Stream insect occupancy-frequency patterns and metapopulation structure

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Abstract An understanding of the distribution patterns of organisms and the underlying factors is a fundamental goal of ecology. One commonly applied approach to visualize these is the analysis of occupancy-frequency patterns. We used data sets describing stream insect distributions from different regions of North America to analyze occupancy-frequency patterns and assess the effects of spatial scale, sampling intensity, and taxonomic resolution on these patterns. Distributions were dominated by satellite taxa (those occurring in ≤10% of sites), whereas the occurrence of core taxa (occurring in ≥90% of sites) determined the overall modality of occupancy-frequency patterns. The proportions of satellite taxa increased with spatial scale and showed positive relationships with sampling intensity (r^2=0.74–0.96). Furthermore, analyses of data sets from New York (USA) showed that generic-level assessments underestimated the satellite class and occasionally shifted occupancy-frequency distributions from unimodal to bimodal. Our results indicate that, regardless of species- or generic-level taxonomy, stream insect communities are characterized by satellite species and that the proportion of satellite species increases with spatial scale and sampling intensity. Thus, niche-based models of occupancy-frequency patterns better characterize stream insect communities than metapopulation models such as the core-satellite species hypothesis.

Keywords Aquatic insect · Core-satellite · Distribution · Sampling intensity · Spatial scale

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Introduction

An understanding of the distribution patterns of organisms (e.g., occupancy-frequency patterns) and the biotic and abiotic factors underlying these remains a fundamental goal of ecology. Since Raunkiaer (1918) first analyzed the frequency distributions of plants (McGeoch and Gaston 2002), numerous studies have shown that regionally widespread species are often locally abundant, whereas regionally rare species are

usually locally uncommon (McNaughton and Wolf 1970; Bock and Ricklefs 1983; Brown 1984; Collins and Glenn 1991; 1997; Gaston and Blackburn 2000). Attempts to explain this pattern include dynamic metapopulation models (Levins 1969; Hanski 1982), niche-based models (Brown 1984), and combinations of the two (Collins and Glenn 1997; McGeoch and Gaston 2002; Heino 2005).

The Core-Satellite Species Hypothesis (CSS) is a dynamic equilibrium model based on local immigration and extinction dynamics. CSS predicts a bimodal pattern of regional occupancy-frequency distributions in which species are either regionally common or regionally rare (Hanski 1982; Gotelli 1991; Hanski and Gyllenberg 1993). Bimodality results from stochastic colonization and extinction dynamics and differences in life history strategies (Ulrich and Zalewski 2006) that produce instability such that most populations are either extinction-prone or relatively stable. Empirical support for this model has been found in a variety of terrestrial taxa (e.g., Hanski 1982; Gotelli and Simberloff 1987; Tokeshi 1992 and references therein; Collins and Glenn 1997).

Brown (1984) criticized the CSS because of its assumptions of habitat homogeneity, its complete dependence on colonization and extinction events, and its reliance on rescue effects (Gotelli 1991). Also, bimodality may result from sampling artifacts rather than biological processes (Nee et al. 1991; van Rensburg et al. 2000; Novotny and Drozd 2001). Instead, Brown (1984) proposed a niche-based model in which species have differing tolerances and physiological requirements. In this model, positive relationships between abundance, frequency, and distribution result from the combinations of biotic and abiotic factors that determine multidimensional niche dimensions and the generally unimodal relationship between abundance (and frequency) and environmental gradients (e.g., Whittaker and Niering 1965). Unlike the CSS, the niche-based model predicts a unimodal occupancy-frequency distribution in which most species are regionally rare. Again, there is considerable empirical support for unimodal occupancy-frequency distributions (Tokeshi 1992 and references therein; Malmqvist et al. 1999; Perelman et al. 2001; Heino 2005).

