

# The effect of urbanization on the quality of remnant habitats for leaf-mining Lepidoptera on *Quercus agrifolia*

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Previous studies suggest that urbanization alters the abundance and species richness of native insects on remnant habitat patches. However, the effects of urbanization on biological communities caused by habitat loss and fragmentation have not been separated from effects caused by altered habitat quality within remnant habitats or by the nature of the urban matrix. To test for an effect of urbanization acting via altered habitat quality or matrix characteristics, we controlled for the effects of habitat loss and fragmentation by comparing remnant habitat patches in urban and agricultural regions experiencing similar levels of habitat loss and fragmentation. We studied the species richness and abundance of the community of leaf-mining Lepidoptera on *Quercus agrifolia* in the San Francisco Bay Area. We measured the extent of five land-use types within a 500 m radius of each study patch. We built generalized linear models to determine if the extent of any of the landscape variables was associated with the species richness and abundance of the leaf-miner community. The extent of urbanization was not associated with species richness or total abundance. However, the abundance of three species of leaf-mining moths was associated with the extent of urbanization, but not in a consistent pattern. The abundances of *Stigmella variella* and *Bucculatrix albertiella* were higher and the abundance of *Dryseriocrania auricyanea* was lower at highly urbanized sites. The absence of a consistent association between urban land-use and both species richness and abundance indicates that the effects of urbanization on the community of leaf-mining moths of *Q. agrifolia* do not differ from the effects of replacing and fragmenting habitats with similar amounts of agricultural land-uses.

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The replacement of natural habitats by urbanization has reduced the abundance or caused the disappearance of some insect species (Adkin 1934, Guichard and Yarrow 1948, Satchell 1965, Hammond 1975, Davis 1978, Taylor et al. 1978). By urbanization we mean all forms of urban land-use including residential, commercial, industrial, and transportation. For example, in the urbanized San Francisco Bay Area counties with a lower proportion of public lands have lower species richness of insects (Connor et al. 2003). In San Francisco, only 57% of the native butterfly species have been seen in the last 10 yr (Hafernik and Reinhard 1995). In Palo Alto, none of the butterflies found in rural sites is

present in the urbanized business district (Blair and Launer 1997).

Replacement of natural habitats by human-dominated areas results in habitat loss and fragmentation. Habitat loss and fragmentation create a landscape of remnant habitat patches that vary in size, shape, and isolation (Abensperg-Traun and Smith 1999). Urban areas are characterized by small, remnant habitat patches that tend to harbor few native species potentially at low abundances (Faeth and Kane 1978, Connor and McCoy 1979, 2001, Connor et al. 2000, Niemelä 2001). Some insects may require a critical patch size in order to persist (MacGarvin 1982, Kareiva

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1983), and patches reduced in area are subject to greater edge effects (Andrén and Angelstam 1988, Paton 1994, Murcia 1995, but see Heliölä et al. 2001).

Patch shape is hypothesized to reduce species richness as habitat fragments become less circular. Baz and Garcia-Boyero (1995) report increased butterfly species diversity as oak forest fragments converged on circularity. However, other studies report no influence of shape on species richness (Faeth and Kane 1978, Blouin and Connor 1985, Abensperg-Traun and Smith 1999), or that shape only becomes relevant at small spatial scales (Kunin 1997).

The isolation of a habitat patch may also be associated with the abundance and diversity of insect species. Habitat fragments isolated by human-dominated regions are less likely to be re-colonized by the native biota (Kozlov 1996, Van Dyck and Matthysen 1999). The isolation of habitat patches can alter insect densities because natural enemies may be unable to track prey in patches isolated and surrounded by a matrix of unsuitable habitat (Frankie et al. 1987, Hanks and Denno 1993, Kruess and Tschardt 1994, Denys and Schmidt 1998).

Replacement of natural habitats by urban land-uses could also result in changes in the quality of the remaining habitat patches (White and McDonnell 1988, Rebele 1994, Oksanen et al. 1996, Denys and Schmidt 1998). Among the activities considered to affect habitat quality is the application of fertilizers and pesticides, increased irrigation, soil compaction, the establishment of non-native species, and emissions from the burning of fossil fuels.

Changes in habitat quality could affect the abundance and diversity of native insects by altering food availability, enemy attack, or microclimate. For example, altered water or nutrient regimes may affect the abundance or persistence of folivorous insects (Connor 1988, McQuate and Connor 1990, Hanks and Denno 1993, Speight et al. 1998). Exotic insects are more likely to be introduced into urban areas because of high rates of visitation by people (Paine et al. 1997). Predation or competition by exotic species may displace or reduce the abundance of native species (Bolger et al. 2000). Use of pesticides in urban areas reduces the abundance of native insects (Luck and Dahlsten 1975, Dreistadt et al. 1990). Furthermore, the proximity of buildings might affect microclimate by altering light levels, which could affect insect species that forage under specific light conditions (Trumble and Denno 1995).

The nature of the matrix surrounding habitat patches can also affect the probability of dispersal between patches (Haddad 1999, Roland et al. 2000, Ricketts 2001). A matrix of urban land-use may be a greater obstacle for dispersal than a matrix of rural land-uses if animals are less likely to move through an urban matrix than through rural habitats, or if

while doing so they experience a higher risk of mortality.

Most studies that have attempted to assess the effects of urbanization on biological communities have compared habitat patches in urban areas to those in rural areas. Many studies array sample sites along a gradient from urban centers with a completely built environment to rural areas with much less built environment (White and McDonnell 1988, McDonnell and Pickett 1990, Oksanen et al. 1996, Blair and Launer 1997, Denys and Schmidt 1998, Blair 1999). These studies implicitly assume that differences between urban and rural study sites are caused by urbanization, since urban land-use is reduced or absent from rural areas. However, the rural areas used as comparison sites are not "pristine". Rural study sites also experience the effects of human use of the land, but mostly as agriculture. Most urban areas are surrounded by agricultural areas so that rural areas may experience substantial, if not equal, effects of habitat loss, fragmentation, and altered habitat quality because of agricultural land-uses.

Since the replacement of natural habitats by both urban and agricultural land-uses results in habitat loss and fragmentation, any unique effects of urbanization must arise because of differences in the quality of the remaining habitat patches or differences in the effects of the "matrix" (urban or agriculture) on dispersal between patches. However, no studies have attempted to separate the effects of habitat loss and fragmentation from those due to altered habitat quality and to the character of the surrounding matrix.

