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Spatial constraint of peatland butterfly occurrences within a heterogeneous landscape

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Abstract The occurrence of ten butterfly taxa (*Clossiana eunomia dawsonii, Clossiana freija, Clossiana frigga, Clossiana titania, Coenonympha inornata, Erebia discoidalis, Incisalia augustinus, Lycaena dorcas, Lycaena epixanthe, Oeneis jutta*) was analyzed within three acid peatland habitat types from the Lake Superior drainage basin of northwestern Wisconsin. Both first- (nearest-neighbor spatial analysis) and second-order (Ripley's K) spatial point process statistics were used to identify the extents over which each distribution pattern significantly deviated from random expectations. Versions of these tests were used that identified significant spatial pattern uncorrelated to habitat location and habitat preference. These analyses documented non-random occurrence patterns in seven species. Deviations from random were largely confined to two extents: <50 km and 70–100+ km. The majority of non-random patterns at <50 km extents were examples of aggregation, while the majority of non-random patterns noted at the 70–100+ km scale were examples of segregation. These results demonstrate that even for winged animals inside a limited landscape, spatially constrained processes can be important determinants of distribution. It is likely that metapopulation dynamics and dispersal limitation help explain why aggregation is dominant at small scales. The mechanisms underlying the predominance of segregation at large scales are less clear, but may be related to migration history and/or weak environmental gradients.

Keywords Butterflies · Metapopulation · Nearest-neighbor spatial analysis · Ripley's K · Spatial pattern

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Introduction

Species occurrence patterns have often been described as a simple reflection of species niche requirements and underlying environmental conditions (MacArthur 1972; Tilman 1988). This idea requires the assumption that dispersal never limits distribution at regional scales, giving all species access to all potential habitats (Krebs 1985). Saur (1988) equated this concept with Beijerinck's Law, which states that "everything is everywhere but the environment selects". In such situations, species occurrences should not have significant spatial pattern beyond that exhibited by the physical environment.

However, the spatial relationship of populations, independent of the physical environment, may also influence occurrence patterns. Supply-side ecology (Roughgarden et al. 1987) and the mass effect (Shmida and Ellner 1984) demonstrate how proximity to potential source populations can positively influence occurrence frequency. Additionally, analyses of distance decay (Nekola and White 1999) and competitive co-equivalency (Shmida and Ellner 1984) demonstrate how habitat isolation can negatively influence population frequency. For these reasons, patch size and isolation can correlate as significantly to patch occupancy as does the physical environment (Moilanen and Hanski 1998). When such spatial factors are at work, non-random spatial occurrence patterns should be evident independent of the physical environment. Identification of such patterns is an important first step in the recognition of situations where spatially constrained processes are (or have been) important (Diggle 1983).

How frequently do populations deviate from random occurrence patterns, independent of their environment? One way of assessing this question is to compare distributions across a well-defined taxonomic group within a particular habitat in a given landscape. This allows for at least partial control of the environmental, geographic, temporal, and phylogenetic templates upon which distributions have developed.

Butterflies of northern Wisconsin acid peatlands represent such a system. Recent and historical investigations have documented ten species [*Clossiana eunomia dawsonii* (Nymphalidae), *Clossiana freija* (Nymphalidae), *Clossiana frigga* (Nymphalidae), *Clossiana titania* (Nymphalidae), *Coenonympha inornata* (Satyridae), *Erebia discoidalis* (Satyridae), *Incisalia augustinus* (Lycaenidae), *Lycaena dorcas* (Lycaenidae), *Lycaena epixanthe* (Lycaenidae), *Oeneis jutta* (Satyridae)], which live out their entire life cycles in these habitats (Masters 1971a, b, 1972; Ferge and Kuehn 1976; Kuehn 1983; Swengel 1995; Nekola 1998). Within the Lake Superior drainage basin of northwestern Wisconsin, three types of acid peatland habitats exist: muskeg, kettlehole, and coastal. Muskeg sites are dominated by open black spruce-cottongrass-wiregrass savanna, are relatively dry (except in the proximity of moats or lakes), and usually have an elevation similar to the surrounding uplands. Kettlehole peatlands are generally wetter, commonly contain floating sphagnum-leatherleaf mats, and are typically found fringing lakes or in kettlehole depressions. Coastal wetlands are limited to estuaries along the Lake Superior coast. Considerable similarity exists within the physical environment, habitat size, and flora of each peatland type, leading to the presence of very similar habitats throughout the region. However, subtle environmental and vegetation differences exist between peatland types, producing slightly different butterfly faunas within each (Nekola 1998).

The following paper analyzes the occurrence patterns of these butterflies within these habitats in order to identify the frequency of non-random distributions that are uncorrelated with environment, and the spatial extents at which the majority of any such non-random patterns occur. These results identify potentially important spatial processes, and can be used to guide conservation strategy.

