

Canopy herbivore community structure: large-scale geographical variation and relation to forest composition

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Abstract. 1. Geographical distributions of individual foliage-feeding forest herbivore species have been found to be aligned closely with the distribution of their host trees, however little is known about the extent to which broad herbivore communities are geographically associated with distinct host communities.

2. Large-scale geographic variation in canopy herbivore communities in a 80 000 km² area (the state of Maine, U.S.A.) was characterised using historical insect survey data. Variation in insect communities was compared with corresponding variation in forest over-storey composition, which was quantified using data from a regional forest inventory survey.

3. Principal components analysis was used to characterise associations among herbivore and tree species. Analysis of the herbivore data identified three main insect groups: group A corresponded to a single species (*Choristoneura fumiferana*), group B corresponded to pine-feeding species including *Semiothisa* sp., and group C corresponded to the spruce-feeding species *Gilpinia hercyniae* and *Pikonema alaskensis*. Analysis of the forest inventory data characterised three important forest types: northern hardwoods, eastern white pine, and northern spruce-fir forest types.

4. Spatial analyses were carried out on the first two components of each of the principal components analyses. Factor 1 of the insect data showed a trend of decreasing values from south to north, while factor 2 of the forest inventory data showed an opposite trend. These inverse trends reflected the distribution of the main contributing species to the principal components analysis, *C. fumiferana* and *Pinus strobus* respectively. These distributions were highlighted further by the significant negative cross-correlations that were found between the two factors up to distances of 120 km.

5. Analyses indicated a parallel between the geographic variation in the insect guilds associated with conifers and the geographic pattern of their conifer hosts. Hardwood-feeding caterpillars, on the other hand, did not form well-defined guilds and showed varying geographical distributions. The survey data showed varying quality in defining large-scale associations in the structures of herbivore and host communities.

6. Implications for biodiversity management are discussed.

Key words. Canopy, diversity, geographic variation, geostatistics, herbivore community, principal components analysis.

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Introduction

Forest canopies support a complex assemblage of herbivores, most of which never reach outbreak levels (Mason, 1987). At any location, the herbivore community is usually represented by species belonging to several different guilds that differ in their feeding habits (Root, 1973). Moran and Southwood (1982) found a remarkable similarity in the proportions of insects in the major guilds sampled in the U.K. and in South Africa, in spite of considerable differences in climate and species composition, however it is recognised widely that specific herbivore communities vary considerably among tree species and forest types. This reflects the plant–herbivore association that is thought to have arisen via island biogeographical processes in which tree species act as islands that herbivore species may colonise (Southwood & Kennedy, 1983).

There is considerable information about associations between individual insect species and their host plants and the extent to which geographical ranges of individual insect and plant species co-vary (Crawley, 1984). Several studies have compared multi-species abundance and diversity among different forest types (e.g. Hysell *et al.*, 1996; Reynolds & Crossley, 1997; Basset & Novotny, 1999; Barbosa *et al.*, 2000) but there have been few attempts to describe and quantify the spatial structure of herbivore communities (Simandl, 1993). Quantification of community structure can be achieved most effectively through the use of multivariate statistical methods (Gauch, 1982; Pielou, 1984; Jongman *et al.*, 1995), as illustrated by recent efforts to apply these methods to characterise animal communities, including arthropods, however most of these studies have focused largely on arthropod composition in relation to forest conditions and management practices (e.g. Schowalter, 1995; Chey *et al.*, 1997; Schowalter & Ganio, 1998; Le Corff & Marquis, 1999; Work & McCullough, 2000). There is a clear lack of information about the geographical variation in herbivore community structure and how that structure relates to plant community structure.

Given the increasing emphasis of biodiversity management efforts beyond the conservation of individual species to include efforts to preserve distinct communities, understanding geographical variation in community structures is of growing importance (Ehrlich, 1996; Knight, 1998). The objective of the work reported here was thus to investigate the use of forest insect and forest tree surveys to characterise geographical variation in forest foliage feeding insect communities over a large area (the state of Maine, U.S.A.) and to determine the extent to which that community structure was associated with over-storey tree community structure.

Methods

The approach to characterising foliage-feeding forest insect defoliator communities in Maine involved the use of multivariate statistical analyses to describe how various insect and tree species co-varied in their abundance, and the use of

geostatistics to determine the geographical pattern of that variation and to identify associations between herbivore and forest communities. Data on both insect species abundance and over-storey forest composition were not available from the same sampling locations, which precluded a combined analysis of multivariate associations directly between insect and tree communities. Therefore, insect and tree data from two separate data-sets were analysed and geostatistical methods were used to quantify spatial associations.