The niche-based and CSS models generate interesting alternative predictions about the pattern of species occupancy-frequency distributions. Most previous tests of these models occurred in terrestrial habitats with varying degrees of fragmentation and in communities of long-lived species with complex life histories (e.g., Collins and Glenn 1997). Stream insect communities provide a level of comparability uncommon in many other analyses of occupancy patterns (Heino 2005). Streams are inherently patchy across landscapes and have discrete boundaries. Also, insects in streams represent diverse assemblages of related, relatively short-lived taxa with high vagility as winged adults. These characteristics make stream insect communities well suited for the analysis of species occupancy-frequency distributions.

Over evolutionary time-scales, occupancy-frequency patterns of stream insect assemblages may result from both niche-based differences in species habitat requirements and metapopulation processes (Heino 2005). Over shorter time- and space-scales, metacommunity structure may be strongly affected by the disturbance regime (Resh et al. 1988; Townsend et al. 1997) or interactions between hydrologic disturbance and productivity (Cardinale et al. 2006). Thus, occupancy-frequency distributions of steam insects may result from the interplay of niche differences, disturbance regimes, and immigration and extinction dynamics.

We analyze here occupancy-frequency distributions of stream insect communities from different regions across North America. Given that streams are discrete entities in the landscape, thereby necessitating colonization from outside of local patches, and subject to frequent disturbances (e.g., drought and flood) that affect local extinction and colonization (e.g., Resh et al. 1988; Reice et al. 1990; Wallace 1990) and that stream insects differ in colonization abilities (Wallace 1990), we hypothesize that site-occupancy patterns will be bimodal at local scales and driven by colonization-extinction dynamics, but that these patterns will become unimodal as the scale increases as a function of niche-based differences and dispersal limitation. In testing this hypothesis, we also assess the influence of taxonomic resolution, a potential artifact, on occupancy-frequency distributions, as many arthropod data sets, particularly for immature stages such as most aquatic insects, are not identified to species.

Methods

Study sites

We used pre-existing stream invertebrate data sets for all analyses, chosen to represent five regions in North America (Table 1). We used only insect taxa and only samples from low-mid-order streams in order to standardize the data sets. Sampling methods were consistent within and among regional data sets (Table 1), and similar mesh and sieve sizes were used in all cases.

Furthermore, all samples were obtained within a short temporal period except for those from the Pacific Coast.

Insect identifications were primarily to the genus level, with the exception of the Chironomidae and early instars of several other taxa that were identified to family, a common trend in freshwater invertebrate data sets. One data set from New York (Table 1) was exceptional in that 3 years of species-level stream insect data were available. Thus, we used this data set to assess the influence of taxonomic resolution (species vs. generic level) on occupancy-frequency distributions and metapopulation models.

Data sets

Alabama Three streams each were sampled in the Cumberland Plateau, the Valley and Ridge province, and the Piedmont provinces of Alabama for a total of nine streams. The taxon-specific data used in the analyses were mean annual abundances that were weighted for relative habitat area.

Alaska The Alaska streams are all north of the Arctic Circle on the north slope of the Brooks Range (Huryn et al. 2005) and are among the least human-impacted streams on the continent. The 32 streams sampled included mountain, glacier, tundra, and spring streams.

Maryland Maryland streams are from the Piedmont region on the northern outskirts of the Washington D.C. metropolitan area. The 65 study streams were located within four watersheds (29–68 km^2) that ultimately drain into the Chesapeake Bay and have historically been dominated by agriculture but are now experiencing urban and suburban growth (Moglen et al. 2004; Moore and Palmer 2005).

New York This data set was based on 30 sites distributed across the Delaware and Hudson River tributaries that drain the Catskill Mountains. All of these sites are unimpaired or only slightly impaired.

Pacific coast This data set was based on 60 low-order streams from the U.S. Pacific Coast ranging from northern Washington to northern California. Data were obtained from the National Aquatic Monitoring Center's BugLab Mapping database (http://www.129.123.10.177/buglab), a Bureau of Land Management and Utah State University collaboration. Data were combined from multiple years (1997–2004) in order to obtain enough sites to analyze the influence of substantial increases in spatial scale on distributional patterns.

