

LETTER

Linking species–area and species–energy relationships in *Drosophila* microcosms

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Abstract

Resource availability is an important constraint on community structure. Some authors have suggested it conceptually links two of the most basic patterns in ecology, the species–area relationship and the latitudinal gradient in species richness. I present the first experimental test of this conjecture, by manipulating both the area and resource concentration of artificial larval drosophilid fly habitats and then allowing colonization from a natural species pool. Both the abundance and species richness of these habitats depended upon the total quantity of resources available, regardless of whether those resources were contained within smaller high-quality habitats or larger poor-quality habitats. While the intercepts of species–area relationships varied with resource concentration, they all collapsed onto the same species–energy curve. These results support the view that energetic constraints are of fundamental importance in structuring ecological communities, and that such constraints may even help explain ecological patterns such as the species–area relationship that do not explicitly address resource availability.

Keywords

Abundance, *Drosophila*, species richness, species–area relationship, species–energy theory.

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INTRODUCTION

Two of the most well-known patterns in geographical ecology are the species–area relationship (e.g. Williams 1943; Preston 1960; Rosenzweig 1995) and the latitudinal gradient in species richness (e.g. Dobzhansky 1950; MacArthur 1972; Willig *et al.* 2003). Both of these patterns have been the subject of extensive empirical documentation and theoretical investigation, as ecologists have sought to understand the variation in species richness across-spatial scales and geographical locations. The increase in richness with area surveyed has been attributed to several different processes including: (1) a sampling effect, because larger areas inherently contain more individuals; (2) an increase in habitat diversity with area (Williams 1964; Connor & McCoy 1979); (3) a dynamic equilibrium between speciation, dispersal and extinction (MacArthur & Wilson 1967; Hubbell 2001); and (4) intraspecific aggregation and dispersal limitation (Plotkin *et al.* 2000). The first of these processes has received the most theoretical treatment, and it

follows straightforwardly from the statistical sampling of individuals from a species abundance distribution (Preston 1962; May 1975). Using such an approach, abundance is assumed to increase linearly with area, and thus in larger areas, a greater number of individuals are sampled from some fixed species abundance distribution. The form of this distribution (e.g. lognormal, log-series and broken stick) leads to mathematical predictions for the form of the species–area relationship.

A variety of hypotheses have been generated to explain the latitudinal gradient in species richness (see reviews in Pianka 1966; Rohde 1992; Willig *et al.* 2003). Although many of these hypotheses are not mutually exclusive, recent reviews suggest that the potential energy of the environment (e.g. productivity; Kaspari *et al.* 2000) may play the primary role in determining species richness over broad geographical extents (Wright *et al.* 1993; Waide *et al.* 1999; Whittaker *et al.* 2001; Hawkins *et al.* 2003). Discussion of the effects of energy on species richness has been complicated by the failure to consistently distinguish between the effects of

potential energy and kinetic energy (i.e. temperature; Turner *et al.* 1988; Allen *et al.* 2002). These two measures of energy are correlated along latitudinal and other environmental gradients, and both exhibit positive correlations with the richness of a variety of plant, vertebrate, and invertebrate taxa (see references in Wright *et al.* 1993; Waide *et al.* 1999; Hawkins *et al.* 2003). The rest of this paper focuses on variation in potential energy available to a group of consumers.

Wright (1983) was the first to propose a link between species–area and productivity–richness patterns in his development of ‘species–energy theory’ (also referred to as the ‘more individuals hypothesis’ and the ‘energy–abundance hypothesis’). Wright (1983) suggested that the species–area relationship was simply the special case of a more general species–energy relationship where resource density does not vary spatially. He reasoned that the total number of individuals supported on an island or within some spatially delimited area should be proportional to the total amount of resources available in that area, or the product of area and resource density. He then invoked the same assumption from species–area theory that an increasingly large sample of individuals from a fixed species abundance distribution will lead to a predictable relationship between the number of individuals and the number of species.

