

Effects of urbanization on butterfly species richness, guild structure, and rarity

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Abstract We evaluated the effects of landscape characteristics associated with urbanization, as well as local features, on butterfly species richness at four spatial scales (50, 150, 500, and 1,000 m from survey plots). We also evaluated these effects separately by butterfly guilds based on their region-wide rarity and on degree of specialization. The distribution of abundances of the 44 species observed showed an excess of uncommon species compared to a log-normal distribution, and the two most abundant species were exotic (*Thymelicus lineola* and *Pieris rapae*). We used an information theoretic approach to model selection to determine the most important correlates of butterfly species richness. Models of mean butterfly richness per visit explained greater variance than did models of cumulative richness across the season. Cumulative butterfly species richness was affected more at larger spatial scales, while richness per visit was affected similarly at all spatial scales. The most consistent local factor affecting butterfly diversity was the number of nectar producing plants that were flowering. The most consistent landscape-level correlates of species richness were number of people (at small spatial scales) and green space. Measures of increased urbanization were associated with decreased butterfly species richness, and rare and specialized species were most affected. Species that were regionally rare, and those that specialized both in host plants and had few broods, disappeared with declining richness across sites 2.9–4.5 times faster than did generalists and less restricted specialists.

Keywords Species diversity · Urbanization · Sprawl · Lepidoptera · Habitat specialist

Introduction

Habitat loss and fragmentation are primary causes of species extinctions (e.g., Wilcove et al. 1998), and urban and suburban sprawl have been identified as primary causes of habitat fragmentation (Wang and Moskovits 2001; Wade et al. 2003). Urbanization also is associated

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with habitat degradation, including decreased plant species diversity, reduced water quality, and increased air and soil pollution (e.g., Bastin 1999; Hall et al. 1999; McKinney 2002). The reduction in amount and quality of natural habitat associated with urban development negatively affects native biodiversity. Studies of the effects of urbanization on biodiversity have focused primarily on vertebrates, including reptiles (Germaine and Wakeling 2001), amphibians (Gibbs 1998; Homan et al. 2004; Clark et al. 2007), mammals (Riley et al. 2003; Jedrzejewski et al. 2004), and birds (Green and Baker 2003; Melles et al. 2003; Miller et al. 2003; Lee et al. 2004). Less attention has been paid to the effects of habitat loss and fragmentation on terrestrial invertebrates (e.g., Gibb and Hochuli 2002; Tschardt et al. 2002), and only a small subset of this work has investigated the effects of urbanization (e.g., Pizl and Josens 1995; McIntyre and Hostetler 2001; Alaruikka et al. 2002; Shochat et al. 2004). For example, carabid beetles are relatively well studied in urban settings, and they exhibit declines in species richness with increasing urbanization, although other measures of diversity and community structure do not follow similarly clear patterns (Gibbs and Stanton 2001; Niemela et al. 2002; Ishitani et al. 2003; Venn et al. 2003; Weller and Ganzhorn 2004).

Our goal was to evaluate butterfly communities at sites with different degrees of urbanization in the surrounding landscape. Butterfly species richness has been suggested as a surrogate for (i.e., to be strongly correlated with) hymenoptera (Kerr et al. 2000) and bird (Robbins and Opler 1997; Pearson and Carroll 1998; Blair 1999) diversity. Butterflies are potentially useful ecological indicators of urbanization because they are readily surveyed, and they are sensitive to changes in microclimate, temperature, solar radiation, and the availability of host plants for ovipositing and larval development (Ehrlich et al. 1972; Singer 1972; Weiss et al. 1988; Thomas et al. 1998; Fordyce and Nice 2003). Increased urban features, including roads, buildings, and mowed lawns, correspond with decreases in butterfly species richness, diversity, and abundance (Ruszczyk 1986; Ruszczyk and DeAraujo 1992; Blair and Launer 1997; Stefanescu et al. 2004). As might be predicted, butterfly species that specialize on particular plant species for ovipositing, and disturbance sensitive species, are more affected by urbanization than are generalist species (Kitahara and Fujii 1994; Hogsden and Hutchinson 2004).

It is likely that multiple aspects of urbanization have pronounced effects on butterfly communities, although there has been limited analysis beyond the effects of habitat loss and the simplification of herbaceous plant diversity described above. Our objectives were to evaluate the effects of urbanization at multiple spatial scales on butterfly distribution by correlating (1) several measures of species richness, (2) feeding and seasonal breeding specialization, and (3) measures of rarity and commonness (cf. Rabinowitz et al. 1986) with local site characteristics (nectar species richness, nectar abundance index, presence of water, and site area) and landscape measures of urbanization, including two measures of road cover, areas of open space and green space, and number of people.

Methods

Study sites

This study was conducted from 20 May–25 August 2004 in the Greater Boston Area in eastern Massachusetts, USA (42°16′–69°N, 70°98′–35°W; Fig. 1). Data were collected from 20 different meadow sites, each at least 1 km from the next nearest site. Sites were open fields with similar major nectar sources; sites differed in landscape contexts surrounding them to represent a range in degree of urbanization. The unmowed portion of each site

