

Why More Productive Sites Have More Species: An Experimental Test of Theory Using Tree-Hole Communities

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ABSTRACT: One of the most common explanations for an increase in species richness with productivity is what we have dubbed the "More Individuals Hypothesis." According to this hypothesis, more productive sites can support higher total abundances and, since species richness is an increasing function of total abundance, so will it be of productivity. This hypothesis assumes that communities are limited by productivity. We tested the More Individuals Hypothesis using the detritivorous aquatic insect communities of tree holes. When tree holes with varying levels of productivity (debris amount) were allowed to be colonized (through oviposition), more productive tree holes did have more species but not more individuals. Neither was total energy use strictly proportional to productivity. Only in communities forced to disassemble through productivity reductions were the predictions of the More Individuals Hypothesis satisfied. Ovipositing adults may prefer productive tree holes not because they contain more resources but because they are anticipated to be less likely to dry out. In tree holes, and more generally, the More Individuals Hypothesis is an insufficient explanation for increases in species richness with productivity because it neither accounts for the different processes of local colonization and extinction nor allows body size to correlate with extinction risk.

Keywords: productivity, species richness, tree hole, detritivores, species-energy theory.

Although patterns between species richness and productivity have been documented for decades, the mechanisms behind these patterns are still largely unresolved (Rosenzweig and Abramsky 1993; Huston 1994; Abrams 1995). One exception might be the increase in species richness with productivity in animal communities. In de-

scribing a unimodal relationship between local species richness and productivity, Rosenzweig and Abramsky (1993, p. 56) write: "Actually, the increase phase of the relationship troubles no one. It is felt to be on a firm theoretical basis: a poor environment supplies too meager a resource base for its would-be rarest species, and they become extinct." For such an "established theory," there have been remarkably few experimental tests in animal communities. Productivity has rarely been manipulated, and when an effect of productivity on species richness has been experimentally established, the mechanisms behind this effect are often unclear. In this article, we first outline the proposed mechanisms for positive productivity-richness correlations in animal communities and describe in detail the predictions made by one of these proposed mechanisms. We then present experimental tests of these predictions using the insect communities of water-filled tree holes. Conveniently, species richness in tree holes only increases with productivity.

Proposed Mechanisms for an Increase in Species Richness with Productivity

The productivity of a given trophic level is traditionally defined as the rate at which it acquires energy for biomass production (e.g., Lindeman 1942). The first productivity-richness patterns documented were of plant communities, in which plant species richness was related to plant productivity. When ecologists began to examine productivity-richness patterns for animals, however, they continued to use plant productivity as an explanatory variable, rather than the analogous animal productivity (see examples compiled by Rosenzweig and Abramsky 1993). Thus, plant ecologists compare the species richness of a certain trophic level (primary producers) with its own productivity, while animal ecologists compare the species richness of a (consumer) trophic level with the productivity of a more basal level. In this article, we continue in the tradition of animal ecologists to compare animal richness with basal level productivity. We concur with the view of Abrams (1995, p. 2020) that, in

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terms of productivity-richness theory, "what is important is the flow into the set of resources for which competition is occurring." Like Abrams, we define the productivity of these resources as the rate at which resources become available to a given trophic level for consumption and use "productivity" as a shorthand for "the productivity of resources."

In animal communities, a variety of patterns in species richness have been observed over productivity gradients, including positive correlations, negative correlations, and unimodal relationships (Rosenzweig and Abramsky 1993; Huston 1994). When positive correlations have been observed, several explanations have been offered. These can broadly be divided into four types (details in table 1). More productive sites could have more species because they contain more individuals, have more opportunities for specialization, have faster population recovery times from disturbance (dynamic equilibrium models), or have smaller population sizes because of the appearance of a higher trophic level. The most ubiquitous explanation of these is arguably the first, which we have dubbed the "More Individuals Hypothesis" and which is the theme of this article. After describing the More Individuals Hypothesis in detail, below, we will explain why tree-hole communities are an ideal system for testing this particular explanation.

The More Individuals Hypothesis

In its simplest form, the More Individuals Hypothesis relates the high species richness of productive sites to the ability of such sites to support large populations of each species. The smaller populations of less productive sites are more extinction prone, and so on balance these sites contain fewer species (e.g., Ricklefs 1973; Huston 1979, 1994; Rosenzweig and Abramsky 1993; DeAngelis 1994; Abrams 1995).

A very basic test for the More Individuals Hypothesis would be simply to search for positive correlations between productivity, total abundance, and richness. Such a test, however, would not be very convincing—any number of covariates could result in spurious correlations between these three variables. A more powerful test requires a mechanistic model that can make specific predictions about the functions linking productivity, abundance, and richness.

Such a model has been described by Wright (1983), as part of his "species-energy theory." Wright argued that increases in productivity (P), analogous to increases in area, should result in proportional increases in the total number of individuals (N). When this trend is coupled to the well-documented power function between species richness (S) and N (i.e., $\log S \propto \log N$; for explanations

see Preston 1962 and MacArthur and Wilson 1967), the result is also a power function between species richness and productivity (i.e., $\log S \propto \log P$). We can extend this reasoning further. Species richness sometimes is a logarithmic function of N (i.e., $S \propto \log N$), rather than a power function, resulting in logarithmic species-productivity curves (i.e., $S \propto \log P$). Differences between power function and logarithmic species-area curves have been related to different species-abundance distributions and sampling scales (May 1975; Rosenzweig 1995). Using Wright's analogy between area and productivity, we therefore predict species richness might also be a logarithmic function of productivity. Although Wright (1983) does not explicitly predict logarithmic productivity-richness relationships, such a relationship is generated by a patch-occupancy model based on the More Individuals Hypothesis (Wright et al. 1993).

Although Wright (1983) originally formulated this theory for islands, it obviously has the same wide applicability as species-area theory (as its central tenet is that productivity and area are analogous). Since species-area curves apply to both local and regional scales, although the details change with scale (Rosenzweig 1995), productivity-species richness curves should also apply at both scales (Wright et al. 1993; but see Currie 1991). Predicted increases in species richness with productivity are incompatible with a unimodal relationship between productivity and local richness: the decrease phase of these relationships may be due to the limitation of factors other than energy (Rosenzweig and Abramsky 1993; Huston and DeAngelis 1994; DeAngelis 1994).

Given the above formulation of the More Individuals Hypothesis, we can make three predictions. In the absence of other effects, (1) species richness will increase with productivity, either as a power or logarithmic function, because (2) total abundances are proportional to productivity. This is a direct consequence of the energy-limitation of the community, that is, (3) the total energy used by the community is directly proportional to the energy available. We do not examine the relationship between richness and abundance to avoid circularity (once predictions 1 and 2 are proven, the relationship between species richness and abundance is determined).

Using Tree Holes to Test Productivity-Richness Theory

The insect communities of water-filled tree holes are well suited for testing productivity-richness theory. Tree holes are small cavities formed either by the aboveground structure of trees or by localized rotting of the wood. Water and leaf litter accumulate in these cavities, and the decaying litter is consumed by a variety of detritivorous insects, most of which are specific to this habitat (Kitch-

Table 1: Four common explanations for an increase in local animal diversity with productivity

<i>Explanation</i>	<i>Features of explanation</i>	<i>References</i>
More individuals	<ol style="list-style-type: none"> 1. Productivity is a limiting factor. 2. More productive sites can support more individuals in total. 3. The number of species generally increases with the number of individuals, for example, because populations with low abundances are more likely to go extinct. 4. Therefore, more species will be found at the more productive sites. 	Wright 1983; Rosenzweig and Abramsky 1993; Abrams 1995
More specialization	<ol style="list-style-type: none"> 1. Productivity is the sum of a variety of resources. 2. A minimum amount of a resource type is needed to support a specialist species. 3. At low productivities, some resource types are too rare to support a specialist species. 4. Increasing productivity increases the amount of each resource type, and so more resource types can support a specialist species. 5. Specialization prevents competitive exclusion, so more productive communities have more species. 	Schoener 1976; DeAngelis 1994
Dynamic equilibrium models	<ol style="list-style-type: none"> 1. More productivity results in faster population growth rates. 2. Faster growth rates result in rapid recovery of population abundances after disturbance. 3. At any point in time, populations with low abundances are more likely to go extinct. 4. Therefore, more productive communities have a higher equilibrium number of species, at least as long as the rate of disturbance prevents populations from becoming so abundant that competitive exclusion occurs. 	Huston 1979, 1994; DeAngelis 1994
One more trophic level	<ol style="list-style-type: none"> 1. The number of trophic levels in a food web is limited by energy. 2. If an increase in productivity allows for the appearance of a trophic level above that being studied (predator, parasite), this reduces population sizes. 3. Competitive exclusion is less likely with reduced population sizes. 4. Therefore, diversity increases with productivity. 	Abrams 1995; Moen and Collins 1996

ing 1983; Kitching and Pimm 1985). There are some trophic complexities in the path between leaves and the insects. Tree-hole leaves are coated in fungi and bacteria, which in turn support a rich protozoan community (Lackey 1940; Walker et al. 1991; J. Birch, unpublished data). Insects appear to feed on all these trophic levels (detritus, fungi, bacteria, protists: Maguire et al. 1968; Fish and Carpenter 1982; Walker et al. 1991) although the dietary contribution of each remains undocumented for most insects. In keeping with our earlier assertion that productivity-richness theory should be based on the productivity of resources available for consumption (see also Abrams 1995), we should logically measure productivity as the sum of energy from detritus, fungi, bacteria, and protists. We make the simplifying assumption that this energy sum is, more or less, proportional to the amount of leaf litter, admittedly glossing over some of the intricacies of trophic dynamics in the process. However, virtually all studies of detritivore insects use the same approximation of leaf litter biomass for total resource energy, for practical reasons (e.g., Pimm and Kitching 1987; Jenkins et al. 1992; Richardson 1992). Although relevant data from tree holes are sketchy, bacterial biomass appears to be related to both the amount and decay rate of leaves (Fish and Carpenter 1982; Walker et al. 1991). Finally, although productivity is strictly speaking a rate measure, most leaves enter tree holes only in a short period in autumn, allowing us to use initial leaf biomass as a productivity measure.