Wright (1983) and subsequent workers supported this theory using correlational data from communities of different kinds of organisms along geographical gradients of latitude, productivity, or other factors. However, the suggestion that species–area and species–energy patterns are merely different facets of the same relationship has never been tested experimentally. *Drosophilid* flies are an excellent taxon for assessing these relationships because: (1) they are an exceptionally diverse group, with *c.* 700 species in the Neotropics (Val *et al.* 1981); (2) larval resource competition has been extensively documented within the genus *Drosophila* (e.g. Bakker 1961; Gilpin *et al.* 1985); (3) a large percentage of Neotropical species utilize banana as a breeding substrate (J. Sevenster, personal communication), and thus the larvae of these species can be made to share a common resource currency; and (4) their small size allows for the construction of artificial larval habitats that can be easily manipulated with respect to the variables of interest. Using *Drosophila* communities from a natural species pool, I tested for the equivalence of species–area and species–energy relationships by experimentally manipulating resource availability of artificial larval *drosophilid* habitats. This approach controls for factors that have confounded previous attempts to evaluate species–energy relationships at geographical scales, such as coarse or inappropriate measures of available energy for the taxon of interest (e.g. net primary productivity

for birds), and co-variation of many additional environmental variables (e.g. temperature, seasonality and habitat structure).

Using these experimental microcosms, I specifically test the following predictions regarding the effect of resource availability on artificial *Drosophila* communities. (1) The total abundance of flies supported in a habitat increases linearly with resource availability. (2) Species richness of a community increases with increasing abundance. This relationship is typically characterized as a power or logarithmic function, with the implicit assumption that the form of the species–abundance distribution remains relatively constant (e.g. lognormal) across habitats varying in resource availability (Srivastava & Lawton 1998; Kaspari *et al.* 2000; Hurlbert 2004). I employ rarefaction curves (see Methods) to test whether an increase in richness occurs primarily via the sampling of more individuals, or whether variation in resource availability systematically alters the species–abundance distribution. (3) Species richness increases as a positive decelerating function of resource availability. (4) If species–area and species–energy relationships are equivalent, then the relationships predicted above should be indistinguishable whether resources are increasing via increases in habitat area or resource concentration.

METHODS

Study site

This research was carried out on Barro Colorado Island (BCI), Panama (9°9′N, 79°51′W) from February through November 2003. BCI is *c.* 1500 ha and is comprised of both old (> 200 years) and young (< 100 years) tropical forest stands (Foster & Brokaw 1982). The island receives an average of 2600 mm rainfall annually, and undergoes a 4-month long-dry period beginning in December (Leigh 1999). Over 40 species of *drosophilid* flies have been identified from BCI, the vast majority of which belong to the genus *Drosophila* (Sevenster 1992).

Larval habitats

Larval habitats were created using cylindrical plastic containers 16, 30, 53, 88 and 140 mm in diameter and *c.* 13 mm in height. Across these five habitat sizes, area varied from 2.0 to 153.9 cm². Habitats were filled with a banana–agar substrate of varying concentration made in the following way. Ripe banana was blended to a homogeneous consistency, and 1 g of baker’s yeast was added per 100 g banana. This banana–yeast combination (hereafter ‘banana’) was mixed thoroughly with an agar solution (3 g agar powder per 100 mL dH₂O) in five different ratios by

weight: 5%, 10%, 20%, 40% and 80% banana. Before setting, 1 mL of the mould inhibitor methyl-paraben (30% w/v in 95% ethanol) was added per 100 g of total substrate. Resource availability was defined as the total grams of banana present in a habitat.

Species pool collection and habitat colonization

Four to nine 20 L bait buckets with a variety of scored fruit (e.g. orange, papaya, tomato, cantaloupe, banana and mango) were hung in the forest at a height of \approx 1.5 m and at roughly 100 m intervals. After 3–4 d, flies were collected from bait buckets (and occasionally from native fruit on the forest floor) using a fine mesh insect net, and brought into the laboratory. Parasitoid wasps (primarily Eucolidae) were removed from the sample. Larval habitats were placed in a large plastic oviposition chamber with dimensions 40 × 58 × 15 cm. The sample of adult drosophilids (hereafter, the ‘species pool’) was introduced into the chamber and allowed to oviposit for \approx 24 h, after which all flies were collected by aspiration and preserved. The species pool typically included \approx 1000 flies and between nine to 14 species of females (Table S1). Each experimental habitat was then placed on moist soil inside an individual, well-ventilated plastic container, and all habitats were stored together in an incubator set to 25 °C with a 12 h light–dark cycle. Every day, any emergent adults were collected, stored in 70% ethanol, and later identified to species.