Materials and methods

Site selection

Identification of all high quality peatlands within or adjacent to the Lake Superior drainage basin (Fig. 1) was accomplished by a fly-over of the study area on 20 May 1996 in a small aircraft. Approximately 5 h of flight time were required to survey the entire region at an altitude of 3,000–5,000 m in north-south transects running approximately 10 km apart. Other high-quality sites were identified through review of the Biological Conservation Database and discussions with the staff of the Wisconsin Department of Natural Resources Bureau of Endangered Resources. While an attempt was made to inventory all high-quality sites, some (like the Kakagon Sloughs) were not visited due to difficulty in political and/or physical access. As few such sites existed, and as they were spread across the study region, we assume that their absence from this analysis has not biased results.

Field sampling

The latitude-longitude location of each surveyed site was determined through digitization of USGS 7.5 min topographic quads using the ATLAS DRAW software package. The centroids for these sites were then converted to Zone 15 UTM coordinates using PC-ARCINFO.

The peatland habitat type represented by each site (muskeg, kettlehole, or coastal) was also recorded. Muskeg peatlands (37 to-

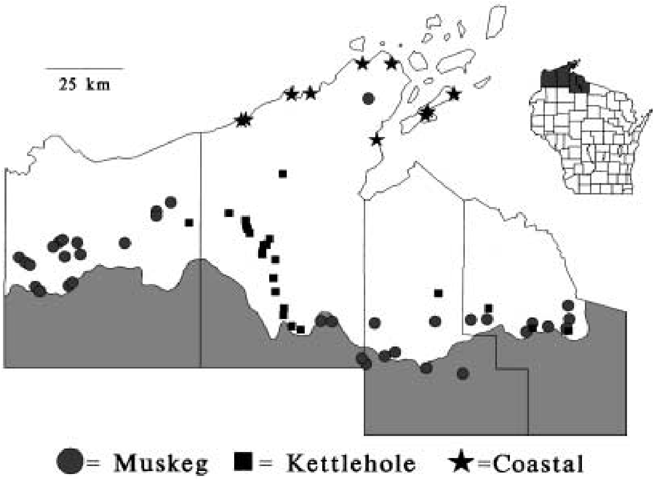

Fig. 1 Distribution of surveyed peatland habitats in northwestern Wisconsin. The *shaded area* in the south of the region represents areas outside of the Lake Superior drainage basin

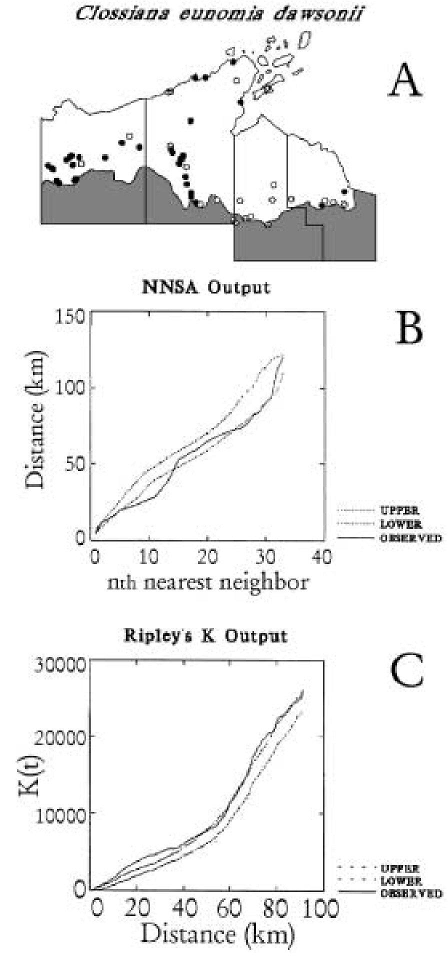

Fig. 2 **A** Occurrence pattern of *Clossiana eunomia dawsoni* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

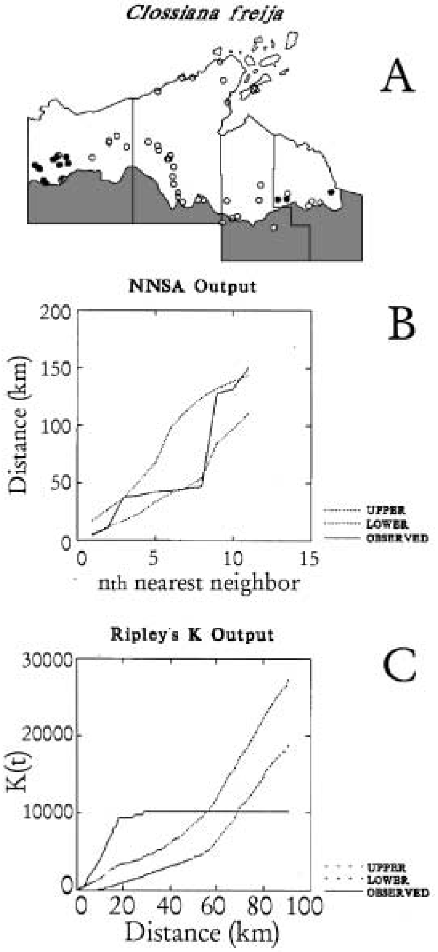

Fig. 3 **A** Occurrence pattern of *Clossiana freija* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

tal inventoried sites) were concentrated along the southern divide basin boundary in the western and eastern sides of the study area and were absent from the pitted outwash plain in the central region. Kettlehole peatlands (23 sites) were generally concentrated in the central outwash plain that lacked muskeg sites, although a few were also scattered throughout the eastern half. Coastal peatlands (10 sites) were limited to the Lake Superior shore in the Bayfield Peninsula and the Apostle Islands (Fig. 1).