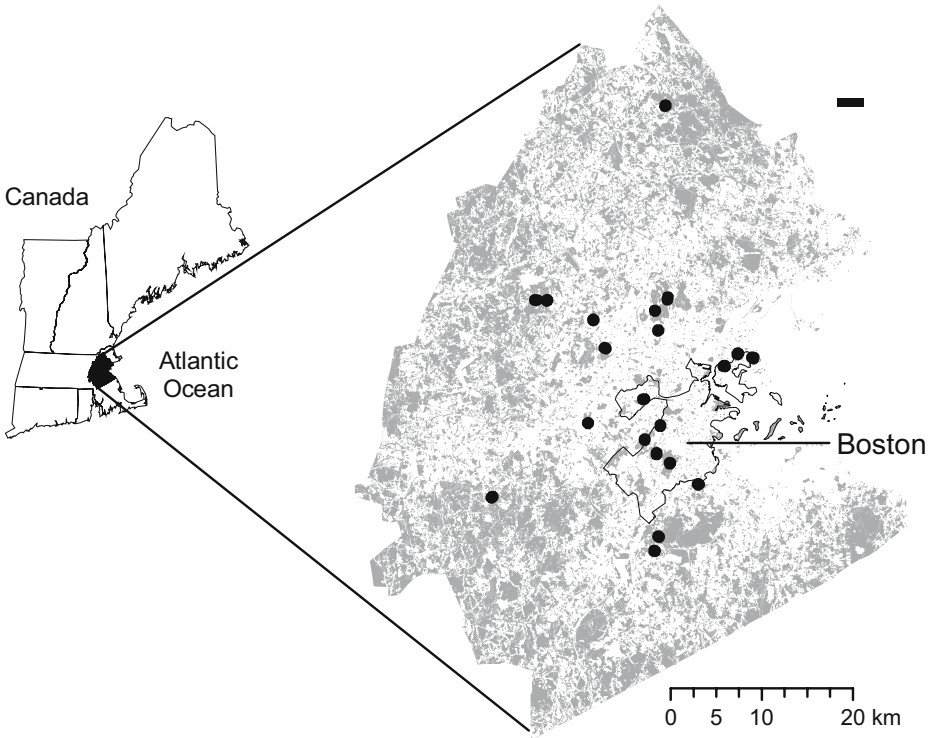


Fig. 1 Field sites in the Greater Boston Area (USA). Dots mark survey sites, and gray shading represents green space (a combination of urban open, pasture, open land, cropland, forest and woody perennial land use categories). The city limits of Boston are shown as solid black lines

ranged in size from 2,660–17,879 m² (\bar{X} =7,657, SD=3,706), but the area surveyed at each site for butterflies and plants was 1,500 m² along two transects of 75×10 m. Each site was visited three to five times during the study period. During each site visit, data were collected on butterfly and nectar source species presence and abundance. Surveys took place between 10:00–17:00 h on days when cloud cover was less than 50%, temperature was greater than 16°C, and there was no precipitation.

Butterfly and flowering plant surveys

Butterfly censuses were conducted using modified Pollard walks (Pollard 1977), traveling at a uniform pace along the 75-m transects, and all butterflies within 5 m to the left, right or in front of the observer were identified and recorded. Transects crossed a representative sample of each site and bisected areas with high nectar source abundance, thus maximizing the chances of encountering butterflies at each site. A single observer (PJC) conducted all butterfly surveys to control for observer bias. When identification on the wing was not possible, butterflies were caught with a net and identified in hand before being released. Nomenclature follows the North American Butterfly Association (NABA 1995). Flowering plant surveys were conducted at each site during each visit to determine nectar source richness (number of species) and abundance (number of individual plants that were flowering) during each visit. Only flowering plants known to be used as nectar sources by butterflies were recorded. Observers walked the butterfly transects and identified each

species of flowering plant encountered within 5 m to either side. When a given species of flowering plant numbered 100 or fewer individuals, each plant was counted. Species with more than 100 individual plants were estimated to fall within one of two categories; 101–1,000 or 1,001–10,000. The abundance of each flowering plant species was then binned into one of four categories: 1–10, 11–100, 101–1,000, or 1,001–10,000. Abundance data were used to create an index of nectar abundance for each site. This was done by taking the mid-point value of the highest abundance class of each species at a site over the course of the field season and summing these values across all flowering species at that site.

Butterfly species richness measures

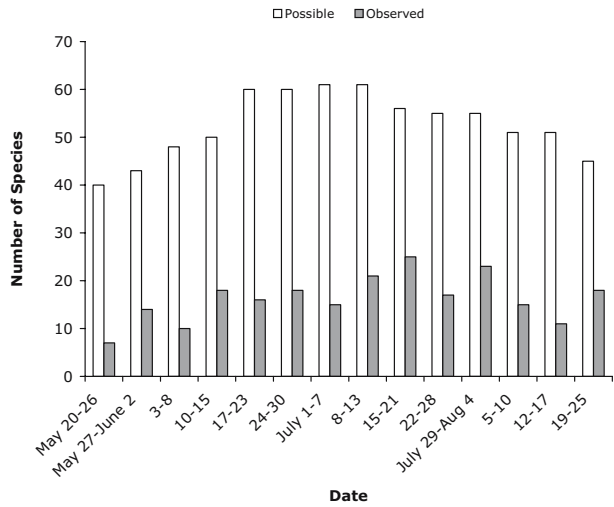
Butterfly data gathered from field surveys were used to create six measures of species richness. The first two measures were (1) cumulative species richness, equal to the total number of species seen at a site across all visits, and (2) mean number of species seen at a site during each visit. As surveys progressed across the season, however, differences in flight times affected the number of species that could be seen. In addition, some sites had habitat features not found at other sites that could have affected butterfly species richness (e.g., a water source). Consequently, the other butterfly species richness measures were adjusted for potential richness at the site at the time of the survey. The first adjustment was to divide observed species richness values at a site by the potential richness at a site, creating (3) adjusted cumulative richness and (4) adjusted mean richness / visit, respectively. Butterfly potential was determined by using information about species habitat use and existing records of flight time and abundance for eastern Massachusetts. For a species to be considered “possible” during a given site visit it needed to fulfill three criteria. First, it needed to be classified as uncommon (one to three observed/location/day), common (4–20 observed/location/day), or abundant (more than 20 observed/location/day) in the eastern half of the state according to data collected by the Massachusetts Butterfly Club (Dodd 1999). Species listed as rare to uncommon or rare to common also were considered possible, but those listed as rare were not. Second, the species needed to exhibit a flight time that overlapped with the site visit. Flight period for these species was recorded as overlapping or not overlapping during each 7-day period from April through October. If a species was not observed during a 7- or 14-day period in the middle of its flight season the species was still considered potentially present during that 1 or 2-week period (Fig. 2 depicts weekly butterfly richness potential based on these two criteria). Finally, for a species to be considered potentially present, it needed a habitat preference that matched the profile of the site or its immediately adjacent habitat, such as presence of deciduous and coniferous trees, freshwater marsh, streams, and ponds. Habitat preferences were based on Klots (1951), Howe (1975), Opler and Malikul (1998), and Glassberg (1999). This adjustment process resulted in a possible species list for each of the 20 sites surveyed during each of the 14 weeks of the survey season.