Experiments

Three separate experiments were conducted to evaluate species–energy relationships, species–area relationships, and the combined effects of resource concentration and area. In the ‘resource concentration experiment’, larval habitats consisted of 60 g of larval substrate in 100 mm Petri dishes (actual inside diameter 88 mm), with resource concentration levels of 5%, 10%, 20%, 40% or 80% banana. Twenty habitats were placed in the oviposition chamber and colonized by a single species pool. Fifteen of these habitats varied with respect to a second variable (habitat heterogeneity) and so are not considered here. The remaining habitats that were used for analysis include a single habitat at each of the five resource concentrations.

In the ‘area experiment’, larval habitats were created with variable areas (2.0, 7.1, 22.1, 60.8 and 153.9 cm²), all with a resource concentration of 40% banana. Five habitats of each of the four smaller sizes and three habitats of the largest size were placed in the oviposition chamber together and colonized by a single species pool.

In the ‘resource–area experiment’, larval habitats were created that varied in resource concentration (10%, 20% and

40% banana) as well as habitat area (7.1, 22.1, 60.8 and 153.9 cm²). A set of 12 habitats representing each combination of resource concentration and area was colonized by a single species pool. This experiment was replicated three times using a different species pool for each replicate.

Data analysis

I used ordinary least squares regression to examine the relationships between log-transformed values of resource availability, abundance, and species richness. For each of these relationships within the resource–area experiment, two analyses of covariance were conducted to test for unequal slopes and/or intercepts among (1) habitats of differing resource concentrations; and (2) habitats of differing areas. In ANCOVA analyses, a full model including dummy variables for differences in slope and intercept was first entered. If there was no evidence for differing slopes ($P > 0.1$), then a model was fit testing for differences in intercept with a common slope. If there was no evidence for differing intercepts, all of the data was fit by a single linear regression.

I calculated rarefaction curves (Hurlbert 1971; Brewer & Williamson 1994) for each of the 35 resource–area experiment habitats (one habitat yielded no adult flies). The shape of rarefaction curves reflects the underlying species–abundance distribution, with the slope of the initial rise being mathematically equivalent to an unbiased measure of evenness (Olszewski 2004). If high-resource environments support more species than low-resource environments via a sampling effect of a greater number of individuals, then the trajectory of rarefaction curves should be similar regardless of resource level (Hurlbert 2004). However, in the one instance where this was tested, Hurlbert (2004) showed that the abundance distributions of bird communities become more even as resource availability increases. If there is a systematic effect of either habitat area or resource concentration on the species–abundance distributions of these experimental *Drosophila* communities, then the rank position of the rarefaction curves should be ordered according to that variable. I tested for the effects of habitat area, resource concentration, and total resource availability on the rank position of the initial slope of rarefaction curves using Kruskal–Wallis and Spearman rank tests.

RESULTS

In the resource–area experiment, the total number of flies supported by a habitat increased with the amount of banana–yeast resource available with a log–log slope indistinguishable from unity [$\log N = 0.93 \cdot \log \text{Banana} + 1.32$, $P < 0.001$, $R^2 = 0.85$; 95% CI for $\beta = (0.79, 1.06)$; Fig. 1a]. ANCOVA analyses failed to detect an effect of

