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Do local processes scale to global patterns? The role of drought and the species pool in determining treehole insect diversity

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Abstract Global patterns in community species richness may represent limitations operating at the local scale, such as competitive exclusion and habitat suitability, or, in the case of unsaturated communities, limitations to the species pool of biogeographic regions. Separating the effects of local and regional processes on community richness requires combining small-scale experiments with broad surveys. I examine limitations to the number of aquatic insect species per treehole at the scale of a single woodland, and between eight biogeographic regions. Variation in species richness at the woodland scale can largely be explained by small-scale differences between treeholes in drought disturbance, as shown for British treehole insects for 2 years. At the global scale, drought disturbance is a relatively poor predictor of patterns in the local richness of treehole mosquitoes. Instead, regional differences in the species pool explain most of the variation in local mosquito richness. Treeholes in at least the most species-poor regions appear to be unsaturated with mosquito species. In this system, therefore, local processes do not necessarily scale to global patterns.

Keywords Community saturation · Disturbance · Biogeography · Mosquito larvae · Habitat permanence

Introduction

Species richness varies markedly around the world, even within the same type of community. There are two general types of explanation for such differences in local richness between regions: habitat or history. First, communities in different regions may occur in habitats that are superficially similar in appearance but differ in ecologically important ways (such as primary productivity, disturbance regimes, temperature). For example, latitudinal gradients in terrestrial diversity have been attributed to differences in solar energy input (Currie 1991) or seasonality (Pielou 1975). Second, different regions of the world have different histories (including time since glaciation, isolation from other regions, chance introductions), all of which affect the current regional species pool. Well-known examples of history-based explanations include attributing depauperate island faunas to low colonization rates (MacArthur and Wilson 1967) or linking high tropical diversity to the equatorial origin of many lineages (Jablonski 1993; Mora et al. 2003).

Habitat-based explanations have often been tested at the local scale. For example, if global variation in local diversity is determined entirely by energy-limitation, reductions in productivity at any site should result in loss of species (Jenkins et al. 1992; Srivastava and Lawton 1998). However, if larger scale effects within regions (e.g. meta-community dynamics, see Inouye 2005 this issue) or between regions (e.g. biogeographic history) have a role in creating variation in local diversity, it will not be possible to scale directly from such local experiments to global patterns. The imprint of history on diversity is most visible in unsaturated communities, that is, communities in which local diversity is limited by (i.e. proportional to) the regional species pool. In such communities, local diversity may be highly dependent on long-distance dispersal within the region, rates of speciation, and invasions from other regions (Ricklefs and Schluter 1993). This study is primarily

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interested in the latter two processes, those that affect the size of the regional species pool.

Habitat-based explanations for differences in local diversity make no assumptions about the importance of interspecific interactions. History-based explanations assume that species interactions are weak, and thus relatively unimportant in limiting local diversity. The counterview is that species interactions set an upper limit to local richness (via competitive exclusion or food web stability). Communities that have reached this asymptote in diversity are said to be saturated with species, and will show little difference in local diversity between regions with different histories.

In this study, I examine variation in the number of insect species per treehole at two spatial scales, within a British woodland and around the world, and contrast a habitat-based (drought) and a history-based (species pool limitation) explanation for each pattern. The results are then interpreted in the context of saturation theory. This study therefore extends the concept of “scaling-up” from experiments to ecosystems, explored in other papers in this Special Feature, to the largest scale, global. Treeholes are useful for this type of comparison as they occur on most continents, are generally consistent in size and resource productivity amongst localities (Kitching 1983, 2000), and contain a discrete and easily measured community of insects (Kitching 2001). Insects in treeholes occupy a range of niches, including several types of detritivore (e.g. syrphid, chironomid, scirtid beetle and tipulid larvae), filter feeders (mosquitoes) and predators (e.g. odonates and *Toxorhynchites* spp. mosquitoes). I concentrate on examining drought and the species pool as potential determinants of local (per treehole) insect diversity, as both have been hypothesized to be main drivers of geographic patterns in phytelm food webs (Kitching 2001), and previous work in Britain has shown that other potential drivers, such as detrital resources (Srivastava and Lawton 1998) and interspecific interactions (Bradshaw and Holzapfel 1992), do not appear to limit local richness. Drought disturbance, by contrast, has frequently been identified as a key determinant of treehole diversity in other areas of the world (Lounibos 1981; Bradshaw and Holzapfel 1988; Fincke 1992; Sota et al. 1994). Finally, current responses to drought disturbance and the species pool may help predict future impacts of, respectively, climate change and species invasions.

The global analysis is limited to mosquitoes to maximize the potential for niche saturation; mosquito species are likely to interact strongly and negatively with each other. Specifically, mosquitoes are the only filter feeding insects in treeholes, and interactions between mosquitoes include both competition and predation (Bradshaw and Holzapfel 1983), whereas interactions with other detritivore insects are typically weak or facilitative (Heard 1994; Paradise and Dunson 1997). Rotifers and protozoa are more important as prey for mosquitoes than as competitors for bacteria and particulate matter (e.g. Addicott 1974).