Only the larval stages of insects are found in tree holes. The adults are terrestrial. The abundance of insects in tree holes is therefore the result of resource limitation on larval survival and of oviposition decisions of adults but is not directly related to population growth. Nonetheless, species with low abundances are still predicted to have a higher chance of local extinction, the key premise of the More Individuals Hypothesis. Dynamic equilibrium models (table 1), on the other hand, which explain productivity-richness correlations on the basis of population growth rates, are clearly inappropriate for tree holes. Nor can productivity-richness relationships be explained by the addition of a trophic level (table 1): no predators of detritivore tree-hole insects have been found in Britain (Kitching 1971; Bradshaw and Holzapfel 1992). The "More Specialization Hypothesis" (table 1) is a potential explanation, and we evaluate the relevant evidence in the "Discussion" section.

Assembly versus Disassembly of Communities

Explanations for positive productivity-species richness relationships do not distinguish between assembling and disassembling communities, yet community assembly

and disassembly may involve quite different processes. By community assembly we mean the progressive accumulation of species over time, by community disassembly the progressive loss of species. Community assembly depends on processes operating on two scales: the between-site process of colonization and the within-site process of local species extinction. Community disassembly, by contrast, in the limit reflects just the within-site process of local species extinctions. Consequently, the effects of productivity may differ between the assembly and disassembly of a community because of priority effects (Kneidel 1983; Shorrocks and Bingley 1994) or because of the effects of productivity on colonization (Tilman 1993). We explored this possibility by examining both the assembly and disassembly of tree-hole insect communities along a productivity gradient.

Methods

We undertook three separate experiments to test the More Individuals Hypothesis. The first experiment examines the effect of productivity on community assembly, the second explores the effect of productivity on community disassembly, and the third separates the effects of productivity on oviposition and larval survivorship. The aims of each experiment are outlined in the following sections.

Assembly Experiment: Productivity and Colonization

Artificial tree holes, designed to mimic the buttress tree holes of European beech (*Fagus sylvaticus*), were used to examine the effects of productivity on species richness in assembling communities. Natural buttress tree holes were not used because the substantial differences that exist among natural tree holes in volume, for example (Sota 1996; Srivastava 1997), could have obscured the effects of productivity. Artificial tree holes have been effectively used to simulate natural tree holes in many parts of the world and are colonized rapidly (e.g., Yates 1979; Jenkins et al. 1992).

Artificial tree holes were each composed of a transparent plastic box (11 cm × 16 cm × 5.5 cm deep; the boxes had a lip, giving an opening of 9 cm × 14 cm) filled with a measured amount of leaf litter (see below) and settled tap water to a total volume of 750 mL. A piece of beech bark (about 8 cm × 4 cm) in each container served as an oviposition site, and garden netting (mesh 1 cm × 1 cm) over the opening prevented entry of falling leaves (but not ovipositing insects). A total of 64 artificial tree holes were set up March 1–3, 1994, and another 16 in early March 1996. The leaf litter added to tree holes was composed of fallen beech (60% dry

weight) and oak (40% dry weight) leaves, a mixture similar to the leaf litter found in nearby natural tree holes. Leaves were collected in early February, air-dried at 80°C for 10 h, and ground in a domestic blender (15 s/500 mL) to a density of 157 g L⁻¹. Leaf fragments were approximately 0.3–0.5 cm in diameter.

All artificial tree holes were set out in a 200 × 80-m wooded area at Silwood Park in south-central England, in a site dominated by silver birch *Betula pendula* Roth. Beech trees (*Fagus sylvatica* L.) with natural tree holes occurred adjacent to the area, providing a pool of potential colonists. In this area, birch trees of greater than 70 cm diameter breast height (diameter at 1.4 m) and at least 5 m apart were selected. One artificial tree hole was sunk into the soil (3 cm deep) at the base of each tree, between the buttresses and as close as possible to the trunk (mimicking natural buttress tree holes that occur close to the ground, at the junction of beech buttress roots and the trunk). Birch trees were selected in preference to beech trees as the natural tree holes of the latter would have interfered with the treatments.

Litter fall in England is very high from September to October (140–320 g dry weight m⁻²), and minimal (<50 g m⁻²) thereafter (Kitching 1983). Leaf litter in tree holes in March was therefore assumed to be largely derived from litter fall over the period beginning in the previous September and ending in late February, a total of 760 g m⁻² (Kitching 1983). As the opening to each artificial tree hole was 9 cm × 14 cm, this results in a natural leaf litter level of 10 g (760 g m⁻² × 0.09 m × 0.14 m) in each. Four levels of leaf litter were selected: 5×, 1×, 1/5×, and 1/25× natural levels, equivalent to 50 g, 10 g, 2 g, and 0.4 g, respectively, per tree hole ($n = 50$ treatment⁻¹). Note that in natural tree holes, leaf litter amounts can differ by two orders of magnitude (even in holes of the same volume).

Every 2 mo between March 1 and November 1, 1994, four randomly selected tree holes for each treatment (5×, 1×, 1/5×, 1/25×) were harvested. The 16 tree holes set up in early 1996 were harvested in the first week of November 1996. The complete contents of each tree hole (water and debris) were sorted in shallow pans and searched thoroughly for species. The abundance of each species was determined by a complete count for all but the most abundant chironomids (abundance of these was determined by subsampling). Mean size was recorded, as length, for each species in each tree hole (in the case of multiple cohorts, size and abundance were recorded separately for each cohort) and then converted into fresh weight using empirically derived relationships (Srivastava 1997; r^2 from 0.91 to 0.98). Distilled water was added to tree holes as often as required to keep water levels constant (as frequently as every 2 wk in the summer).

Leaf litter amounts in the artificial tree holes changed over the season, especially during autumn leaf fall. By July 1994, the 1/25× treatment had increased from the initial 0.40 g dry weight to 1.45 g (± 0.91 ; $\bar{X} \pm SD$), but the amount of leaf litter in the other treatments had not changed. In September 1996, the 1/25× treatment had only marginally more debris, an average of 2.14 g (± 0.67). By November 1994, the 1/25× treatment had increased further to 4.60 g (± 1.48), becoming indistinguishable from the 1/5× (2.0 g original) treatment with 5.17 g (± 2.89) leaf litter. The most productive treatment (50.0 g original) had decreased to 34.1 g (± 3.18), but the 1× treatment (10.0 g original) was unchanged at 10.57 g (± 0.93). The experiment was terminated at this point because of the change in treatment levels. It is not possible to simply correct for the new leaf litter amount in this case because the species richness of a given month integrates effects of leaf litter over the previous months, particularly during peak oviposition periods.

There was no effect of productivity on water pH ($r = 0.00$, $p > .05$, $n = 16$) and indeed little difference in pH among tree holes ($\bar{X} \pm SE = 7.37 \pm 0.05$, September 1996).

Estimating Energy Utilized. The total energy use of a community is the sum of the energy used by its component species. The energy used by a species is frequently not proportional to its relative abundance (Brown and Maurer 1986; Pagel et al. 1991), so simply summing abundances over species will not accurately reflect community energy use. We therefore corrected abundances for body size. The exponent of body size–metabolic rate relationships has been argued to be both 0.67 (Brown and Maurer 1986) and 0.75 (Peters 1983). Specific studies of insects reflect this uncertainty, reporting exponents between 0.62 (Kayser and Heusner 1964, summarized by Peters 1983) and 0.76 (Zotin and Konoplev 1978, summarized by Peters 1983). We used as the exponent the midpoint of this empirical range, 0.69, but similar results would have been obtained by any of these exponents. We chose to compare the energy use of all individuals with that of one of the commonest animals in the tree holes, a typical third instar *Metriocnemus martinii* chironomid (mass 0.00054 g):

$$\text{chironomid-equivalent abundance} = 0.69 \log (\text{individual weight}/0.00054 \text{ g}). \quad (1)$$

We do not convert chironomid-equivalent units into Joules d⁻¹ as we do not have the appropriate physiological data for *Metriocnemus*. For comparative purposes, the units are irrelevant. This approach ignores potential differences in energy requirements or efficiency between

filter feeders and detritus chewers or the effects of resource processing chains. Such effects are presumed to be only minor modifications to the larger patterns driven by body size.

Statistical Analysis. All analysis was based on generalized linear models, using GLIM version 3.77 (1985—see Crawley 1993). The distribution of species richness, abundance, and energy use data necessitated using models with a Poisson error structure. Significance of terms was determined by sequential deletion (Crawley 1993) in all cases. Log-link functions were used in preference to logarithmic transformations (the latter were often not possible, in any case, because of 0 values). Residual plots were routinely checked for heteroscedasticity, and overdispersion was corrected in Poisson models using an empirically derived scale parameter (Crawley 1993).