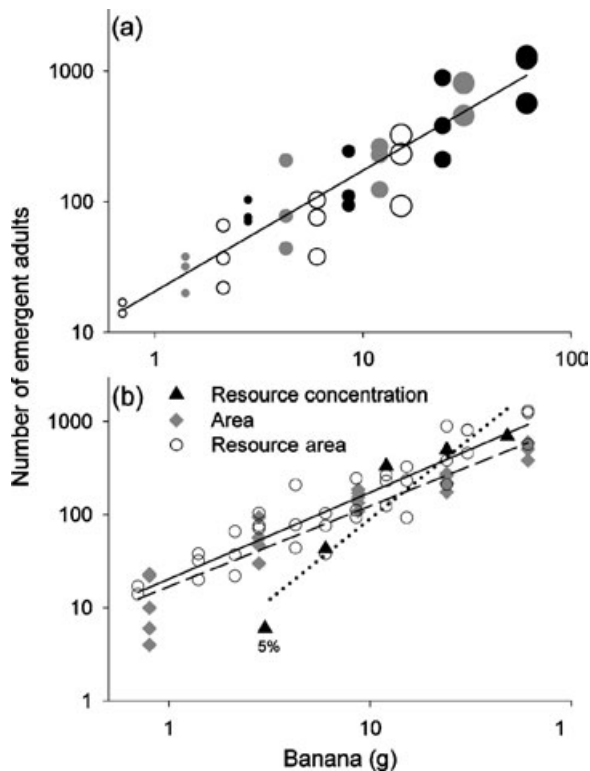


Figure 1 The relationship between the number of adult flies emerging from artificial larval habitats and the amount of banana–yeast resource available in the habitat. (a) Resource–area experiment; circle shade indicates resource concentration: open, 10%; grey, 20%; black, 40%; circle size indicates habitat area: small, 7 cm²; medium-small, 22 cm²; medium-large, 61 cm²; large, 154 cm². (b) Data for all three experiments compared.

habitat area (all P -values > 0.15) or resource concentration (all P -values > 0.2) on the parameter estimates of this relationship. Fly production per gram of banana was on average 20.0 ± 1.6 SE individuals. In the area experiment, the resource–abundance slope was slightly lower [$\log N = 0.87 \cdot \log \text{Banana} + 1.22$, $P < 0.001$, $R^2 = 0.88$; 95% CI for $\beta = (0.73, 1.01)$; Fig. 1b] but still included unity. In contrast, the resource–abundance slope in the resource concentration experiment was much steeper due primarily to exceptionally high mortality on the habitat with only 5% banana (A. Hurlbert, unpublished data). The number of emergent adults on the other habitats in the resource concentration experiment was generally similar to that observed in the other two experiments for a given amount of resource (Fig. 1b).

As predicted, species richness increased as a positive decelerating function of abundance across experimental drosophilid habitats varying in both area and resource concentration ($\log S = 0.24 \cdot \log N - 0.03 + 0.09 \cdot a$, $P < 0.001$, $R^2 = 0.55$; where $a = 1$ for habitats of 61 cm² and

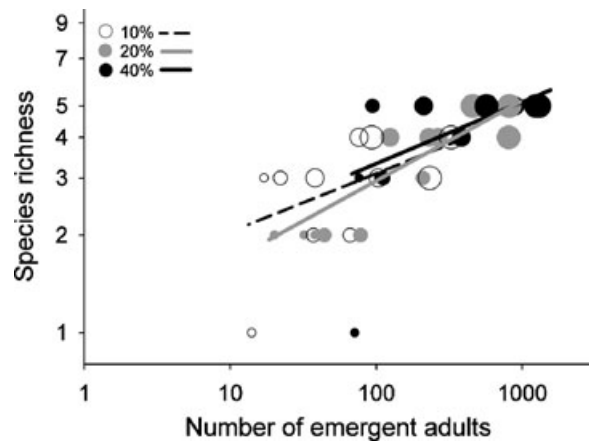


Figure 2 The relationship between the total number of adult drosophilids and the number of different species supported by habitats varying in both area and resource concentration (resource–area experiment). Symbols as in Fig. 1a. Regression lines shown for habitats of differing resource concentration are statistically indistinguishable (see text).

$a = 0$ otherwise; Fig. 2). An ANCOVA found a slightly higher intercept for habitats of the second largest size (P -values for dummy variables and interaction terms for other habitat sizes were > 0.15). A separate ANCOVA found no effect of resource concentration on the abundance–richness relationship (P -values for all concentration related dummy variables and interaction terms were > 0.5 ; Fig. 2).

The accumulation of species richness with number of individuals sampled for the various larval habitats is shown in the rarefaction curves of Fig. 3. While the shape of these curves varied, there was no systematic effect of either habitat area (Kruskal–Wallis, $H = 0.3$, d.f. = 3, $P = 0.96$) or resource concentration (Kruskal–Wallis, $H = 0.21$, d.f. = 2, $P = 0.90$) on the rank position of these curves at a subsample of two individuals. Similarly, there was no correlation between the total amount of resource available in the habitat and the rank position of the curves ($r_s = 0.07$, $P = 0.68$). These results suggest that the way in which species richness increased with abundance was generally similar across habitats.

