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The diversity and abundance of North American butterflies vary with habitat disturbance and geography

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Abstract

Aim We used data from the annual Fourth of July Butterfly Count for the years 1989–97 to examine patterns of species richness and total butterfly abundance across North America and within topographically diverse and disturbed landscapes.

Location We analysed counts from 514 different locations in North America. The counts represent all areas of the USA and southern Canada, with a few Mexican sites as well, although most counts were in the eastern USA.

Methods First, we standardized published count data according to the effort expended per count (total party-hours). Using regression analysis and analysis of variance, we then examined the impact of latitude, longitude, topographical relief, habitat disturbance and different climatic measures on the species richness and total abundance of butterflies per count. We also examined the abundance of exotic species in disturbed landscapes.

Results Our analyses suggest that: (1) species richness is highest at low latitudes and near Rocky Mountain longitudes; (2) the total abundance of individuals is highest in northern US latitudes and Great Plains longitudes; (3) species richness but not total abundance increases with greater topographical relief; (4) species richness and diversity indices are lower in more disturbed habitats; and (5) the abundance of the introduced *Pieris rapae* (L.) is greater in more disturbed habitats.

Main conclusions Different factors control the abundance and species richness of North American butterflies. Along with geographical location, habitat disturbance and topographical variability affect species richness. Our analysis also shows the value of broad-based monitoring regimes, such as the North American Fourth of July Butterfly Count.

Keywords
Species richness, Fourth of July Butterfly Count, disturbed habitats, *Pieris rapae*.

INTRODUCTION

Butterflies are conspicuous components of open habitats and indicators of habitat quality. Some patterns in their distribution and abundance are well known. For example, widespread species are often locally abundant and fluctuate more than geographically restricted species (Brown, 1987; Gaston, 1988; Gaston & Lawton, 1988); also, short-term changes in butterfly abundance result from variation in weather, whereas long-term changes are due to modification of habitat quality and availability (Thomas, 1984). Less is known about factors other than resource partitioning that affect the community structure of butterflies (Gilbert & Singer, 1975; Gilbert, 1989). Most taxonomic groups are represented by more species at lower latitudes (Fischer, 1960; MacArthur, 1965; Pianka, 1966; Schall & Pianka, 1978; Brown & Lomolino, 1998), and species richness in butterfly communities is likely to correlate inversely with latitude as well. Greater diversity of habitats should also support a greater number of species. Elevational range is correlated with habitat diversity because variation in elevation provides different climatic, edaphic and vegetative conditions. In contrast to species richness, individual abundance is apt to show different correlations.

Where humans have altered the landscape, less habitat diversity and less native vegetation remain, and so species

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richness of butterflies is likely to be less (Kitahara & Fujii, 1994). Providing support for this expectation, Blair & Launer (1997) found fewer species and reduced overall abundance with increasing urbanization in California, while Ruszczyk & de Araujo (1992) found reduced butterfly diversity in urbanized and developed areas of Brazil, with the butterfly species in cities being those that depend on urban vegetation. Total abundance is not necessarily reduced in disturbed landscapes, however, because agricultural monocultures can provide excellent conditions for growth of selected species, particularly of good colonizers that feed on crops and invasive host plants. Two such species in North America are *Pieris rapae* (L.), which oviposits on cabbage relatives in gardens and farms, and *Thymelicus lineola* (Ochsenheimer), which is associated with *Phleum pratense*, an abundant grass in agricultural fields (Scott, 1986). These butterflies are known in the US as the Cabbage White and the European Skipper, respectively, and both thrive in disturbed areas.

For butterflies, as for other organisms, monitoring is important for conservation and understanding distributions (New, 1991; Pollard & Yates, 1993), while biogeographical patterns provide insight into the ecology of a species (New, 1991). Despite some difficulties with data from broad-scale monitoring schemes (Butcher *et al.*, 1990; Swengel, 1990), the public monitoring of butterflies (Opler & Brown, 1990–1991; Opler & Swengel, 1992–1993, 1994–1998; Pollard & Yates, 1993) and birds (Butcher, 1990; Droege, 1990) provides extensive information that is unobtainable in any other way. Such survey data have been used to study population trends of single butterfly species (Swengel, 1990) as well as broader patterns in their distribution and abundance (Swengel, 1998; Blair, 1999). To examine patterns of butterfly distribution further, we analysed data from the annual Fourth of July Butterfly Count, a monitoring scheme sponsored by the Xerces Society and the North American Butterfly Association (NABA). We used survey data to determine primarily: (1) the geographical locations of greatest butterfly species' richness and individual abundance; and (2) whether habitat disturbance reduces richness and abundance.