Methods

Effect of drought on insects in British treeholes

Study site

All fieldwork was carried out at Silwood Park, Ascot, a 100-ha estate in Berkshire, Britain (51°25'N, 0°35'W) with over a hundred treeholes. In this area, almost all the treeholes are bark-lined buttress holes found near the base of European beech trees (*Fagus sylvaticus*).

Prevalence of drought in British treeholes

A total of 97 beech buttress treeholes were mapped at Silwood Park. All of these treeholes contained water at least once in 1995 or 1996. The mapped treeholes were examined for standing water (minimum 4 mm depth) every 2–3 days from 25 April to 15 September 1995, and from 3 April to 4 September 1996 (with the exception of a 2-week period in late May 1995). Drought disturbance is less significant in the remaining months of the year because of high rainfall and cold temperatures.

Effects of drought on insect diversity in Britain

Drought varies naturally between treeholes at Silwood Park, largely because of differences in treehole depth (Srivastava 1997). Deep treeholes are the least drought-prone, both because they collect more rainwater, and because they have slower evaporation rates (Srivastava 1997). This natural gradient in drought frequency provides a useful opportunity to examine the relationship between drought and diversity, after correcting for differences in treehole size. Local loss of a species is the endpoint of a gradual decline in abundance, so I also examine the corollary, that drought affects total abundances.

The effects of drought disturbance on insects were monitored over the summers of 1995 and 1996 in a set of 16 treeholes. These treeholes were all surveyed for biota once in each of four study periods. The periods started on 5 July 1995, 15 September 1995, 23 April 1996, and 10 July 1996, and lasted for ca. 4 days each. In each case, treeholes were examined a few days after the end of a drought period, when all 16 treeholes had become water-filled due to heavy rainfall. When debris is dry, up to 50% of insects (except mosquitoes) hide in inaccessible bark crevices, and so are missed in samples of detritus and water (Srivastava 1997). When treehole detritus is saturated with water, insects quickly leave the bark crevices. Within 4 days of rewetting, >99% of aquatic insects are captured in samples of detritus and water (Srivastava 1997). It is clear from the size distribution of these insects that oviposition over these 4 days is not an important contributor to abundance of any species save

Aedes geniculatus, whose drought-resistant eggs are simulated to hatch by submersion (Yates 1979). Insects were also surveyed in these 16 treeholes on two randomly chosen dates in June and August (17 June 1995 and 21 Aug 1995), to provide additional seasonal data for the mosquito richness estimate (used in the global analysis).

The effect of drought on diversity was further examined in an independent set of 20 treeholes on 9–10 August 1995, when many treeholes were drought-stressed. This second dataset was needed to both increase the power of the analysis, and to assess treehole biota at the height of the drought. Treeholes were filled to capacity with distilled water exactly 4 days prior to sampling to ensure that most treehole insects were captured in the debris and water sample. The long-term dynamics of the treehole community are artificially changed by watering, so these treeholes were not examined on any further dates (this is why the set of 16 repeated-measure treeholes were never artificially watered). The drought history of all these treeholes was recorded as part of the larger treehole drought survey described shortly.

Insects were sampled as follows. The standing water in each treehole was removed using a 60-ml syringe fitted with a 15-cm length of 12-mm hose. The leaf debris was then scooped out, leaving only a basal sand layer. The volume of debris (excluding intact leaves and beech nuts) was measured. Insects in all the water and debris were counted and identified. Debris was sorted in small amounts on a white tray, diluted if necessary with distilled water (the added water was subsequently removed with a 150- μ m sieve after sorting). In the case of highly abundant species, especially the chironomid *Metricnemus cavicola*, the debris was mixed and a subsample used for abundance determination. Sub-sampling for species richness is not appropriate, so species richness was determined by examining all the debris and water. At the end of the sampling procedure, the debris, insect larvae, and original treehole water were returned to the appropriate treehole, ready for the next sample period.

Statistical analysis

The effects of drought on species richness and abundance were examined using both the 20-treehole dataset, from August 1996, and the 16-treehole dataset with repeated observations. In both cases, the data was count-based and thus best approximated by a Poisson distribution. For the 20-treehole dataset, analysis involved generalized linear models (GLMs) with a log link function. GLMs do not accommodate non-normal repeated measures data, so for the second dataset an extension of GLMs, generalized estimation equations (GEEs), were used (Liang and Zeger 1986). These analyses both use R version 1.8.0 (<http://www.r-project.org>), with the add-on Geepack version 0.2-7 package for GEE analysis (<http://cran.r-project.org/doc/packages>). In the GLM, entered

variables were: detrital volume, treehole permanence (see below), and their interaction. In the GEE, entered variables were: detrital volume, date, permanence, and all two-way and three-way interactions between these variables. In all models, detrital volume was entered before permanence to correct for effects of habitat size and resource levels before correlating diversity and drought. Treehole permanence was quantified as the proportion of days that the treehole contained water, over the two census periods (27 April–15 September 1995, and 3 April–8 July 1996). Overall, this measure of treehole permanence explained more of the variance in species richness than other plausible measures including: water content of the debris, water-filled days in the 20 day-period before the survey, or water-filled days in the current summer. The results of the GLM and GEE analyses are difficult to display graphically because of multiple continuous explanatory variables. I therefore separated treeholes into categories simply for graphical display (not analysis): dry (water-filled < 20% of days) versus wet treeholes, and small (< 300 ml debris) versus large treeholes.

