioning. Because ecosystems around the world are being degraded and as a result species are disappearing, it is important to understand spatial and temporal patterns of biodiversity and the mechanisms that drive these patterns. While biodiversity is difficult to quantify, it has several measurable aspects. Species richness is a straightforward count of the number of species that occur in a given area; species evenness is a measure of the relative abundance of species; heterogeneity indices measure both richness and evenness (Magurran 1988). Taking all three measures into account provides a complete picture of ecosystem diversity.

Waide et al. (1999) suggests that productivity is a determinant of biodiversity. As productivity increases, the resource base increases and can support higher biodiversity. Several empirical curves have been constructed, though the shape of these curves is far from universal. Some studies have found both unimodal and linear patterns, while others have found no relationship (Mittelbach et al. 2001).

One drawback of the empirical patterns is that sampling methods often vary across multiple sites, so it is difficult to make comparisons among available diversity data. We used identical sampling methods at four different sites in Costa Rica to characterize the productivity-diversity relationship for macro invertebrates.

METHODS

We sampled invertebrate populations at four sites in Costa Rica: Palo Verde National Park on 13 January 2004, Monteverde National Park on 21 January 2004, Corcovado National Park on 3 February 2004, and La Selva on 13 February 2004. All samples were collected between 0830 and 0930. At each site, ten sweep net samples were collected along forest edges, defined as areas where vegetation changes from grass and shrubs to trees. Each invertebrate sample was taken with 16 continuous sweeps of a net, covering an area of approximately 2 m^2.

Macro-invertebrates in each sample were identified to order and grouped by morphospe-

cies. Morphospecies identities were consistent across all samples at each site, but not between sites.

We calculated three diversity measures to evaluate the relationship between biodiversity and productivity. Species richness was calculated as the total number of unique morphospecies in each sample. The heterogeneity index used to calculate diversity was the Shannon-Weiner index (H', hereafter referred to as diversity)

$$H' = -\sum (p_i)\ln(p_i)$$

where p_i is the proportion of individuals found in the ith species. Evenness was calculated using the formula

$$J = H' / H'_{max}$$

where H'_{max} = ln(number of unique species).

Data were analyzed at scales of both individual sample (10 per site) and site. Estimates of above-ground net primary productivity (ANPP) for Palo Verde and Corcovado National Parks were obtained from Oak Ridge National Laboratory Active Archive Center's Net Primary Productivity database <http://www.daac.ornl./gov/NPP>, and estimates for Monteverde and La Selva biological stations were obtained from M. Kaspari (pers. comm.).

RESULTS

We found no relationship between species richness of invertebrates and ANPP at the level of individual samples within a site (r = 0.03, df = 39, P = 0.83; Fig. 1A) or total cumulative richness from all samples within a site (r = 0.50, df = 3, P = 0.50; Fig. 1B). Species evenness increased significantly with productivity at the individual sample level (r = 0.35, df = 39, P = 0.03; Fig. 2A), but not at the site level (r = 0.66, df = 3, P = 0.35; Fig. 2B). Diversity was not related to productivity at the individual sample level (r = 0.14, df = 39, P = 0.38; Fig. 3A), but increased significantly with productivity in sites overall (r = 0.98, df = 3, P = 0.02; Fig. 3B).