The final two butterfly richness measures were adjusted in a similar fashion, but butterfly species never seen on any survey were omitted from the list of potential species, creating conservative measures referred to as (5) subset adjusted cumulative richness at each site, and (6) subset adjusted mean richness / visit, respectively.

Identifying feeding and seasonal breeding specialists and generalists

To allow us to look for effects of urbanization on butterfly richness for species with different degrees of specialization, we placed each species into one of four guilds using the

Fig. 2 Maximum number of species that could be seen per week across all sites visited, based on flight time, available microhabitat, and historic abundance (*open bars*), and total number of species observed (*filled bars*). Observed species are summed across 20 field sites during each week of the census period; the number of sites surveyed each week was not constant



methods of Kitahara and Fujii (1994). Butterfly species were categorized in one of four types based whether or not they were host-plant specialists and whether or not they were time specialists. Host-plant specialists were those where larvae use ten or fewer host plant species, and time specialists were those that produce fewer than three broods per year. Species that specialized in both ways were referred to as dual specialists; some species specialized only in one or the other category, and generalist species specialized on neither. Information on larval resource breadth and number of broods was taken from Klots (1951), Forbes (1960), Howe (1975), Opler and Malikul (1998), and Glassberg (1999).

Determining butterfly species rarity

We also were interested in determining if guilds of species with different regional distribution and abundance patterns were associated differently with measures of urbanization. Using a scheme similar to that proposed by Rabinowitz (1981; Rabinowitz et al. 1986), butterfly species were placed into one of eight rarity categories based on their geographic range, habitat specificity, and local population size. Geographic range of butterflies was taken from the US Geologic Service Butterflies of North America distribution maps (Opler et al. 1995), which shows species as present or absent in each county in the USA. Determining the cutoff between broad and narrow geographic distributions is not well defined, so we considered a range to be large if it exceeded the area of a large natural disturbance (Reed 1992). We used the threat posed by ice storms to overwintering butterfly survival as a means of identifying geographic range. An ice storm in 1998 affected approximately 160,000 km² of the Northeastern United States and Canada (Federal Emergency Management Agency 1998; Canadian Forest Service 2003), so this was considered the cutoff between large and small ranges. Of the 44 species observed during this study, however, all have geographic ranges larger than this. Habitat specificity was characterized as broad or restricted based on the number of different habitat types that a species was reported to use. Species described as using only meadows or woodlands, swamps, wetlands, or more specific habitats (Klots 1951; Howe 1975; Opler and Malikul 1998; Glassberg 1999) were categorized as restricted. Species described as being commonly found in two or more habitat types were characterized as having broad habitat specificity. The local population size of each species was determined

using the Massachusetts Butterfly Club checklist (Dodd 1999). Only species listed as abundant (more than 20 observed/location/day) were classified as having sometimes large populations. Using these three binomial variables, each species' rarity type was classified using Rabinowitz's (1981) rarity scheme.

Variables, landscape scales, and analyses

Local variables included nectar species richness, nectar abundance index, water (present or absent), and unmowed area. Landscape variables included single-lane road length, which is the total length of single lane undivided roads; total road length, which includes all paved road types; area of open space, which was a combination of urban open, pasture, open land, and cropland; area of green space, which was open space (as just defined) plus forest and woody perennial categories; and number of people. Landscape variables were quantified at spatial scales of 50, 150, 500, and 1,000 m from the perimeter of the study sites using ESRI ArcGIS software. Spatial scales were selected based on published butterfly dispersal distances from mark-release-recapture studies (Chew 1981; Schneider 2003). By matching spatial scales with dispersal distances, we attempted to capture landscape characteristics most likely to affect butterfly species richness. Road type and length data were taken from Census 2000 TIGER Linework shapefiles, human population abundance was calculated from Census 2000 Blocks shapefiles, and land use data were taken from the Office of Geographic and Environmental Information (MassGIS), Commonwealth of Massachusetts Executive Office of Environmental Affairs (<http://www.mass.gov/mgis/>) land use data layer (updated 1999). The land use data layer was created from 1:25,000 aerial photography and land use was identified into one of 21 different categories.

We compared the six butterfly species richness measures to local and landscape variables at each spatial scale. Models were created in a manner similar to that of Hostetler and Knowles-Yanez (2003) although we compared model fit using an information theoretic approach (Burnham and Anderson 2002). Specifically, within each spatial scale we first determined bivariate correlation coefficients for each of the independent variables compared to the dependent variable. The variable with the best correlation coefficient was entered into a regression model and its AICc score determined (calculated from AIC score from PROC REG, SAS 2004). We then compared all possible two-variable models that included the first independent variable. If any model decreased the AICc value by more than 2.0 (Burnham and Anderson 2002), the best model was kept and the procedure was repeated for three-way models, and so on until there was no significant improvement in model fit based on AICc scores. In the one instance where alternative models had identical AICc scores (to two decimal places), we report the model with fewer parameters. Once best models were identified for each spatial scale, a combined model was made using the same procedure, but considering only the variables that were significant at each spatial scale. For final models, we also report an R^2 value to provide an indication of how well each model fit the data. With this type of analysis, there exists the potential problem that independent variables could be correlated, leading to a problem with multicollinearity in the analysis. To evaluate the degree of multicollinearity within each spatial scale we ran a condition index (the COLLIN option in PROC REG, SAS Institute 2004). For our independent variables for each measure of richness, the maximum value for the condition index was 24.2, so there was no indication of a multicollinearity problem within each spatial scale for our regressions (Belsley et al. 1980).