The relationship between local and regional richness in treeholes

Local-regional richness plots are commonly used to test for species saturation (Srivastava (1999). Linear relationships between local and regional richness are often interpreted to reflect limitation of local richness by the regional species pool, whereas if local richness reaches an asymptote, species interactions are suspected to limit local richness.

A local-regional richness plot was developed for treeholes mosquitoes (defined as Culicidae and Co-rethrellidae after Bradshaw and Holzapfel 1983). Local richness for temperate-region treeholes (Britain, Japan, and Pennsylvania) was based on samples collected in the period April–September. The richness and abundance of temperate treehole mosquitoes is highest at this time of year (Kitching 1971; Sota et al. 1994; Paradise 2005) suggesting that this is the most likely time of year for niche saturation and competitive exclusion. Repeated measures for a treehole were first averaged before calculating local richness as mean richness per treehole. The analysis excluded treeholes that never contained water during the entire study, but included all other treeholes, irrespective of size or drought frequency. Regional richness refers to the total number of treehole-dwelling mosquito species recorded for the region, and was obtained from the studies or researchers directly. Region was defined in this study as the surrounding county, state or island, and ranged in area from ca. 1,600 (Kenya) to 8,000 (Peru) km². Artefactual results can occur when local areas occupy a substantial fraction of the regional area (Srivastava 1999; Hillebrand and Blenckner 2002), but in this analysis, local areas were < 1% of the respective regional areas. Pseudoreplication

arises when multiple estimates of local richness for the same region are used in local-regional richness plots, and can affect the discrimination between saturated and unsaturated curves (Srivastava 1999). Therefore, in the two cases where there were multiple values of local richness per region (Britain and Kenya), the local data was averaged before analysis. Meteorological data was obtained from weather stations as close as possible to the local collection sites (Table 1).

All analysis for this section used Genstat v. 6.1 (Numerical Algorithms Group, Oxford, UK). Logistic models were fit with binomial errors, a logit link function, and an empirically derived asymptote; other models were fit with normal errors after appropriate transformation. As sample sizes were low for these analyses, I also calculate statistical power for each test using G-Power v. 2.0. (Erdfelder et al. 1996).

Results

Effect of drought on insects in British treeholes

Over the course of the Silwood Park survey, nine species of larval aquatic insects were encountered in treeholes. The most abundant larvae were the chironomids *M. cavicola* Kieffer (formerly *M. martini* Thienemann) and a *Diamesa* sp., and the syrphid *Myiatropa florea* L. Larvae of the scirtid beetle *Prionocyphon serricornis* Müller and the mosquitoes *A. geniculatus* Olivier, *Culex torrentium* Martini, and *Anopheles plumbeus* Stephens were also common. Larvae of psychodid fly larvae (*Pericoma* sp.) and an unidentified tabanid were rare inhabitants. Species differed in their sensitivity to drought. Both *A. geniculatus* and *P. serricornis* were restricted to the most permanent treeholes, *M. cavicola* was found in all but the most drought-prone treeholes, and *Diamesa* sp. and *M. florea* occurred in treeholes irrespective of their drought history.

Species richness and abundance were highest in the most permanent treeholes (Fig. 1a, b). In the longitudinal dataset of 16 treeholes, examined on four dates, more species were found in treeholes that were more permanent (Fig. 1a; Wald statistic=9.29, $df=1$, $P=0.002$), after correcting for positive correlations between species richness and volume of detritus (Fig. 1c; Wald statistic=7.15, $df=1$, $P=0.007$). The strength but not direction of these effects differed between dates. Treeholes examined in September 1995, after the extensive summer drought, had overall lower species diversity than in either July date (Fig. 1e; Wald statistic=5.91, $df=1$, $P=0.015$), especially in less permanent treeholes with little detritus (September detritus: Wald statistic=7.82, $df=1$, $P=0.005$; September detritus \times proportion days wet: Wald statistic=4.83, $df=1$, $P=0.028$). Similarly, treeholes in April 1996 had marginally lower richness than in either July date (Wald statistic=3.83, $df=1$, $P=0.050$), particularly the less permanent treeholes (Wald statistic=5.90, $df=1$,

$P=0.015$). Species richness was similar between July 1995 and July 1996.

Insect abundance tended to follow similar patterns as species richness. Overall, abundance was greater in the more permanent treeholes (Fig. 1b; Wald statistic=29.6, $df=1$, $P<0.0001$) after correcting for differences in volume of detritus (Fig. 1d; Wald statistic=20.17, $df=1$, $P<0.0001$). Abundance in September 1995 was lower than in other dates (Fig. 1f; Wald statistic=5.19, $df=1$, $P=0.023$); there were no further differences between dates.