We conducted a study of the species richness and abundance of the community of leaf-mining moths associated with *Quercus agrifolia* in the San Francisco Bay Area (SFBA). We compared study sites experiencing a variety of levels of urbanization, where the effects of habitat loss, fragmentation, and altered habitat quality are confounded, to sites with similar levels of habitat loss and fragmentation caused by agricultural land-use that are largely free of the effects of urbanization. Therefore, we were able to determine if one need invoke an effect of urbanization on habitat quality or an effect of the urban matrix that differs from that caused by replacing and fragmenting habitats with agricultural land-uses. We did not attempt to compare "pristine" sites to sites experiencing the effects of urbanization. Such a comparison, if possible, would confound the effects of altered habitat quality with the effects of habitat loss and fragmentation since pristine sites have not experienced habitat loss and fragmentation. Also, comparisons to "pristine" sites would be confounded with the effects of distance and elevation since the nearest *Q. agrifolia* forests that might be considered to be pristine are > 100 km from the SFBA and at higher elevation.

## Methods

### The insects and the host plant

There are 18 native and no exotic species of leaf-mining Lepidoptera associated with *Q. agrifolia* throughout California (Opler 1974a, Opler and Davis 1981, Powell 1992, Table 1).

Because attributes of leaf mines are species-specific, we were able to identify, record, and count each species of leaf miner simply by inspecting foliage (Opler 1974a). The leaf-mining moths on *Q. agrifolia* display a variety of voltinism patterns, but the leaf mines persist on the tree beyond the death of the larvae or emergence of the adult. Therefore, estimates of abundance and species richness can be made virtually throughout the growing season.

*Quercus agrifolia* Neé (coast live oak) is distributed along the western coast of North America from Mendocino County, CA to Baja California, Mexico (Pavlik et al. 1991). *Quercus agrifolia* is evergreen with new leaves produced annually in March and April. Leaves are slowly lost beginning one year after their appearance, but may persist for up to two years.

### Study sites and their attributes

We defined a study site to be a remnant patch of *Q. agrifolia* and the surrounding landscape within a 500 m radius measured from the center of the patch (78.54 ha). We used a radius of 500 m since other studies suggest that leaf miners seldom disperse > 500 m (Kozlov 1996, Connor unpubl.). We randomly selected fifty

study sites varying in their degree of urbanization from among the available stands of *Q. agrifolia* located within the SFBA. Study sites were located within 70 km of the coast from Santa Cruz County to Napa County ranging between 38.55° and 36.96°N latitude and between 122.90° and 121.96°W longitude (Fig. 1).

To estimate site attributes at both the patch and landscape scale, we used aerial photographs in the form of United States Geological Survey Digital Orthophoto Quadrangles (1:24 000 scale). We located each study site on the photo, and used Sigma Scan 5.0 to trace the perimeter of each patch and land-use type and to calculate their areas. The patch attributes we measured were area and shape ( $4\pi \times \text{area}/\text{perimeter}^2$ ). The landscape attributes we measured were the areas of urban land-use, oak woodland, non-oak woodland, cropland, and grassland within the 500 m radius (Table 2). We defined agricultural land-use as the sum of the areas of cropland and grassland. We estimated the isolation of each site as the distance from the edge of the study patch to the nearest oak woodland.

### Estimating species richness and abundance

To estimate the species richness and abundance of leaf-mining Lepidoptera, we sampled foliage between May and September 1999. At each site, we randomly sampled 3–6 trees (dbh > 5 cm). From the canopy of each tree within 2 m of the ground, we clipped three randomly selected branches, each with a minimum of 50 leaves. We examined every leaf for the presence of leaf mines and recorded the number of individual mines

Table 1. Taxonomy, life-history syndrome and average density of leaf-mining lepidoptera associated with *Quercus agrifolia* in the SFBA (Density = number of mines/100 leaves, SE = standard error).

Family	Species	Density	SE	Life history type
Eriocraniidae	<i>Dryseriocrania auricyanea</i>	0.310	0.00075	Univoltine
	<i>Eriocraniella xanthocara</i>	0.134	0.00028	Univoltine
Nepticulidae	<i>Stigmella variella</i>	0.387	0.0012	Multivoltine
Incurvariidae**	<i>Vespina quercivora</i> ***	0.00	0.00	Univoltine
Heliozelidae**	<i>Coptodisca powellella</i> ***	0.00	0.00	Univoltine
Tischeriidae**	<i>Tischeria discreta</i> **	0.033	0.00014	Univoltine
Bucculatricidae	<i>Bucculatrix albertiella</i>	0.824	0.00041	Bivoltine
Gracillariidae	<i>Caloptilia reticulata</i>	0.311	0.00091	Multivoltine
	<i>Caloptilia agrifoliella</i>	1.319	0.0037	Univoltine
	<i>Caloptilia</i> spp.*	0.674	0.0017	Varied
	<i>Neurobathra bohartiella</i> **	0.004	0.00003	Bivoltine
	<i>Acrocercops insulariella</i> ***	0.00	0.00	Univoltine
	<i>Phyllonorycter inusitatella</i> **	0.035	0.00014	Univoltine
	<i>Phyllonorycter sandraella</i> **	0.035	0.00016	Bivoltine
	<i>Phyllonorycter antiochella</i>	0.902	0.0025	Univoltine
	<i>Phyllonorycter</i> spp.*	0.012	0.000058	Varied
	<i>Cameraria agrifoliella</i>	0.090	0.00022	Multivoltine
	<i>Cameraria wislizeniella</i> ***	0.00	0.00	Multivoltine
	<i>Cameraria anomala</i> ***	0.00	0.00	Univoltine
Cosmopterigidae**	<i>Stilobosis dulcedo</i> **	0.005	0.00003	Univoltine

\**Caloptilia* and *Phyllonorycter* species whose mines could not be identified to species level due to leaf damage.

\*\*Found at <20% of all 50 sites therefore not used in individual species analyses.

\*\*\*Never found at any of the 50 sites in this study, which concurs with Green (1979) and Opler and Davis (1981).