We conducted principal components analysis on the landscape variables at each spatial scale and across scales in an attempt to reduce the number of independent variables.

However, due to poor variable reduction (the first principal component never explained more than 24.5 of the variation) the principal components were not used in regression analyses.

In order to expand our exploration of the possible relationships between butterfly diversity and landscape variables, statistical significance was considered to be $\alpha=0.10$. Similar analyses were done on mean species richness/visit values for the different ecological guilds. Specifically, we created a combined model for each of the following: dual specialist species, species that were not dual specialists, rare species (cf. Rabinowitz 1981; Rabinowitz et al. 1986), and common species (those not classified as “rare”). Results of the combined model are reported, unless a model at a specific spatial scale was superior ($\Delta\text{AICc}<-2.0$), which can occur depending on the order of variables entered into the model.

Results

During our surveys we recorded 44 species of butterfly from six families (Table 1). Sites ranged in cumulative richness from 4–26 species ($\bar{X}=14.0$, $\text{SD}=4.9$) and mean species richness per visit ranged from 2.2–11.0 ($\bar{X}=6.1$, $\text{SD}=2.2$). During each week of the study, we observed from 17.5–44.6% ($\bar{X}=30.8$, $\text{SD}=8.1$) of the potential observable species (Fig. 2; note that this figure shows the number of species possible by week, combined across all sites, while analyses were done on the possible species list determined each week separately for each site). Cumulative abundances of each species across the entire study ranged from 1–1,937 individuals, with the only two exotic species being the most abundant (*Thymelicus lineola*, 1,937 individuals; *Pieris rapae*, 689); species ranked abundances fit a log linear distribution ($r^2=0.95$). If the axes are reversed and number of species are grouped into abundance octaves (Magurran 1988), our distribution was significantly different than that expected from a log-normal distribution (Kolmogorov–Smirnov test, $D=0.147$, $P=0.018$), with an overabundance of uncommon species and the modal abundance in the lowest octave of two or fewer individuals.

Sites ranged in nectar species richness from 6–34 species ($\bar{X}=21.5$, $\text{SD}=6.8$) and the nectar abundance index ranged from 1,150–82,050 ($\bar{X}=28,385$, $\text{SD}=19,585$). Because of strong similarities of the butterfly richness indices subset adjusted cumulative richness and subset adjusted mean richness/visit to other measures of richness, both here and in their results of subsequent analyses, we do not report their results for further analyses.

All regression models yielded significant results, but the variables included in each model differed by species richness measure and spatial scale (Table 2). Models of cumulative species richness consistently had lower explanatory power than did models of mean number of species/visit. Models of cumulative species richness improved (assessments of model fit are based on AICc scores) with increasing spatial scale. At smaller spatial scales, cumulative species richness was most correlated with number of people (50, 150 m scales) and total road length (500 m scale). The best model for this butterfly richness variable, however, occurred at the 1 km scale, and included green space and the number of nectar plants that were flowering ($R^2=0.49$). Adjusting cumulative species richness by the number of species that could be seen had no effect on variables included in the model or model fit at the first three spatial scales. At the 1 km spatial scale the model included only the length of single-lane roads, and explained less variability than did the unadjusted richness model. Using this butterfly richness measure, there was almost no difference in model fit across spatial scales. Relationships between butterfly richness and independent variables were predictable: negative relationships with number of people and road length, and positive relationships with green space and the number of flowering plants.

Table 1 Species detected on surveys, cumulative numeric abundance across sites (*N*), number of sites where species were recorded (out of 20), and information required to determine degree of specialization based on Kitahara and Fujii (1994) and regional rarity based on Rabinowitz (1981) (geographic range excluded from table because all species have wide geographic distributions)