Each site was visited 4–7 times during the 1996 flight season. Surveys were only conducted during sunny, dry weather when temperatures were 18°C or higher. Surveys were made at weekly intervals early in the flight season when a number of closely spaced adult emergences occur. Later in the season, when species emergence periods were more temporally separated and individual populations were in flight for longer periods of time, the survey interval increased to 3 weeks. Each site visit lasted for 15–90 min, depending upon site size, and all encountered peatland butterfly taxa were recorded. Voucher specimens are housed in the first author's collection at the University of Wisconsin-Green Bay. Nomenclature follows that of Miller and Brown (1981).

Cumulative presence-absence species lists for all peatland taxa from each site were compiled from site visit lists combined with any additional collections archived at the Milwaukee Public Museum and element occurrence records maintained by the Wisconsin Bureau of Endangered Resources.

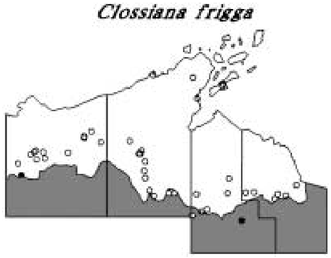

Fig. 4 Occurrence pattern of *Clossiana frigga* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time

As weather and logistical constraints prevented visitation of all sites during a given flight time, only sites inventoried during the flight duration for a given species were used for statistical analysis. Flight times for a given species were determined by noting the earliest and latest dates of adult encounters in the study region during 1996.

Statistical analyses

Two general approaches exist to analyze spatial point patterns: first-order statistics consider the mean distances between points, while second-order statistics consider the variance in these distances. One of the most commonly used first-order statistics is nearest-neighbor analysis (Diggle 1983; Manly 1991), while one of the most commonly used second-order statistics is Ripley's K analysis (Ripley 1977; Haase 1995). As little has been written to suggest whether first- or second-order statistics are more effective at identifying non-random patterns, both were used.

Both methods, as commonly employed, generate random null models from the assumption that occurrence is possible anywhere within the study region (e.g. Diggle 1983; Manly 1991). This is not appropriate for acid peatland butterflies, which cannot reside outside of peatland habitats. If peatlands are non-randomly distributed (as is the case in northwestern Wisconsin), it will be impossible to determine from such null models whether a non-random occurrence pattern for a given species is due to habitat distribution or other spatially constrained processes. Additionally, the physical environment may lead to significant non-random pattern when differences exist between habitats (as is also the case for peatland butterflies in our study). To more clearly test for non-random distributions uncorrelated to such environmental pattern, the first- and second-order statistics used in this study constrained random null models to actual peatland locations and to the actual occurrence frequencies of each species within each peatland type.

Nearest-neighbor spatial analysis (NNSA; Davis et al. 2000) was chosen as the first-order statistic. This method is related to the nearest-neighbor method described by Manly (1991), in which the average distance between 1st, 2nd, 3rd to *n*–1 nearest neighbors (where *n* equals the total number of occurrences of that species in the landscape) is calculated and compared to expected values generated from random distributions. Unlike Manly's test, the NNSA method generates random expectations based upon the subsampling of a larger finite set of points within a landscape. This permits factoring out spatial pattern caused solely by habitat distribution. This method also constrains random subsamples to be drawn at the same frequencies for which taxa were observed in that given habitat type. This allows any spatial pattern caused by habitat differences to be factored out (Davis et al. 2000).

NNSA null expectations were based on 5,000 Monte Carlo simulations. Two-tailed 95% confidence intervals were generated from this process, and plotted versus observed nearest-neighbor distances (Figs. 2, 3, 4, 5, 6, 7, 8, 9, 10, 11). From these, the total

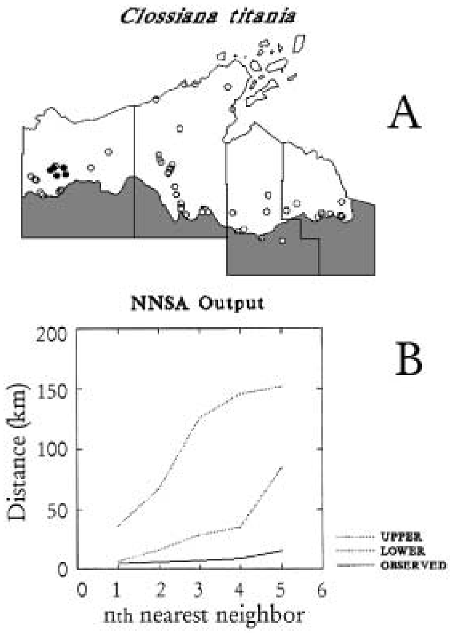

Fig. 5 **A** Occurrence pattern of *Clossiana titania* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations

range of distances were determined over which observed distributions deviated from random.