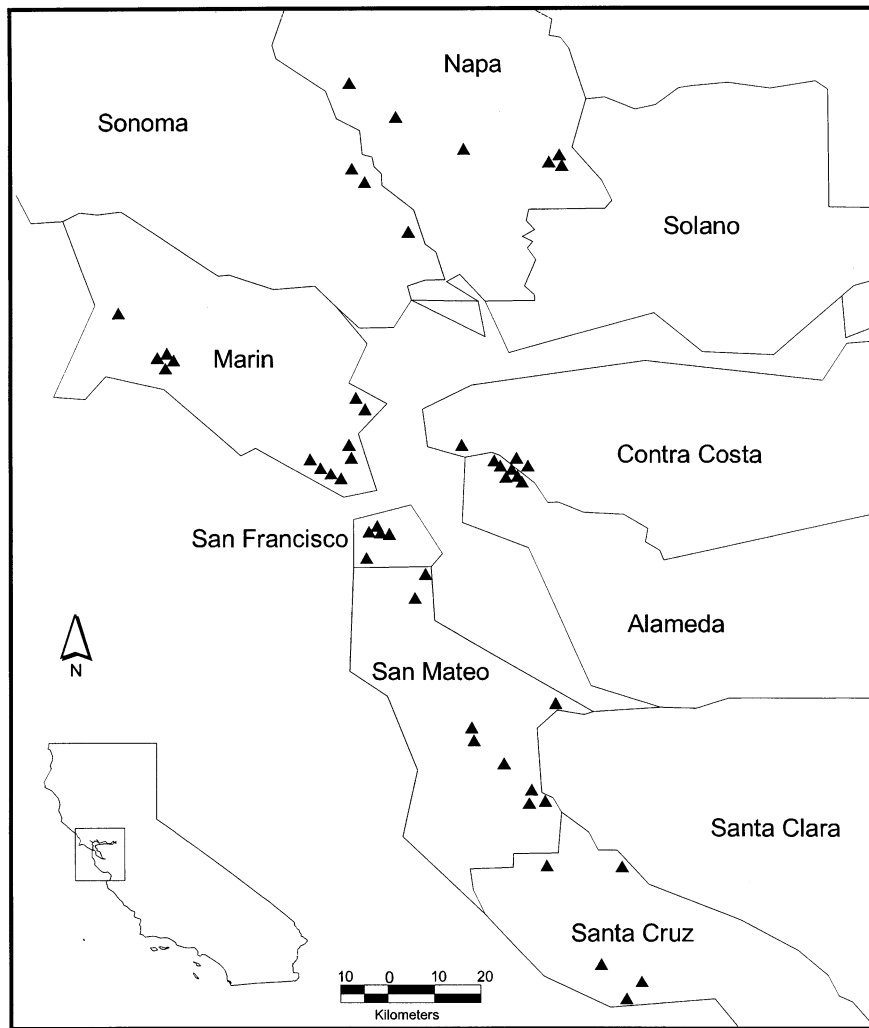


Fig. 1. Location of the 50 study sites in the San Francisco Bay Area.

Table 2. The range, mean, coefficient of variation, and average percent of site area for all landscape and patch attributes [Urban = area of roads and buildings, Oak woodland = area of oak woodland within the study site excluding the sample patch, Non-oak woodland = area of other forest and shrubland, Cropland = area of vineyard and row crops, Grassland = area of managed and unmanaged grasses, Isolation = distance to nearest oak patch from sample patch, Patch Area = area of sample patch, Shape =  $(4\pi \times \text{area}/\text{perimeter}^2)$ ]. Average percent of total area based on 500 m radius = 78.54 ha. Water bodies comprised <1% of the area of each study site and therefore were not examined in our analyses.

Variables	Abbreviation	Range	Mean (n = 50)	Coefficient of Variation	Average % of area
<b>Landscape:</b>					
Urban	urb	0–75.8 ha	15.7 ha	143.0	20.0
Oak woodland	oak	0–10.9 ha	3.7 ha	80.8	4.6
Non-oak woodland	non	0–70.3 ha	38.0 ha	51.3	48.4
Cropland*	crp	0–63.4 ha	6.0 ha	243.4	7.6
Grassland*	grs	0–41.9 ha	9.6 ha	105.2	12.2
Isolation	iso	0–0.3 km	0.1 km	76.4	N/A
<b>Patch:</b>					
Area	area	0.04–43.4 ha	3.0 ha	221.8	3.8
Shape	shp	0.09–0.8	0.4	46.3	N/A

\*Agriculture (ag) was estimated as the sum of cropland and grassland.

of each species for each site. We estimated species richness simply as the number of taxa found at each site. We estimated abundance as the total number of individual leaf mines counted for each species at a site. To account for differences in sampling effort between sites, we estimated the leaf area sampled at each site (m<sup>2</sup>) from digital images of the sampled leaves using Sigma Scan 5.0.

### Data analysis

To examine the effects of urbanization on the leaf-mining Lepidoptera on *Q. agrifolia*, we built linear models for the species richness and abundance of the leaf-miner community, and for the abundance of individual species. For individual species, models were built only if the species was present in at least 20% of the study sites (Table 1). Because species richness and abundance tend to follow a Poisson distribution (Agresti 1996), we used a generalized linear model assuming the response variable to be Poisson distributed (Vincent and Haworth 1983, Connor et al. 1997). Models were corrected for over dispersion to accurately estimate the standard errors of the regression coefficients (McCullagh and Nelder 1989).

We built models that accounted for variation in sampling effort and study site attributes at the patch scale before examining the influence of urbanization and other landscape attributes. First, the leaf-area sampled at each study site was forced into the model to adjust for variation in sampling effort. Second, the contribution of patch attributes such as area and shape were examined before we assessed the effects of landscape or regional conditions. Accounting for patch-scale or local effects before testing for landscape or regional effects is the most common practice in tests for landscape scale effects (Dueser et al. 1988, Pearson 1993, Saab 1999, Cam et al. 2000). Patch attributes with significant partial t-values ( $p < 0.05$ ) were retained in the model. Finally, we assessed the contribution of landscape or regional conditions such as the amount of urban, agricultural, or other land-use categories after accounting for sampling effort and patch scale attributes. Landscape-scale attributes with significant partial t-values ( $p < 0.05$ ) were retained in the model. We examined the final model for each variable using a deviance difference test and by inspection of residual plots.