Finally, species richness increased as a power function of resource availability in all three experiments (Fig. 4). This relationship was similar whether resources increased via an increase in habitat area or an increase in resource concentration (Fig. 4, Table 1). ANCOVA analyses failed to detect an effect of habitat area (all P -values > 0.25) or resource concentration (all P -values > 0.5) on the parameter estimates of this relationship. The habitat with only 5% banana in the resource concentration experiment (Fig. 4b) showed a strong negative deviation from the trend line consistent with the low total abundance supported on this

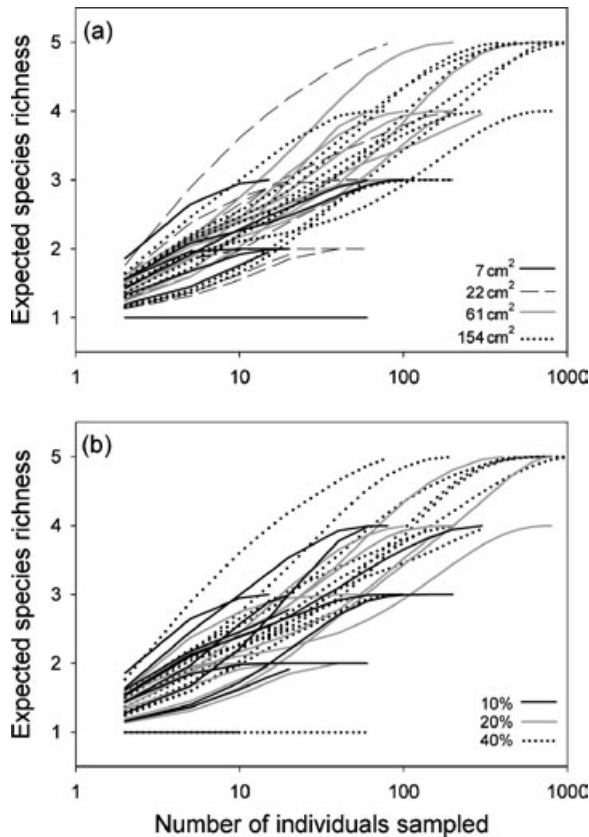


Figure 3 Rarefaction curves showing how species richness accumulates with the number of individuals sampled for each habitat in the resource–area experiment. Note that the x -axis is presented on a logarithmic scale. (a) Communities coded by habitat area. (b) Communities coded by resource concentration.

habitat. Again, this result suggests that somewhere between 5% and 10% lies a threshold for the minimum usable resource concentration for most of the *Drosophila* larvae in this experiment.

DISCUSSION

Here I have shown that within discrete artificial habitats, energy is a fundamental currency that constrains community abundance and richness in the manner predicted by species–energy theory. Both the abundance and species richness of communities in artificial larval *Drosophila* habitats depended upon the total quantity of resources available, regardless of whether those resources were contained within smaller high-quality habitats or larger low-quality habitats. While these relationships were inherently noisier for certain subsets of the data (e.g. for habitats of the smallest size), they were all consistent with this effect of resource availability. The fact that the rank position of rarefaction curves was not related to resource variables suggests that the

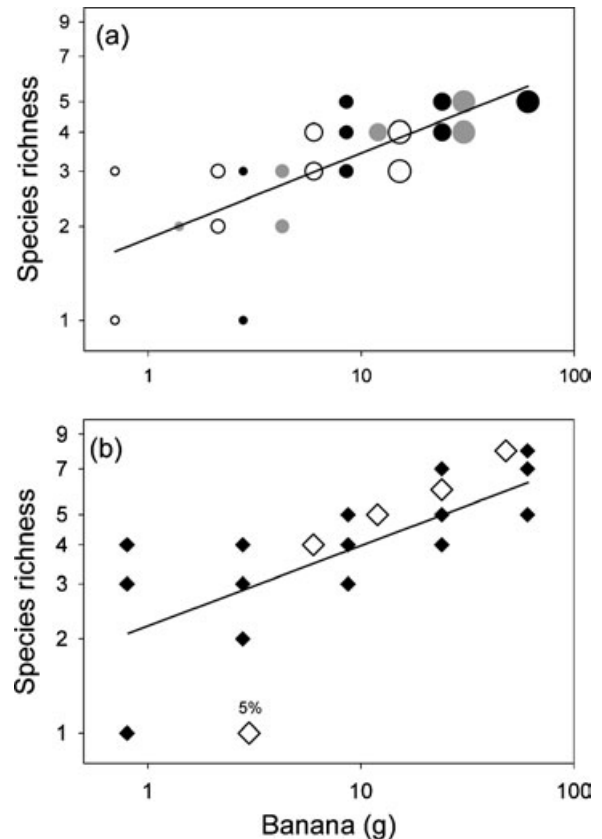


Figure 4 The relationship between the number of fly species and the amount of banana-yeast resource available in the habitat. (a) Resource–area experiment, symbols as in Fig. 1a, regression equations given in Table 1. (b) Area experiment (filled symbols) and resource concentration experiment (open). Regression line shown is for the area experiment (see Table 1).