These results are partially supported by a separate analysis of an additional 20 treeholes examined once, in August 1995. Species richness was unrelated to detrital volume (Fig. 1c; $F_{1,17}=1.69$, $P=0.21$; detritus \times permanence interaction, $F_{1,16}=0.52$, $P=0.48$) on this date, but increased with the proportion of days the treehole contained water (Fig. 1a; $F_{1,18}=7.79$, $P=0.012$). Abundance, conversely, was unrelated to treehole permanence (Fig. 1b; $F_{1,17}=2.60$, $P=0.12$; detritus \times permanence: $F_{1,16}=0.13$, $P=0.72$) but increased with detrital volume (Fig. 1d; $F_{1,17}=5.18$, $P=0.036$).

Differences between regions in treehole drought

Water levels in treeholes were extremely variable over the summer months in Britain (Fig. 2). On most summer days in 1995 and 1996, less than half of the 97 treeholes contained standing water (mean percent of treehole with water: 1995: 26%, 1996: 41%). For a period of 4 weeks in 1995, not a single treehole contained standing water.

Compared with Britain, drought appears to be more prevalent in Kenya, slightly less prevalent in Pennsylvania and much less prevalent in Japan and Florida (Fig. 3). It should be cautioned that the drought data for these other countries is, except for Japan, based on single-year surveys. However, long-term meteorological data for these countries corroborates these trends (Table 1). Amongst regions, the mean proportion of treeholes with water is strongly correlated with precipitation (annual: $r=0.90$, $P=0.037$; driest 6 months: $r=0.88$, $P=0.049$) but not temperature (annual: $r=-0.12$, $P=0.85$; driest 6 months: $r=0.10$, $P=0.87$).

The relationship between local and regional richness in treeholes

A local-regional richness plot (Fig. 4) was developed for treehole mosquitoes, based on data from eight regions of the world (Table 1). Local richness in the analysis refers to the average number of mosquito species per treehole (the scale at which interaction is most likely).

Both local and regional richness are lowest in Britain, Pennsylvania, and Australia (many treeholes have one species or no mosquitoes). The remaining regions have larger species pools, and treeholes in these regions contain on average one to two species of mosquito per

Table 1 Data used for the global comparisons of treehole mosquitoes

Local site	Region	Local richness	Regional richness	Insect data source	Weather station (years)	Mean daily temperature and monthly precipitation for driest 6 months (year)
Silwood Park and Wytham Woods (51°25'N, 0°35'W and 51°46'N, 1°20'W)	Berkshire, Britain	0.300 (Silwood Park, $n = 16$), 0.225 (Wytham Woods, $n = 20$)	3 ^a	Current study, and Kitching (1969)	Wallingford, Britain (1853–2002)	(9.5) °C, 48.0 (48.5) mm
Lamington National Park (28°50'S, 153°E)	New South Wales and Queensland, Australia	0.57 ^b ($n = 28$)	3 ^c	Kitching (1982)	Springbrook Park, Qld., Australia (unspecified)	21.0 (18.9) °C, 155 (149) mm
Center County, Pennsylvania (40.5°N, 77.4°W)	Pennsylvania, USA	0.57 ($n = 27$)	5 ^d	C. Paradise (personal communication)	Lewistown, Pennsylvania, USA (1961–1990)	18.1 (10.4) °C, 90.1 (80.9) mm
Lowland forests near Iquitos, Peru (3°5'S, 73°1'W)	100 km radius around Iquitos, Peru	1.22 ($n = 50$)	15	S. Yanoviak (personal communication)	Iquitos, Peru (1949–1990)	25.8 (26.1) °C, 216 (240) mm
Sites at BCI, Panama (9°N, 79°W)	Barro Colorado Is., Panama	1.86 ($n = 65$)	17	Yanoviak (2001 and personal communication)	Balboa Heights, Panama (1969–2003)	26.8 (26.6) °C, 75.3 (157) mm
Kombeni and Makadara Forests (3°55'S, 39°34'E and 4°16'S, 39°22'E)	Kilifi and Kwale Districts, Kenya	1.65 (Kombeni, $n = 132$) 2.40 (Makadara, $n = 163$)	19	Lountbos (1981)	Shauri Moro/Simakeni, Kenya (1976–1977)	28.5 (27.2) °C, 67.8 (73.8) mm
Tajima Shrine (33°33'N, 129°53'E)	Kabeshima Island, Japan	2.09 ($n = 86$)	12	Sota et al. (1994, and personal communication)	Saga, Japan (1988–1992)	20.5 (15.1) °C, 232 (169) mm
Tall Timbers Research Station (30°36'N, 84°12'W)	North Florida, USA	1.39 ($n = 35$)	7	Bradshaw and Holzapfel (1983)	Tallahassee, Florida (1961–1990)	24.8 (19.5) °C, 158 (139) mm

^a*Orthopodomyia pulchripalpis* was not included in the species pool, although it is occasionally recorded from British treeholes, as it is restricted to large rot holes in very old pollarded trees [a habitat not examined in this study or by Kitching (1972)]

^bInferred from Kitching (1982) who found *Aedes canadoscuttellum* in 8/28 samples, as well as an undescribed *Aedes* species as whose “frequency of occurrence was much the same” (2×8/28 = 0.57)