METHODS

We analysed the data published for the annual Fourth of July Butterfly Counts (JBC) held from 1989 through 1997 (Opler & Brown, 1990–1991; Opler & Swengel, 1992–1993, 1994–1998). The JBC is a 1-day census of all butterflies seen within 25-km (15-mile) diameter circles established throughout the United States, Canada and Mexico. The JBC provides the most extensive observation and monitoring of butterflies in North America. We chose to analyse years in which there were at least 100 counts (1989 on). Count sites are located throughout the USA and southern Canada, with the greatest concentration in the eastern U.S.A. (Fig. 1). For each count circle, participants recorded the location, maximum and minimum altitude and land use of each count circle, as well as weather conditions and count effort. Effort was reported by party-miles (sum of miles covered by all separate groups of counters during the count in all modes of transportation, including walking, driving, etc.) and by party-hours (number of hours spent making observations in the field summed across all groups in a single count circle). These characteristics served as independent variables for examining patterns of species' richness (total number of species) and individual abundance (total number of individuals). To maintain similarity in timing of counts and coverage, we excluded Mexican counts except as noted (the number of Mexican counts in any single year ranged from 0 to only 5).

The set of all 1989–97 counts provided the largest sample (2006 counts) and therefore the most information. Counts in the same count circle from one year to the next may correlate temporally; therefore, for each factor, we added the analysis of a second data set that, although smaller, comprised fully independent observations. For geographical patterns and the effect of weather, we analysed the set of single most recent counts from each count circle (514 counts). For the effect of disturbance, we analysed the set of 1997 counts (330 counts).

Prior to assessing the impact of habitat disturbance and geographical location on species richness and butterfly abundance, we standardized all observations by measures of count effort recorded as party-miles and party-hours. We divided total abundance by party-hours, because a linear relationship over time is expected in the observation of individuals. Significant variance in abundance was explained by this measure of count effort ($t = 29.588$, $P < 0.0001$, $r^2 = 0.307$). We standardized measures of species richness by dividing by log party-hours, because of a negative exponential in the discovery rate of new species. In fact, more variance in species richness was explained by log party-hours than by party-hours alone (log, $t = 38.786$, $P < 0.0001$, $r^2 = 0.432$; linear, $t = 35.302$, $P < 0.0001$, $r^2 = 0.387$). For both abundance and richness, party-miles explained less variance than did party-hours.

In addition to geographical patterns, we analysed the impact of observer experience and weather. For bird counts, abundance and species richness are affected significantly by the experience of the observers, as measured by the number of years a count has been held (Butcher & McCulloch, 1990). Butterfly observers also report improved identification ability with more years of conducting counts (Swengel, 1990), but in our analysis the number of years that a count had been held did not affect the JBC data significantly ($P > 0.05$ for both abundance and richness). We examined the effect of cloud cover, maximum and minimum temperature and maximum wind speed by looking for significant regressions of the dependent variables (the standardized measures of richness and abundance) on these independent variables.

To evaluate the impact of habitat disturbance, we analysed data from 1994 on, which include counts with descriptions of land use sufficient to categorize most count circles as predominantly disturbed or undisturbed. Using the percentages given for land use or general descriptions of the count area, we classified count circles as disturbed if more than half the land was modified by human activity through agricultural, residential, commercial or urban development. Using analysis of variance, we then examined the effect of habitat disturbance on richness, abundance and the relative abundance of the alien species *P. rapae* and *T. lineola* in the butterfly fauna.

Figure 1 Map of all Fourth of July Butterfly Count circles for 1989–97.

To provide a different analysis of diversity patterns, we calculated diversity indices (Simpson's *D*, Shannon's *H*; Begon *et al.*, 1996) for each count in 1997, the most recent year for which we had complete data. For a comparison of biogeographical patterns derived from JBC data, we analysed the data of Pearson & Cassola (1992), who summed the distributions of all North American butterfly species shown by Scott (1986) into 275-km^2 squares. To eliminate the effects of differing land areas within each square, we eliminated all coastal squares from these analyses.

Data were analysed with Microsoft Excel 5.0 (Microsoft Corp.) and StatView 5.0 (Abacus Concepts) for Macintosh. For cases in which we predicted a linear relationship between continuous variables, we used regression analysis. For cases in which a linear relationship was not justified, continuous variables, such as longitude, were converted to discrete nominal variables for tests by analysis of variance. Percentages (sunshine during the count period, the abundance of alien species) were arc-sine transformed for analysis. Geographical maps of butterfly distribution were created using ArcView GIS 3.0 (ESRI, Inc.), with breakpoints classified by natural breaks in the data.