Ripley's K (Ripley 1977) was chosen as the second-order statistic. This test evaluates the expected number of points within a distance *t* of an arbitrary point in the area being evaluated (Haase 1995). If occurrences are randomly distributed, the expected value of $K(t)=\pi t^2$.

The unbiased estimate of $K(t)$ for an observed spatial point pattern is:

$$\hat{K}(t) = n^{-2} A \sum_{i\neq j} \sum_{i\neq j} w_{ij}^{-1} I_t(u_{ij})\ ,$$

where n is the number of points in the landscape area A; u_{ij} is the distance between events i and j; $I_t(u)$, the counter variable, equals 1 if $u<=t$ and 0 if $u>t$; w_{ij} is the proportion of the circumference of a circle centered at the event i with radius u_{ij} lying within A; and the summation is over all pairs of a given species occurrence (Ripley 1977).

Random expectations for $K(t)$ were based upon a random subsample of n peatlands in the landscape, with n representing the number of species occurrences, as is outlined in Kraft et al. (in press). Randomly chosen sites were selected according to the actual proportion of sites colonized by each species within each peatland type. In this way, spatial pattern due to habitat distribution and preference were factored out.

S-Plus was used for estimating Ripley's K (Venables and Ripley 1997). Null expectations were based on 5,000 Monte Carlo simulations. Two-tailed 95% confidence intervals were generated and plotted against observed values (Figs. 2, 3, 4, 5, 6, 7, 8, 9, 10, 11). From these, the total range of distances was determined over which observed deviated from random.

Because our null expectations are based upon randomly selected subsets of given peatland sites, the expectation that $K(t)$ will approximate πt^2 is not valid. Thus, the boundary issues considered by Haase (1995) do not apply to our analysis, as occurrences are constrained to actual peatland locations. Any such boundary-based biases should be accounted for by our use of Monte Carlo simulations to estimate the 95% confidence interval for $K(t)$.

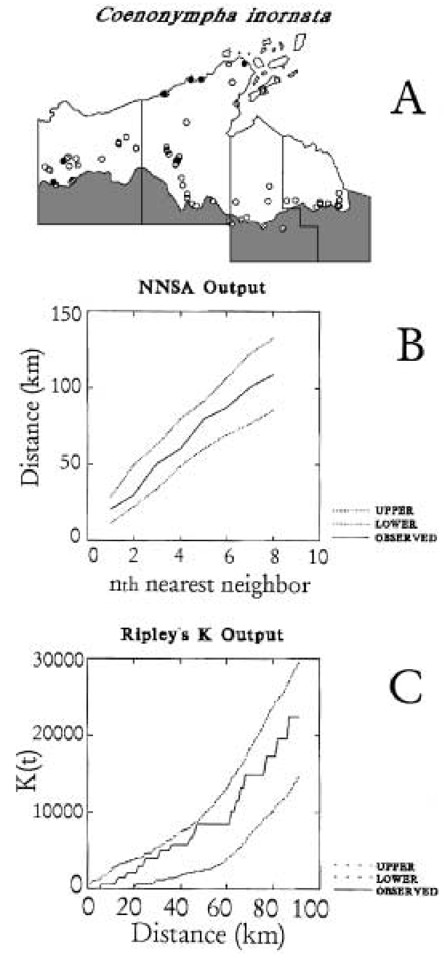

Fig. 6 **A** Occurrence pattern of *Coenonympha inornata* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows $K(t)$ for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

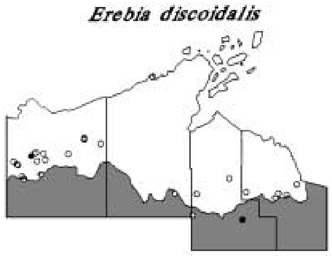

Fig. 7 Occurrence pattern of *Erebia discoidalis* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time

Results were summarized across all species via histograms documenting the total number of significant aggregations and segregations at each analyzed distance for both methods (ca. 0–150 km for NNSA, 0–91 km for Ripley's K).

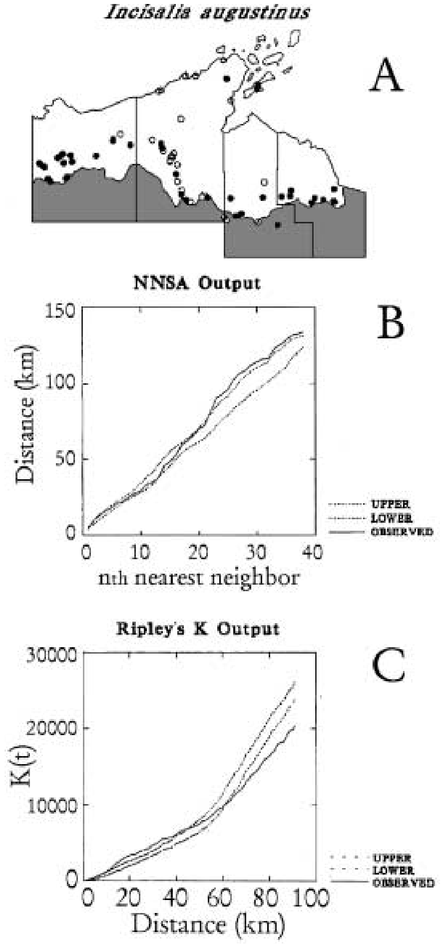

Fig. 8 **A** Occurrence pattern of *Incisalia augustinus* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