Data analyses

To assess occupancy-frequency distributions in each region, we plotted the number of species occurring in ten classes, represented by 10, 20, 30%, and so on up to 100% of the stream sites sampled in each region. Following Hanski (1982), we considered taxa that occurred in ≥90% of the sites to be core taxa, and those that occurred in ≤10% to be satellites. We used Tokeshi's (1992) test to first determine the exact probability of obtaining an observed frequency value for the left- and right-most classes (≤10% and ≥90% of sites) under the null hypothesis of random occurrence of taxa (uniform distribution) within a site using the following equation:

$$P_c = \sum_{i-n_l}^{N-n_r} \sum_{j-n_r}^{N-i} \frac{N! h^{i+j} (1-2h)^{N-i-j}}{i! j! (N-i-j)!},$$

where N is the total number of species, h is the class interval ($0 < h < 1$), and i and j are the left- and right-most class values, respectively. Following Tokeshi (1992), we then analyzed the left- and right-most classes separately to measure the significance of the core and satellite modes:

$$P_l = \sum_{i-n_l}^{N} \binom{N}{i} h^i (1-h)^{N-i},$$

$$P_r = \sum_{i-n_r}^{N} \binom{N}{i} h^i (1-h)^{N-i}.$$

Table 1 Location, years sampled, sampling method, number of sites sampled, and area covered for each data set

Location	Years sampled	Sample area (km^2)	Number of sites	Number of samples	Sampling method	Sampling interval	Mesh size (μm)	Number of taxa
Alabama	1990, 1991	1,500	9	4	Surber, core	Quarterly	250	140
Alaska	2000, 2001	11,000	32	3–5	Surber	Annually	243	63
Maryland	2001, 2002	500	65	6	Surber	Annually	250	73, 75
New York	2000, 2001, 2002	2,800	30	16	Surber	Annually	250	186, 175, 179
N.W. Pacific Coast	1997–2004	73,000	60	1	Surber	Once	250	100

Number of sites and number of samples refer to the number of streams and number of samples taken in each, respectively

When $P<0.05$ for the first test (P_c), the distribution has a mode in either the left- or right-most class, or both. For the second test, $P<0.05$ for either the left- or right-most class (P_1 or P_r) indicates a mode at that class, while $P<0.05$ for both the left- and right-most classes indicates bimodality. We also ranked patterns of modality along a continuum from ''strong'' to ''weak'' based on P values (Tokeshi 1992). Standard linear and non-linear regression techniques were used to examine the effect of sample intensity and spatial scale on modality (SAS ver. 9.1.2; SAS Institute, Cary, N.C.).

Spatial scales and sampling intensity

We analyzed the Pacific Coast (60 sites) and Maryland (65 sites) data sets at multiple spatial scales and sampling intensities. To standardize the number of sites between data sets, we did not use the five outermost sites in the Maryland data set for these analyses.

We performed spatial scale analyses by first assessing modality using just the 20 center-most sites, determined by their latitude and longitude. For this analysis, we kept sampling intensity constant at 20 sites to isolate this variable from spatial scale. Twenty sites were then randomly chosen with replacement from the center-most 30, 40, 50, and, finally, all 60 sites. Thus, increasing spatial scale was analyzed as 20 of 30 sites, 20 of 40 sites, etc. The area measurements and increments were estimated from latitudinal and longitudinal coordinates of sites, as was the Gaussian area covered by the center-most 20, 30, 40, 50, and 60 sites.

In order to isolate spatial issues from the sampling intensity analyses, we held the sample area constant as the area encompassing all 60 sites of each data set. We next completely randomized all of the samples and analyzed these at intervals of 20, 30, 40, 50, and 60 sites, similar to a reshuffling without a replacement procedure. Hence, the 30-site interval was comprised of ten randomly selected sites added to the original 20 random sites, and so on.