To ensure spatial independence of counts for statistical analysis, we transformed latitude/longitude data to Universal Transverse Meridian (UTM) coordinates and produced variograms (Isaaks & Srivastava, 1989) of all counts in North American zones 17 and 18 (the eastern side of the continent) using Geo-EAS software (version 1.2.1, U.S.E.P.A.).

RESULTS

General patterns

Summed results of general patterns are presented in Table 1. With data standardized to count effort as described above, species richness increased from northern Canada towards

Table 1 The effects of geographical location, elevation and weather on butterfly richness and abundance. Analysis by linear regression. Three data sets were analysed: all 1989–97 counts (all); the set of only the most recent count from each count circle (single); and data from Pearson & Cassola (1992). Richness = ln(species/hour); abundance = individuals/hour.

Factor	Data	*n*†	Effect on: Richness	Abundance	Interpretation
Latitude	All§	1997/2001	****	n.s.	More species but less abundance (?) at lower latitudes
	Single§	511	**	*	
	P & C	174	****		
Longitude	All	1974	n.s.	n.s.	No linear patterns¶ with longitude
	Single	502	n.s.	n.s.	
	P & C	174	n.s.		
Elev. range	All	1822	****	*	More species with greater elev. range
	Single	458	*	n.s.	
Max. elev.	All	1864	****	n.s.	Unclear result
	Single	467	n.s.	n.s.	
Cloud cover	All	1976/7	n.s.	(*)	No effect of cloud cover (but see text)
	Single	502	n.s.	n.s.	
Max. temp.	All	1944/5	**	n.s.	Fewer individuals at higher max. temps.?
	Single	493	n.s.	*	
Min. temp.	All	1900/1	****	n.s.	More spp. seen with higher min. temps.
	Single	485	**	*	
Max. wind	All	1643	n.s.	*	Perhaps more individuals seen when windier
	Single	423	n.s.	n.s.	

† When the sample sizes differed for analyses of richness and abundance, both are shown.
**** $P < 0.0001$; ** $P < 0.01$; * $P < 0.05$; (*)$P < 0.10$.
§ Analysis of latitudinal effects included data from Mexican counts (all, 23; single, 9); the same results were found when Mexican counts were excluded (see text).
¶ Consistent patterns of maximum richness and abundance occurred at middle longitudes (see text).

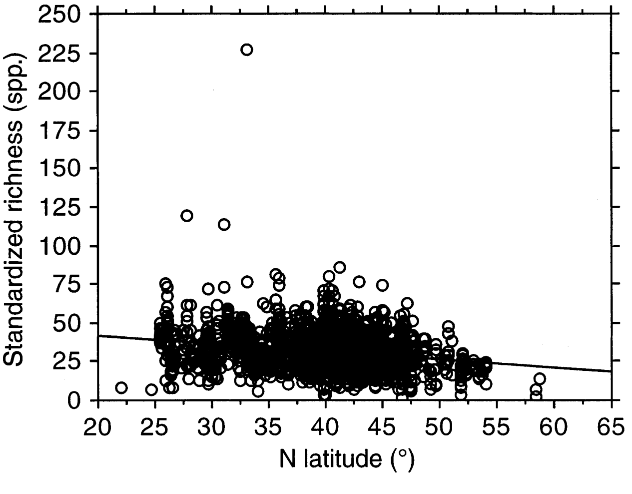

Figure 2 Latitudinal gradient in butterfly species richness using standardized data from JBC. $P < 0.0001$, $r^2 = 0.050$.

Mexico (Fig. 2; all counts: $F[1,1995] = 283.08$, $P < 0.0001$, $r^2 = 0.124$; single counts: $F[1,509] = 7.635$, $P < 0.01$, $r^2 = 0.015$). The same results occurred even when Mexican counts were excluded (e.g. all counts: $F[1,1971] = 104.15$, $P < 0.0001$, $r^2 = 0.05$), indicating that this pattern exists even without the counts from species-rich Mexico. Species richness also varied significantly by longitude, with the highest richness occurring between the Mississippi River and the Rocky Mountains (Fig. 3; all counts: $F[11,1962] = 14.651$, $P < 0.0001$; single counts: $F[11,488] = 3.667$, $P < 0.0001$). Analysis of the data given by Pearson & Cassola (1992) showed parallel results; species richness regressed significantly against latitude (Fig. 4; $F[1,172] = 214.89$, $P < 0.001$, $r^2 = 0.56$), with curvilinear change against longitude (Fig. 5).