Disassembly Experiment: Productivity Loss and a Species-Rich Community

This experiment examines the effect of productivity reduction on an established species-rich community. We designed a community typical of high productivity conditions, based on six 5× productivity artificial tree holes examined in late October 1994 (set up alongside or as part of the assembly experiment). Our “typical” community had a species richness of four, like the 5× tree holes (modal richness = 4, \bar{X} = 4.3, total of seven species). The typical community was composed of the four most common species from the 5× tree holes: the syrphid *Myiatropa florea* (modal abundance 29 larvae/5× tree hole) and the mosquitoes *Aedes geniculatus* (1 larva/tree hole), *Anopheles plumbeus* (12 larvae/tree hole), and *Culex torrentium* (13.5 larvae/tree hole). All possible species pairs coexist in nature.

The typical community was assembled in each of 16 small plastic containers (8.5 cm × 8.5 cm × 5.0 cm), half the volume of the original 5× tree holes. Abundances of the species in the typical community were therefore approximately half modal values for the 5× tree holes: 10 *Myiatropa* container⁻¹, (about 0.08 g live weight), 1 *Aedes* container⁻¹ (predominantly third instar), 5 *Anopheles* container⁻¹ (predominantly second instar), and 6 *Culex* container⁻¹ (predominantly fourth instar). This reduction in volume, although compensated for by reductions in abundance, may still have affected the community (e.g., through decreased volume:area ratios, etc.). This would be problematic if we intended to compare disassembled communities to the original community, but we are simply interested here in documenting the disassembly process (i.e., we need only assume any volume effects are similar between treatments).

Both larvae and leaf litter for this experiment were obtained from the pooled contents of the six 5× tree holes described above and two additional 5× productivity tree holes (also set up alongside the assembly experiment). The 16 experiment containers were divided into four productivity levels, 1/25×, 1/5×, 1×, and 5×, which contained (respectively) 1.4 g, 7.0 g, 35 g and 175 g wet weight leaf litter per container. These leaf litter amounts were based on the assembly experiment tree holes in late October but were adjusted slightly to ensure a 125-fold difference across treatments. (In the assembly experiment, detrital entry and decomposition had reduced the difference between treatments by late October.) As with abundances, leaf amounts were half that of the analogous assembly experiment tree holes because of the smaller container size.

Water was obtained from another eight artificial tree holes (also set up alongside the assembly experiment), comprising two each of 1/25×, 1/5×, 1×, and 5× productivity. Productivity may affect water quality and, as some of the study species are filter feeders, we wanted to preserve this effect in this experiment. The water from each pair of tree holes of the same treatment was mixed and then added to containers of the analogous treatment level in this experiment to constant height (4 cm).

The containers were covered in mesh and kept in a small unheated shed with windows. Temperatures were near natural. Light levels were low but comparable to those that tree-hole insects experience in dense woodland.

Survival and size (measured as length and converted to mass, as in the assembly experiment) of all larvae were examined after 1 wk, and then every 2 wk, until a constant number of individuals was obtained at 11 wk after community assembly. For *Culex* individuals, time of pupation and time of emergence were also recorded (no other species pupated during the experiment).

Species richness and abundance are both count data, and so were analyzed in models with Poisson errors. Energy use is a continuous variable and was analyzed in models with normal errors. Larval survivorship for each species, in the form of proportion data, was modeled with binomial errors and a logistic link function.

Oviposition Experiment: Productivity, Syrphids, and Mosquitoes

The effects of productivity on oviposition decisions and subsequent larval survivorship can be separated by manipulating productivity after oviposition but before the eggs have hatched or larvae are large enough to be resource limited. Adults could oviposit in artificial tree holes of two productivities: “low” or “high” (described

in detail below). Larvae similarly developed in either low or high productivity. The three experimental treatments were LL (adults and larvae both encounter low productivity), HH (adults and larvae both encounter high productivity), and LH (adults encounter low productivity, debris added after oviposition, and larvae encounter high productivity). The fourth treatment that would have made this a full factorial design (HL, where adults encounter high productivity but larvae encounter low productivity) was not practical: debris cannot be removed without the possibility that the minute newly hatched larvae are removed with it.

One artificial tree hole of each of the three treatments (LL, HH, LH) was placed against each of 10 large oak trees in Silwood Park (total of 30 artificial tree holes). That is, treatments were crossed with blocks without replication, where each oak tree serves as a block. The oak trees were >9 m apart and the artificial tree holes were >0.8 m apart around each tree. Oak trees were used in preference to neighboring large beech trees, as the natural tree holes in the beech might have affected oviposition decisions. The base of the trees, including artificial tree holes, were enclosed by poultry netting to prevent disturbance by rabbits.

Each LL, LH, and HH artificial tree hole was composed of a plastic container (as in the disassembly experiment), oak bark (about 8 cm × 3 cm, for insects to oviposit upon), crushed leaves, and water. The LL and LH tree holes received 2 g dry weight of crushed beech/oak leaves (prepared as described for assembly experiment), and the HH tree holes received 10 g. The combined weight of crushed leaves, including those added later to the LH tree holes, had been incubated for 2 wk prior to the experiment in distilled water (30 mL water g⁻¹ dry leaves). The water drained from the leaves was added directly to the HH tree holes, or diluted fivefold before being added to the LL or LH treatments (in both cases, to a total volume of 300 mL). The quantity of debris affects water color in artificial tree holes, and we wanted to preserve this difference in this experiment.

The tree holes were available for oviposition for 2 wk. Less time would have meant too little oviposition for statistical analysis, while more time would have meant that the larvae would have started to be resource limited. The experiment was repeated three times, with oviposition allowed either from August 3 to 17, 1995, May 21 to July 4, 1996, or July 10 to 26, 1996 (most oviposition by tree-hole species occurs in July and August). The first run captured a peak of *C. torrentium* oviposition and the third a peak of *M. florea* oviposition. Oviposition was too rare for analysis in the second run, which is not described further. At the end of the *Culex* run, most eggs had only just begun to hatch (the initial census was de-

layed until after all had hatched). At the end of the *Myiatropa* run, most eggs had just hatched. Other species were present infrequently and were removed.

After the oviposition period, the artificial tree holes were moved into two mesh cages (50 cm × 50 cm × 50 cm, containers randomly rearranged every week) and the tree-hole openings were sealed with further mesh. Crushed leaves (8 g dry mass, incubated in water for several weeks; see above) were added to each of the LH tree holes. *Culex* containers were examined 2, 4, 6, 10, and 12 wk after the end of the oviposition period. *Myiatropa* containers were examined on the very last day of the oviposition period, and 12, 24, and 36 d thereafter. At each census, the abundance of each species was completely counted.

The high and low productivity treatments of this experiment have the same amounts of leaf litter as the 1× and 1/5× treatments, respectively, of the assembly experiment, but the containers are half the volume. They are therefore not completely analogous to any treatment of the assembly experiment.

Statistical Analysis of Oviposition versus Survivorship. Larval abundance was compared between treatments and blocks with a generalized linear model approximation of ANOVA, using a Poisson error distribution (abundances are count data, with numerous 0 values). Although data are presented for all dates, only the initial and a later treatment are analyzed, to avoid too many repeated measures. The last census for *Myiatropa*, 36 d after oviposition, is used as this later date to maximize the chance of effects on larval survivorship, and the later date for *Culex* was chosen to be comparable to *Myiatropa*: 42 d after oviposition and 28 d after the initial census. A Bonferroni layering technique (Darlington 1990) was used to correct for repeated measures. There were two planned comparisons: LH + LL versus HH and LH + HH versus LL. These were not orthogonal, and so significance levels were also corrected by a Bonferroni layering technique. Note that the combination of both Bonferroni corrections could lead to a maximum correction factor of 4, and a minimum of 1.

Statistical Analysis of Larval Survivorship. Larval survivorship was also analyzed for only those containers in which oviposition occurred. As this substantially restricts the data set and so reduces statistical power, we included data from additional tree holes run alongside the above experiment (two per blocked tree). These tree holes were identical to the tree holes described above, except that they initially contained less water (a treatment that has no bearing in the present context). By the end of the oviposition period, though, leaf litter and water were added

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so that larvae encountered either low or high productivity conditions, exactly as for the LL, LH, and HH treatments.

For this analysis, all containers in which larvae experienced high productivity conditions (HH, LH, and extras) were combined, and all containers in which larvae experienced low productivity conditions (LL and extras) were similarly combined. By including initial density as a covariate, we believe we account for all the obvious differences between the various treatments that occurred during the oviposition period. Block effects cannot usefully be examined in this restricted analysis (as there would be too many missing values), but substantial differences between blocks are similarly accounted for by using initial density as a covariate (recall that, postoviposition, the containers were moved together, so there are no blocks during the time larvae are growing). Even though initial density is accounted for, large differences in sex ratios between oviposition treatments or blocks might influence results. In mosquitoes, protandry (early emergence of males) is common and may be exaggerated by resource limitation (Kleckner et al. 1995). Although protandry occurred in *Culex*, by the end of the experiment treatments did not differ noticeably in the sex ratio of emerged adults. *Culex* was examined until almost all the individuals had either died or emerged, and survivorship is based on total numbers rather than rates.

Results

Species Composition of Artificial Tree Holes

Our artificial tree holes were colonized by virtually the same suite of insect larvae as their natural counterparts, with the exception of the coleopteran *Prionocyphon serricornis* Müller (occurs only in natural tree holes). All insects species described below are Diptera larvae, unless indicated otherwise. The most common species in both natural and artificial tree holes are the chironomids *Metriocnemus martinii* Thien and a *Diamesea* sp., the syrphid *Myiatropa florea* L., and the culicids *Aedes geniculatus* Oliver, *Culex torrentium* Martini, and *Anopheles plumbeus* Stephens. Psychodid larvae, *Pericoma* spp., occur occasionally in both, and tabanids very occasionally. A few species occurred in artificial but not natural tree holes, all rarely: the chironomid *Chironomus thummi* Kieff, the culicid *Culiseta annulata* Schrank, the anisopodid *Sylvicola* sp., the chironomid *Anatopynia (Macropelopia) fulva* Kieff, and adults of a dytiscid coleopteran. (The last two species are small predators but occurred very rarely—respectively, one and four tree holes out of 80—and in each case as only one to four individuals; their effects on the results should be minimal.)