Taxonomic resolution

For most data sets, the majority of insect taxa were identified to genus, with a few early instars and chironomids identified to family. This level of taxonomic resolution is characteristic for stream insect data sets, as these assemblages are composed of primarily immature stages, many of which are early instars. Generic- and species-level keys to groups of immature aquatic insects, when available, are usually based on final instars. To assess the potential influence of taxonomic resolution on occupancy-frequency patterns, the New York data sets were analyzed at both generic and species levels.

Results

All data sets showed significant modal occupancy-frequency distributions (Table 2). Bimodality was evident in the Alabama and New York (Figs. 1a, 2) data sets, while communities represented by the remaining data sets were dominated by satellite taxa and thus showed unimodal, left-skewed distributions (Figs. 1b–d, 2).

Spatial scale and sampling intensity

Incremental increases in the spatial scale of the Maryland and Pacific Coast data sets generally resulted in increasing proportions of satellite taxa and stronger unimodal patterns reflected by decreasing P_1 values (Table 3). This increase in the proportion of satellite taxa was relatively monotonic for the Pacific Coast data set. The Maryland data set showed a similar, but less consistent trend (Table 3).

Increases in sampling intensity by increments of ten sites resulted in a logarithmic increase in the proportion of rare, satellite taxa (Table 4). The Maryland 2001 and Pacific Coast patterns remained strongly unimodal throughout all levels of sampling intensity and also showed consistently decreasing P_1 values. As a

Table 2 Tokeshi (1992) test results for stream insect data sets

[a] P_c, P_1, and P_r represent the results of the overall, left-, and right-most class tests, respectively

[b] An (L) behind a diagnosis indicates that the left-most class was dominant in the pattern

Location	P_c[a]	P_1[a]	P_r[a]	Diagnosis[b]
Alabama	<0.001	0.012	<0.001	Strongly bimodal
Alaska	<0.001	<0.001	0.957	Strongly unimodal (L)
Maryland 2001	<0.001	<0.001	0.850	Unimodal (L)
Maryland 2002	<0.001	<0.001	0.905	Unimodal (L)
New York 2000	<0.001	<0.001	0.537	Weakly bimodal (L)
New York 2001	<0.001	<0.001	0.255	Weakly bimodal
New York 2002	<0.001	<0.001	0.183	Bimodal
Pacific Coast	<0.001	<0.001	0.998	Strongly unimodal (L)

Table 3 Tokeshi (1992) test results for Maryland years 2001 and 2002 and Pacific Coast data sets analyzed at increasing spatial scales

Area (km²)	P_c[a]	P_l[a]	P_r[a]	Diagnosis[b]
Maryland 2001				
105	0.229	0.207	0.511	Uniform
150	0.035	0.017	0.871	Unimodal (L)
209	0.367	0.278	0.755	Uniform
422	0.069	0.062	0.494	Uniform
531	0.011	0.006	0.729	Unimodal (L)
Maryland 2002				
105	0.026	0.049	0.193	Bimodal
150	0.016	0.013	0.421	Weakly bimodal
209	0.142	0.079	0.871	Uniform
422	0.024	0.021	0.444	Weakly bimodal
531	5.9E-05	4.2E-06	0.967	Strongly unimodal (L)
Pacific Coast				
17,030	3.2E-05	1.0E-05	0.917	Unimodal (L)
23,527	3.7E-05	1.2E-05	0.887	Unimodal (L)
32,261	8.3E-06	2.3E-06	0.998	Strongly unimodal (L)
64,256	9.7E-07	2.5E-07	0.998	Strongly unimodal (L)
72,829	1.7E-06	4.5E-07	0.962	Strongly unimodal (L)

[a] P_c, P_l, and P_r are P values for assessing the strength of the overall, left-, and right-most classes, respectively

[b] An (L) behind a diagnosis indicates that the left-most class was dominant in the pattern

result, there were significant, negative relationships between sampling intensity and the P_l values for Maryland 2001 ($r^2=0.96$, $P=0.032$) and the Pacific Coast ($r^2=0.94$, $P=0.006$), and this relationship was marginally significant for Maryland 2002 ($r^2=0.74$, $P=0.060$).