## Results

Study patches in areas dominated by urban or agricultural land-use were similar in size and degree of isolation, and experienced similar levels of habitat loss and fragmentation (Table 2). The average area of the study patches was 3.00 ha. The average distance from each study patch to the nearest patch of oak forest was 0.10 km ( $\pm 0.01$ ). On average, both urban and agricultural land-uses comprised 20% of the area within 500 m of each study patch. Study sites in more urbanized areas were located on private land or in parks adjacent to residential neighborhoods. Study sites in areas dominated by agriculture included parks and sites on private land, and were surrounded by grassland and vineyards.

The number of leaves sampled at each site ranged between 450 and 2500 with over 50 000 being examined in this study. We identified 2426 individual leaf mines representing 13 species of Lepidoptera. The average density of a species ranged between 0.004 and 1.32 mines/100 leaves (Table 1) and the average density of the community was 5.2 mines/100 leaves. On average we found 5.9 ( $\pm 0.37$ ) species of leaf-mining moths at each study site.

### Species richness and total abundance

Neither urbanization nor any of the other landscape characteristics were useful in explaining variation in the species richness or abundance of the leaf-mining community on *Q. agrifolia* (Table 3). However, patch area was positively associated with species richness and total abundance after accounting for variation in sampling effort (Table 3).

### Individual species

Five of the 18 species associated with *Q. agrifolia* in the SFBA were not found in any of the study sites, which is consistent with both Opler (1974a) and Green's (1979) studies of this community along a transect from San Francisco to Antioch, CA (Table 1). These five species are distributed further inland at the latitude of the SFBA and only reach the coast further south. Of the remaining 13 species of leaf miners, only eight were found in at least 20% of our 50 study sites. Of these eight, the abundances of only three species were associ-

Table 3. Final regression models for Species richness and Total abundance of the leaf-mining moths on *Q. agrifolia*. "None" indicates that none of the explanatory variables had significant partial t-statistics ( $\alpha = 0.05$ ) therefore they did not enter into the final model.  $\chi^2$  is the difference in residual deviances between the null and final models.

Response variables	Intercept	Leaf area	Patch variables	Landscape variables	$\chi^2$	p
Species richness	1.00	0.75	0.05 (area)	None	12.41	0.002
Total abundance	2.75	0.72	0.17 (area)	None	495.44	$< 1 \times 10^{-22}$

Table 4. Final regression models for the abundance of the eight individual species of leaf-mining moths on *Q. agrifolia*. "None" indicates that none of the explanatory variables had significant partial t-statistics ( $\alpha = 0.05$ ) therefore they did not enter into the final model. Patch and landscape variables are listed in order of significance.  $\chi^2$  is the difference in residual deviances between the null and final models. Abbreviations for variable names are given in Table 2.

Response variables	Intercept	Leaf area	Patch variables	Landscape variables	$\chi^2$	p
<i>Dryseriocrania auricyanea</i>	1.47	0.85	0.18 (area)	-0.05 (urb) -0.03 (non) -0.04 (ag)	182.95	$< 1.0 \times 10^{-22}$
<i>Eriocraniella xanthocara</i>	-0.77	1.07	None	None	3.29	0.07
<i>Stigmella variella</i>	-1.25	2.21	None	0.022 (urb)	57.67	$3.00 \times 10^{-13}$
<i>Bucculatrix albertiella</i>	-2.56	3.39	None	0.05 (urb)	520.94	$< 1.0 \times 10^{-22}$
<i>Caloptilia reticulata</i>	0.34	-0.05	0.24 (area)	None	67.09	$2.70 \times 10^{-15}$
<i>Caloptilia agrifoliella</i>	0.86	0.93	0.27 (area)	None	361.02	$< 1.0 \times 10^{-22}$
<i>Phyllonorycter antiochella</i>	1.03	-0.27	0.21 (area)	5.85 (iso)	173.73	$< 1.0 \times 10^{-22}$
<i>Cameraria agrifoliella</i>	-0.75	0.52	None	None	0.48	0.49

ated with the degree of urbanization, *Stigmella variella*, *Bucculatrix albertiella*, and *Dryseriocrania auricyanea* (Table 4). The best fit models of *S. variella* and *B. albertiella* only included the degree of urbanization. The residual plots for both species indicate that urbanization has a small positive effect on their abundance (Fig. 2A and B, respectively). The abundance of *D. auricyanea* was positively associated with patch area, but negatively associated with urbanization, agriculture and the area of non-oak forest (Table 4 and Fig. 2C). Among the five species that occurred at  $< 20\%$  of the study sites, none were found more commonly at sites with either low or high amounts of urban land-use. Examination of the patterns of presence and absence of all 13 species indicated that the composition of the community did not vary systematically in relation to the degree of urbanization.

None of the landscape variables accounted for variation in the abundances of the remaining five species. However, the abundances of *Phyllonorycter antiochella*, *Caloptilia reticulata*, and *Caloptilia agrifoliella* were positively associated with patch area (Table 4).

## Discussion

### The effect of patch attributes

Patch attributes were more useful than landscape attributes in explaining variation in the species richness and abundance of the community of leaf-mining moths on *Q. agrifolia*. We found a positive association between the species richness of leaf-mining moths on *Q. agrifolia* and patch area in the SFBA. Patch area was also useful in explaining variation in the abundance of the whole community of leaf-mining moths as well as for four individual species. These results indicate that

the density of the community of leaf-mining moths on *Q. agrifolia* is higher on large patches as was found by Connor et al. (2000) for many other insect species. However, consistent with previous studies, patch shape was not useful in explaining variation in species richness and abundance (Faeth and Kane 1978, Blouin and Connor 1985).

### The effect of landscape attributes: urbanization and altered habitat quality

The absence of an association between urban land-use and both species richness and total abundance indicates that the effects of urbanization on the community of leaf-mining moths on *Q. agrifolia* do not differ from the effects of replacing and fragmenting habitats with similar amounts of agricultural land-uses. That only three species show an association between abundance and urbanization and that these effects are not consistent in sign also supports this interpretation.