Total abundance revealed different geographical patterns from species richness. Abundance did not differ conspicuously with latitude (all counts: $F[1,1999] = 0.840$, n.s.; single counts: $F[1,509] = 6.231$, $P < 0.05$, $r^2 = 0.012$, more at higher latitudes), with the greatest abundance between 45° N and 50° N latitude (along the US–Canada border). Abundance fluctuated by longitudinal category (all counts: $F[11,1966] = 3.467$, $P < 0.0001$; single counts: $F[11,488] = 1.071$, n.s.), with the highest abundance between 90° W and 105° W (Great Plains; Fig. 6).

Variogram analysis revealed no evidence of spatial autocorrelation within 1997 JBC data of the standardized measures of richness and total abundance. A variogram of species richness within North American UTM zone 17, which contains 76 counts, displays no range (distance) effect (Fig. 7). Similar analysis of richness in zone 18 (73 counts) and total abundance in zones 17 and 18 produced similar variogram patterns.

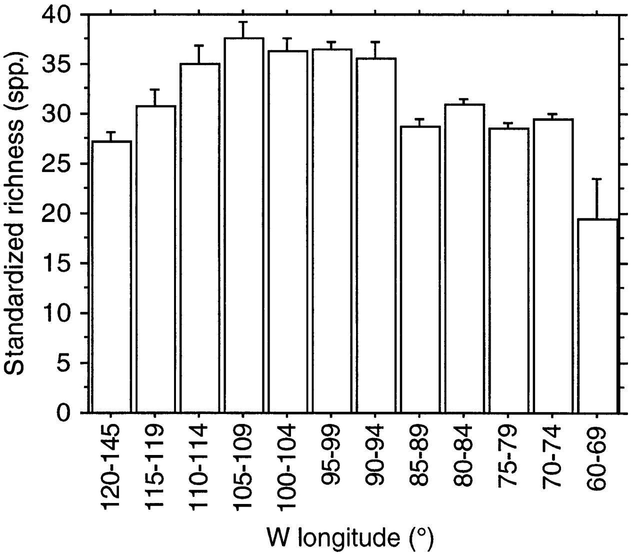

Figure 3 Longitudinal pattern in butterfly species richness using standardized data from JBC. The highest richness occurs 105°W to 109° W longitude.

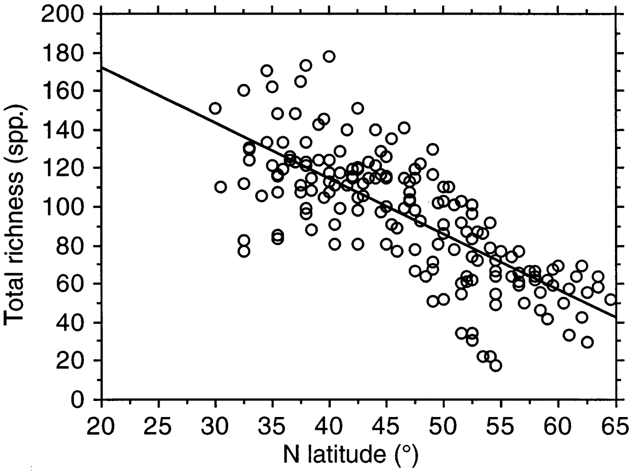

Figure 4 Latitudinal gradient in butterfly species richness taken from 275 × 275 km squares based on range maps. The data are from Pearson & Cassola's (1992) summed results of species distributions as given in Scott (1986). Coastal squares were excluded from the analysis so that land area was constant among squares.

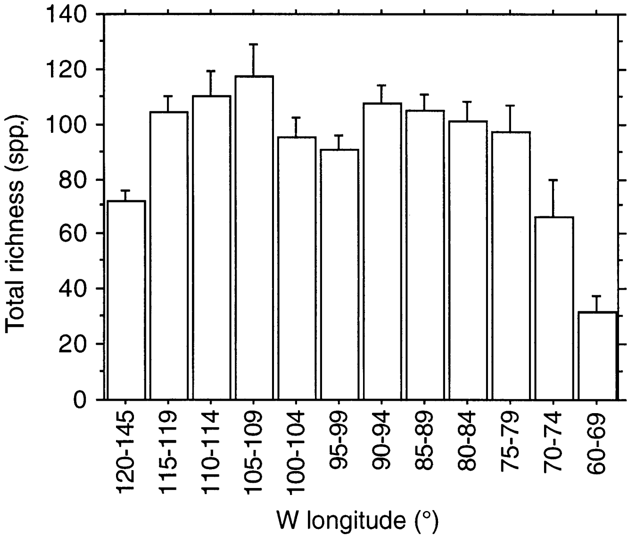

Figure 5 Longitudinal pattern in butterfly species richness from 275-km × 275-km squares from range maps. The data are from Pearson & Cassola's (1992) summed results of species distributions as given in Scott (1986). Coastal squares were excluded from the analysis so that land area was constant among squares. Species richness peaks at 105–109° W longitude.