Taxonomic resolution

When we changed the analyses of the New York data sets from generic-level to species-level analyses, the patterns shifted from significant bimodal patterns to significantly strong unimodal patterns because the number of satellite taxa increased and the proportion of core taxa decreased (Fig. 2). In general, the size of the satellite classes was reduced by about half when species were lumped into genera. The core class increased only slightly in actual size but more considerably in

proportion. Patterns at both taxonomic levels for the New York data sets were consistent for the 3 years examined (Fig. 2).

Discussion

In our analyses, stream insect assemblages in different regions of North America showed significant bimodal and unimodal occupancy-frequency distributions with generally high proportions of rare taxa. Although the New York data set showed that satellite taxa were generally underestimated by generic-level analyses, our data sets were dominated by rare taxa at most scales, particularly the largest scales. Patterns of bimodality (e.g., Tokeshi 1992 and references therein; Hanski and Gyllenberg 1993; Collins and Glenn 1997;

Table 4 Tokeshi (1992) test results for Maryland and Pacific Coast data sets analyzed at increasing sampling intensities

Sample number	P_c[a]	P_l[a]	P_r[a]	Diagnosis[b]
Maryland 2001				
20	0.365	0.323	0.643	Uniform
30	0.123	0.074	0.823	Uniform
40	0.007	0.003	0.832	Unimodal (L)
50	0.001	4.3E-04	0.841	Unimodal (L)
60	4.4E-04	1.7E-04	0.850	Unimodal (L)
Maryland 2002				
20	3.0E-04	8.3E-05	0.997	Strongly unimodal (L)
30	0.086	0.043	0.955	Strongly unimodal (L)
40	2.0E-05	5.4E-06	0.969	Strongly unimodal (L)
50	1.2E-07	2.5E-08	0.974	Strongly unimodal (L)
60	9.2E-10	1.9E-10	0.946	Strongly unimodal (L)
Pacific Coast				
20	7.4E-05	2.1E-05	0.993	Strongly unimodal (L)
30	1.2E-05	3.3E-06	0.985	Strongly unimodal (L)
40	6.2E-12	1.1E-12	0.995	Strongly unimodal (L)
50	2.6E-15	4.0E-16	0.996	Strongly unimodal (L)
60	8.2E-17	1.2E-17	0.997	Strongly unimodal (L)

[a] P_c, P_l, and P_r are the results of the overall, left-, and right-most class tests, respectively