As many species have summer oviposition peaks, colonization of the artificial tree holes was slow, and by May only 31% of the tree holes contained insects, mainly chironomids. By July, though, 88% of tree holes were colonized, and in September (both years) and November all tree holes contained insects. Species richness in July, September (both years), and November was also comparable to natural tree holes (zero to seven species), so our analysis is based on these four dates.

Community-Level Patterns. Species richness increased with productivity on all dates (fig. 1A–C). The More Individuals Hypothesis predicts that, in the absence of other productivity-related effects, species richness should increase as a power, or even logarithmic, function of productivity (see the introduction to this article). Indeed, on three of the four dates (July 1994, September 1994, and September 1996), power and logarithmic functions provided a substantially better fit than linear or exponential functions (table 2; note that as there is no difference in degrees of freedom between these four models, differences in r^2 values cannot be formally tested). When these three dates are analyzed together (table 2), it is evident that species richness increases with productivity in a similar fashion (ln productivity \times date interaction is not significant: $\chi^2 = 2.24$, $df = 2$, $p > .05$), but the actual magnitude of species richness differs between dates (date $\chi^2 = 6.39$, $df = 2$, $p < .05$). There were fewer species in all treatments in July, compared with the September dates, probably because most mosquito oviposition peaks occur after July.

Species richness in November 1994 did not conform to the same pattern. Although species richness increased with productivity, a linear or exponential function describes this increase better than a power or logarithmic function (table 2). By November, debris entry had obscured differences in productivity between 1/25 \times and 1/5 \times for several weeks (see "Methods"), and it may be that this reduced range in productivity resulted in a reduced range of species richness. Using final debris amounts rather than initial amounts for the other dates does not change the best fit function.

The More Individuals Hypothesis predicts that increases in species richness with productivity will be accompanied by increases in total abundance. There is little evidence for this in our data (fig. 2). Although a linear regression of total abundance on productivity is significant and fits the data no worse than other models (logarithmic, power, and exponential functions), this is entirely due to the results of one date, September 1996 (combining results of other dates does not affect the fit

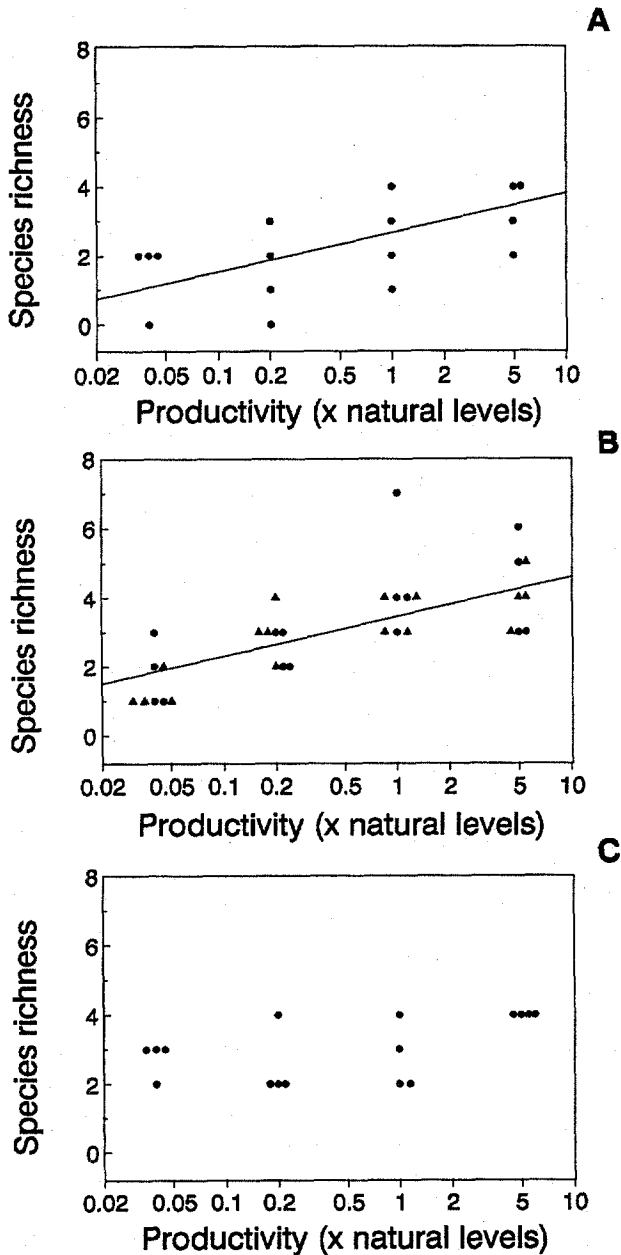


Figure 1: Species richness increases with productivity in assembling tree-hole communities in (A) July 1994, (B) September 1994 (circles) and 1996 (triangles), and (C) November 1994. Note that productivity is plotted on a logarithmic scale. Equations of the plotted regression lines are given in table 2. No regression line is plotted for (C) November 1994 as there may have been some slippage in the productivity treatments by this date.

A of model, $\chi^2 = 2.2$, $df = 4$, $p > .05$). The effect of productivity on abundance for the other dates is not significant (slope estimate: -0.66 ± 6.13) so the simplified model is: abundance = $112.5 (+71.66 \times \text{productivity}$, if date is September 1996). A reanalysis of the data without November, by which time there may have been some slippage in the treatments (see above), yields virtually identical results: abundance = $118.9 (+68.6 \times \text{productivity}$, if date is September 1996). It is not obvious to us why productivity and abundance were correlated in September 1996, unlike all the 1994 dates; species composition is similar between years. Finally, the model itself explains much less of the total deviance in abundance ($r^2 = 0.28$ with November, 0.27 without November) than expected from the strength of the productivity–richness model ($r^2 = 0.45$, without November). Note that no reformulation of the More Individuals Hypothesis would be able to overcome the fact that, on most dates, there simply are not more individuals in the more productive tree holes.

The final prediction of the More Individuals Hypothesis is a linear relationship between total energy use by the community and productivity. The energy use of communities may not be proportional to their total abundance if species differ considerably in body size and the distribution of abundance among body sizes differs between communities. We therefore correct abundances for body size using allometric relationships, as described in “Methods.” We chose to express these corrected abundances as the number of *Metriocnemus* chironomids that would use an equivalent amount of energy. The combination of 0 values and correlations between variance and mean values necessitated using generalized linear models with a Poisson error structure and a logarithmic link function (Crawley 1993).

Community energy use increased with productivity (fig. 3), either as a power or exponential function ($r^2 = 0.33$ and 0.39 , respectively; $\chi^2 > 28.1$, $df = 1$), irrespective of month (month $\chi^2 < 4.37$, $df = 2$; month \times productivity $\chi^2 = 2.43$, $df = 2$; month \times log productivity $\chi^2 = 3.78$, $df = 2$; all $p > .05$). Forcing a proportional function between energy use and productivity (i.e., setting the power function exponent to 1) significantly reduces the fit of the model ($\chi^2 = 42.2$, $df = 1$, $p < .05$). Therefore, although energy use increases with productivity, a proportional relationship is poorer than a curvilinear relationship in describing this increase.

In addition, the energy use–productivity data are clearly delimited by a triangular space in figure 3: although maximum energy use increases with productivity, minimum energy use is comparable between productivity treatments. When similar bounded relationships have been observed in plots of abundance against body size (reviewed by Lawton 1989), they have been interpreted

Table 2: Various functions between species richness (S) and productivity (P) in assembling tree-hole communities and associated r² values

	Logarithmic	Power	Linear	Exponential	Best-fit model
July 1994	.23	.24	.22	.21	$\ln S = .18 \ln P + .88$
September 1994	.49	.46	.23	.21	$S = .62 \ln P + 3.75$
September 1996	.68	.60	.40	.41	$S = .60 \ln P + 3.42$
November 1994	.24	.26	.41	.41	$S = .28 P + 2.56$
July 1994 + September 1994 + September 1996	.48	.46	.32	.30	July 1994: $S = .50 \ln P + 2.72$; September 1994, 1996: $S = .50 \ln P + 3.44^*$

Note: The equation presented for the multivariate model is for a simplified version of the full logarithmic model and, hence, has a slightly lower r² than the full logarithmic model. For all regression models presented in this and subsequent tables, p < .05 unless otherwise indicated.

*r² = .45. This value is for the three-date model, which is presented as two separate equations for clarity.