Analysis of all count circles showed species richness increasing with greater elevational range ($F[1,1820] = 20.293$, $P < 0.0001$, $r^2 = 0.011$) and with greater maximum elevation ($F[1,1863] = 88.63$, $P < 0.0001$, $r^2 = 0.045$). Single count results showed an effect of elevational range ($F[1,458] = 5.875$, $P < 0.05$, $r^2 = 0.013$), but not of maximum elevation ($F[1,465] = 0.125$, n.s.). Average abundance showed little effect of elevational range (all counts: $F[1,1820] = 5.065$, $P < 0.05$; single counts: $F[1,456] = 0.062$, n.s.) or maximum elevation (all counts: $F[1,1864] = 1.061$, n.s.; single counts: $F[1,465] = 0.613$, n.s.).

Weather on the day of the count explained little of the total variance. Percentage cloud cover affected neither species richness (all counts: $F[1,1974] = 0.001$, n.s.; single counts: $F[1,500] = 0.010$, n.s.) nor total abundance (all counts: $F[1,1975] = 3.042$, n.s.; single counts: $F[1,500] = 0.264$, n.s.). Maximum wind speed did not affect the number of species found (all counts: $F[1,1641] = 1.706$, n.s.; single counts: $F[1,421] = 0.893$, n.s.), but, unexpectedly, more butterflies may have been seen on counts that reported stronger winds (all counts: $F[1,1642] = 5.082$, $P < 0.05$; single counts: $F[1,421] = 2.508$, n.s.).

The effects of temperature were mixed. Species richness was greater at higher maximum temperatures with all counts ($F[1,1942] = 10.022$, $P < 0.01$, $r^2 = 0.005$), but not with single counts ($F[1,491] = 0.006$, n.s.). More species were clearly seen, though, at higher minimum temperatures (all counts: $F[1,1898] = 63.765$, $P < 0.0001$, $r^2 = 0.033$; single counts: $F[1,483] = 7.275$, $P < 0.01$, $r^2 = 0.015$). Total abundance showed a different pattern, possibly being lower with higher maximum temperatures (all counts: $F[1,1943] = 0.355$, n.s.; single counts: $F[1,491] = 6.644$, $P < 0.05$, $r^2 = 0.013$) and higher minimum temperatures (all counts: $F[1,1899] = 0.510$, n.s.; single counts: $F[1,483] = 5.651$, $P < 0.05$, $r^2 = 0.012$).

Effects of disturbance

Using the description of land use within each count circle, we judged 304 of 1183 counts (25.7%) to be mostly disturbed and 794 (67.1%) mostly undisturbed, with 85 counts (7.2%)