[b] An (L) behind a diagnosis indicates that the left-most class was dominant in the pattern
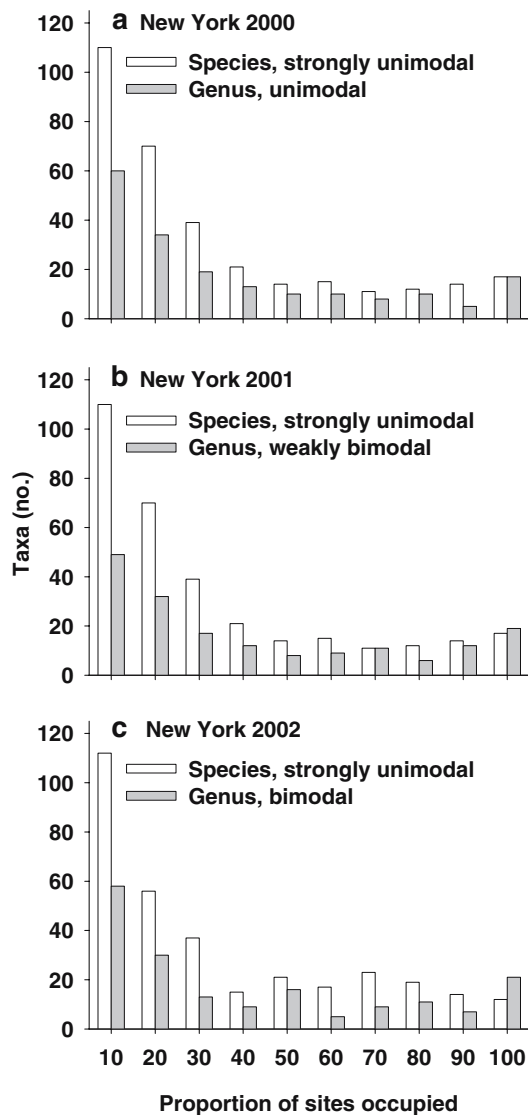
Fig. 1 Occupancy-frequency distributions and modality results of taxa for ten classes of stream insect data sets from: **a** Alabama 1990–1991, **b** Alaska 2000–2001, **c** Maryland 2001, **d** Maryland 2002, **e** the Pacific Coast 1997–2004. Modality designations are based on Tokeshi ([1992](#)). The proportion of sites occupied was divided into occupancy-frequency classes (i.e., the first class represents 0–10% of sites occupied, the second represents 10.01–20% occupied, etc.). **a** is sized for the nine streams sampled from Alabama
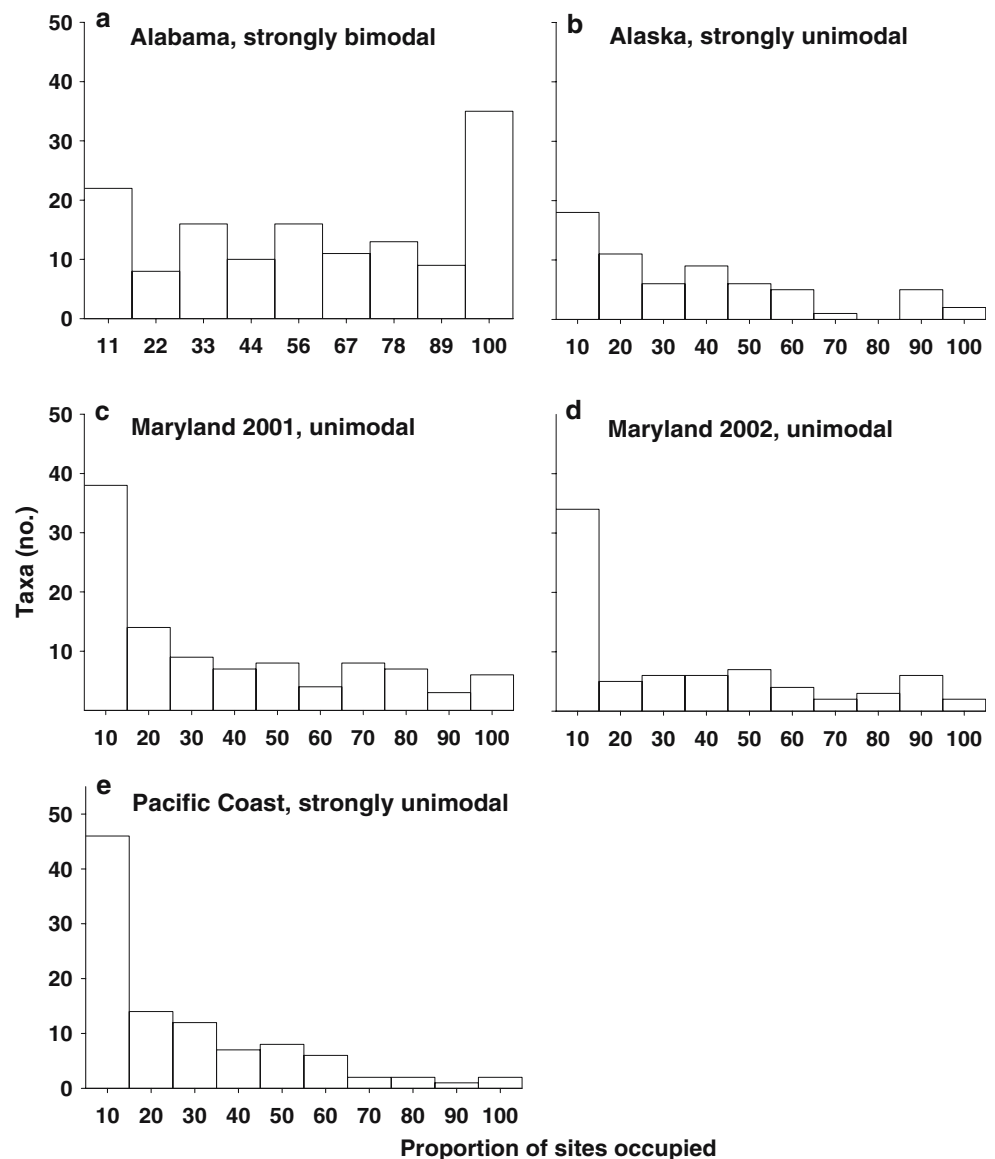
Gibson et al. [1999](#)) and dominance by rare taxa (Tokeshi [1992](#) and references therein; Malmqvist et al. [1999](#); Perelman et al. [2001](#); Storch and Šizling [2002](#); Heino [2005](#)) have been very common worldwide. Hence, the overall distributional patterns that we observed with stream insects are consistent with other studies encompassing a wide variety of flora and fauna and a diverse array of systems.