Maine Forest Insect and Disease Survey

The Maine Forest Insect and Disease Survey is a programme conducted by the Maine Department of Forestry and is designed to measure regional trends in forest insect populations across the state (Donahue & Murray, 1999). As part of that effort, insect count data were obtained as branch beating samples from 1971 to 1996. Each year, samples were taken from arbitrarily selected trees at sample locations situated irregularly across the state. Each sample was taken from a single branch of a single tree. Samples from successive years did not necessarily arise from the same stand or tree, but the same tree species were sampled in successive years. Samples were collected by placing a tarpaulin below the tree canopy and striking a single branch with a stick (Morris, 1955). The number of insects falling on the tarpaulin was recorded by taxa. Several hundred samples were taken each year. Altogether, over 80 000 samples, including more than 150 000 insect entries, were collected (Donahue & Murray, 1999).

This huge amount of information contained a number of potential sources of error and limitations. For these reasons, the data were summarised in the following ways. The 20 most abundant foliage (or cone)-feeding taxa that had been identified at least to the genus were selected for further analysis (Table 1). Because sample locations were not geo-referenced, the latitude and longitude of the centroid of the township where samples were collected was used as the spatial location of samples. The density of each insect species was calculated for each township as the total number of insects collected in the township over all years from 1971 to 1996, divided by the total number of trees sampled. Data were pooled over the whole study period as only a limited number of locations was sampled each year. This pooling of data over time and the rather coarse spatial scale of townships ensured that the dataset contained a good geographical distribution of the branch beating collections. All but a few of Maine's townships were sampled, amounting to about 900 locations. By pooling data across years, however, spatio-temporal patterns or associations could not be identified. For example, it could not be determined whether insects showed high localised abundances at different locations in different years.

1995 Forest Inventory and Analysis Survey

Data on forest over-storey composition were obtained from the 1995 USDA Forest Service Forest Inventory and

Table 1. Total number and densities (number of insects per branch) of the 20 most abundant foliage-/cone-feeding insect species collected in Maine's Forest Insect and Disease Historical Database (1971–1996), summarised by tree genus.

Order	Family	Genus or species	Density													
			Abies	Larix	Picea	Pinus	Tsuga	Acer	Betula	Fagus	Fraxinus	Populus	Quercus			
Coleoptera	Chrysomelidae	<i>Syneta extorris borealis</i>	0.03	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Homoptera	Aphididae	<i>Cinara</i> sp.	0.05	0.11	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Homoptera	Cercopidae	<i>Aphrophora cribrata</i>	0.03	0.04	0.04	0.34	0.03	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hymenoptera	Diprionidae	<i>Gilpinia hercyniae</i>	0.03	0.04	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hymenoptera	Diprionidae	<i>Neodiprion abietis</i>	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hymenoptera	Diprionidae	<i>Diprion similis</i>	0.00	0.00	0.01	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hymenoptera	Tenthredinidae	<i>Pristiphora gemiculata</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	50.00	0.00	0.00	0.00
Hymenoptera	Tenthredinidae	<i>Pristiphora erichsonii</i>	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hymenoptera	Tenthredinidae	<i>Pikonema ataskensis</i>	0.00	0.01	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lepidoptera	Coleophoridae	<i>Coleophora serratella</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.04	0.01
Lepidoptera	Geometridae	<i>Semiothisa</i> sp.	0.10	0.10	0.06	0.32	0.34	0.34	0.00	0.04	0.04	0.04	0.04	0.00	0.01	0.04
Lepidoptera	Geometridae	<i>Lambdina fuscicollaria fuscicollaria</i>	0.04	0.01	0.04	0.02	0.59	0.10	0.09	0.03	0.03	0.46	0.00	0.00	0.02	0.03
Lepidoptera	Geometridae	<i>Eupithecia</i> sp.	0.04	0.01	0.04	0.09	0.10	0.10	0.00	0.02	0.01	0.01	0.00	0.00	0.01	0.01
Lepidoptera	Geometridae	<i>Operophtera bruceata</i>	0.01	0.00	0.00	0.00	0.00	0.00	1.58	0.01	0.64	0.00	0.00	0.85	0.00	0.00
Lepidoptera	Geometridae	<i>Protoboarmia porcellaria</i>	0.03	0.01	0.02	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lepidoptera	Lasiocampidae	<i>Malacosoma dissirta</i>	0.00	0.00	0.00	0.01	0.00	0.00	0.07	0.07	0.01	0.01	0.00	1.09	0.12	0.12
Lepidoptera	Lymantriidae	<i>Lymantria dispar</i>	0.00	0.04	0.01	0.05	0.01	0.01	0.19	0.02	0.02	0.02	0.00	0.06	0.06	1.88
Lepidoptera	Noctuidae	<i>Elaphria versicolor</i>	0.03	0.00	0.02	0.01	0.01	0.01	0.00	0.01	0.01	0.01	0.00	0.00	0.00	0.01
Lepidoptera	Pyralidae	<i>Dioryctria abietivorella</i>	0.01	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lepidoptera	Tortricidae	<i>Choristoneura fumiferana</i>	1.68	0.60	1.23	0.02	0.46	0.46	0.01	0.02	0.06	0.00	0.00	0.07	0.07	0.00
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Analysis Survey for the state of Maine (Griffith & Alerich, 1996). In this survey, 3001 fixed area plots were used to estimate over-storey basal area by species. Latitude and longitude of the inventory plots were recorded to the nearest 100'. In order to identify the major patterns of forest cover, the basal area of the 20 most common species was summarised for each plot (Table 2).