Common name	<i>N</i>	No. of sites	Rarity class		Degree of specialization	
			Habitat specificity	Local population Size	Broods/ year	No of larval hosts
Papilionidae						
Black swallowtail (<i>Papilio polyxenes</i>)	28	11	Broad	Small	2	>10
Eastern tiger swallowtail (<i>P. glaucus</i>)	25	14	Restricted	Small	2	>10
Spicebush swallowtail (<i>P. troilus</i>)	5	3	Restricted	Small	2	≤10
Pieridae						
Cabbage white (<i>Pieris rapae</i>)	689	20	Broad	Large	3	>10
Clouded sulphur (<i>Colias philodice</i>)	77	16	Broad	Large	>3	>10
Orange sulphur (<i>C. eurytheme</i>)	135	15	Broad	Large	>3	>10
Lycaenidae						
Harvester (<i>Feniseca tarquinius</i>)	0	0	–	–	2	≤10
American copper (<i>Lycaena phlaeas</i>)	91	8	Broad	Large	3	≤10
Coral hairstreak (<i>Satyrum titus</i>)	5	1	Restricted	Small	1	≤10
Acadian hairstreak (<i>S. acadicum</i>)	0	0	–	–	1	≤10
Edward's hairstreak (<i>S. edwardsii</i>)	1	1	Restricted	Large	1	≤10
Banded hairstreak (<i>S. calanus</i>)	6	1	Restricted	Large	1	≤10
Striped hairstreak (<i>S. liparops</i>)	0	0	–	–	1	>10
Juniper hairstreak (<i>Callophrys gryneus</i>)	0	0	–	–	2	≤10
Frosted elfin (<i>C. irus</i>)	0	0	–	–	1	≤10
Gray hairstreak (<i>Strymon melinus</i>)	0	0	–	–	2	>10
Eastern tailed blue (<i>Everes comyntas</i>)	94	14	Broad	Large	>3	>10
Spring azure (<i>Celastrina ladon</i> spp.)	3	2	Broad	Large	1	>10
Silvery blue (<i>Glaucopteryx lygdamus</i>)	0	0	–	–	1	>10
Nymphalidae						
Variiegated fritillary (<i>Euptoieta claudia</i>)	0	0	–	–	2	>10
Great spangled fritillary (<i>Speyeria cybele</i>)	11	6	Broad	Small	1	≤10
Aphrodite fritillary (<i>S. aphrodite</i>)	0	0	–	–	1	≤10
Silver-bordered fritillary (<i>Boloria selene</i>)	0	0	–	–	1	≤10
Harris' checkerspot (<i>Chlosyne harrisii</i>)	0	0	–	–	1	≤10
Pearl crescent (<i>Phyciodes tharos</i>)	42	11	Broad	Large	2	≤10
Question mark (<i>Polygonia interrogationis</i>)	1	1	Restricted	Small	2	≤10
Eastern comma (<i>P. comma</i>)	1	1	Restricted	Small	2	≤10
Mourning cloak (<i>Nymphalis antiopa</i>)	1	1	Broad	Small	2	>10
Red admiral (<i>Vanessa atalanta</i>)	11	6	Broad	Small	>3	≤10
American lady (<i>V. virginensis</i>)	13	9	Broad	Large	2	>10
Painted lady (<i>V. cardui</i>)	6	4	Broad	Small	>3	>10
Common buckeye (<i>Junonia coenia</i>)	4	2	Broad	Small	2	>10
Red-spotted purple (<i>Limenitis arthemis astyanax</i>)	1	1	Restricted	Small	2	>10
Viceroy (<i>L. archippus</i>)	0	0	–	–	2	≤10
Northern pearly eye (<i>Enodia anhedon</i>)	0	0	–	–	1	≤10
Eyed brown (<i>Satyrodes eurodice</i>)	0	0	–	–	1	≤10
Appalachian brown (<i>S. appalachia</i>)	1	1	Restricted	Small	1	≤10
Little wood satyr (<i>Megisto cymela</i>)	141	11	Restricted	Large	1	≤10
Common ringlet (<i>Coenonympha tullia</i>)	100	9	Restricted	Large	2	≤10

Table 1 (continued)

Common name	N	No. of sites	Rarity class		Degree of specialization	
			Habitat specificity	Local population Size	Broods/ year	No of larval hosts
Common wood nymph (<i>Cercyonis pegala</i>)	57	9	Restricted	Large	1	≤10
Monarch (<i>Danaus plexippus</i>)	13	5	Broad	Large	>3	≤10
Hesperiidae						
Silver-spotted skipper (<i>Epargyreus clarus</i>)	35	12	Broad	Large	1	>10
Hoary edge (<i>Achalarus lyciades</i>)	0	0	–	–	1	≤10
Southern cloudywing (<i>Thorybes bathyllus</i>)	3	1	Restricted	Small	1	>10
Northern cloudywing (<i>T. pylades</i>)	2	2	Restricted	Small	1	>10
Dreamy duskywing (<i>Erynnis icelus</i>)	2	2	Restricted	Small	1	≤10
Juvenal's duskywing (<i>E. juvenalis</i>)	0	0	–	–	1	≤10
Horace's duskywing (<i>E. horatius</i>)	1	1	Restricted	Small	2	≤10
Wild indigo duskywing (<i>E. baptisiae</i>)	0	0	–	–	2	≤10
Common sootywing (<i>Pholisora catullus</i>)	0	0	–	–	2	>10
Least skipper (<i>Ancylorhynchus numitor</i>)	17	5	Restricted	Small	3	≤10
European skipper (<i>Thymelicus lineola</i>)	1937	18	Restricted	Large	1	≤10
Leonard's skipper (<i>Hesperia leonardus</i>)	0	0	–	–	1	≤10
Indian skipper (<i>H. sassacus</i>)	0	0	–	–	1	≤10
Peck's skipper (<i>Polites peckius</i>)	165	16	Broad	Large	2	≤10
Tawny-edged skipper (<i>P. themistocles</i>)	16	7	Broad	Small	2	≤10
Crossline skipper (<i>P. origenes</i>)	5	3	Restricted	Small	1	≤10
Long dash (<i>P. mystic</i>)	4	2	Restricted	Small	1	≤10
Northern broken dash (<i>Wallengrenia egeremet</i>)	50	10	Restricted	Small	1	≤10
Little glassywing (<i>Pompeius verna</i>)	8	6	Restricted	Small	1	≤10
Delaware skipper (<i>Anatrytone logan</i>)	0	0	–	–	1	≤10
Mulberry wing (<i>Poanes massasoit</i>)	0	0	–	–	1	≤10
Hobomok skipper (<i>P. hobomok</i>)	1	1	Restricted	Small	1	≤10
Broad-winged skipper (<i>P. viator</i>)	3	2	Restricted	Small	1	≤10
Black dash (<i>Euphyes conspicuus</i>)	0	0	–	–	1	≤10
Dun skipper (<i>E. vestris</i>)	12	4	Restricted	Large	1	≤10
dusted skipper (<i>Atrytonopsis hianna</i>)	0	0	–	–	1	≤10
Pepper and salt skipper (<i>Amblyscirtes hegon</i>)	0	0	–	–	1	≤10
Libytheidae						
American snout (<i>Libytheana carinenta</i>)	1	1	Restricted	Small	2	≤10