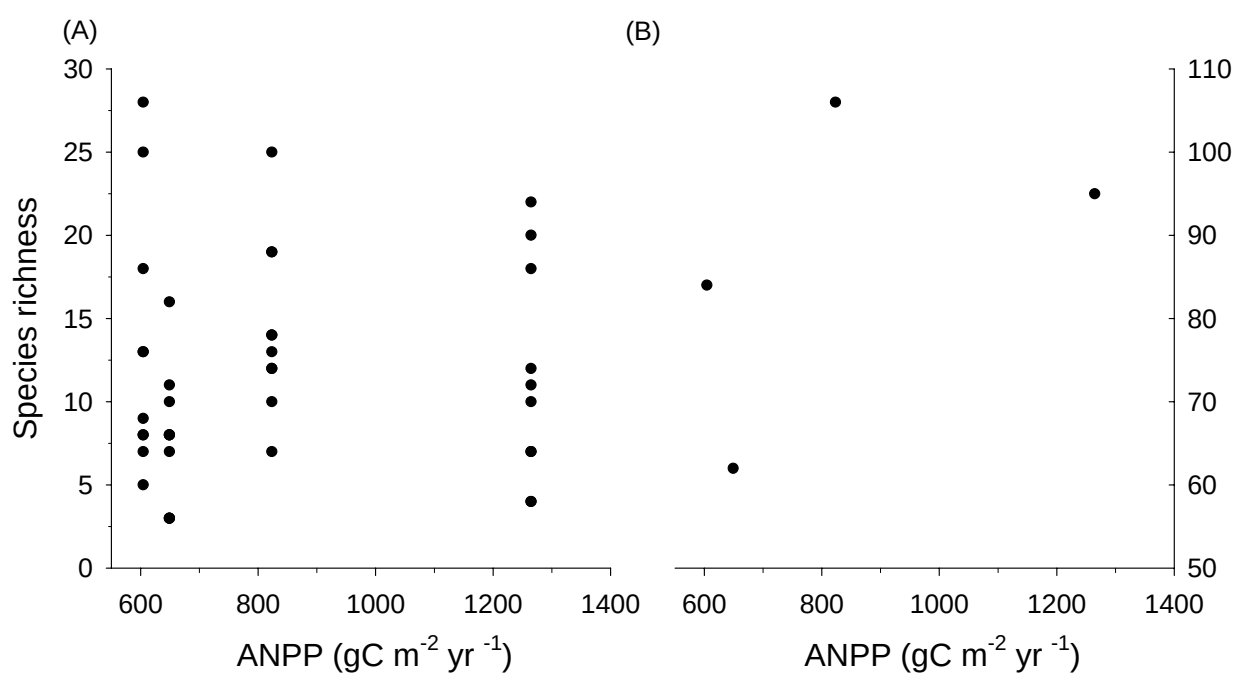

Figure 1. Species richness of invertebrates vs. productivity (above-ground net primary productivity) at each of four sites in Costa Rica: Palo Verde, Monteverde, Corcovado, and La Selva (in order of increasing productivity). Richness was calculated as (A) the total number of species in each of 10 sweep net samples at each site, and (B) the total number of species per site. Some data points are overlapping.

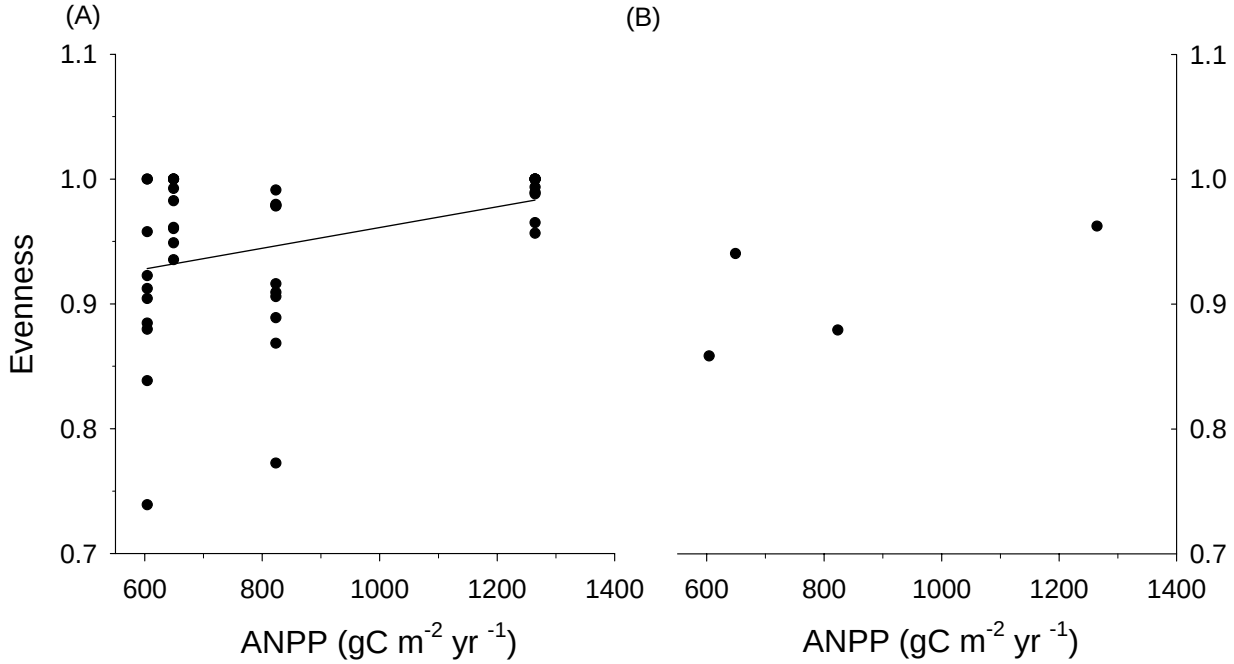

Figure 2. Evenness of invertebrates vs. productivity (above-ground net primary productivity) at each of four sites in Costa Rica: Palo Verde, Monteverde, Corcovado, and La Selva (in order of increasing productivity). Evenness was calculated for (A) each of 10 sweep net samples at each site, and (B) each site overall. A regression line indicating a significant relationship is shown in (A) for evenness of individual samples vs. productivity. Some data points are overlapping.