The ability of leaf-mining moths to persist in small remnant habitat patches is the most likely reason we observed no effect of urbanization. Small insects can maintain large, persistent populations even in relatively small habitat patches (Hafernik 1992, Abensperg-Traun and Smith 1999). It is unlikely that the persistence of the community of leaf-mining moths on *Q. agrifolia* in the SFBA is due to high rates of inter-patch dispersal. Although the average distance of our study sites to the nearest patch of oak woodland was only 0.1 km, leaf-mining moths are small and are not strong fliers. Connor (unpubl.) determined that populations of a leaf-mining moth feeding on oak in Virginia that were separated by as little as 0.2 km of an agricultural matrix display population dynamics that are largely independent. The leaf-mining moths that feed on *Q. agrifolia*

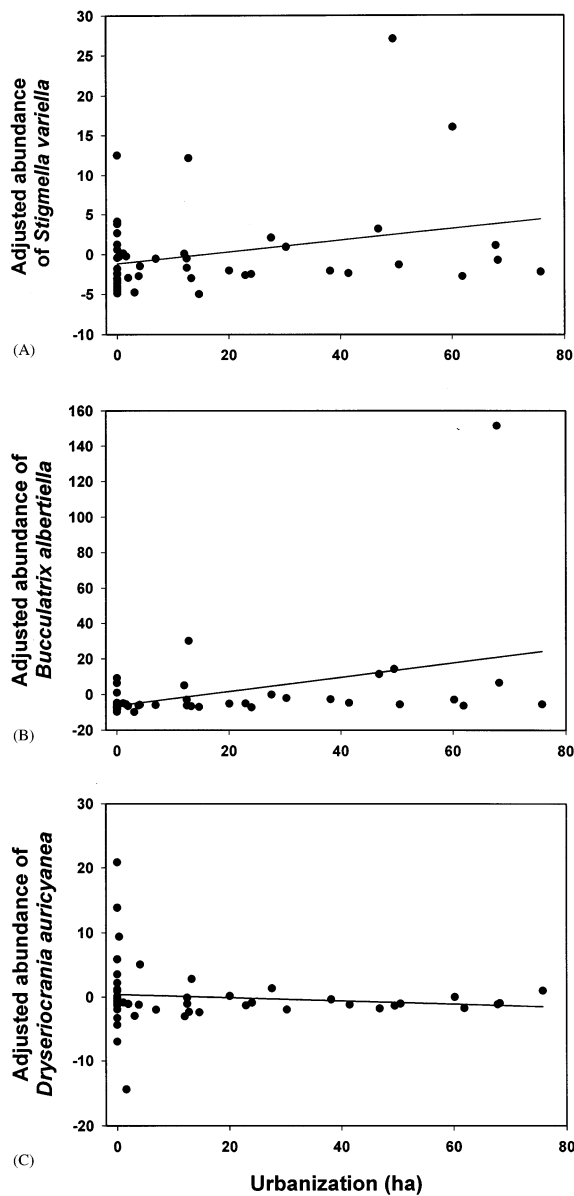


Fig. 2. The relationship between the abundance of species of leaf-mining lepidoptera (adjusted for the effects of leaf area) and urbanization (area of urban land-use). Adjusted estimates of abundance are the residuals derived from the regression of abundance on leaf area. **A.** *Stigmella variella* – the positive slope indicates that *S. variella* is more abundant in areas with a greater extent of urban land-use. The model for the abundance of *S. variella* and the signs of the regression coefficients are not changed by removing the apparent outlier. **B.** *Bucculatrix albertiella* – the positive slope indicates that *B. albertiella* is more abundant in areas with a greater extent of urban land-use. When the apparent outlier is removed, both urban and grassland land-use enter the model for the abundance of *B. albertiella* with positive regression coefficients. **C.** *Dryseriocrania auricyanea* – the negative slope indicates that *D. auricyanea* is less abundant in areas with a greater extent of urban land-use.

are either host-specific or feed exclusively on oaks, so the presence of alternative hosts is unlikely to contribute to their persistence (Opler 1974b). However, since *Q. agrifolia* is planted in residential yards, this may increase the probability that leaf-mining moths will persist in urban areas.

It is possible that the methods we employed to test for an effect of urbanization or our choice of study sites lead to a bias against detecting an effect. Our approach to quantifying urbanization assumes that the quality of remnant habitat patches will be influenced only by the amount of urban land-use within 500 m of the center of the study patch. Our methods also assume that all types and intensities of urban land-use contribute equally to altering habitat quality. While we have argued that 500 m is the relevant scale for measuring landscape effects on leaf-mining insects, other ways of estimating the effects of urbanization on the quality of remnant habitat patches may reveal more subtle effects. Furthermore, we selected our study sites to include a wide range of urban and agricultural land-use. Given that both the mean and variance in the extent of urban and agricultural land-use were quite similar, we achieved this goal (Table 2). Therefore, the absence of an effect of urbanization cannot be attributed to having selected a narrow range of variation in the extent of urban land-use relative to other land-use categories.

Besides the lack of an effect of altered habitat quality or differences in the effects of an urban or agricultural matrix on the community of leaf-mining moths on *Q. agrifolia*, our data suggest that this community has suffered little from the effects of habitat loss and fragmentation other than reductions in the abundance of individual species. We do not have strong, direct evidence that population densities and species richness of leaf-mining Lepidoptera on *Q. agrifolia* have not been reduced relative to levels that existed prior to European settlement. However, our data combined with observations by Opler (1974a) and Green (1979), as well as data on communities of leaf-mining insects on other oak species, provides weak indirect evidence consistent with this interpretation. The population densities of leaf-mining moths that we observed on *Q. agrifolia* are greater than that observed for other communities of leaf-mining insects on evergreen oaks, even though all other studies have been conducted in less urbanized regions (Table 5). Furthermore, over half of the 13 species found on *Q. agrifolia* in the SFBA occurred at a greater proportion of the study sites than was found by Green (1979) in a more intensive, multi-year survey of the leaf-mining Lepidoptera on *Q. agrifolia* throughout California. Finally, none of the 13 species of leaf-mining insects that occur on *Q. agrifolia* and whose geographic ranges include the SFBA were absent from our study sites, which suggests that no local extinctions have occurred.

Our results are difficult to compare to both single species and community level studies that have examined

Table 5. Estimates of average density of the whole community of leaf-mining insects on species of evergreen oaks (*Quercus* sp.) located throughout the United States (Density = number of mines/100 leaves).

Authors	Evergreen host plant	Average density of mines
This study	<i>Q. agrifolia</i>	5.23
Faeth et al. (1981)	<i>Q. hemisphaerica</i>	2.45
Connor et al. (1983)	<i>Q. virginiana</i>	15.0 (ca)
Bultman and Faeth (1986)	<i>Q. emoryi</i>	<5.0
Boecklen and Spellenberg (1990)	<i>Q. rugosa</i>	3.89
	<i>Q. emoryi</i>	1.81
Aguilar and Boecklen (1992)	<i>Q. grisea</i>	1.88

the effects of urbanization on insects. This is in part because we examined the effects of urbanization acting via altered habitat quality and the nature of the urban matrix while controlling for habitat loss and fragmentation. On the other hand, other studies confound habitat loss and fragmentation with the effects of urbanization caused by altered habitat quality and the nature of the urban matrix.