Multivariate analyses

Principal components analysis was chosen over other methods because it requires few formal assumptions, even though it has several limitations in the case of non-linear data (James & McCulloch, 1990; Jongman *et al.*, 1995). Consequently, it was used for descriptive purposes only. Separate principal component analyses were used to describe patterns of community composition for the counts of insect species and for the basal area of tree species. For the herbivore data, the analysis used the 20 variables representing the density of the selected taxa, normalised using a $\log(x+1)$ transformation. The principal components analysis on the forest data was carried out using the percentage basal area per plot of the 20 most common tree species after arcsin-square-root transformation.

Before analysis, variables were also standardised to a mean of 0 and a standard deviation of 1 in order to prevent the most abundant species from exerting undue influence on the principal components analysis (Pielou, 1984): counts of *Choristoneura fumiferana* would otherwise overwhelm all other data, as this species comprised 67% of all collected

individuals, while the second most abundant species, *Gilpinia hercyniae*, amounted to only 7% of collections.

Measurement of spatial dependence

Geostatistical methods were used to explore the geographical variation of the herbivore and forest communities. Spatial patterns were described using the variogram and the cross-correlogram (Rossi *et al.*, 1992; Liebhold *et al.*, 1993). The variogram models the variability among observed values of a given variable as a function of their separation distance. The cross-correlogram describes the correlation between two different variables as a function of the distance between samples (Rossi *et al.*, 1992). When the distance between samples is zero (both variables are sampled at the same location), the cross-correlogram yields the ordinary (non-spatial) Pearson correlation coefficient. In this study, pseudo-cross-correlograms were computed because insect and forest surveys were conducted at different sample locations (Deutsch & Journel, 1998). The variograms characterised the spatial structure of the insect and forest communities whereas the pseudo-cross-correlograms described the spatial correlations between herbivore occurrence and forest composition. All geostatistical calculations were made on the first two axes of the principal components analyses as variables using the GSLIB software (Deutsch & Journel, 1998).

Results

Insect abundance

The abundance of the 20 dominant herbivore taxa and their mean densities per tree for each tree genus are shown in Table 1. Lepidoptera and Hymenoptera caterpillars dominated the samples, both in terms of diversity (85% of sampled taxa) and abundance (95% of samples). The spruce budworm *Choristoneura fumiferana* was by far the most abundant species, with more than 28 000 specimens collected over the 25 years of the survey. It was followed by an exotic diprionid, the European spruce sawfly *Gilpinia hercyniae*, with 3000 specimens collected. Both species' densities were highest on conifers, as *C. fumiferana* was found mostly on balsam fir and spruce and *G. hercyniae* on spruce. Other taxa were collected in much lower numbers, with only *Semiothisa* sp. (Lep., Geometridae) and *Coleophora serratella* (Lep., Coleophoridae) exceeding 1000 specimens.