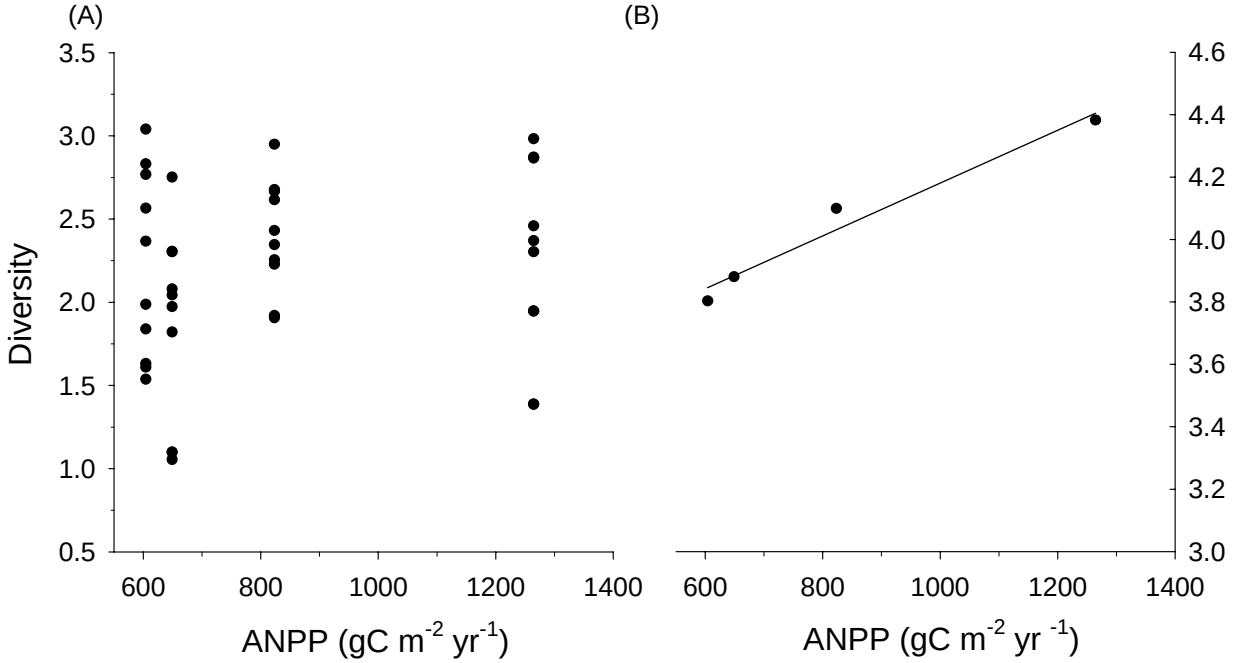

Figure 3. *H'* (Shannon-Wiener index of diversity) of invertebrates vs. productivity (above-ground net primary productivity) at each of four sites in Costa Rica: Palo Verde, Monteverde, Corcovado, and La Selva (in order of increasing productivity). Diversity was calculated for (A) each of 10 sweep net samples at each site, and (B) each site overall. A regression line showing a significant relationship is shown in (B) for diversity at each site vs. productivity. Some data points are overlapping.

DISCUSSION

We calculated three measures of biodiversity (diversity, richness, and evenness) from this data set at two spatial scales, by sample and by site. When analyzed using the individual samples (n = 10 at each site; alpha diversity), neither diversity nor richness changed with in-

creased productivity. Evenness, however, increased with increasing productivity. If increased productivity does not lead to an increase in range of niche-limiting resources, but rather, an increase in the amount of similar resources, it is possible that no new species would be added even though individual species may increase in abundance (Begon et al. 1990). More comprehensive measurements of resource availability and resource variety, and how species use the resources within each environment could clarify the causes of patterns in richness, diversity, and evenness.

When analyzed at the site level (gamma diversity), diversity increased with productivity. This was a mathematical result of increases in both richness and evenness (although neither was significantly correlated with productivity by itself). Increased productivity may lead to an increase in resources that can support both a greater number of species and of individuals. This is consistent with the global trend of high biodiversity in areas of high primary productivity.

Our results indicate the difficulty in identifying a single biodiversity index and that the relationship between productivity and biodiversity is affected by scale. Since our study sites represent only a fraction of the global productivity range, future studies should compare a broader range of sites to better determine the shape of the productivity-biodiversity curve. This study contributes to our understanding of patterns in biodiversity, an area which should be a priority for further study because humans are changing biodiversity at a high rate and changes in biodiversity can produce feedbacks that further influence ecosystem structure and function.

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