Studies focusing on individual species examine the effects of urbanization by altering habitat quality and report higher insect abundances in urban environments. However, in studies reporting data on a single insect species, the decision to study that species is almost always biased by the perceived high abundance of the species in urban areas (Nuckols and Connor 1995). Also, few single species studies report data on insect abundance in remnant habitat patches in both urban and non-urban habitats (Frankie and Ehler 1978, McIntyre 2000). Increases in insect abundance in urban areas are attributed to such causes as higher plant "stress", lower diversity plantings (mono-culture), and altered natural enemy complexes in urban regions (Root 1973, Kareiva 1983, Houston 1985, Dreistadt et al. 1990, Hanks and Denno 1993). Plant "stress" in urban areas has been attributed to air pollution and an altered hygrothermal environment that may increase a plant's susceptibility to insect attack (Houston 1985, Schmitz 1996, Oksanen et al. 1996, Kozlov 1996, van Rensburg et al. 1997, Speight et al. 1998). Conversely, a lack of plant stress caused by increased fertilization, water availability, and sunlight has also been hypothesized to increase population densities of insect species in urban areas (Marino et al. 1993). If the natural enemies of herbivorous insects are less successful at colonizing urban regions or suffer greater mortality from pesticide use, then populations of herbivorous insects might increase in urban areas (Vôte 1946, Frankie et al. 1987, Kahn and Cornell 1989, Hanks and Denno 1993).

Studies examining the community-wide effects of urbanization on insects focus on the effects of habitat loss and fragmentation, and report either no effect or reductions in insect species richness and abundance in urban areas (Taylor et al. 1978, Vincent and Frankie 1985, Wolda et al. 1994, Hafernik and Reinhard 1995, Nuckols and Connor 1995, Panzer et al. 1995, Kozlov 1996, Denys and Schmidt 1998, Blair and Launer 1997, Bolger et al. 2000, Niemelä et al. 2002). No general synthesis has emerged from past studies to predict which groups of species are more likely to show effects of urbanization, and most studies have confounded the effects of urbanization caused by altered habitat quality or the nature of the urban matrix with the effects of habitat loss and fragmentation. For example, although a few studies have compared the species richness of butterfly communities in urban areas to sites presumably less urbanized (Hafernik and Reinhard 1995, Blair and Launer 1997, Blair 1999), these studies usually have not quantified the extent of urbanization in the vicinity of the study sites, nor have they attempted to test for an effect of urbanization above and beyond that caused by the loss and fragmentation of habitats. That the species richness and abundance of butterflies in San Francisco and Palo Alto, CA is less than in habitats on the periphery of these cities largely reflects the nearly complete loss of habitat containing suitable host plants, not an effect of urbanization on habitat quality in remnant habitat patches. However, regardless of a study's design, examinations of insect communities in urban areas find, as we did, that the response of insects to urbanization is species specific (Wolda et al. 1994, Hafernik and Reinhard 1995, Panzer et al. 1995, Kozlov 1996, Blair and Launer 1997, Denys and Schmidt 1998).

For many species of small, herbivorous insects, the presence of host-plants in sufficient numbers may constitute a patch of sufficient quality to permit persistence in highly fragmented urban and rural locations. However, for those species of insects that commonly move across the landscape foraging for resources, the habitat matrix through which they disperse might affect the propensity to disperse and the probability of surviving dispersal (Haddad 1999, Roland et al. 2000, Ricketts 2001). While we argue that leaf-mining moths are sedentary and unlikely to disperse substantial distances across any habitat matrix, some species of butterflies, larger moths, dragonflies and damselflies, and perhaps bees and wasps may be among those flying insects whose probability of successful dispersal may be less across a matrix of urban land-uses. Non-flying and epigeic insects may also face barriers to dispersal across a matrix of urban land-uses, but whether these barriers are greater than those posed by a matrix of agricultural land-uses requires further study.

## Conclusion

The absence of an association between urban land-use and species richness and abundance indicates that the effects of urbanization on the community of leaf-mining moths on *Q. agrifolia* do not differ from the effects of replacing and fragmenting habitats with similar amounts of agricultural land-uses. Neither altered habitat quality nor the character of the urban matrix has different effects on the community of leaf-mining moths on *Q. agrifolia* than does a matrix of agricultural land-use.

Further study will be necessary to determine if the absence of an effect of urbanization caused by altered habitat quality and the character of the urban matrix is a result that applies to other insect communities. For those few species of leaf-mining moths whose abundance was associated with the extent of urban land-use, mechanistic studies could help reveal the processes that underlie these patterns. However, future studies should acknowledge that the effects of urbanization caused by altered habitat quality and the character of the urban matrix can only be measured relative to the effects of other human land-uses that occupy the matrix in a landscape that has experienced similar levels of habitat loss and fragmentation.