Yearly insect densities of four selected taxa are shown in Fig. 1. The first three graphs correspond to the three most abundant species in the survey, while the fourth graph represents the least abundant species, *Pikonema alaskensis*. A spruce budworm outbreak occurred in Maine all through the 1970s (Fig. 1a), while *G. hercyniae* population levels were highest in 1993 (Fig. 1b). Other species mostly showed yearly fluctuations of little importance.

Table 2. The 20 most abundant tree species, ranked on basal area, surveyed in the Forest Inventory and Analysis Project 1995 survey of Maine.

Species	Common name	Basal area (m ² ha ⁻¹)
<i>Abies balsamea</i>	Balsam fir	14.171
<i>Acer rubrum</i>	Red maple	11.859
<i>Picea rubens</i>	Red spruce	11.060
<i>Thuja occidentalis</i>	Northern white cedar	10.111
<i>Pinus strobus</i>	White pine	6.572
<i>Acer saccharum</i>	Sugar maple	6.495
<i>Betula papyrifera</i>	Paper birch	5.346
<i>Betula alleghaniensis</i>	Yellow birch	5.113
<i>Fagus grandifolia</i>	American beech	5.086
<i>Tsuga canadensis</i>	Eastern hemlock	4.943
<i>Populus tremuloides</i>	Quaking aspen	2.837
<i>Picea glauca</i>	White spruce	1.847
<i>Quercus rubra</i>	Red oak	1.818
<i>Picea mariana</i>	Black spruce	1.503
<i>Fraxinus americana</i>	White ash	1.403
<i>Populus grandidentata</i>	Bigtooth aspen	1.359
<i>Acer pennsylvanicum</i>	Striped maple	0.778
<i>Betula populifolia</i>	Gray birch	0.684
<i>Larix laricina</i>	Tamarack	0.670
<i>Fraxinus nigra</i>	Black ash	0.521

Multivariate analyses

Principal components analysis was performed on insect densities of the 20 dominant herbivorous taxa from Table 1. The first three principal components explained 20.9% of the insect density variability (8.0% for factor 1, 6.7% for factor 2, 6.2% for factor 3), while the first five components accounted for 32% of the total variability.

The projection of the variables on the planes defined by the first three principal components is shown in Fig. 2. *Choristoneura fumiferana* and *Semiothisa* sp. delimited the extremes of the first principal component. They were respectively correlated negatively and positively with factor 1. In the second principal component, *G. hercyniae*

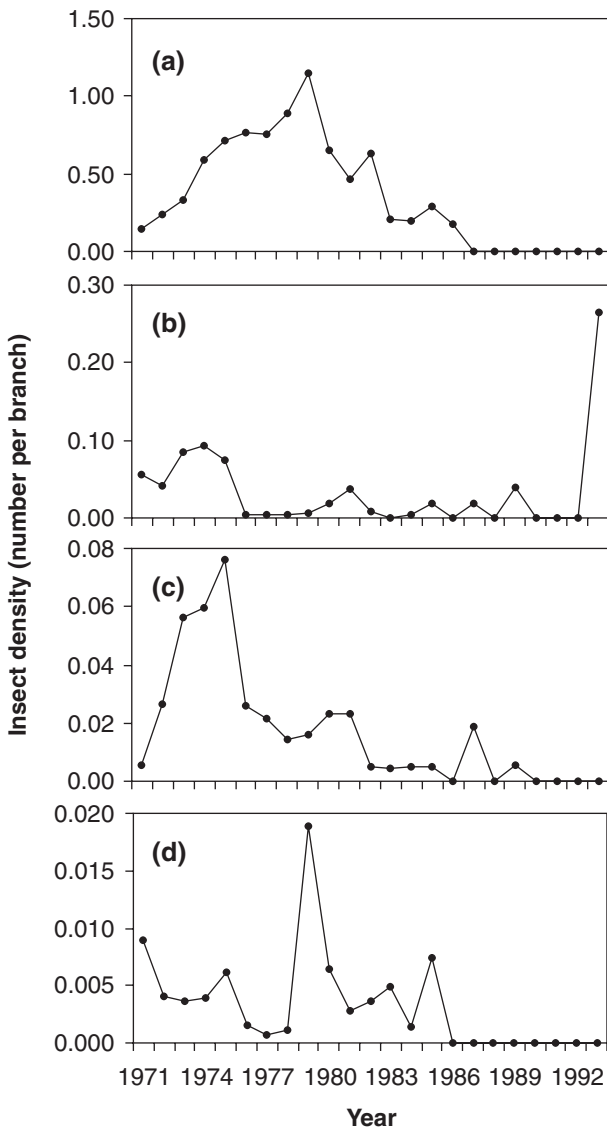


Fig. 1. Yearly densities (number of insects per tree) of four selected insect species for 1971 to 1993: (a) *Choristoneura fumiferana*, (b) *Gilpinia hercyniae*, (c) *Semiothisa* sp., (d) *Pikonema alaskensis*.