We hypothesized that occupancy-frequency patterns of stream insects would be bimodal as an effect of colonization and extinction dynamics fueled by frequent hydrologic disturbances, which may greatly reduce or eliminate populations at local scales (e.g., Resh et al. [1988](#); Reice et al. [1990](#); Dodds et al. [2004](#)). It has also been suggested that recolonization of localized stream patches is a continuous process (Mehranvar and

Jackson [2001](#)) that can rescue extinction-prone, local populations and also generate bimodal occupancy-frequency patterns (Gaston and Lawton [1989](#); Bossuyt et al. [2004](#)). However, despite frequent disturbances, dynamic equilibria, external and unequal recolonization, and discreteness of streams in the landscape, bimodality was rare in our data sets. We found overwhelmingly unimodal, satellite-dominated patterns or, more rarely, bimodal patterns with a larger satellite mode. We therefore conclude that the frequent natural disturbances of streams that were hypothesized to contribute to the co-occurrence of rare and common insects may instead reduce the occurrences of core taxa and facilitate greater proportions of satellite taxa, as per the intermediate disturbance hypothesis (Connell [1978](#)) and dynamic equilibrium models (Huston [1979](#)).

Fig. 2 Three years of occupancy-frequency distributions and modality results at the species and genus level of identification for stream insect data sets collected from New York in: **a** 2000, **b** 2001, **c** 2002. Modality designations are based on Tokeshi (1992). The proportion of sites occupied was divided into occupancy-frequency classes (i.e., the first class represents 0–10% of sites occupied, the second represents 10.01–20% occupied, etc.)

The effect of larger proportions of satellite taxa with increasing sampling area has long been predicted (Raunkiaer 1934; Williams 1964; Brown 1984) and commonly linked to increased habitat heterogeneity (Brown 1984; Hanski and Gyllenberg 1993; Collins and Glenn 1997; although see Gibson et al 2005). Collins and Glenn (1997) observed bimodality at small spatial scales in tallgrass prairie assemblages of plants, grasshoppers, small mammals, and birds, but these bimodal patterns disappeared as the sampling area was enlarged. From this, they hypothesized that the CSS may

be valid at smaller scales (e.g., the patch scale), and Brown's (1984) niche-based model may be valid at larger scales, thus reconciling two seemingly opposed hypotheses (Hanski 1982; Gotelli 1991; Collins and Glenn 1997).