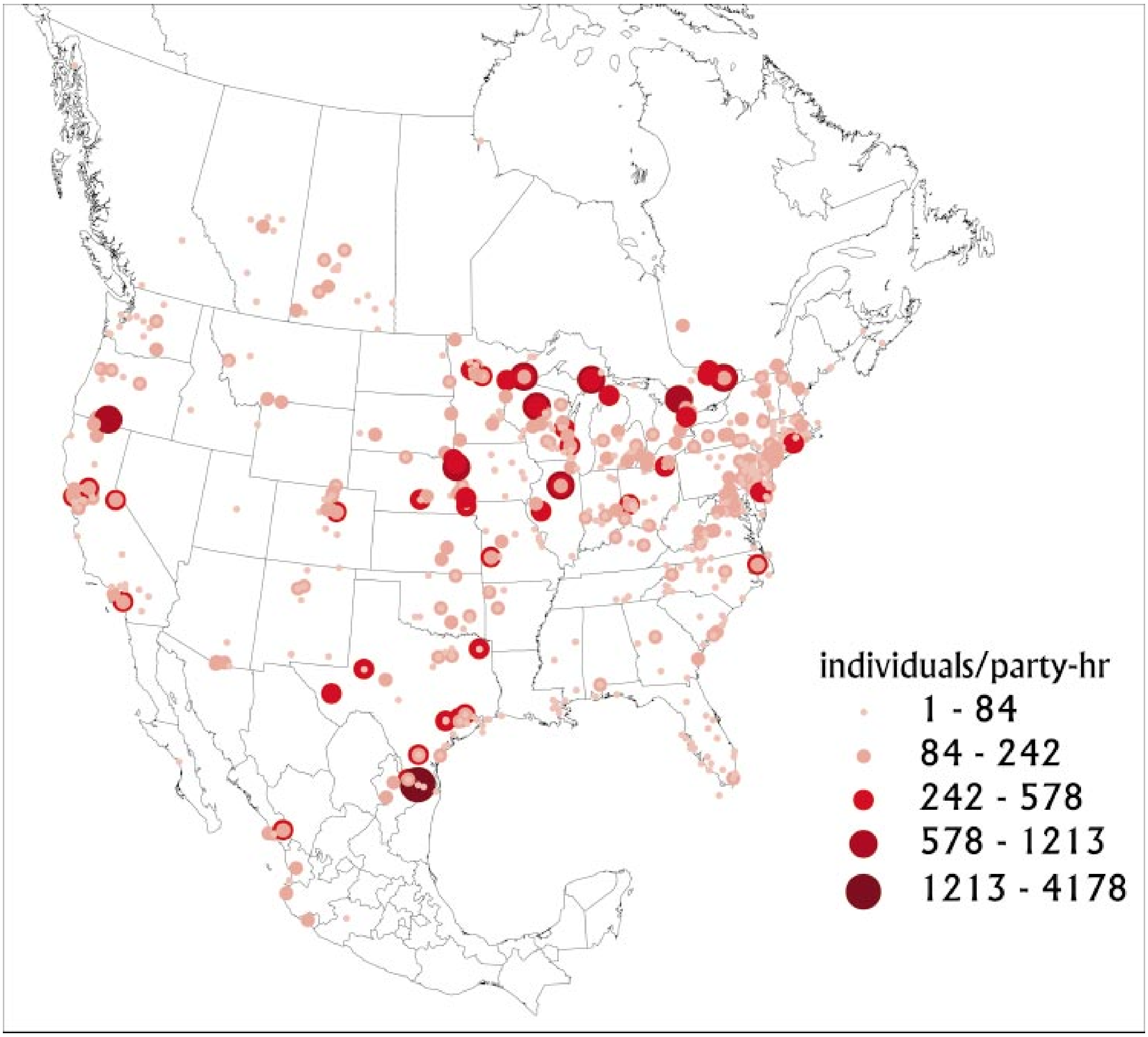

Figure 6 Map of butterfly abundance using standardized data from JBC held 1989–97. Dots of different sizes represent different rates of observing total butterflies, as shown.

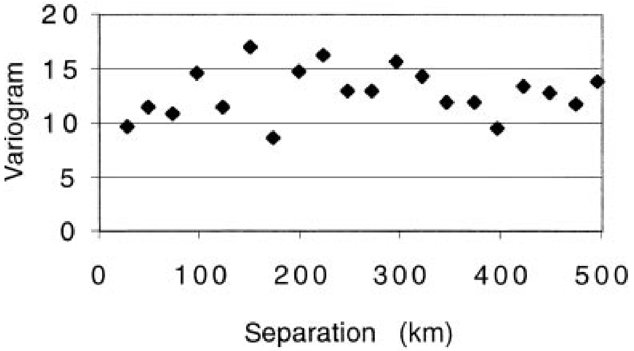

Figure 7 Variogram of species richness from the 76 counts in 1997 within North American UTM zone 17. The first point represents 23 data pairs; all other points were calculated from at least 30 data pairs. The separation distance of pairs is also known as 'lag'.

excluded for lack of sufficient information. The summed results of our analyses are given in Table 2. Species richness was found to be significantly lower in more disturbed habitats (all counts: $F[1,1095] = 22.808$, $P < 0.0001$; 1997 counts: $F[1,280] = 4.502$, $P < 0.05$). The pattern of reduced diversity also appears in plots of species vs. abundance (Fig. 8). Total abundance did not differ with habitat disturbance, however (all counts: $F[1,1096] = 1.572$, n.s.; 1997 counts: $F[1,280] = 0.035$, n.s.). The two introduced species combined were represented at greater relative abundance in disturbed areas in an analysis of all counts ($F[1,1095] = 11.211$, $P < 0.001$), although that relationship disappeared when considering only 1997 counts ($F[1,280] = 2.690$, $P = 0.10$). Among the introduced species, *P. rapae* was discernibly more numerous in disturbed habitats (all counts: $F[1,1095] = 23.299$, $P < 0.0001$; 1997 counts: $F[1,280] = 5.704$, $P < 0.05$).

Table 2 The effects of habitat disturbance on richness, abundance, the proportion of exotic species and diversity indices using one-factor analysis of variance. Count circles were categorized as mostly disturbed or undisturbed depending on whether more than half the land area within the circle was modified for agricultural, residential, commercial or urban uses. Two data sets were analysed: all counts from 1994 to 1997 and those from only 1997. Richness = ln(species/hour); abundance = individuals/hour.