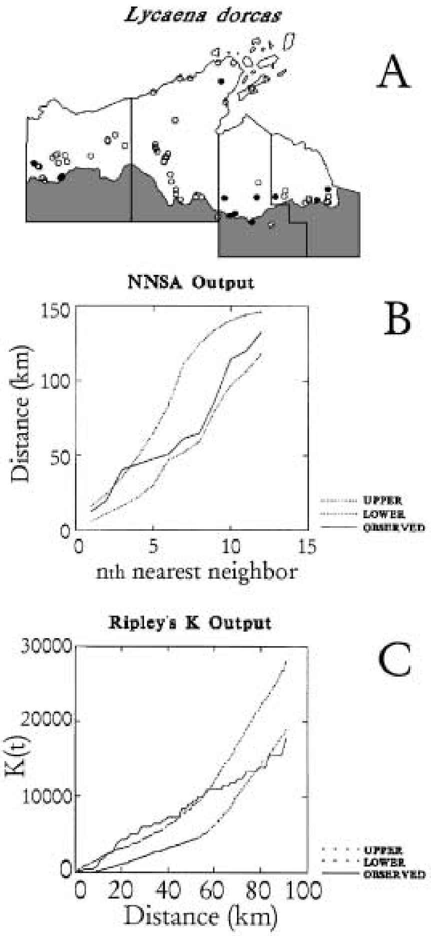

Fig. 9 **A** Occurrence pattern of *Lycaena dorcas* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

Results

Two taxa (*Clossiana frigga* and *Erebia discoidalis*) were only twice encountered. Their populations were limited to muskeg sites in the west and east. Although their distributions have been mapped for sake of completeness (Figs. 4, 7), their few occurrences precluded further statistical analysis.

Significant deviations from random were noted in the occurrences of seven of the remaining eight taxa. The only species which did not significantly deviate from random in either test was *Coenonympha inornata*, which was located at nine scattered sites (4 muskeg, 1 kettlehole, 4 coastal; Fig. 7).

Clossiana eunomia dawsonii was located at 34 sites (14 muskeg, 14 kettlehole, 4 coastal), with the majority being located in the western half of the study region (Fig. 2). NNSA identified significant aggregation in these occurrences from the 6th–14th (min. $P<0.0005$; 21–44 km), 25rd–27th (min. $P=0.008$; 73–77 km), and 29th ($P=0.021$; 85 km) nearest neighbors. Ripley's K identified significant clustering (min. $P<0.0005$) in these occurrences from 1–48 km and 67–87 km extents.

Clossiana freija was located at 12 muskeg sites, with populations being restricted to the far west and east (Fig. 3). NNSA identified significant aggregation over the 1st–2nd (min. $P=0.012$; 5–11 km) and 8th ($P=0.017$; 47 km) nearest neighbors. Significant segregation was noted at the 11th ($P=0.001$; 150 km) nearest neighbor. Ripley's K identified significant aggregation from 4–55 km (min. $P<0.0005$), and significant segregation from 69–91 km (min. $P<0.0005$).

Clossiana titania was located at 6 muskeg sites in the far west (Fig. 5). NNSA identified significant aggre-

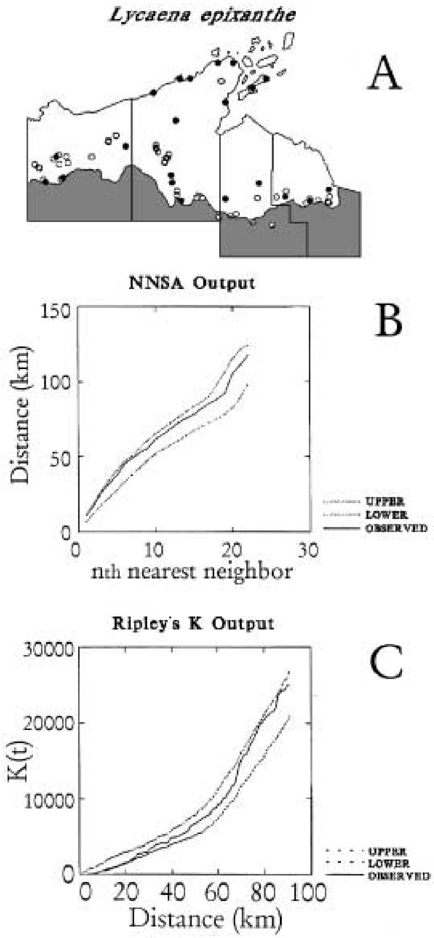

Fig. 10 **A** Occurrence pattern of *Lycaena epixanthe* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed* lines show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