^cThe predatory mosquito *Toxorhynchites* sp. is included in species pool, although it was not found in the treeholes examined in the Kitching (1982) or Kitching (2000). This genus is recorded from treeholes in the region (Kitching 2000)

^dAlthough only three species were encountered by Paradise (2005), an additional two are recorded for central Pennsylvania, albeit very infrequently (Barrera 1996)

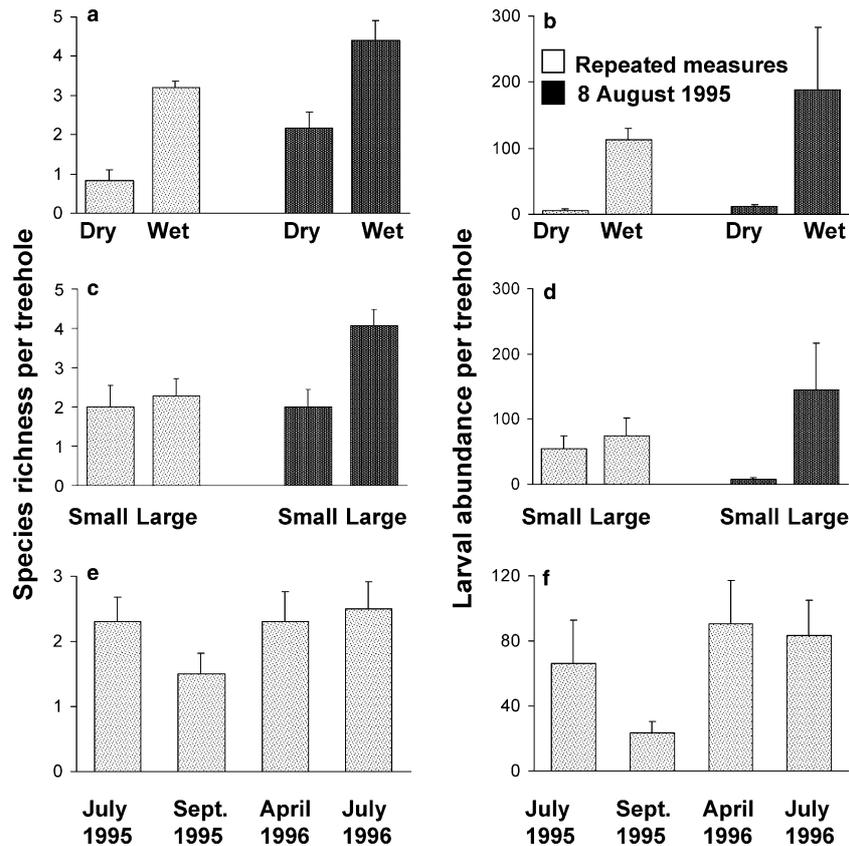


Fig. 1 Differences in the species richness and abundance of treehole insects with **a, b** treehole permanence, **c, d** volume of debris, and **e, f** date. Results for two independent groups of treeholes are shown, including one group repeatedly measured ($n=16$) and one group sampled only on 8 August 1995 ($n=20$). Permanence and debris are shown as categorical variables to

simplify the figure, but are analysed as continuous variables in the GLM and GEE models (see text). Dry treeholes contained water $\leq 20\%$ of days, wet contained water $>20\%$ of days. Small treeholes contained <300 ml debris, large treeholes contained ≥ 300 ml debris. Values are means + SE

treehole. Local richness is positively correlated with regional richness ($r=0.85$, $P=0.008$; Fig. 4) and, to a lesser degree, dry season temperature ($r=0.74$, $P=0.035$). Local richness is not correlated with yearly temperature ($r=0.64$, $P=0.087$), dry season precipitation ($r=0.28$, $P=0.51$), or yearly precipitation ($r=0.32$, $P=0.44$). The statistical power (ability to detect a true effect) of these analyses is variable, ranging from 99% (local-regional correlation) to 67–87% (correlations with dry season climate) to just 33–44% (correlations with yearly climate). If the analysis is restricted to the five regions for which drought data is available, local richness is also correlated with regional richness ($r=0.87$, $P=0.01$, power = 92%) not drought frequency ($r=0.29$, $P=0.64$, power = 13%).

Although it appears that regional richness can explain much of the variation in local richness, it is less evident whether local richness in the richest regions is approaching an asymptote. Two curvilinear functions, a power function ($r^2=0.80$, $F_{1,6}=23.51$, $P=0.008$; Fig. 4) and a logistic function ($r^2=0.78$, $F_{1,6}=20.93$, $P=0.004$, asymptote of three species; Fig. 4), both explain more of the variance than a linear function ($r^2=0.72$, $F_{1,6}=15.33$, $P=0.008$) but the exponent of the power

function (0.888 ± 0.183 SE) approaches that of a straight line (straight lines are power functions with exponent 1.0). Some authors have recommended testing for curvilinearity in local-regional plots by evaluating a quadratic term for regional richness (Cresswell et al. 1995). By this criterion, the relationship is linear (quadratic term: $F_{1,5}=1.73$, $P=0.245$). However, the statistical power for this test is very low. The current analysis has only a 23% chance of detecting a quadratic relationship even if it exists.