Measure	Data set†	Comparison of disturbed and undisturbed circles	Interpretation
Richness	All 1997	**** *	Fewer species in disturbed circles
Abundance	All 1997	n.s. n.s.	No difference in total abundance
% introduced species	All 1997	*** (*)	Perhaps a higher percentage in disturbed circles
% *P. rapae*	All 1997	**** *	Higher percentage of *P. rapae* in disturbed circles
Shannon's *H*	1997	*	Less diversity in disturbed circles
Simpson's *D*	1997	(*)	

† n(all) = 1098; n(1997) = 282.

**** $P < 0.0001$; *** $P < 0.001$; * $P < 0.05$; (*) $P < 0.10$.

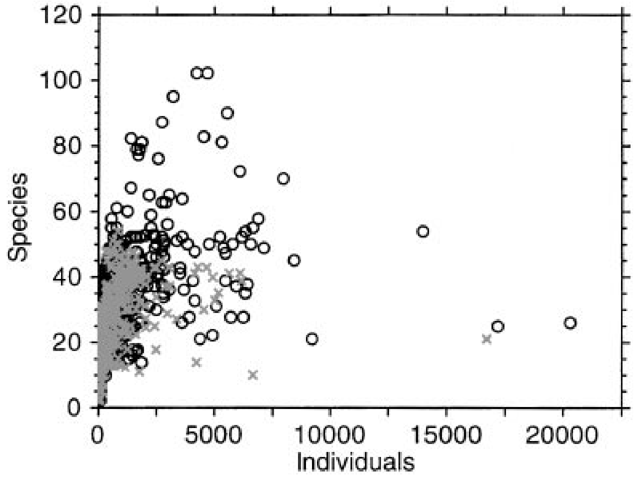

Figure 8 Species richness vs. total abundance from JBC 1989–97 in predominantly natural or disturbed count circles (see text): ×, natural counts; ○, counts in disturbed areas.

Analysis of the diversity indices *D* and *H* for all 1997 counts showed higher diversity in less disturbed habitats, as expected. The difference was significant for *H* ($F[1,280] = 4.083$, $P = 0.044$), but just missed significance for *D* ($F[1,280] = 3.429$, $P = 0.065$). These indices vary only slightly, with *H* being more independent of the underlying distribution of relative abundance (May, 1976).

DISCUSSION

General patterns

As expected, species richness of butterflies increases at lower latitudes. This is consistent with the latitudinal gradient found in most organisms, despite uncertainty about the reasons for this increase (Fischer, 1960; Pianka, 1966; Currie, 1991; Rohde, 1992; Brown & Lomolino, 1998). Some (Gilbert, 1989; Brown & Opler, 1990) have attributed the greatest effect on butterfly diversity to plant species diversity, although that begs the question why plant diversity increases at low latitudes (Currie & Paquin, 1987). The latitudinal pattern in butterflies fails in peninsulas, in which distal regions may have fewer species (Brown, 1987; Brown & Opler, 1990; Martin & Gurrea, 1990), although reduced topographical variability may explain this effect. Cardillo (1999) has argued that an increased rate of speciation accounts for greater richness towards the equator. Despite the causes of either latitudinal or longitudinal diversity gradients, our analysis of Pearson & Cassola's (1992) data provides independent support for the biogeographical patterns found in JBC data. Using the coarser analysis of counting the number of resident butterfly species in each state, Robbins & Opler (1997) found support for the same latitudinal gradient, and also concluded that the highest diversity by longitude was in the Rocky Mountain region.

Species richness of butterflies also increases with greater elevational range. This effect appears both in the longitudinal gradient across North America, in which the highest diversity is found near the Rocky Mountains, as well as in the analysis by elevational range within count circles. These results suggest that elevational range impacts the diversity of butterflies through habitat diversity (Martin & Gurrea, 1990; Robbins & Opler, 1997).

The dissimilarity in patterns of richness and abundance points to different factors regulating these two components of butterfly communities. Abundance of individuals may be tied more strongly to productivity, whether in total carbon fixed per year or in the flush of productivity near the beginning of the growing season. Higher abundance in the Great Plains, where there is extensive agriculture, supports this conclusion. Currie (1991), Wilson (1992) and Kerr *et al.* (1998) have argued for the importance of energy flow, measured by potential evapotranspiration, on species richness, although others have challenged the general importance of this factor (Latham & Ricklefs, 1993). Whatever the impact of productivity on richness, the impact on abundance is certainly more direct.