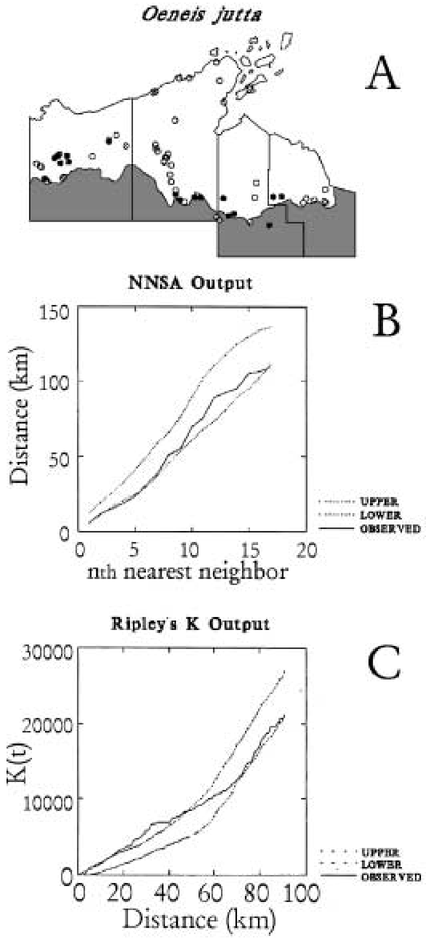

Fig. 11 **A** Occurrence pattern of *Oeneis jutta* within the study region. *Black circles* represent occupied sites; *open circles* represent sites vacant during flight time. **B** *Black line* shows distance to nearest neighbor for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo NNSA simulations. **C** *Black line* shows *K(t)* for observed distribution of occupied sites; *dashed lines* show upper and lower 95% confidence intervals from 5,000 Monte Carlo Ripley's K simulations

gation (minimum $p<0.0005$) across all neighbors (5–15 km). Too few occurrences were present to allow calculation of Ripley's K.

Incisalia augustinus was located at 39 sites (30 muskeg, 8 kettlehole, 1 coastal), which were most frequently encountered in the west and east (Fig. 8). NNSA identified significant segregation (min. $P<0.0005$) from the 22nd–38th nearest neighbors (81–133 km). Ripley's K identified significant aggregation in occurrence at 5 km ($P=0.023$) and from 10–44 km (min. $P<0.0005$), and significant segregation from 61–91 km (min. $P<0.0005$).

Lycaena dorcas was located at 13 muskeg sites, with the majority of populations being found in the eastern half (Fig. 9). NNSA identified significant ($P=0.003$) segregation at the 3rd nearest neighbor (40 km). Ripley's K identified significant aggregation in its occurrence from 16–60 km (min. $P<0.0005$), and significant segregation from 81–82 km (min. $P=0.013$) and 86–91 km (min. $P=0.006$).

Lycaena epixanthe was located at 23 sites (7 muskeg, 7 kettlehole, 9 coastal), with populations sporadically occurring throughout the entire region (Fig. 10). No significant deviations from random were noted by NNSA. However, Ripley's K identified significant segregation (min. $P<0.0005$) in its occurrences from 3 to 21 km.

Oeneis jutta was located at 18 sites (15 muskeg, 3 kettlehole), with populations being noted in the west and south central (Fig. 11). NNSA identified significant aggregation from the 3rd–5th (minimum $p=0.009$; 15–23 km) nearest neighbors. Ripley's K identified significant aggregation from 5–8 km (min. $P=0.008$), 10 km ($P=0.022$), 13 km ($P=0.022$), 16 km ($P=0.024$), and from 18–49 km (min. $P=0.001$).

Comparison of these results across species (Fig. 12) show that significant deviation from random was most apparent at three extents. At <20 km, NNSA identified non-random aggregation for two taxa (*C. freija*, *C. titania*), while Ripley's K identified significant aggregation

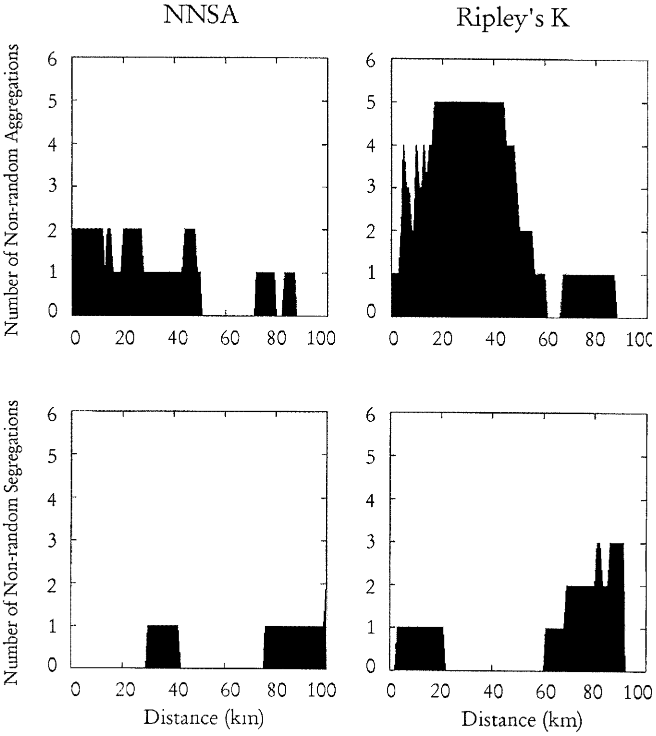

Fig. 12 Frequency of non-random aggregation and segregation patterns from 0–100 km extents for both NNSA and Ripley's K analyses