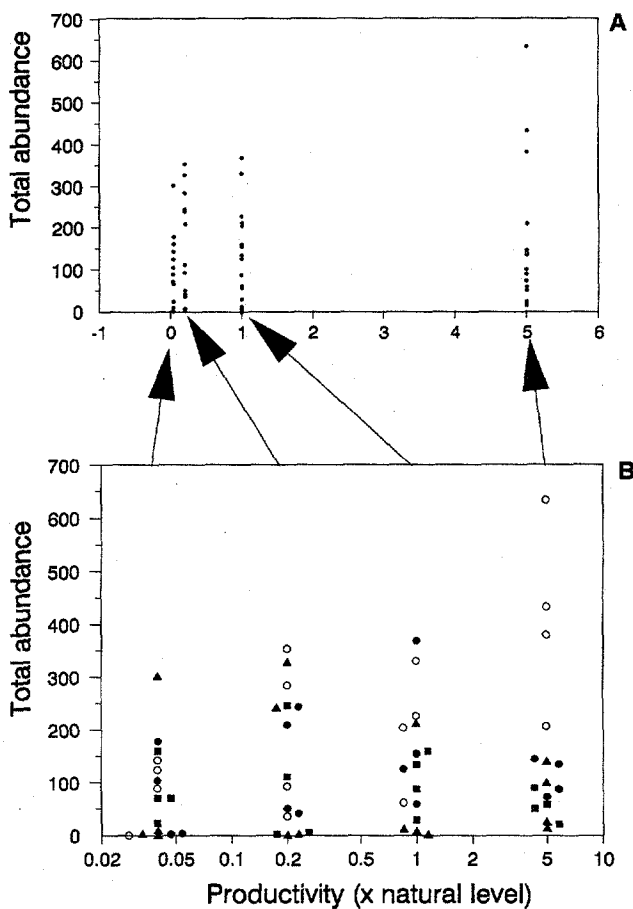


Figure 2: There is only weak linear relationship between total abundance and productivity in assembling tree-hole communities. A, This linear relationship is due to the results from only one date, September 1996. The data are replotted on a logarithmic scale (B) simply to allow the date markers to be clearly displayed. Abundance was measured in July 1994 (triangles), September 1994 (solid circles) and 1996 (open circles), and November (squares).

to mean that other factors—in addition to body size—are important constraints on population abundance (Lawton 1989; Brown 1995). We interpret figure 3 to mean that productivity sets an upper limit to community energy use (i.e., an energetic carrying capacity), but the energy use of many communities falls far below this upper limit because of other limiting factors or chance events.

In summary, total abundance is not strongly related to productivity, and total energy may be only partially determined by productivity. The More Individuals Hypothesis is therefore an insufficient explanation for the logarithmic productivity-richness relationship observed in this experiment.

Species-Specific Patterns. No species occurred preferentially in low productivity tree holes (fig. 4). Most species occurred preferentially in high productivity tree holes (*Myiatropa*, *Aedes*, *Anopheles*, *Diamesea*; $r > 0.40$, $p < .05$), although *Metrioconemus* and *Culex* occurrences were not significantly correlated with productivity ($r < 0.12$, $p > .05$). There is little evidence to suggest that the preferential absence of many species from the low productivity tree holes is due to resource limitation of larval survivorship. If it were, larval abundances in the few low productivity tree holes where such species are present would be expected to be near zero as well. This is clearly not the case for most species, with the striking exception of the syrphid *Myiatropa* (fig. 4).

Disassembly Experiment: Productivity Loss and a Species-Rich Community

Community-Level Response. The species richness of a typical high productivity community was decreased by large reductions in productivity (fig. 5A). By the last census (11 wk after the experiment began) there was a logarithmic

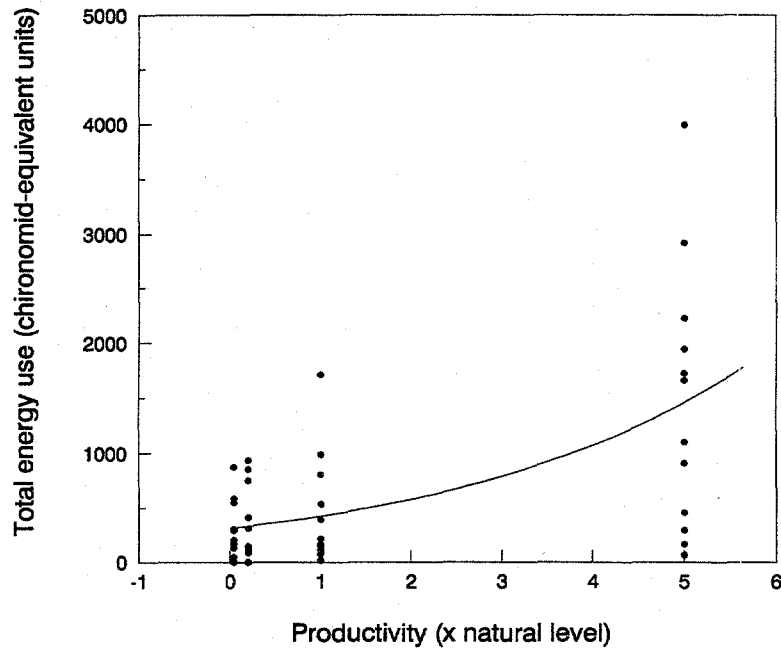


Figure 3: Maximum energy use by assembling tree-hole communities is proportional to productivity, but the energy use of most communities falls well below the maximum values. The equation of the plotted line is $\ln \text{Energy} = 0.309 \text{ Productivity} + 5.74$.

mic (or power) function between species richness and productivity (other functions had poorer fit; table 3, "All productivity treatments"). The following results are based on this final census, when abundances had stabilized.

Initially, it appears that the second and third predictions of the More Individuals Hypothesis do not hold. Both abundance and energy use, predicted to be linear functions of productivity, are better described as logarithmic or power functions (fig. 5B, C; table 3, "All productivity treatments"). Total abundance and total energy use are constrained, though, by the initial community. If abundances or energy use were not at their maximum value in the original 5 \times community, as seems likely given their wide ranges in 5 \times energy utilization (fig. 3), the 5 \times treatment may have lower abundances and energy use than expected from physiological constraints alone. When the 5 \times community is removed from the analysis, the best richness-productivity function remains logarithmic, but both abundances and energy use become linearly related to productivity (table 3, "1/25 \times , 1/5 \times , and 1 \times productivity treatments"; fig. 5D–F). Although a power function formally has the best fit for the energy use and productivity data, the estimated exponent is 1.008 (± 0.1214) so the curve is essentially linear, and the linear equation is presented instead. The intercept of the linear equation is not significantly different from 0 ($F = 0.096$, $df = 1, 10$, $p > .05$) so energy use is exactly proportional to productivity.

Species-Specific Response. Differences in species richness between productivity levels were caused by the complete loss of *Myiatropa* or *Aedes* from some of the less productive tree holes. This loss was related to significant reductions in larval abundance with decreases in productivity (equations given in fig. 6; *Myiatropa* $\chi^2 = 95.9$, $df = 1$, $p < .01$; *Aedes* $\chi^2 = 4.92$, $df = 1$, $p < .05$). By contrast, there was no significant effect of productivity on the survivorship of larval *Anopheles* (fig. 6; $\chi^2 = 0$, $df = 1$, $p > .05$). All *Culex* emerged before the end of the experiment (mainly between weeks 3 and 5) and so this species plays no role in any of the foregoing analyses. Note, however, that there was no effect of productivity on the proportion of *Culex* larvae that successfully emerged ($\chi^2 = 1.62$, $df = 1$, $p > .05$; details in fig. 6).

Oviposition Experiment: Productivity, Syrphids, and Mosquitoes

Separating Oviposition and Larval Survivorship. Adults of both the syrphid *M. florea* and the mosquito *C. torrentium* preferred to oviposit in high rather than low productivity containers (fig. 7A, B). Specifically, initial values of mean larval abundances differed among the three treatments (*Culex* $\chi^2 = 8.29$, $df = 2$, $p < .05$; *Myiatropa* $\chi^2 = 14.46$, $df = 2$, $p < .002$; Bonferroni corrections) and most of the deviance (89% in both species) was due to more larvae occurring in containers perceived by adults as high productivity (HH) than in containers