Discussion

On an average summer day in south England, less than half of all treeholes contain water. Drought has major effects on the diversity and abundance of treehole insects. The effects of drought on diversity are seen spatially (the most frequently dry treeholes have fewest species throughout the year; Fig. 1a) as well as temporally (diversity is most reduced after a major drought in August 1995; Fig. 1e). Of course it is possible that these patterns are caused by other, unexamined factors, although care was taken to prevent artifacts (such as

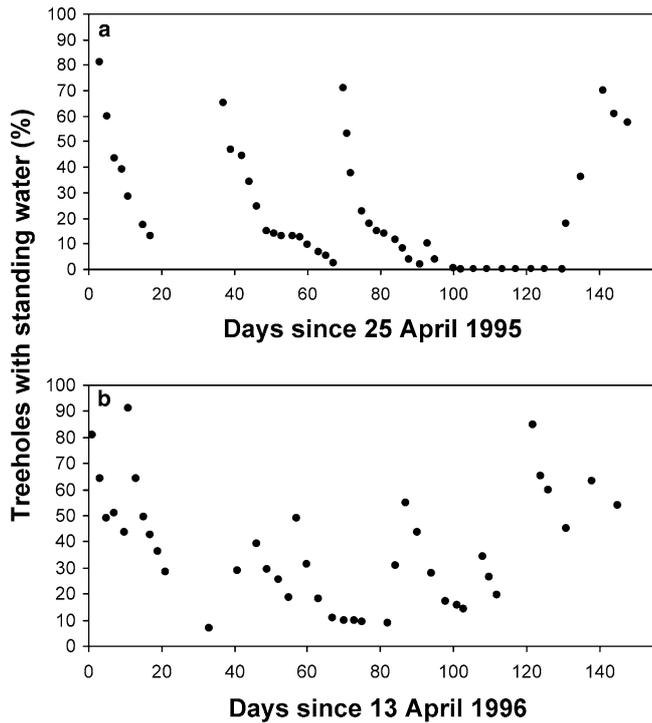


Fig. 2 Temporal dynamics of treeholes with standing water at Silwood Park, UK in **a** 1995 and **b** 1996

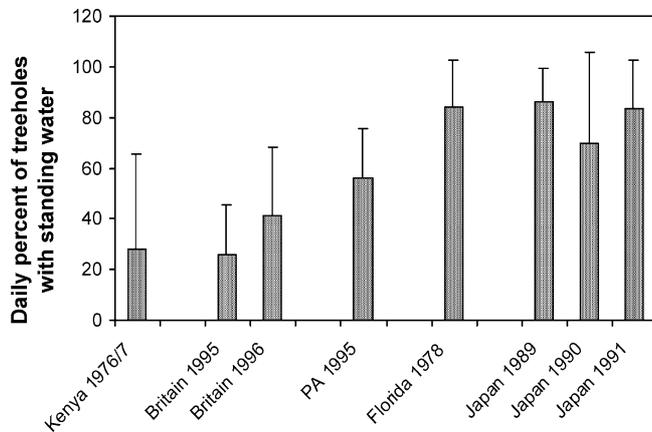


Fig. 3 The mean (+SD) daily percent of treeholes with standing water, calculated for the six summer or dry season months of the year, for five regions: Kenya, Britain, Japan and, in the USA, Pennsylvania (PA) and Florida. See Table 1 for data sources. In all cases, SD was based on data collected at monthly intervals

ensuring larvae were not in inaccessible bark crevices) and to control for covariates (such as debris volume). For example, treeholes in September may have had low diversity not just because of drought but also because of phenology (Kitching 1971). However, the loss of species in the driest September treeholes appears to exceed that due to phenology alone: interaction terms between date, treehole permanence, and debris volume indicate that small, dry treeholes lost proportionately more species

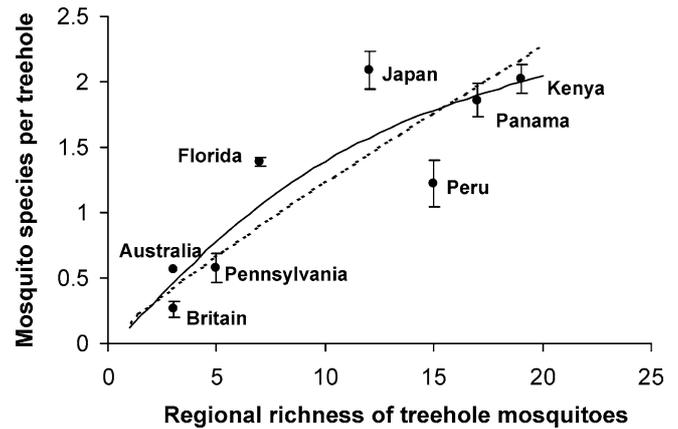


Fig. 4 Local and regional richness of treehole mosquitoes for eight regions of the world (details of datasets in Table 1). Standard errors of local richness are shown for all regions except Australia (data not available). Power (dotted line) and logistic (solid line) regressions are based on mean values of local richness for each region

than did large, wet treeholes over the August 1995 drought period. Reductions in species richness may have been due to a variety of factors. Adult insects may choose not to oviposit in treeholes which are dry or likely to experience drought, perhaps using oviposition cues such as water colour as reliable indicators of drought frequency (Bradshaw and Holzapfel 1988; Srivastava and Lawton 1998). In a dry treehole, insect larvae may die due to desiccation, or may become easy prey for terrestrial predators such as centipedes and beetle larvae. Even before a treehole completely dries out, larvae that feed in the water column, like mosquitoes, may face increased competition as water volume becomes reduced.