Habitat specificity is based on Klots (1951), Howe (1975), Opler and Malikul (1998), and Glassberg (1999), and local population size is based on Dodd (1999)

Models of mean butterfly species richness per visit had consistently higher explanatory power (R^2 ranged from 0.50 to 0.77; Table 2). The best models of mean butterfly species richness per visit at every spatial scale included green space. The best models (based on AICc) were at the 50 and 150 m spatial scales, with decreasing fit with increasing spatial scales. Models showed positive relationships between butterfly richness and green space, nectar species richness (number of species of nectar-producing plants that were flowering), and number of flowering plants. Both models showed a negative relationship with the presence of water. Models where mean butterfly richness was adjusted for possible butterfly species showed a similar pattern, with the 1 km spatial scale having the poorest fit. Models

at the three smaller spatial scales were virtually identical, including water, the number of flowering plants, and measures of undeveloped space (open space for 50 m, unmowed area and green space for 150 and 500 m). The two smallest spatial scales also included number of people in their models. Variables differed in their relative importance at each spatial scale, with number of people being the most important at the two smaller spatial scales (negative relationship), and green space being the most important at the larger spatial scales (positive relationship; Table 2).

Table 2 Best models (based on AICc scores) from linear regressions of butterfly species richness

	Significant variables	AICc score	R^2	p value
Cumulative species richness				
50 m	–Number of people	60.37	0.23	0.019
150 m	–Number of people	60.03	0.23	0.018
500 m	–Total road length	58.19	0.31	0.006
1 km	+Green space, +total plant	53.54	0.49	0.001
Combined	+Green space 1 km, +total plant	53.54	0.49	0.001
Adjusted cumulative species richness				
50 m	–Number of people	83.38	0.24	0.017
150 m	–Number of people	83.30	0.24	0.016
500 m	–Total road length	80.84	0.33	0.005
1 km	–Single-lane road length	81.72	0.30	0.007
Combined	–Total road length 500 m	80.84	0.33	0.005
Mean number of species/visit				
50 m	+Nectar species richness, –water, +total plant, +green space	8.47	0.77	<0.001
150 m	+Green space, +total plant, –water	8.97	0.74	<0.001
500 m	+Green space, +total plant, +unmowed area, –water	11.52	0.74	<0.001
1 km	+Green space	19.33	0.50	<0.001
Combined	+Green space 1 km	19.33	0.50	<0.001
Adjusted mean number of species/visit				
50 m	–Number of people, –water, +total plant, +open space	43.59	0.72	<0.001
150 m	–Number of people, –water, +total plant, +unmowed area, +green space	43.56	0.75	<0.001
500 m	+Green space, +unmowed area, +total plant, –water	42.32	0.74	<0.001
1 km	+Green space, +unmowed area	49.86	0.55	<0.001
Combined	+Green space 1 km, +unmowed area, +total plant	47.68	0.62	<0.001
Mean number of species/visit, best combined or single-spatial-scale model for				
Dual specialists	–Water, –number of people 150 m, +total plant, +green space 150 m	–	0.77	<0.001
Not dual specialists	–Water, +total plant, +open space 150 m	–	0.72	<0.001
Rare species	+Green space 1 km, +unmowed area	–	0.70	<0.001
Common species	+Total plant, +open space 50 m, –water, –single-lane road length 50 m	–	0.65	<0.001

Cumulative species richness measures refer to total species richness summed across all site visits, and adjusted measures represent the percent of species observed out of those possible (corrected for flight time, rarity, and site characteristics). The definitions of guilds (dual specialists and rarity) are given in the text. Results are given for each spatial scale and across spatial scales (“combined” models); independent variables are placed in order of relative importance to the model, and are distinguished by whether they were positively (+) or negatively (–) associated with species richness. AIC_c scores can be compared only within a single species richness type; values are not given for models that are not subsets of other models. R^2 values are adjusted for degrees of freedom; error df for all models = 20–number of variables in reduced model–1

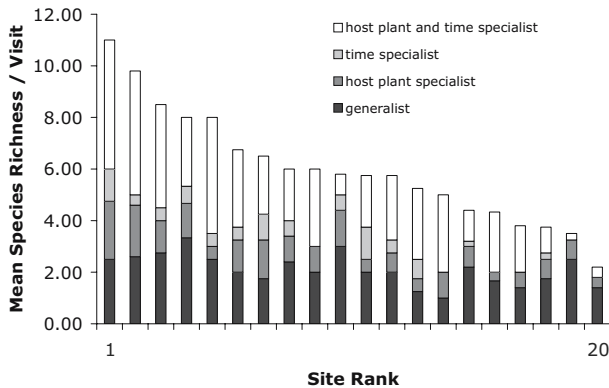


Fig. 3 Mean species richness per visit, with sites ranked from highest to lowest richness and subdivided by site into specialization category. Generalist species used greater than ten host plant species and had three or more broods per year; host plant specialists used ten or fewer host plant species but had greater than two broods per year; time specialists used greater than ten host plant species but had less than three broods per year; and host plant and time specialists used 10 or fewer host plants and had less than three broods per year. Error bars were omitted for clarity of the figure

Of the 44 butterfly species recorded, five were classified as generalists, four as host plant specialists, ten as timing-of-reproduction specialists, and 25 were dual specialists on both host plant and timing (Table 1). When survey sites were ranked by species richness (Fig. 3), we found that the rate of species richness disappearance across sites by species that were dual specialists was 2.9 to 4.5 times faster than for generalists or other types of specialists (combined specialists: slope = -0.190 , $r^2 = 0.67$; generalists: slope = -0.062 , $r^2 = 0.36$; number-of-brood specialists: slope = -0.065 , $r^2 = 0.55$; host plant specialists: slope = -0.042 , $r^2 = 0.37$). Because of the similarity of slopes, generalists, number-of-brood specialists, and host plant specialists were aggregated for analysis of the effects of site and landscape variables on richness, while species that had few broods and specialized in host plants (dual specialists) were analyzed separately. The best fit model for mean species richness per visit for dual specialists ($R^2 = 0.77$) occurred at the 150 m spatial scale and included local and landscape variables: negative relationships with number of people and water, and positive associations with the number of flowering plants and green space (Table 2). Species that were not dual specialists had a similarly strong model ($R^2 = 0.72$) that also showed the best fit at the 150 m spatial scale and included a negative relationship with water and positive associations with the number of flowering plants and open space (Table 2).