and *P. alaskensis* were the major contributing variables and were both correlated negatively with factor 2 (Fig. 2a). *Protoboarmia porcelaria* was the main contributor to factor 3 (Fig. 2b). While the first component isolated one species, *C. fumiferana* (group A), the second and third components identified groups of species according to their known host associations: group B encompassed four species feeding on pine (*Aphrophora cribrata*, *Diprion similis*, *Eupithecia* sp., *Semiothisa* sp.), group C comprised two nearly exclusively spruce-feeding species (*G. hercyniae*, *P. alaskensis*), and group D consisted of *Abies*-feeding species (*C. fumiferana*, *Eupithecia* sp., *P. porcelaria*, *Semiothisa* sp.).

The values of the first two principal components for each township are mapped in Fig. 3e,f, together with maps of the densities of the four major contributing insect species (Fig. 3a–d). These values illustrate clearly the influence of *C. fumiferana* on axis 1 and of *G. hercyniae* and *P. alaskensis* on axis 2. Overall, the values of factor 1 (Fig. 3e) showed a decreasing trend from south to north, corresponding to increasing populations of *C. fumiferana*. In contrast, values of factor 2 increased from the south-east to the north-west, corresponding to decreasing densities of *G. hercyniae* and *P. alaskensis* (Fig. 3f).

A principal components analysis was also carried out on the data from the Forest Inventory and Analysis (Table 2). The two first principal components explained 20.1% of the tree species variability (11.2% for factor 1, 8.9% for factor 2), while the first five components addressed 40.0% of the variation in data. The first two principal components clearly separated the variables, as shown in Fig. 4. Factor 1 was highly correlated negatively with northern hardwoods or beech–birch–maple types (*Fagus grandifolia*, *Acer saccharum*, *Acer pennsylvanicum*, *Betula alleghaniensis*) (Eyre, 1980), while factor 2 was highly correlated negatively with *Quercus rubra* and *Pinus strobus*, two species belonging to the eastern white pine forest type. Species of the northern spruce–fir forest type (*Picea* spp., *Abies balsamea*, *Thuja occidentalis*, *Larix laricina*) were correlated positively with both factors 1 and 2. The remaining species were largely uncorrelated with factor 1 but correlated negatively with factor 2, and belonged to other hardwood forest types, including mixed northern hardwoods or the aspen–birch group (Eyre, 1980).

The values of the principal component analysis for the 3001 sampling locations and the percentage basal area of the four tree species that had the greatest influence on the principal components (*Fagus grandifolia*, *Pinus strobus*, *Abies balsamea*, *Picea rubens*) are mapped in Fig. 5. Axis 1 exhibited a trend of increasing values from north to south while axis 2 showed the opposite trend.

Measurement of spatial dependence

The spatial structure of the principal components is illustrated in Fig. 6. The four graphs show the variogram values, standardised by the sample variance, for the first two principal components of the insect and forest inventories.