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## References

- Abensperg-Traun, M. and Smith, G. T. 1999. How small is too small for small animals? Four terrestrial arthropod species in different-sized remnant woodlands in agricultural western Australia. – *Biodiv. Conserv.* 8: 709–726.
- Adkin, R. 1934. Some lost suburban hunting grounds. – *Proc. of the South London Entomol. and Nat. Hist. Soc.* 1934: 25–131.
- Agresti, A. 1996. An introduction to categorical data analysis. – Wiley.
- Aguilar, J. M. and Boecklen, W. J. 1992. Patterns of herbivory in the *Quercus grisea* × *Quercus gambelii* species complex. – *Oikos* 64: 498–504.
- Andrén, H. and Angelstam, P. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. – *Ecology* 69: 544–547.
- Baz, A. and Garcia-Boyero, A. 1995. The effects of forest fragmentation on butterfly communities in central Spain. – *J. Biogeogr.* 22: 129–140.
- Blair, R. B. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity. – *Ecol. Appl.* 9: 164–170.
- Blair, R. B. and Launer, A. E. 1997. Butterfly diversity and human land use: species assemblages along an urban gradient. – *Biol. Conserv.* 80: 113–125.
- Blouin, M. and Connor, E. F. 1985. Is there a best shape for nature reserves? – *Biol. Conserv.* 32: 277–288.
- Boecklen, W. J. and Spellenberg, R. 1990. Structure of herbivore communities in two oak (*Quercus* spp.) hybrid zones. – *Oecologia* 85: 92–100.
- Bolger, D. T. et al. 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. – *Ecol. Appl.* 10: 1230–1248.
- Bultman, T. L. and Faeth, S. H. 1986. Leaf size selection by leaf-mining insects on *Quercus emoryi* (Fagaceae). – *Oikos* 46: 311–316.
- Cam, E. et al. 2000. Relative species richness and community completeness: birds and urbanization in mid-Atlantic states. – *Ecol. Appl.* 10: 1196–1210.
- Connor, E. F. 1988. Plant water deficits and insect response: the preference of *Corythucha acruate* (Heteroptera: Tingidae) for the foliage of white oak (*Quercus alba*). – *Ecol. Entomol.* 13: 318–375.
- Connor, E. F. and McCoy, E. D. 1979. The statistics and biology of the species-area relationship. – *Am. Nat.* 113: 791–832.
- Connor, E. F. and McCoy, E. D. 2001. Species-area relationships. – In: Levin, S. A. (ed.), *Encyclopedia of biodiversity*. Vol. 5. Academic Press, pp. 397–412.
- Connor, E. F., Faeth, S. H. and Simberloff, D. 1983. Leafminers on oak: the role of immigration and in situ reproductive recruitment. – *Ecology* 64: 191–204.
- Connor, E. F. et al. 1997. Tests for aggregation and size-based sample-unit selection when sample units vary in size. – *Ecology* 78: 1238–1249.
- Connor, E. F., Courtney, A. C. and Yoder, J. M. 2000. Individuals-area relationships: the relationship between animal population density and area. – *Ecology* 83: 734–748.
- Connor, E. F. et al. 2003. Insect conservation in an urban biodiversity hotspot: the San Francisco Bay Area. – *J. Insect Conserv.* 6: 247–259.
- Davis, B. N. K. 1978. Urbanisation and the diversity of insects. – In: Mound, L. A. and Waloff, N. (eds), *Diversity of insect faunas*. Blackwell, pp. 126–138.
- Denys, C. and Schmidt, H. 1998. Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. – *Oecologia* 113: 269–277.
- Dreistadt, S. H., Dahlsten, D. L. and Frankie, G. W. 1990. Urban forests and insect ecology. – *BioScience* 40: 192–198.
- Dueser, R. D., Dooley, J. L. and Taylor, G. J. 1988. Habitat structure, forest composition and landscape dimensions as components of habitat suitability for the Delmarva fox squirrel. – In: Szaro, R. C., Severson, K. E. and Patton, D. R. (eds), *Management of amphibians, reptiles, and small mammals in North America*. United States Dept of Agriculture, Gen. Tech. Rep. RM-166, pp. 414–421.
- Faeth, S. H. and Kane, T. C. 1978. Urban biogeography. City parks as islands for Diptera and Coleoptera. – *Oecologia* 32: 127–133.
- Faeth, S. H., Mopper, S. and Simberloff, D. 1981. Abundances and diversity of leaf-mining insects on three oak host species: effects of host-plant phenology and nitrogen content of leaves. – *Oikos* 37: 238–251.
- Frankie, G. W. and Ehler, L. E. 1978. Ecology of insects in urban environments. – *Annu. Rev. Entomol.* 23: 367–387.
- Frankie, G. W. et al. 1987. Abundance and natural enemies of the spindle gall midge *Pinyonia edulicola* Gagne, in natural and urban stands of pinyon pine in Colorado (Diptera: Cecidomyiidae). – *J. Kansas Entomol. Soc.* 60: 133–144.
- Green, D. S. 1979. Ecology and host-specificity of parasitoids of leafmining Lepidoptera on *Quercus agrifolia* (Fagaceae) in California. – Ph.D. thesis, Univ. of California, Berkeley.
- Guichard, K. M. and Yarrow, J. H. H. 1948. The Hymenoptera Aculeata of Hampsted Heath and the surrounding district, 1832–1947. – *Nature* 27: 81–111.