increase in richness with resource availability occurs primarily via the sampling of more individuals from the species pool. Furthermore, I have shown that species–area relationships over homogeneous habitats varying in area by nearly two orders of magnitude are consistent with this same energetic framework. While the intercepts of species–area relationships varied with resource concentration, they all collapsed onto the same species–energy curve (Fig. 4). These results support the view that energetic constraints play a major role in structuring ecological communities, and that such constraints may even help explain ecological patterns such as the species–area relationship that do not explicitly address available energy.

Recent evaluations of species–energy theory (Srivastava & Lawton 1998; Kaspari *et al.* 2000; Currie *et al.* 2004; Hurlbert 2004) have found mixed support. While a strong positive relationship exists between richness and available potential energy in these studies, the intermediate links through abundance are often equivocal. For example, the abundance

Table 1 Regression results for log species richness as a function of log grams of banana for three experiments

Experiment*	Treatment	Resource variable	<i>n</i>	Intercept	Slope ± SE	<i>P</i> -value	<i>R</i> ²
RA	10% conc.†	Area	11	0.29	0.25 ± 0.085	0.016	0.49
RA	20% conc.	Area	12	0.23	0.30 ± 0.040	< 0.001	0.85
RA	40% conc.	Area	12	0.26	0.28 ± 0.086	0.009	0.51
RA	7 cm ² ‡	Concentration	8	0.27	0.13 ± 0.317	0.700	0.03
RA	22 cm ²	Concentration	9	0.19	0.39 ± 0.157	0.043	0.47
RA	61 cm ²	Concentration	9	0.33	0.25 ± 0.067	0.008	0.66
RA	154 cm ²	Concentration	9	0.30	0.23 ± 0.071	0.015	0.60
RA	all†	Both	35	0.26	0.27 ± 0.036	< 0.001	0.63
A	40% conc.	Area	23	0.35	0.25 ± 0.051	< 0.001	0.55
R	61 cm ² ‡	Concentration	4	0.34	0.33 ± 0.021	0.004	0.99

*RA, resource–area; A, area; R, resource concentration.

†One habitat yielded no flies, and was thus omitted from the analysis.

‡Excluding data point at 5% banana, see text. Regression equation including this data point is as follows: $\log S = 0.66 * \log \text{Banana} - 0.11$, $P = 0.042$, $R^2 = 0.80$; SE of slope = 0.192.

of aquatic invertebrates did not increase with the productivity (amount of leaf litter) of artificial tree holes in a similar community assembly experiment (Srivastava & Lawton 1998), and tree density appears to be invariant with latitude (Enquist & Niklas 2001). Hurlbert (2004) found that the increase in avian richness along a productivity gradient was greater than expected from simply sampling more individuals. In many of these studies, however, the relationships predicted by species–energy theory may be affected by other variables such as habitat complexity and temperature that co-vary along the productivity gradient. Habitat complexity typically increases over the global productivity gradient as vegetation becomes more three-dimensional, just as the addition of litter to artificial tree holes simultaneously increased the structural complexity of the tree holes (Srivastava & Lawton 1998). Habitat complexity can affect the species–abundance distribution and alter the way individuals are partitioned among species (Hurlbert 2004), and could potentially affect the way organisms convert resources into total abundance or biomass. Temperature is also closely correlated with productivity over broad scales, and may influence patterns of diversity via its effects on evolutionary rates (Rohde 1992; Gillooly *et al.* 2005, A.P. Allen *et al.*, unpublished manuscript) and population energy use (Allen *et al.* 2002).