With regards to regional rarity classification based on Rabinowitz's (1981; Rabinowitz et al. 1986) criteria, we categorized 11 species as common and the rest as some type of rare: seven species had restricted habitat specificity and sometimes large local populations, seven had broad habitat specificity and everywhere small local populations, and 19 had restricted habitat specificity and everywhere small local populations (Table 1). When survey sites were ranked by mean butterfly species richness/visit (Fig. 4), both common and rare species (collectively) declined across sites mean species per visit, but rare species declined at almost twice the rate (common sites: slope = -0.136 , $r^2 = 0.71$; rare species: slope = -0.223 , $r^2 = 0.80$). The mean number of rare species per visit was best explained by a model that include a local variable, unmowed area, and green space at the 1 km spatial scale ($R^2 = 0.70$). In contrast, common species were most affected at the smallest spatial scale, with

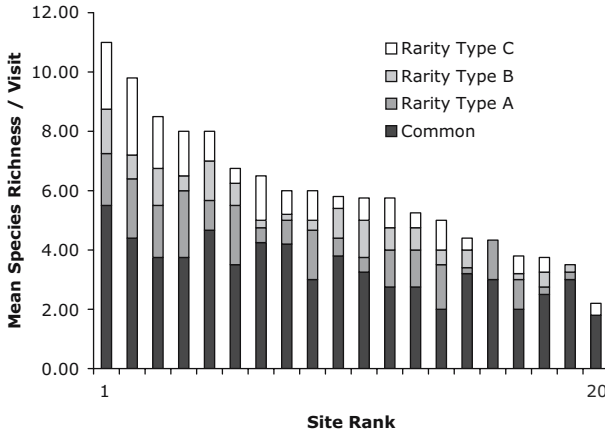


Fig. 4 Mean species richness per visit, with sites ranked from highest to lowest richness and subdivided by site into rarity category (cf. Rabinowitz 1981). Species in all categories had wide geographic distributions. Common species were characterized by broad habitat specificity and sometimes large local populations; rarity type A species had restricted habitat specificity and sometimes large local populations; rarity type B species had broad habitat specificity and everywhere small local populations; and rarity type C species had restricted habitat specificity and everywhere small local populations. Error bars were omitted for clarity of the figure

positive associations with the number of nectar-producing plants and open space at 50 m, and negative associations with water and single-lane road length ($R^2=0.65$).

Discussion

Regardless of our measure of species richness, most best-fit models included both local and landscape variables. Models of cumulative species richness consistently explained less of variability than did models of mean species richness per visit. Cumulative species richness was best explained by a model that included the total number of plants that produce nectar used by butterflies and green space at the 1 km spatial scale. The spatial-scale-specific models at smaller spatial scales were poorer model fits, but those models included number of people and total length of all paved road types. In contrast, the best models explaining mean butterfly richness per visit were those at smaller spatial scales (50 and 150 m), although they also included the total number of plants that produce nectar used by butterflies and green space. These models also included a variable that indicated the presence of water, and the 50 m spatial scale model also included nectar species richness. These results are consistent with studies that have found plant and butterfly species richness to positively covary (e.g., Hawkins and Porter 2003; Hogsden and Hutchinson 2004) and the number of plant communities to correlate positively with the presence of regionally rare butterfly species (Lovett-Doust et al. 2003). Summerville and Crist (2001) experimentally manipulated the degree of habitat fragmentation and found that butterfly species richness was positively correlated with increasing patch area. They also noted that plots with greater flowering plant abundance showed higher use by butterflies.

Our adjustment of richness measures by the number of butterflies expected as a maximum each week had little effect on the explanatory power of the models or of the patterns revealed. For cumulative species richness, the only effect was at the 1 km spatial scale, where single-

lane road length replaced green space and flowering plant abundance. For models of mean butterflies per visit models adjusted for estimated potential butterfly richness, there were more model changes over unadjusted models. At the 50- and 150-m spatial scales, number of people became the most influential variable, as with cumulative species measures, and the area of unmowed habitat (locally) became important at the larger spatial scales.

As anticipated, we that found variables associated with increasing urbanization (roads, number of people) were negatively correlated with butterfly richness, while measures associated with areas of less development (green space, open space) were positively correlated. These results are consistent with those of Ruszczyk (1986; Ruszczyk and DeAraujo 1992) and Stefanescu et al. (2004) who found lower species diversity with increased urbanization. Similarly, Kitahara and Fujii (1994, 1997) found an increased proportion of generalist butterfly species with greater urbanization. In contrast, Blair and Launer (1997) found that species richness peaked at sites with intermediate disturbance, where disturbance was defined as a variety of factors associated with urbanization (e.g., amount of cover of pavement). Hogsden and Hutchinson (2004) note, however, that these results may be spatial scale dependent with peaks in richness and diversity at moderately disturbed sites when spatial scale was larger (6 ha) and peaks at the least disturbed sites when the scale was smaller (0.75 ha). Collinge et al. (2003) found that although grassland type and habitat quality strongly influence butterfly richness and abundance, the extent of urban development was not related to species richness. They note, however, that their study area consisted of relatively contiguous grasslands surrounded by 5–30% urban development and that studies considering isolated habitat patches within a more urban setting might yield different results. This argument is consistent with that made by Hagan and Meehan (2002) for forest birds, where they found stand (local) characteristics were more important in explaining bird diversity within a forested landscape compared to the importance of landscape features when forest patches occurred in an agricultural or urban habitat matrix (e.g., Robbins 1980, Villard et al. 1999). Our only surprise was a consistently negative relationship between the presence of water and mean butterfly richness per visit. We were anticipating the reverse pattern, assuming water would be associated with plant species diversity, so we do not have an explanation for this result.