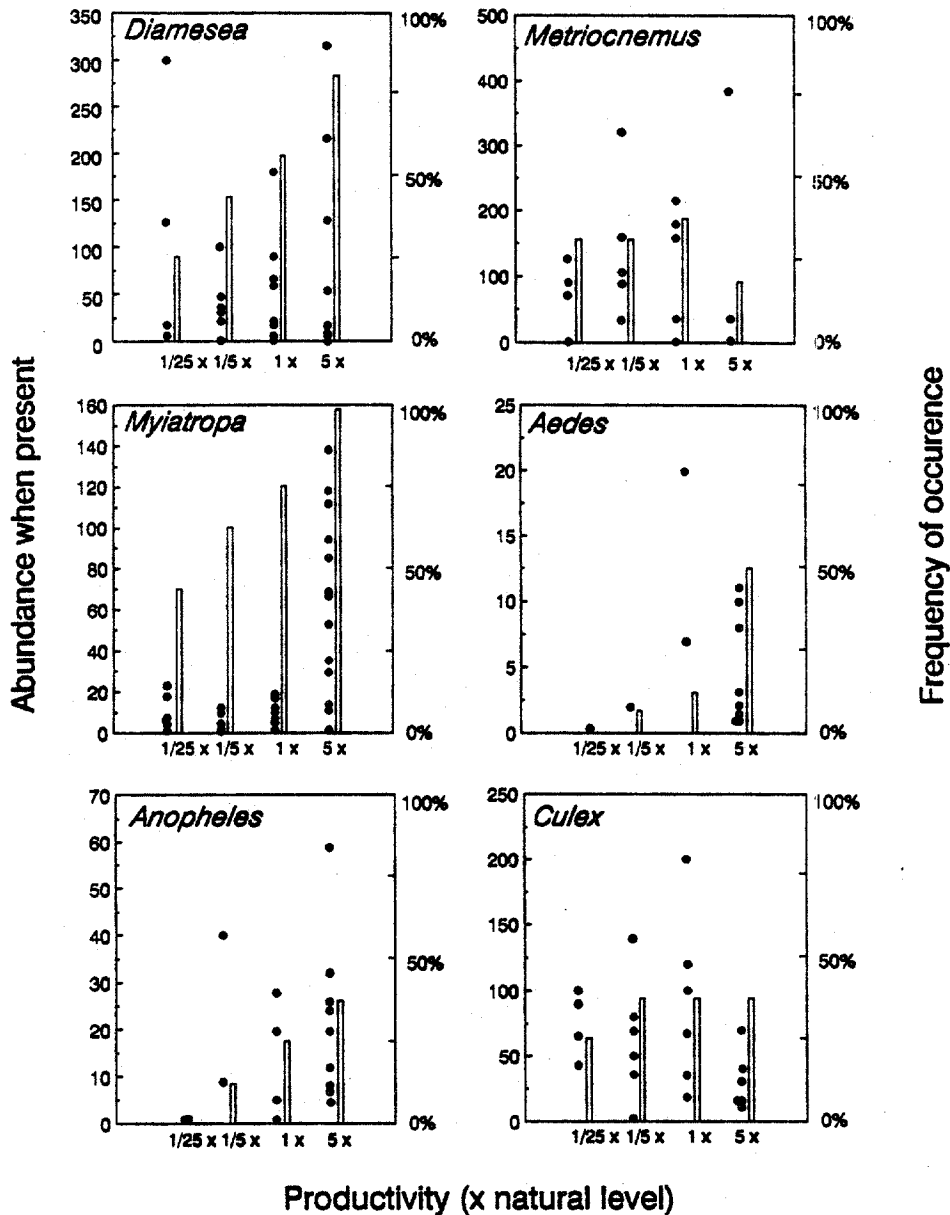


Figure 4: Response of the six most common species to the four levels of productivity of the assembly experiment. Both abundances and frequencies are based on 16 tree holes per productivity level (pooled over all dates), and 0 values of abundance are not shown.

perceived as low productivity (LL and LH). Combining LL and LH into a single treatment level (i.e., ignoring differences in larval food supply) did not significantly affect the fit of the model for either species (*Culex* $\chi^2 = 0.92$, $df = 1$; *Myiatropa* $\chi^2 = 1.52$, $df = 1$; both $p > .05$).

The difference in mean larval abundance between treatments held over time in *Myiatropa* (fig. 7A, at 36 d, treatment $\chi^2 = 14.18$, $df = 2$, $p < .001$, Bonferroni corrections). The oviposition-dependent differences at the beginning of the experiment continued to dominate: at

the final census date, combining LL and LH into a single treatment level (i.e., ignoring differences in larval food supply) still did not significantly affect the model ($\chi^2 = 0.33$, $df = 1$, $p > .05$). It is noteworthy that the mean abundance of LL appeared to decline faster than that of LH (fig. 7B), suggesting that there may be some small effect of productivity on larval survivorship (which we discuss further in the next section). The important point, though, is that the magnitude of this effect pales in comparison to the overwhelming effect of productivity on

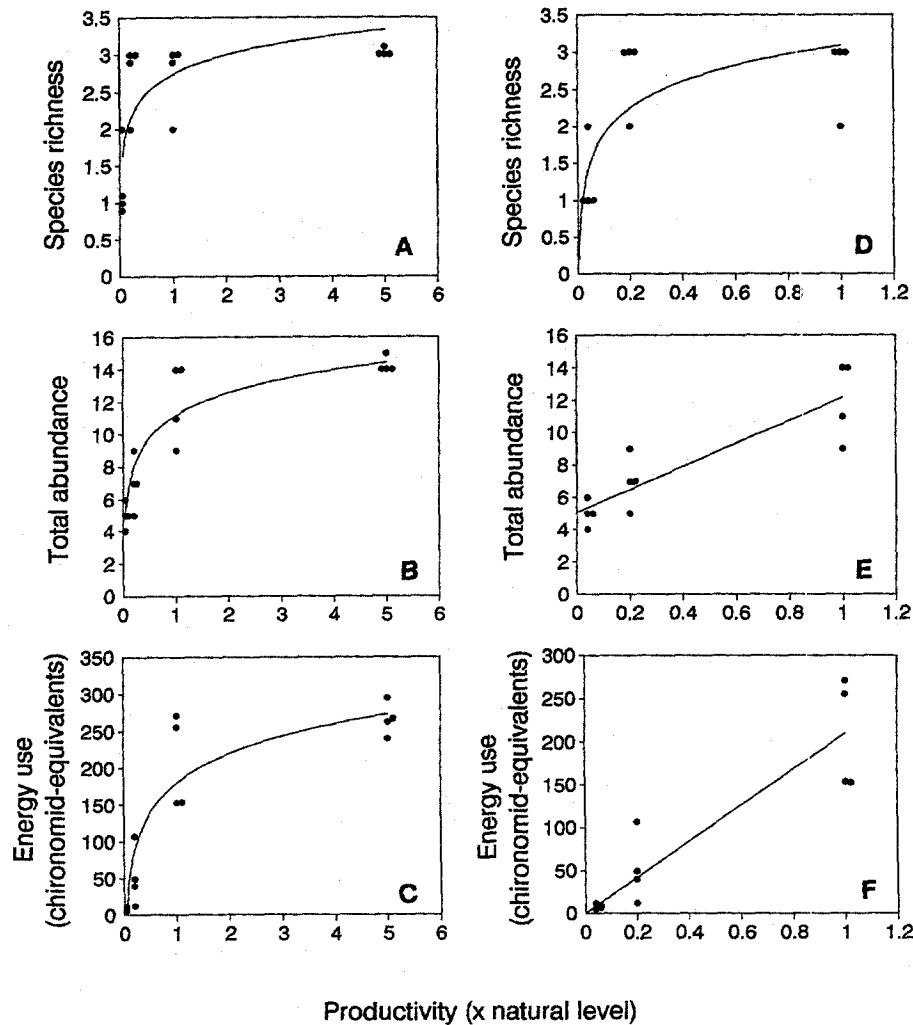


Figure 5: The analyses of the disassembly experiment were either based on all productivity treatments (A–C) or on all but the 5× productivity treatment (D–F). Loss of productivity resulted in decreases in (A, D) species richness, (B, E) total abundance, and (C, F) energy use. Equations of the plotted regression lines are given in table 3.

oviposition decisions. It is clearly impossible to ignore productivity levels encountered by ovipositing females (i.e., combine LH and HH) without substantially decreasing the fit of the model ($\chi^2 = 11.42$, $df = 2$, $p < .002$, Bonferroni corrections). By contrast, in *Culex* the initial differences between treatments in mean larval abundance disappeared within a few weeks (fig. 7B, treatment effect at 42 d $\chi^2 = 4.97$, $df = 2$, $p > .05$). The block effect was significant for *Myiatropa* ($\chi^2 = 23.75$, $df = 9$, initially, 29.16 on day 48, $p < .002$, Bonferroni corrections), and initially for *Culex* ($\chi^2 = 22.76$, $df = 9$, $p < .02$, Bonferroni corrections) but not for *Culex* after 42 d ($\chi^2 = 14.03$, $df = 9$, $p > .05$).

Productivity and Larval Survivorship and Emergence. Even if larval survivorship did not dominate differences between treatments in this experiment, it does not follow that productivity has no effect on larval survivorship. Productivity could have important but relatively small effects on larval survivorship, the time span of the experiment could have been too short (for *Myiatropa*), or the effects of larval survivorship could have been obscured by stochasticity in the frequency of oviposition.

The effect of productivity on larval survivorship can be examined independently of the frequency of oviposition if the analysis is restricted only to those containers in which eggs were oviposited. As this substantially reduces

Table 3: Regressions between species richness (*S*), total abundance (*A*), energy use (*E*), and total productivity (*P*) after 11 wk of disassembly for all productivity treatments and for the 1/25×, 1/5×, and 1× productivity treatments

Regressions	Logarithmic r^2	Power r^2	Linear r^2	Exponential r^2	Best-fit model
All productivity treatments:					
<i>S</i> and <i>P</i>	.55	.48	.21	.20	$S = .369 \ln P + 2.74$
<i>A</i> and <i>P</i>	.85	.84	.60	.55	$A = 2.00 \ln P + 11.2$
<i>E</i> and <i>P</i>	.86	.85	.62	.46	$E = 57.7 \ln P + 180$
1/25×, 1/5×, and 1× productivity treatments:					
<i>S</i> and <i>P</i>	.57	.50	.27*	.25*	$S = .524 \ln P + 3.09$
<i>A</i> and <i>P</i>	.75	.79	.79	.77	$A = 7.09 P + 5.07$
<i>E</i> and <i>P</i>	.76	.87	.84	.76	$E = 210 P$

Note: Although a power function formally has the best fit for the energy use and productivity data in the 1/25×, 1/5×, and 1× productivity treatments, it is so linear (see text) that the linear model is given instead.

*Not significant at $\alpha = .05$.