Because butterflies fly less in low temperatures, rain and cloudy conditions, we expected to see a significant effect of weather on count results. Distributional patterns in Britain (Turner *et al.*, 1987) illustrate the potential impact of weather, although the effect of wind is unclear (Pollard & Yates, 1993). Because butterfly behaviour depends so strongly on ambient conditions (Shreeve, 1984; Thomas, 1984), counts are usually not conducted under poor conditions (Pollard, 1977). The results we evaluated were made under moderate conditions, so the effects of wind, rain and cold have largely been removed from consideration. High variance in the data obscures the remaining small effects of weather.

Despite the fact that spatial data of living organisms may show autocorrelation (Legendre, 1993), our variogram analysis did not reveal any such effects in JBC data. Undoubtedly, the butterflies in one field influence the butterfly communities in neighbouring fields, but counts based on 15-mile diameter circles are separated sufficiently so that local autocorrelation is not apparent. In particular, the closest two count centres could be, without the circular areas around them overlapping, is 33 km. The spatial scales of field to field and count circle to count circle differ significantly.

Effects of anthropogenic disturbance

People change the natural landscape in numerous ways, through loss and degradation of habitat (the most important factor according to New, 1991), modification of natural disturbance regimes, introduction of exotic species, facilitation of the spread of invasives, alteration of population size and structure, decreases in air and water quality, effects on local climate and thus phenological patterns (McDonnell & Pickett, 1990) and creation of fragmented patches that cannot be successfully exploited (Thomas, 1995). Human-produced disturbance may or may not mimic natural disturbance. In either case, low levels of disturbance promote species diversity by maintaining a mosaic structure of habitats across a heterogeneous landscape (Connell, 1978; Petraitis *et al.*, 1989). Extensive disturbance, on the other hand, may increase homogeneity of the land by returning it to earlier successional stages or may produce physiological stress that restricts the growth of some species. Of particular importance to butterflies is that native vegetation may be converted to widespread exotic species and monocultures.

Anthropogenic disturbance can therefore affect butterfly communities in multiple ways. The uniformity of agricultural and residential areas is apt to lead to reduced species richness, a reduction exacerbated by pesticide use in these areas. Whatever the causes may be, we found reduced butterfly diversity in disturbed areas. Kitahara & Fujii (1994) also found reduced butterfly diversity in urbanized areas, and reported the decrease to be particularly within specialist species, with generalists represented more evenly across a gradient of disturbance. Ruszczyk & de Araujo (1992) found similar patterns around Porto Alegre, Brazil; reduced butterfly diversity correlated with greater human disturbance, which produces habitats characterized by stronger sunlight, lessened air and water quality, more non-native plants and greater homogeneity. Because we divided count circles into only two categories of disturbance (more and less than 50% disturbed), our analysis did not have sufficient precision to assess Connell's (1978) intermediate disturbance hypothesis. Blair & Launer (1997), however, did find the highest diversity (both richness and Shannon's diversity *H*) at an intermediate point along a gradient of urbanization.

The reduction of species in disturbed habitats may be related to the significantly greater relative abundance of exotic species. Shapiro & Shapiro (1973) showed, for example, that urbanization on Staten Island, New York, led to a shift to more invasive species. Along a gradient of increasing urbanization, Blair (1996) found for birds that exotics and good colonizers increased in more disturbed areas, while diversity, measured both as richness and as Shannon's diversity *H*, was highest at intermediate disturbance. Blair & Launer (1997) and Blair (1999) also found lower overall abundance and fewer butterfly species in disturbed areas. Through the reduction of natural habitats, anthropogenic change in the landscape has led to the reduction and endangerment of some habitat specialists (Swengel, 1996), 'urban-avoiders' in the description of Blair & Launer (1997), and increasing similarity of butterfly communities across the landscape (Thomas, 1991). The broad patterns seen in JBC data reflect these effects.

Use of JBC data

The quality of the data is less when many people contribute broad-scale observations, as in the Christmas Bird Count (CBC) and the JBC, than in more tightly controlled scientific studies. Species identification may be problematic, for example, and count routes may not be the same from one year to the next. Both bird and butterfly counts have procedures that are sufficiently standardized, however, to make the data valuable. Through comparisons with a scientific survey, Butcher *et al.* (1990) have illustrated the reliability of trends found in CBC data. Recommendations for the use of CBC data also apply to JBC data, including the importance of analysing numerous locations and multiple years (Butcher, 1990). The advantage of survey data sets is that they provide more information over wider geographical regions and over longer time periods than would otherwise be available. As long as their limitations are recognized, they provide important results for ecology and conservation in which large sample sizes can overcome some inconsistencies in the data (Swengel, 1990).

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