in four taxa (*C. eunomia dawsonii*, *C. freija*, *I. augustinus*, *O. jutta*). Additionally, Ripley's K identified significant segregation over this range for *L. epixanthe*. From 20–50 km, NNSA identified aggregation for three taxa (*C. eunomia dawsonii*, *C. freija*, *O. jutta*), while Ripley's K identified aggregation for five taxa (*C. eunomia dawsonii*, *C. freija, I. augustinus*, *L. dorcas*, *O. jutta*). Significant segregation was identified at this scale by NNSA for *L. dorcas*. Few non-random occurrence patterns were identified by either method from 50–70 km. However, at larger scales both methods identified significant aggregation in *C. eunomia dawsonii*. Significant segregation at this scale was identified by both methods for *C. freija* and *I. augustinus*, and by Ripley's K for *L. dorcas*.

Discussion

Perhaps the most obvious and important finding from these analyses is the simple realization that in northwestern Wisconsin, across a broad range of spatial scales (0–90 km), most acid-peatland butterflies appear to possess non-random occurrences independent of habitat location and preference.

As we did not sample physical environmental variables from these sites (e.g. soil and water chemistry, local climate, amount and type of plant cover), it is possible that some of these distribution patterns may be related to such factors. If present, however, these factors must be cryptic, as habitats appeared to be homogeneous within each peatland type, possessing similar (if not identical) microhabitats, vascular plant, and bryophyte species. Additionally, given the small total extent of the sample region (ca. 150 × 75 km), it is unlikely that strong climatic gradients exist. Thus, we believe that the patterns of peatland butterfly occurrence are likely related to other factors.

Assuming that peatlands within a given type have approximately similar environments for these butterflies, the existence of non-random occurrence patterns independent of habitat location and preference would be unlikely if dispersal allowed equal access to all suitable sites. The frequent presence of significant non-random occurrence pattern in these species suggests that within this landscape spatial limitation of butterfly dispersal is common.

Inference of spatial process from spatial pattern

The local clustering of occurrences is not surprising as many ecological processes show some degree of spatial autocorrelation over relatively small extents (Shmida and Ellner 1984; Burrough 1986; Okubo and Levin 1989). In particular, limitations on butterfly movement contribute to patchy occurrences in a number of European taxa, including *Clossiana* (*Boloria*) *aquilonaris* (Mousson et al. 1999), *C.* (*Proclossiana*) *eunomia* (Nève et al. 1996a), *Hesperia comma* (Hill et al. 1996), and *Melitaea cinxia* (Hanski et al. 1994). When dispersal limitation is coupled with other aspects of metapopulation dynamics, local aggregations of butterfly occurrence, independent of the physical environment, are often evident. For instance, *M. cinixa* occurrences on the main Åland island in southwestern Finland demonstrate what visually appears to be strong aggregation over 1–10 km extents among appropriate habitat patches (Moilanen and Hanski 1998). Occurrences of *H. comma* in the North Downs, Surrey, UK, also appear to be aggregated over 2–6 km extents within appropriate sites (Hill et al. 1996). The metapopulations of all five edaphically-restricted butterfly taxa of Sierra Nevada (California) serpentine barrens also demonstrate apparent spatial aggregation in their occurrences among known sites (Gervais and Shapiro 1999).

Much of the previous work on occurrence patterns in Lepidoptera has focused on the factors predicting habitat occupancy or vacancy (Ehrlich and Murphy 1987; Thomas et al. 1992; Hanski et al. 1994). While these studies have elucidated the processes influencing individual patches, none have investigated the spatial patterns in occurrence generated by these processes across an entire landscape. Analyzing such patterns may prove a useful tool for identifying those species whose distribution is influenced by spatial processes (Hanski 1999). For instance, *C. eunomia* is known to exist in discrete metapopulations within Belgium and France, with individuals capable of traversing up to 8 km of unfavorable habitat within a season (Nève et al. 1996b). Our analyses demonstrate strong aggregation for this species at relatively small (<50 km) scales. A previous investigation on

Coenonympha tullia (often lumped with *C. inornata*) distribution in Northumberland, UK, documented that occurrences were more strongly related to habitat quality than geographic factors (Dennis and Eales 1999). In northwestern Wisconsin, this species was the only one that exhibited random occurrence patterns at all scales. These examples, in conjunction with our analysis of spatial distribution pattern, illustrate how analyses of spatial pattern can reflect potential processes underlying organism distribution. While Real and McElhaney (1996) note that spatial pattern analysis, alone, cannot distinguish between all processes capable of producing a given pattern, we believe that the analysis of spatial pattern provides an instructive first step that can help improve field experiments or modeling efforts used to evaluate the processes affecting distribution.