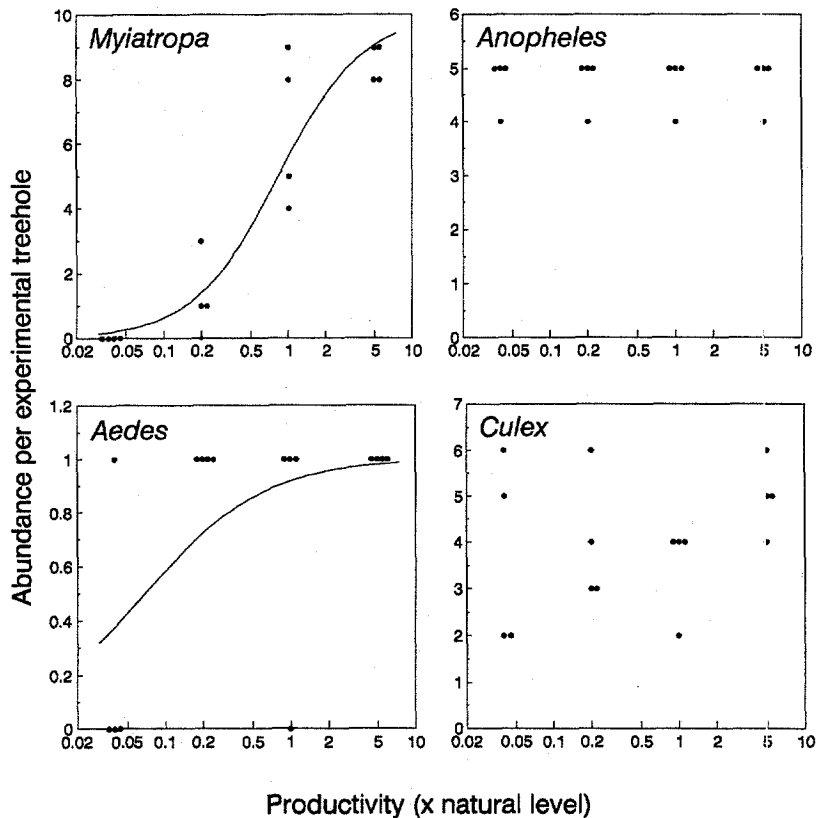


Figure 6: Abundance of each species at four levels of productivity in the disassembly experiment. For *Myiatropa*, the equation of the plotted line is: $\ln(\text{larvae alive}/\text{larvae dead}) = \ln \text{productivity} \times 1.27 + 0.230$. For *Aedes*, the equation is: $\ln(\text{larvae alive}/\text{larvae dead}) = \ln \text{productivity} \times 0.907 + 2.42$. Similar regression equations for *Anopheles* and *Culex* were not significant and so are not plotted. Only *Culex* larvae emerged during the experiment; for this species, “abundance” refers to adult not larval abundance.

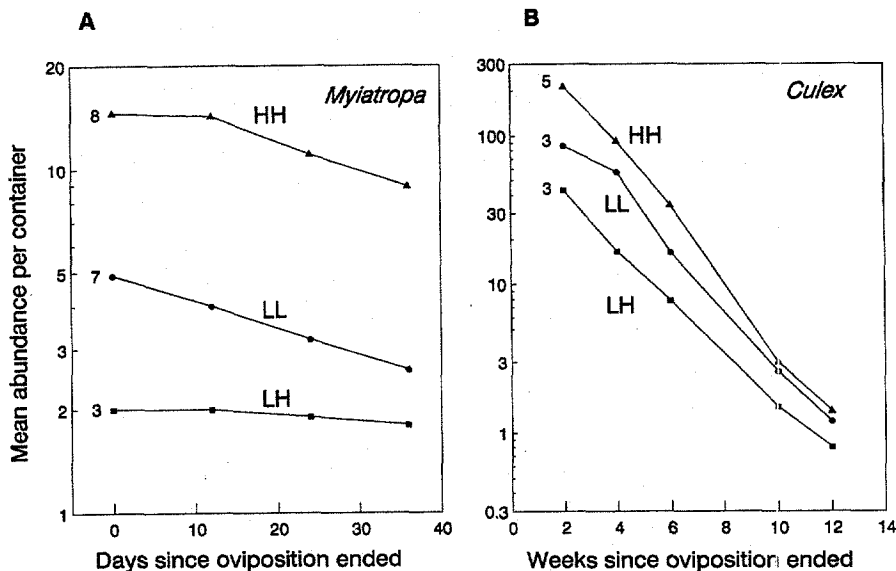


Figure 7: Mean larval abundances ($n = 10$) of (A) *Myiatropa* and (B) *Culex* at various times after oviposition, in the three productivity treatments LL, LH, and HH described in the text. Numbers next to initial abundance data refer to the number of containers with eggs (out of 10). Note that abundances are plotted on a logarithmic scale (a log-link function was used in the analysis).

the number of data points, observations on additional containers are included to increase the power of this analysis (see "Methods"). Initial density is used as a covariate to account for differences between tree holes in oviposition and block treatments (see "Methods").

For both *Myiatropa* and *Culex*, the number of larvae that died during the experiment was linearly related to the initial larval density (fig. 8A, B). A full model of initial density, productivity encountered by larvae, and their

interaction was fitted for both species, and nonsignificant terms removed by sequential deletion for the final models (r^2 of simplified models: 0.82 for *Myiatropa*, 0.97 for *Culex*). For both species, the covariate of initial density was highly significant (*Myiatropa* $F = 30.1$, $df = 1, 24$; *Culex* $F = 710$, $df = 1, 19$; $p < .001$).

For *Myiatropa*, there was a significant interaction between initial density and productivity: although the intercept did not vary between the two productivity levels ($F =$

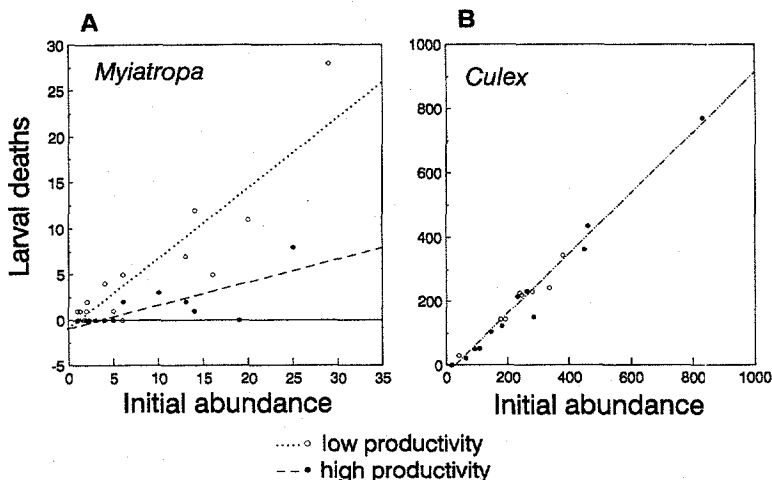


Figure 8: A, A greater proportion of *Myiatropa* larvae died in tree holes in which larvae encountered low productivity compared with high productivity (at low productivity, *Myiatropa* deaths = $0.782 \times$ initial density $- 1.03$; at high productivity, *Myiatropa* deaths = $0.252 \times$ initial density $- 1.03$). B, There was no difference in *Culex* mortality between low and high productivity tree holes (at low and high productivity, *Culex* deaths = $0.940 \times$ initial density $- 30.0$).

0.23, $df = 1, 22, p > .05$), the slope for the low productivity containers was almost twice as steep as for the high productivity containers (fig. 8A; $F = 34.5, df = 1, 23, p < .01$). In *Culex*, by contrast, larval deaths did not differ between low and high productivity containers once initial density had been accounted for (fig. 8B; interaction, $F = 0.54, df = 1, 17$; productivity, $F = 0.34, df = 1, 18$; both $p > .05$).

Finally, this restricted data set was used to look at the effect of productivity encountered by larvae on adult emergence as a possible reason for oviposition preference. Only *Culex* can be analyzed here, as insufficient *Myiatropa* larvae (total = 10) had pupated by the end of the experiment to permit comparisons. The number of *Culex* adults emerged (total = 259) was not related to initial density ($F = 1.08, df = 1, 19, p > .05$), productivity ($F = 2.01, df = 1, 18, p > .05$), or their interaction ($F = 0.13, df = 1, 17, p > .05$).

Discussion

Productivity-Richness Relationships in Tree-Hole Communities

Species richness in artificial tree holes increased with resource productivity (figs. 1, 5). In artificial tree holes in Australia, species richness also increased with productivity over a 100-fold range in productivity (Jenkins et al. 1992) but not a fourfold range (Pimm and Kitching 1987). Although it has been argued that unimodal relationships are the norm for local productivity-richness relationships (Rosenzweig and Abramsky 1993), there is no evidence for such a relationship in tree holes. If unimodal relationships require strong interspecific competition as a central mechanism to their generation (e.g., Rosenzweig 1971; Huston 1979, 1994; Tilman 1982; DeAngelis 1994), our simple positive productivity-richness relationship is perhaps not surprising: among the British tree-hole species, significant effects of interspecific competition have not been found for any species combination examined to date (Bradshaw and Holzapfel 1992). Note that our study does not explicitly examine direct or indirect interactions between species. The hypothesis we wish to test relies on patterns in overall community attributes (total individuals, total energy use) rather than the interactions between particular species.

Increases in species richness with productivity are predicted by what we have dubbed the More Individuals Hypothesis. In its most specific form, this hypothesis predicts logarithmic or power functions between species richness and productivity (prediction 1; see the introduction to this article). This is a result of coupling proportional relationships between productivity and total abundance (prediction 2) with standard power or logarithmic

functions between richness and abundance. The underlying assumption is that communities are energy limited, that is, energy use is proportional to productivity (prediction 3). Consistent with the first prediction, species richness increased as logarithmic or power functions of productivity, both when a community was allowed to assemble (all dates save November) or forced to disassemble through productivity reductions.