Landscape variables and the effects of spatial scale, especially larger spatial scales, on the other hand, have been largely ignored in previous studies of urbanization effects on butterflies. Blair and Launer (1997) characterized their plots based on coverage of lawn, grassland, buildings, pavements, and woody plants at a small spatial scale (<50 m radius from each survey site). Hogsden and Hutchinson (2004) used similar land use variables, but aggregated them into a gray space - green space ratio, and analyses were done at two small spatial scales (0.75 and 6 ha surrounding transects). We evaluated the relationships between butterfly diversity and landscape features at much larger spatial scales, including up to a 1-km radius around the study sites. We found landscape variables to be included in best models at all spatial scales investigated. We found green space and road cover correlated with cumulative butterfly richness measures at the 1 km and 500 m scales, while human abundance was most often significant at the 150 and 50 m scales; green space was included in models at all spatial scales for mean butterfly richness per visit. It is not clear what mechanism(s) associated with human abundance might be affecting butterfly diversity, or if human abundance merely acts as an indicator of a suite of effects associated with urbanization. Blair and Launer (1997) and McKenna et al. (2001) investigated specific human activities, including pedestrian, bicycle, and car traffic. Although the former study only used these measures as a correlate of urbanization, the latter found that increased traffic volume can differentially increase butterfly mortality. It is not clear, however, if these direct effects are sufficient to alter butterfly species richness or community composition.

Of the butterfly species richness measures we evaluated, the two mean species per visit measures yielded the best model fits (as compared to the cumulative species measures). The “by visit” portion allowed one control for sampling effort. A priori, we found the standardized mean/visit measure to be biologically compelling. By using site characteristics and butterfly natural history information (habitat used, flight times) to create a list of species that might be encountered at each site, we were judging richness as it related to biotic potential at each site. This adjustment, however, did not improve the explanatory power of our models.

The two exotic species recorded during the study, *Pteris rapae* and *Thymelicus lineola lineola*, had the greatest cumulative abundances. In their study of butterfly species diversity and abundance patterns across North America, Kocher and Williams (2000) noted that these two species were found in higher abundances in disturbed habitats than undisturbed habitats. It has been suggested that the spread of *P. rapae* to urban areas has been aided by their use of naturalized, weedy species that are often associated with urban and suburban settings. (Chew 1981), and recent population modeling has supported this suggestion (Keeler et al. 2006). The North American range of *T. lineola* overlaps with that of its preferred host plant, Timothy grass (*Phleum pratense*), which is a non-native species in the northeastern USA and eastern Canada grown for hay, pasture, and silage. Since its introduction in Canada in 1910, the spread of *T. lineola* has paralleled the spread of *P. pratense* in agricultural and urban settings (Layberry et al. 1998). Possibly consistent with the high abundance of the exotic butterfly species at our sites, we also noted an excess of uncommon species compared to that predicted by the log-normal distribution. This might be predicted, as the log-normal distribution is consistent with a large, mature and varied natural community (Magurran 1988), indicating that our relatively urban setting contains a simplified complex of species. This pattern has been noted for other taxa (e.g. Blair 1996; McIntyre and Hostetler 2001).

As species richness decreased across sites, regionally rare species and species that are dual specialists (on host plants and on timing of breeding) disappeared at a faster rate than did common and non-dual specialist species. Interestingly, our statistical models had much higher explanatory power for rare species and for dual specialists than for other guilds. This result is consistent with previous work on other taxa, which has shown rare and specialist species to be sensitive to habitat fragmentation and human disturbance (e.g., Rabinowitz et al. 1986; Reed 1992; Tschamtko et al. 2002), and in studies of butterflies. Summerville and Crist (2001) noted that rare butterfly species were disproportionately affected by fragmentation and that many common species appeared to be unaffected. Kitahara and Fujii (1994, 1997; see also Kitahara et al. 2000), who developed the specialist-generalist categorization scheme we used here, also found a strong negative correlation between the number of dual specialists and degree of human disturbance and that generalist species were not significantly affected by disturbance. Similarly, Hogsden and Hutchinson (2004) found only weak associations between any single local or landscape variable and the presence of disturbance adaptable (generalist) butterfly species. Additionally, their composite variable of the ratio of gray space to green space allowed moderately successful explanation of variance in species richness, diversity, and individual abundances. Our observations add to the body of work suggesting that disturbed habitats will be occupied primarily by generalist and common species and that rare and specialist species are more susceptible to loss as urban sprawl expands. If the particular mechanisms of loss can be identified, it should allow amelioration through appropriate planning of greenways and habitat networks (Erickson 2004).

Similar local and landscape variables affected dual-specialist and non-dual specialist species richness, but a different pattern was found for regional rare and common species. Rare species were most associated with green space at the largest (1 km) spatial scale and local habitat (unmowed) area. In contrast, species categorized as common were affected

most by local features and those at the 50-m spatial scale. Although we did not test specific mechanisms in this study, our results suggest that reduction in number of nectar-producing plants, increased number of people, and loss of green space are the most important factors limiting butterfly diversity in our area. We also found that rare species (as categorized based on distribution, abundance, and specialization, *sensu* Rabinowitz 1981) are most vulnerable to local and landscape-level changes associated with urbanization.

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