It is not clear for the majority of the fauna why aggregation is essentially limited to <50 km extents. This is especially interesting given the fact that many of these species appear to share similar niches: in the region *Clossiana freija*, *C. eunomia*, *C. titania*, *L. dorcas*, and *L. epixanthe* all are obligate cranberry consumers, while *Coenonympha inornata*, *E. discoidalis*, and *O. jutta* appear limited to cottongrass and/or wiregrass (Nekola 1998). While these species might thus be expected to demonstrate some form of competitive exclusion, they instead appear to show largely coincident occurrence patterns at regional scales. Such correspondence between occurrence patterns is likely related to factors that have equally influenced all taxa, such as habitat and host plant distribution. If related to cryptic environmental gradients, the location of colonies may be expected to remain static over time. However, if shifting metapopulation dynamics are responsible, the location of occurrence clusters may change over ecological time scales within the landscape.

Another enigma is the presence of significant small-scale segregation in occurrences of *L. epixanthe*. While it is possible that colonies may have become segregated due to competitive interactions, such processes are generally thought to be limited to small extents within sites (Shmida and Ellner 1984). It is difficult to envision how such mechanisms could operate at distances up to 20 km.

A number of other spatial mechanisms may underlie larger scale (70–150 km) segregated spatial distributions. Migration history may provide one explanation. For instance, migration of *C. eunomia dawsonii* out of Minnesota (beyond the study area boundaries) could help account for its higher occurrence frequencies in the west. Likewise, the absence of species from the center (e.g., *C. freija*, *L. dorcas*, *O. jutta*) could be due to dual migration pathways from peatland-rich landscapes to the west and east. However, these patterns could also be related to cryptic soil and water chemistry or climate gradients that our statistical methods could not control for. In this event, identification of such cryptic gradients would be a useful result, given their difficulty in direct detection.

Teasing apart the historical and environmental influences on distribution at large scales may prove difficult due to covariation between these factors. Population genetics analyses may provide one possible avenue to distinguish between them. If historical factors are responsible for the observed large-scale pattern, it seems likely that significant genetic differences may occur across the study region due to differences in initial population source pools. However, if dispersal is not limiting and contemporaneous environmental gradients are responsible for the observed pattern, differences in allele frequency should be diminished from more thorough genetic mixing.

Conservation implications

Relatively few populations (e.g., <25 stations) of these taxa (except *I. augustinus*) have been previously reported from Wisconsin (Ebner 1970; Masters 1971a, b, 1972; Ferge and Kuehn 1976; Kuehn 1983; Swengel 1995). As acid peatlands are frequent in the northern Wisconsin landscape, it has been generally assumed that these species were simply undercollected and would eventually be found within most appropriate sites (Wisconsin Rare Butterfly Working List 1996). As such, none of these species have been granted endangered or threatened species protection within the state (Wisconsin Endangered Species List 1999).

The existence of complex spatial structure in the occurrence of these taxa suggests that such expectations may be false. The aggregation of most inventoried taxa indicates that, at some scale, high-quality sites will be unoccupied. Modifications to sites within limited areas of occurrence would have profound implications to the long-term survival of those species across the entire landscape. For example, *C. freija* and *C. titania* are essentially restricted to a small cluster of sites in the far west of the study region. Unfortunately, peatlands in this same area were observed to be undergoing the heaviest “all terrain vehicle” abuse within the entire region. Thus, even though appropriate habitat for these species exists throughout the study region, the correspondence of high levels of disturbance in the region where most colonies occur suggests that their continued existence within this landscape may be in jeopardy.

In this region, the vulnerability of peatland butterfly species appears to be generally unrelated to habitat frequency. Such patterns may be common at range edges where increased environmental stress and patch isolation lead to lower habitat occupancy rates (Thomas et al. 1992). When species distribution does not simply mimic habitat abundance, determination of population vulnerability to extirpation can only be assessed by conducting geographically systematic inventories and documenting the actual distribution of taxa. Additionally, repeated monitoring of distribution may be necessary if shifting metapopulations exist.

Comparison of first- and second-order spatial point statistics

Given the different assumptions and algorithms underlying these methods, the general robustness of the results suggests that the underlying patterns are quite strong. Only one species (*L. dorcas*) exhibited a major discrepancy in outcomes, with NNSA identifying segregation in the same 30–40 km extent where Ripley's K showed strong aggregation. Based upon visual inspection of this taxon's occurrences, the Ripley's K result appeared more accurate. Perhaps NNSA was unable to identify aggregation for this species as occurrences were concentrated on a region of widely separated sites.

Comparing results across species, Ripley's K identified more non-random distributions at a given extent, and identified larger regions for non-random distribution, as compared to NNSA. It would thus appear that NNSA is the more conservative of the two tests. However, visual inspection of maps suggests that NNSA might be overly conservative, as it failed to identify areas of apparent aggregation or segregation at some scales (e.g., *C. freija*, *I. augustinus*, *L. epixanthe*, *O. jutta*). A more rigorous comparison of these methods would help to better determine their relative strengths and weaknesses.

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