In the assembly experiment, there was little support for predictions 2 and 3. Total abundance was uncorrelated with productivity on most dates. Not even the most general formulation of the More Individuals Hypothesis would be able to overcome the fact that there are simply not more individuals in the most productive tree holes. And although total energy utilization of the community did generally (but not proportionally) increase with productivity, the effect of productivity was more obvious as an upper limit to energy utilization. Most tree holes actually had energy utilization rates much lower than this upper limit, suggesting other constraints than energy.

In the disassembly experiment, by contrast, there was strong evidence for the More Individuals Hypothesis (once the analysis was restricted to treatments where productivity could begin to limit energy use). In this experiment, abundance and energy utilization not only increased with productivity but increased in the predicted way as well: as linear functions.

There are two explanations for this difference between the assembly and disassembly experiments. First, the difference in results might simply be an artifact of community composition. Syrphid abundance was strongly correlated with productivity in both experiments, unlike the abundance of most other species. In the disassembly experiment, where syrphids happened to be the most abundant species, this resulted in correlations between total insect abundance (all species) and productivity. In the assembly experiment, where syrphids were usually not the most abundant species, variation in the abundance of other species between treatments appears to have masked this trend.

Second, although resource limitation can account for the productivity-richness correlation of the disassembling community, other mechanisms might have been more important in the assembling community. Recall that productivity could have influenced species richness in the assembly experiment through either effects on adults (oviposition decisions) or larvae (survivorship, growth, and emergence), but only through larval effects in the disassembly experiment (as the initial composition was experimentally imposed). In assembling communities, oviposition decisions seem to be extremely important in causing differences in larval abundance between productivity levels. For example, for both the mosquito, *Culex*, and the

syrphid, *Myiatropa*, differences in abundance between high and low productivity tree holes were dominated by oviposition decisions not by effects on larval survivorship or emergence (at least over the course of several weeks; see oviposition experiment, fig. 7). Oviposition decisions by adults are presumably based on expectations of larval survivorship (as one component of reproductive success), and so it could be argued that all productivity effects must ultimately depend on resource limitation of larval survivorship. Indeed syrphid larval survival was higher in the same high productivity tree holes that adults prefer for oviposition (oviposition experiment, disassembly experiment). Yet there are several lines of evidence that suggest this is not true for all tree hole species.

In the oviposition experiment, *Culex* mosquitoes preferred to oviposit in high rather than low productivity tree holes, even though there was no significant effect of this productivity difference on subsequent larval survivorship or emergence success. Even with the much larger range of productivity in the disassembly experiment (125-fold rather than fivefold), there was no evidence of productivity effects on the larval abundance, survivorship, or emergence of either *Culex* or *Anopheles* mosquitoes (although *Culex* larvae were already fourth instar when the disassembly experiment was set up). Yet both species were most frequent in the higher productivity treatments of the assembly experiment, apparently as a direct result of adult oviposition decisions.

The discrepancy between oviposition decisions and actual larval survivorship/emergence success in *Culex* (and perhaps *Anopheles*) may represent natural covariance between productivity and a low risk of drought disturbance. Drought disturbance is very important in British tree holes and can cause substantial decreases in larval abundance (Srivastava 1997). Drought-free tree holes tend to be deep (Srivastava 1997) and relatively full of leaves (permanence correlated with the ratio of debris volume to tree-hole opening area, $r = 0.66$, $n = 36$ natural tree holes) and contain dark water (Bradshaw and Holzapfel 1988; Srivastava 1997). Drought avoidance may explain why tree-hole mosquitoes typically show oviposition preferences for tree holes with a high density of organic debris and dark-colored water (Williams 1962; McDaniel et al. 1976; Ahmadi and McClelland 1983). The artificial tree holes of this study varied in both these measures. For example, in the assembly experiment, water darkness (measured as optical density at 460 nm, after Bradshaw and Holzapfel 1988) was strongly correlated with productivity (both log transformed; July 1996 and September 1996: $r > 0.96$, $p < .001$, $n = 16$ on both dates). Tree-hole mosquitoes may therefore have preferentially oviposited in the high productivity tree holes of our experiment expecting them to be low disturbance tree

holes. In our experiment they were not: all tree holes were kept topped-up with water. It is also possible that mosquitoes simply cannot detect tree holes low in dissolved organic matter. Such a proximate explanation may still be consistent with the evolutionary explanation given above.

By contrast, two other covariates of high productivity tree holes, lower water volume and greater structural complexity, were probably less important in generating the observed patterns. High productivity tree holes had less water than low productivity tree holes, simply because the large leaf volume displaced some water. However, reduced habitat volume is usually associated with fewer species, not more as seen in this study. High productivity tree holes, by virtue of their greater leaf surface area, may also have been habitats with greater structural complexity. However, other studies of aquatic insects suggest that leaf debris affects insect diversity and density more through resource inputs than through contributions to structural complexity (Richardson 1992; Warren and Spencer 1996; L. Rowe and J. Richardson, unpublished data).

Does the More Specialization Hypothesis Apply to Tree Holes?

According to the More Specialization Hypothesis (table 1), generalists (species consuming a variety of different resources) dominate low productivity communities as each resource is too scarce in itself to support viable specialist populations. As generalists overlap in resource use, interspecific competition for resources will be fierce, and competitive exclusion will depress species richness. High productivity communities, in contrast, can support many specialists. Competitive exclusion between specialists using different resources is unlikely (only the generalists will be excluded), so such high productivity communities can have higher species richness.

Like the More Individuals Hypothesis, therefore, the mechanism of the More Specialization Hypothesis is differential survivorship. Specialist species, found preferentially at high productivities, should have higher survivorship rates (and hence abundances) at these productivities. Generalist species should occur preferentially at low productivities, and survivorship and abundances should be greatest at these low productivities. Only *Myiatropa*, and less convincingly *Aedes*, have the characteristics of high productivity specialists: they preferentially occur at high productivities, where larval survivorship and abundances are highest (assembly, disassembly experiments). Most tree-hole species fit neither of these definitions: larval survivorship and abundance of *Anopheles*, *Diamesa*, *Culex*, and *Metriocnemus* appears to be uncorrelated with productivity (assembly, disassembly, oviposition experi-

ments). Thus, although the More Specialization Hypothesis may be a partial explanation for the patterns observed in tree holes (via *Myiatriopa*, *Aedes*), it cannot be the whole story.

Implications for the More Individuals Hypothesis

These results from artificial tree holes have three main implications for the general applicability of the More Individuals Hypothesis for positive productivity-richness correlations. First, in order for total abundance to be proportional to productivity, the More Individuals Hypothesis must assume that species have similar body sizes (Blackburn and Gaston 1996). This is not true in tree holes and may not be true in many other systems. There is often large variation in body size at each trophic level of animal communities (Peters 1983; Brown 1995). In assembling tree holes, the large body size of syrphids meant that they dominated energy utilization in tree holes yet often were a relatively low proportion of total abundance. Consequently, the preferential loss of syrphids in low productivity tree holes often led to decreases in both total energy utilization and species richness without significant changes in total abundance (contrary to the More Individuals Hypothesis). Large-bodied species often dominate energy utilization in animal communities, despite being a small proportion of total abundance (Brown and Maurer 1986; Pagel et al. 1991). In general, this will mean that productivity reductions can cause large reductions in community energy use, but only trivial reductions in total abundances, when it is also the largest species that are the most sensitive to productivity loss. This could occur if large species have a higher maintenance threshold (minimum amount of energy intake needed to match an individual's metabolic expenditure). The evidence for this is mixed (Lawton 1991). Large-bodied animal species could also be preferentially lost because of life-history correlates of body size: they tend to be both the least abundant species and the species with the slowest rates of population growth (Lawton 1989, 1990; Blackburn and Lawton 1994; Brown 1995). In plant communities, the situation may be even more complex, as increases in plant size with productivity necessitate decreases in plant abundance per unit area (Gorham 1979; Tilman and Pacala 1993). This change in abundance, in fact, may not only obscure positive productivity-richness correlations but has also been argued to be responsible for an artifactual humped productivity-richness relationship (Abrams 1995; Oksanen 1996).

Second, the More Individuals Hypothesis assumes that no important factors covary with productivity. Even in artificial tree holes, composed of identically sized containers and filled with a standard quality of debris, this

condition could not be met. High productivity tree holes may appear to be low disturbance tree holes to ovipositing adults. Such covariance might explain why some mosquito species (notably *Culex*, and perhaps *Anopheles*) preferentially oviposited in high productivity tree holes even though the larvae did not perform better in such tree holes under nondrought conditions. An analogous situation has been described by Sousa (1979) for the algal assemblages on stones. In this system, changes in species diversity with stone size are not entirely due to larger stones having larger surface area but are also due to larger stones having lower disturbance probabilities.

Finally, the More Individuals Hypothesis ignores the variety of processes affecting species richness. In tree holes, species richness is determined both by adult oviposition decisions and by larval survivorship, but only one of these processes—larval survivorship—conforms to the More Individuals Hypothesis. Historically, ecologists have paid more attention to the effects of productivity on local extinction than colonization processes (Tilman 1993). However, productivity may also affect colonization through effects on propagule establishment (Tilman 1993) or historical effects on the composition of the regional species pool (Taylor et al. 1990; Latham and Ricklefs 1993). A comprehensive theory of productivity-richness relationships must allow for such a variety of processes operating on different spatial scales.

In summary, our experiments with insect communities of tree holes conclude that, although the most productive tree holes have more species, this is not just a matter of more individuals. Our results, together with recent reappraisals of the energetic assumptions of (Blackburn and Gaston 1996) and observational evidence for (Latham and Ricklefs 1993) the More Individuals Hypothesis, suggest that explanations for increases in richness with productivity cannot be as simple as commonly believed.

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