- Haddad, N. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. – *Ecol. Appl.* 9: 612–622.
- Hafernik, J. E. 1992. Threats to invertebrate biodiversity: implications for conservation strategies. – In: Fiedler, P. L. and Jain, S. K. (eds), *Conservation biology: the theory and practice of nature conservation, preservation, and management*. Chapman and Hall, pp. 171–195.
- Hafernik, J. E. and Reinhard, H. 1995. Butterflies of the bay: winners and losers in San Francisco's urban jungle. – *Am. Butterflies* 3: 4–11.
- Hammond, P. M. 1975. Seventeenth century British Coleoptera from the collection of Leonard Plukenet (1642–1706). – *Entomol. Gaz.* 26: 261–268.
- Hanks, L. M. and Denno, R. F. 1993. Natural enemies and plant water relations influence the distribution of an armored scale insect. – *Ecology* 74: 1081–1091.
- Heliölä, J., Koivula, M. and Niemelä, J. 2001. Distribution of carabid beetles (Coleoptera: Carabidae) across a boreal forest–clearcut ecotone. – *Conserv. Biol.* 15: 370–377.
- Houston, D. 1985. Dieback and decline of urban trees. – *J. Arboricult.* 11: 65–72.
- Kahn, D. M. and Cornell, H. V. 1989. Leafminers, early leaf abscission and parasitoids: a tritrophic interaction. – *Ecology* 70: 1219–1226.
- Kareiva, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. – In: Denno, R. F. and McClure, M. S. (eds), *Variable plants and herbivores in natural and managed systems*. Academic Press, pp. 259–289.
- Kozlov, M. 1996. Patterns of forest insect distribution within a large city: Lepidoptera in St. Petersburg, Russia. – *J. Biogeogr.* 23: 95–103.
- Kruess, A. and Tscharntke, T. 1994. Habitat fragmentation, species loss, and biological control. – *Science* 264: 1581–1584.
- Kunin, W. E. 1997. Sample shape, spatial scale and species counts: implications for reserve design. – *Biol. Conserv.* 82: 369–377.
- Luck, R. F. and Dahlsten, D. L. 1975. Natural decline of a pine needle scale [*Chionaspis pinifoliae* (Fitch)] outbreak at South Lake Tahoe, California, following cessation of adult mosquito control with malathion. – *Ecology* 56: 893–904.
- MacGarvin, M. 1982. Species-area relationships of insects on host plants: herbivores on rosebay willowherb. – *J. Anim. Ecol.* 51: 207–223.
- Marino, P., Cornell, H. V. and Kahn, D. H. 1993. Environmental and clonal influences on host choice and larval survival in a leafmining insect. – *J. Anim. Ecol.* 62: 503–510.
- McCullagh, P. and Nelder, J. A. 1989. *Generalized Linear Models*, 2nd ed. – Chapman and Hall.
- McDonnell, M. J. and Pickett, S. T. A. 1990. Ecosystem structure along urban-rural gradients: an unexploited opportunity for ecology. – *Ecology* 71: 1232–1237.
- McIntyre, N. E. 2000. Ecology of urban arthropods: a review and a call to action. – *Ann. Entomol. Soc. Am.* 93: 826–835.
- McQuate, G. T. and Connor, E. F. 1990. Insect responses to plant water deficits. I. Effect of water deficits in soybean plants on the feeding preference of Mexican bean beetle larvae. – *Ecol. Entomol.* 15: 419–431.
- Murcia, C. 1995. Edge effects in fragmented forests; implications for conservation. – *Trends Ecol. Evol.* 10: 58–62.
- Niemelä, J. 2001. Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review. – *Eur. J. Entomol.* 98: 127–132.
- Niemelä, J. et al. 2002. Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. – *Landscape Ecol.* 17: 387–401.
- Nuckols, M. S. and Connor, E. F. 1995. Do trees in urban or ornamental plantings receive more damage by insects than trees in natural forests? – *Ecol. Entomol.* 20: 253–260.
- Oksanen, J. et al. 1996. Levels of damage to Scots pine and Norway spruce caused by needle miners along a SO<sub>2</sub> gradient. – *Ecography* 19: 229–236.
- Opler, P. 1974a. Biology, ecology, and host specificity of Lepidoptera associated with *Quercus agrifolia* (Fagaceae). – *Univ. of California Publications in Entomology*. 75: 1–83.
- Opler, P. 1974b. Oaks as evolutionary islands for leaf-mining insects. – *Am. Sci.* 62: 67–73.
- Opler, P. and Davis, D. R. 1981. The leafmining moths of the genus *Cameraria* associated with Fagaceae in California (Lepidoptera: Gracillariidae). – *Smithsonian Contributions to Zool.* 333: 1–58.
- Paine, T. D. et al. 1997. Enlisting an underappreciated clientele: public participation in distribution and evaluation of natural enemies in urban landscapes. – *Am. Entomol.* 43: 163–172.
- Panzer, R. et al. 1995. Prevalence of remnant dependence among the prairie and savanna-inhabiting insects of the Chicago region. – *Natural Areas J.* 15: 101–116.
- Pavlik, B. M. et al. 1991. *Oaks of California*. – Cachuma Press, Los Olivos, Ca.
- Pearson, S. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. – *Landscape Ecol.* 8: 3–18.
- Powell, J. A. 1992. Recent colonization of the San Francisco Bay Area, California, by exotic moths (Lepidoptera: Tineoidea, Gelechioidea, Torticoidea, Pyraloidea). – *Pan-Pacific Entomol.* 68: 105–121.
- Rebele, F. 1994. Urban ecology and special features of urban ecosystems. – *Global Ecol. Biogeogr. Lett.* 4: 173–187.
- Ricketts, T. 2001. The matrix matters: effective isolation in fragmented landscapes. – *Am. Nat.* 158: 87–99.
- Roland, J., Keyghobadi, N. and Fownes, S. 2000. Alpine *Pamassius* butterfly dispersal: effects of landscape and population size. – *Ecology* 81: 1642–1653.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). – *Ecol. Monogr.* 45: 95–120.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. – *Ecol. Appl.* 9: 135–151.
- Satchell, J. E. 1965. Extinctions and invasions—some case histories and conclusions. – *Symp. of the Monks Wood Exp. Station No. 1, Abbots Ripton*, pp. 19–28.
- Schmitz, G. 1996. Urban ruderal sites as secondary habitats for phytophagous insects. – *Verh. Ges. Okol.* 26: 581–585.
- Speight, M. R. et al. 1998. Horse chestnut scale (*Pulvinaria regalis*) (Homoptera: Coccidae) and urban host tree environment. – *Ecology* 79: 1503–1513.
- Taylor, L. R., French, R. A. and Woiwod, I. P. 1978. The Rothamsted insect survey and the urbanization of land in Great Britain. – In: Frankie, G. W. and Koehler, C. S. (eds), *Perspectives in urban entomology*. Schmid-McCormick, Berwyn, PA, pp. 31–65.
- Trumble, R. B. and Denno, R. F. 1995. Light intensity, host-plant irrigation, and habitat-related mortality as determinants of the abundance of azalea lace bug (Heteroptera: Tingidae). – *Environ. Entomol.* 24: 898–908.
- Van Dyck, H. and Matthysen, E. 1999. Habitat fragmentation and insect flight: a changing 'design' in a changing landscape? – *Trends Ecol. Evol.* 14: 172–174.
- van Rensburg, L. et al. 1997. A phytocentric perspective of *Asterolecanium quercicola* Bouche infestation on *Quercus robur* L. trees along an urbanization gradient. – *S. Afr. J. Bot.* 63: 25–31.
- Vincent, L. S. and Frankie, G. W. 1985. Arthropod fauna of live oak in urban and natural stands in Texas IV. The spider fauna (Araneae). – *J. Kansas Entomol. Soc.* 58: 378–385.

- Vincent, P. J. and Haworth, J. M. 1983. Poisson regression models of species abundance. – *J. Biogeogr.* 10: 153–160.
- Vôte, A. D. 1946. Regulation of the density of the insect-populations in virgin-forests and cultivated woods. – *Neth. J. Zool.* 7: 435–470.
- White, C. S. and McDonnell, M. J. 1988. Nitrogen cycling and soil characteristics in an urban versus a rural forest. – *Biogeochemistry* 5: 243–262.
- Wolda, H. et al. 1994. Diversity and variability of Lepidoptera populations in urban Brno, Czech Republic. – *Eur. J. Entomol.* 91: 213–226.