With increasing spatial scales, our results appear to support niche-based theories of patch occupancy better than metapopulation models. For example, we found that the patterns shifted monotonically toward greater proportions of satellite taxa with increased spatial scale. However, the strong, positive relationship that we observed with sampling intensity and the significance of the satellite class suggest that the incorporation of range edges alone is insufficient to explain the increase of rare insects as spatial scale increases. Unfortunately, an accurate assessment is difficult because we cannot delineate the distributions of all the stream insects and cannot discount the effects of introduced heterogeneity and patchily distributed environmental factors that may accompany larger study areas (Brown 1984; McGeoch and Gaston 2002).

We identified some problems with applying the CSS to stream insects not addressed by Brown (1984). First, the CSS requires that year-to-year variability of environmental conditions must be negligible for the colonization of patches to prevent local extinctions (Hanski 1994). The inherent temporal variability of streams makes this unlikely; however, it is exceedingly difficult to determine the level of variability that constitutes a disturbance to a stream (Resh et al. 1988). Additionally, the CSS assumes that the probability of extinction is negatively correlated with the number of sites occupied (Gaston and Lawton 1989). However, the variability of parameters, such as flow and temperature, is likely more responsible for the absence of insects from patches than density-dependence and competitive exclusion.

The different effects that were observed with increasing spatial scale for the Pacific Coast and Maryland data sets demonstrates that scaling effects may be unique for different stream situations and that the mechanisms influencing distributional patterns may change with the scale of observation. The satellite mode in the Pacific Coast data set increased consistently with increasing spatial scale, whereas the satellite mode of the Maryland data was not as predictable within and among years. The most obvious difference between the two data sets is the spatial scales involved, from approximately 100 to approximately 500 km^2 and approximately 17,000 to approximately 73,000 km^2 for the Maryland and Pacific Coast, respectively. If these scales may be considered local and regional, our results are similar to those obtained

with other studies of scale effects (e.g., Sale 1988; Sherry and Holmes 1988; Collins and Glenn 1997). Furthermore, the interaction of hydrology and production (Huston 1979) should certainly be more unpredictable at local scales. Therefore, the scale of the Pacific Coast data set may transcend the impacts of individual disturbances, resulting in more predictable patterns as a result of climate, geography, and resource availability.

Taxonomic resolution presents a potential problem with aquatic invertebrate data sets because immature stages, which dominate these assemblages, are rarely identified to the species level – the taxonomic unit assumed in most models and hypotheses regarding distributional patterns. The influence of taxonomic resolution was evident in our study, as shown by the reduced satellite mode when the species-level New York data set was analyzed at the generic level. Based on the patterns we observed, generic-level analyses are informative, but they underestimate the satellite mode, a factor that should be acknowledged in studies of distributional patterns at this coarser taxonomic level. Our analyses of generic-level data sets also included some unresolved taxa (e.g., mostly generic level identifications with a few groups such as midges or some early instars at the family or subfamily level). Analyses with and without these unresolved groups did not significantly alter distributional patterns (data not shown), indicating they may not alter overall patterns unless they constitute a large component of an assemblage.

In conclusion, our results demonstrate that stream insects conform to the predictions of a variety of species distribution models and that both biological and artifactual mechanisms can influence patterns. We examined entire assemblages of organisms at large scales, dispersed across much of North America. Further, the assemblages we examined are truly patchily distributed, as the terrestrial habitats between streams in a landscape are completely uninhabitable to immature stream insects. This provides a unique perspective, as most analyses of distributional patterns and associated models focus on communities from more contiguous terrestrial systems, such as grasslands or forests. By limiting our analyses to stream insects, we also focused on diverse assemblages of relatively closely related taxa that were all likely operating at similar scales. Although some mechanisms underlying distributional patterns of stream insects and other groups are still in need of further study, our results demonstrate that taxonomic resolution, sampling intensity, and spatial scale all affect the occupancy-frequency distributions of stream insect communities.

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