Drought disturbance has also been shown to have a major impact on treehole insect communities in Florida (Bradshaw and Holzapfel 1988), Japan (Sota et al. 1994), Australia (Jenkins et al. 1992), Kenya (Lounibos 1981), and even in the tropical moist forests of Panama (Fincke 1992, 1994; Yanoviak 1999), that is, in most of the regions examined in the second half of this study. In some regions, drought has both direct and indirect effects on species. For example, in Florida, drought removes several mosquitoes species including the predatory *Toxorhynchites rutilus* from treeholes, indirectly benefiting two mosquito species, *Aedes triseriatus* and *Aedes hendersoni*, both of which are predator-sensitive but have drought-resistant eggs (Bradshaw and Holzapfel 1983, 1985).

Despite the importance of drought within sites, globally there is no correlation between the number of mosquito species per treehole and drought frequency of the site. For example, during the summer Kenyan treeholes dry out more frequently than British treeholes (Fig. 3), but have much higher local (per treehole) richness (Fig. 4). Treeholes in Florida and Japan have similar drought regimes (Fig. 3), yet Floridian treeholes contain only half the species than their Japanese coun-

terparts (Fig. 4). Although dry season temperature is positively correlated with local richness, the direction of this correlation is opposite to that predicted by drought-limitation of richness (warmer temperatures should increase drought frequency). The other climatic variables show no correlation with local richness (though low sample size limits power of these analyses).

It should be cautioned that the results might have been different if another subset of the treehole biota, rather than mosquitoes, had been examined. For example, Kitching (2000) found that the number of treehole predator species per site correlates negatively with latitude. Predators in treeholes are larger than their prey, and larger body sizes require either longer or warmer periods of development. This is seen in the extreme in odonate species, which require multiple months of continuous water to develop (Fincke 1994) and thus are found in only the most permanent treeholes in tropical rain forests (Kitching 2000). Odonates are voracious predators of mosquitoes in treeholes (Fincke et al. 1997), and such effects of trophic structure may be one of the sources of noise in the local-regional richness plot for mosquitoes.

The weak global correlations between treehole mosquito richness and climate also should not be inferred to mean that geographic patterns in treehole mosquito richness are never strongly influenced by climate. Indeed, there is plenty of evidence that climate plays an important role at the scale of continents. Along the eastern coast of the United States, drought and freezing appear to be well correlated with the occurrence of different treehole mosquito species (Bradshaw and Holzapfel 1983, 1984, 1985). On the west coast of Australia, the species richness of treehole macrofauna (insects and amphibians) is highly correlated with latitude (Kitching 2000). However, when treehole macrofauna is examined at a global scale, the significant correlation between species richness and latitude is lost, except for the predators (Kitching 2000), suggesting that biogeographic effects between continents obscure simple climatic effects. For treehole mosquitoes, biogeography appears to have been particularly effective at decoupling species pools from climatic control. For example, despite having similar climates, Japan and the south-eastern United States have very different species pools of treehole mosquitoes (Japan: 32, south-eastern United States: 7). Presumably the richness of the Japanese pool reflects proximity to species-rich faunas of tropical Asia. Bradshaw and Holzapfel (1985) have argued that the relative impoverishment of the treehole mosquito fauna of the south-eastern United States is due to physical barriers (Caribbean Sea, Great Plains, Sonoran Desert) separating this fauna from the species-rich Central and South American faunas. Other insect communities show similar patterns of strong latitudinal gradients within continents but not globally, such as galling insects (Price 1991) and bracken herbivores (Lawton et al. 1993). In both of these systems, analysis of local-regional richness plots suggests that the

communities are unsaturated (Cornell 1985; Lawton et al. 1993).

Treehole mosquito communities also appear to be unsaturated, at least in southern Britain, Pennsylvania, and Queensland (Fig. 4). In these three regions, both local and regional richness is low. In fact, many treeholes lack any mosquitoes. Florida has intermediate values of local and regional richness. The final four regions have a much higher species pool. In these four regions, it is not clear whether treehole mosquito richness is approaching a local asymptote of two or three species, with a slight outlier of Peru at 1.22 species, or whether there is simply noise around a linear increase of local with regional richness. The problem is threefold. First, there are virtually no models that explicitly predict how a community should approach saturation, so any curvilinear function can be viewed as evidence for saturation. Second, the assessment of curvilinearity in this study had very low statistical power. This is a general problem with this test for saturation, since for many taxa there are limited numbers of independent, well-studied, biogeographic regions in the world. Thirdly, local-regional richness functions in interactive communities can change shape as communities assemble (Mouquet et al. 2003) and, due to their high rate of disturbance, treehole communities are likely in a continual process of assembly. Other models have also shown that species interactions can create both linear and curvilinear local-regional richness plots (Shurin and Allen 2001; Mouquet and Loreau 2002). There are additional problems with this graphical test for saturation. Correlations between local and regional richness may just reflect an underlying common covariate, rather than a causal relationship (though in this study we have discounted drought, temperature and precipitation as this covariate). Local-regional richness plots are also susceptible to a variety of artifacts arising from examining richness at improper scales (Srivastava 1999; Hillebrand and Blenckner 2002; Shurin and Srivastava 2005). Together, these observations suggest that patterns in local and regional richness are most convincing when corroborated by additional evidence for the role of competition or biogeography in limiting local richness (Srivastava 1999).