In addition to the existence of variables potentially confounded with productivity, productivity may drive observed gradients in species richness in ways independent of the relationships proposed by species–energy theory. MacArthur (1972) and others have argued that the number of specialist species that can be supported in an area increases with productivity. This effect could be facilitated in part by an increase in the diversity of resource types as productivity increases (MacArthur 1972). In addition, the productivity of discrete, ephemeral habitat patches (e.g.

aquatic treeholes, decaying fruit and carrion) may also affect the ability of organisms to detect such patches, thus tying productivity to colonization rates. While some of these factors that co-vary with productivity in natural systems also undoubtedly affect community structure, this study demonstrates that when non-resource related variables are controlled for, the mechanisms hypothesized to underlie species–energy theory are well supported.

The results described here apply to coexistence of *Drosophila* species at the scale of individual fruits and over a single generation of larval competition. Multigenerational coexistence at the forest scale has been attributed to intraspecific aggregation over ephemeral fruit patches (Shorrocks & Sevenster 1995; Krijger & Sevenster 2001), as well as to a trade-off between developmental rate (competitive ability) and adult lifespan (colonization ability; Sevenster & van Alphen 1993). While the structure and dynamics of local communities have often been examined in isolation, recent work has suggested that many ecological systems are more appropriately described by considering the entire set of local communities within a region that might be connected by dispersal (e.g. Hubbell 2001; Mouquet & Loreau 2003; Leibold *et al.* 2004). This metacommunity approach is a promising framework that may help to explain community patterns at different spatial scales. However, an important first step toward understanding regional scale patterns lies in identifying the important ecological constraints shaping local communities. Building upon this understanding, ecologists can then address the metacommunity dynamics of dispersal and species turnover to explain how local diversity patterns scale up to the regional level (e.g. Chase & Leibold 2002). While the mechanisms proposed by species–energy theory may operate in most communities, they will generally be insufficient for explaining the full complexity of

positive productivity–richness relationships. A complete understanding of spatial variation in community richness will require investigation of the interaction of other environmental variables with energetic factors, and consideration of the role of dispersal and metacommunity dynamics.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from <http://www.Blackwell-Synergy.com>:

Table S1 The number of female flies of each species in the species pools used in each of the three experiments.

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Table S1 The number of female flies of each species in the species pools used in each of the three experiments. Bold indicates species with individuals that successfully emerged as adults from experimental habitats.

Species	Experiment*				
	R	A	RA-1	RA-2	RA-3
	18 Feb 2003	28 Jun 2003	29 Sep 2003	1 Oct 2003	3 Oct 2003
<i>calloptera</i>	0	0	0	0	1
<i>cardinoides</i>	0	2	0	0	0
<i>converga</i>	0	0	1	0	0
<i>cuaso</i>	0	0	18	15	8
<i>equinoxialis</i> [†]	282	54	416	247	474
<i>fumipennis</i> [‡]	0	m [§]	4	4	4
<i>latifasciaeformis</i>	m	1	0	0	0
<i>malerkotliana</i>	162	5	26	21	37
<i>melanogaster</i>	m	1	0 [¶]	0	0
<i>moju</i>	1	0	0	0	m
<i>nebulosa</i> [‡]	1	0	m	1	1
<i>neomorpha</i>	1	3	0	0	0
<i>paraguayensis</i>	1	0	0	0	0
<i>paranaensis</i>	5	0	0	0	0
<i>paulistorum</i> [†]	0	2	18	23	25
<i>septentriosaltans</i>	2	0	0	0	0

<i>simulans</i>	3	0	0	0	0
<i>sturtevanti</i>	18	298	48	147	350
<i>tropicalis</i> [†]	141	25	3	5	4
unid. <i>Drosophila</i> sp. 2	0	0	0	m	0
<i>willistoni</i> [†]	106	23	34	32	53
<hr/>					
Number of females	723	414	568	494	957
No. species of females	14	10	10	9	10
Total number of flies	1131	617	1016	1180	1712
Total species richness	15	11	11	10	11

* R - resource concentration experiment; A - area experiment; RA - resource-area experiment.

[†] I was unable to distinguish among females of these species, and thus abundances were assigned based on the relative abundance of males in each sample.

[‡] I was unable to distinguish among females of these species, and thus abundances were assigned based on the relative abundance of males in each sample.

[§] The letter 'm' indicates that some males but no females were identified in the species pool.

[¶] In each experiment at the end of the colonization phase, some species pool flies (typically 20-50) either escaped or were smashed beyond recognition during collection. This explains how in a few instances, successful offspring arise in experiments where no females of that species were documented in the pool.