There is additional evidence to suggest that British and Floridian treehole mosquito communities are unsaturated. First, theory indicates that non-interactive communities will not be saturated with species (Cornell and Lawton 1992; Hubbell 2001). Manipulations of treehole mosquitoes in both Britain and Florida have failed to find evidence of strong interspecific competition (Bradshaw and Holzapfel 1983, 1992). Second, if communities are saturated with species, the expectation is that exotic species are either unsuccessful at invading the community, or their invasion results in the loss of native species. Britain was invaded by *C. torrentium* in the late 1940s (Mattingly 1951) with no competitive exclusion of native species. *C. torrentium* is now common in Silwood Park (this study, Bradshaw and Holzapfel 1992). In the

mid-1980s, treeholes in the southeastern United States were similarly invaded by *Aedes albopictus*, which entered North America from Asia through the used tire trade (Reiter and Sprenger 1987). The most similar native species is *Aedes aegypti*, and there are reports of loss of *A. aegypti* from specific areas after *A. albopictus* invasion (reviewed in Juliano 1998). However, competitive exclusion may be occurring primarily in tires and other artificial containers inhabited by both species (Livdahl and Willey 1991; Juliano 1998), rather than treeholes (Schreiber et al. 1988; Livdahl and Willey 1991; Juliano 1998). In total, the above evidence suggests that treeholes contain relatively few mosquito species on average (a maximum of two species in Kenya) not because of competitive exclusion (i.e. saturation) but rather the high rate of drought disturbance in the system.

Unsaturated communities are often linked to “vacant niches”, that is niches that are as yet unfilled because the appropriate species has not yet entered the species pool, or has not had time to disperse to most localities in the region (Lawton 1984). Of particular interest in treehole mosquitoes is the predatory genus *Toxorhynchites*, as it exploits a different niche than most other treehole mosquitoes (which are browsers and filter feeders). The genus does not occur in Britain, and in fact there are no aquatic insect predators in British treeholes. Kitching (Kitching 1983; Kitching and Pimm 1985; Kitching 2000) suggests that the less predictable environment of British treeholes may select against multi-trophic food webs. Biogeography may also be important. The genus *Toxorhynchites* originated in the tropics (Gutsevich et al. 1971), and does not occur in any of the Palearctic region (Europe, North Africa, Middle East, Northern Asia) except for a single rare species found just north of eastern China (Stone et al. 1959; Gutsevich et al. 1971). Dispersal barriers and climatic factors in regions far distant from Britain appear to be ultimately responsible for the current absence of *Toxorhynchites* predators from British treeholes.

In summary, this study has shown that the determinants of local diversity are scale-dependent. There is some analogy here with studies of community invasibility, which have shown that species interactions explain between-patch invasibility patterns at small spatial scales but this effect is obscured by the effects of environmental heterogeneity at larger landscape scales (Shea and Chesson 2002). In treeholes, although drought (i.e. environmental heterogeneity) determines between-treehole differences in insect richness within forest patches, or even continents, the simple effects of drought are obscured by biogeography at the global scale. In general, the results of local habitat-manipulations will not scale easily to global patterns when at least some unsaturated communities are included in the analysis. There is no consensus yet as to the relative prevalence of saturated versus unsaturated communities (Cornell and Karlson 1997; Srivastava 1999; Shurin and Srivastava 2005). By contrast, several of the papers in this Special Feature demonstrate that small-scale manipulations of habitat

can, with some ingenuity, be used to predict landscape-scale patterns (Melbourne and Chesson 2005; Petersen and Englund 2005; Schmitz 2005). At spatial scales greater than landscapes, however, not only habitat changes (see Helms and Hunter 2005, this issue) but also species identity within communities. Could some of the effects of biogeography, like habitat, be tested with small-scale experiments? Dispersal between biogeographic regions is routinely simulated in biocontrol experiments, although the pool of potential invaders is small and heavily biased to species with particular traits. Ethical considerations prohibit the experimental release of a larger and more representative suite of species between biogeographic regions. Within a region, experimental dispersal of species has been carried out directly (Levine 2000; Shurin 2000) or indirectly, by using landscape structure (Cottenie et al. 2003). Note that such within-region experiments will only be relevant to predicting the effects of dispersal between regions when the dispersing species have similar traits at both scales (Shurin and Srivastava in press). In most systems, local manipulations of habitat and dispersal will have to be carefully combined with global analyses of patterns. Only then will we be able to separate the relative impact of habitat and history on diversity.

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