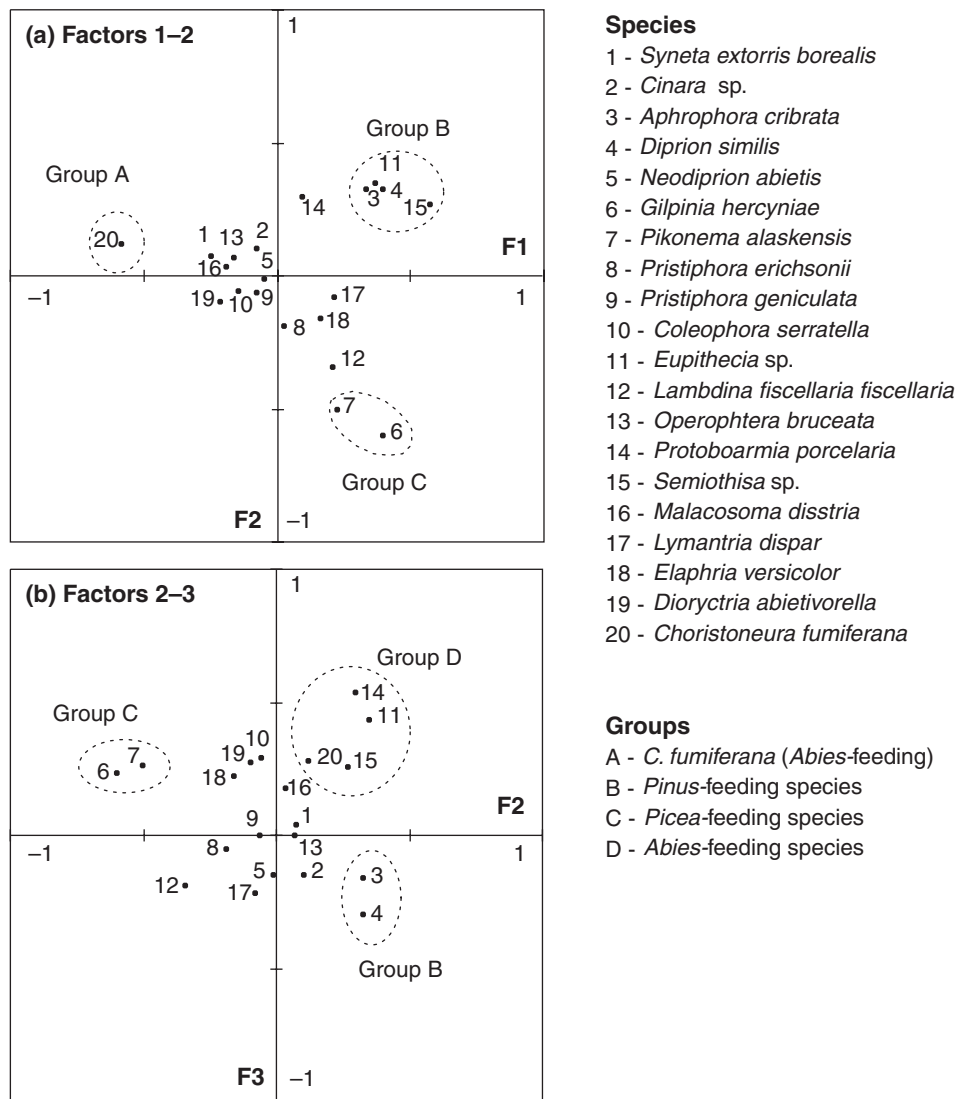


Fig. 2. Projection of the herbivore species on the plane defined by the first three factors of the principal components analysis: (a) corresponds to the projection of the first two factors, (b) shows factors 2 and 3. The first principal component singles out one species, *Choristoneura fumiferana*. The second and third principal components group species according to their known host associations. Group A corresponds to *C. fumiferana*, group B to mostly *Pinus*-feeding species, group C to *Picea*-feeding species, and group D to mostly *Abies*-feeding species.

The spatial dependence of factors 1 and 2 of the herbivore data are described in Fig. 6a,b. For the first axis (Fig. 6a), the variogram reflects the presence of a spatial structure at lag distances less than 20 km and of non-stationarity caused by a north-south linear trend over 60 km. The main contributor to the trend reflected in axis 1 was *C. fumiferana*, the spruce budworm being most abundant in the north of Maine but rare in the south (Fig. 3). The spatial structure at short distances could be due to the spatial pattern of *Semiothisa* sp., which was distributed throughout Maine, but with an aggregative pattern over small distances (Fig. 3c). Factor 2 (Fig. 6b) is characterised by low variogram values at short lags, reflecting a well-defined spatial structure up to distances of ≈ 35 km. This is probably the result of the contribution of

G. hercyniae and *P. alaskensis* to the second principal component (see Fig. 3). Both species were distributed mostly in the central part of southern Maine, with an increasingly scattered presence to the north.

Variograms generated from the forest inventory principal components analysis results are presented in Fig. 6c,d. They indicate the presence of spatial dependence up to distances of 50 km for factor 1 and a strong linear trend for factor 2. The spatial structure of both axes can be explained by the spatial distribution of their major contributing tree species (see Fig. 5). *Fagus grandifolia* and *Abies balsamea* were negatively and positively correlated respectively to factor 1, and both exhibited some degree of spatial correlation. *Pinus strobus* and *Picea rubens* were correlated with factor 2, and

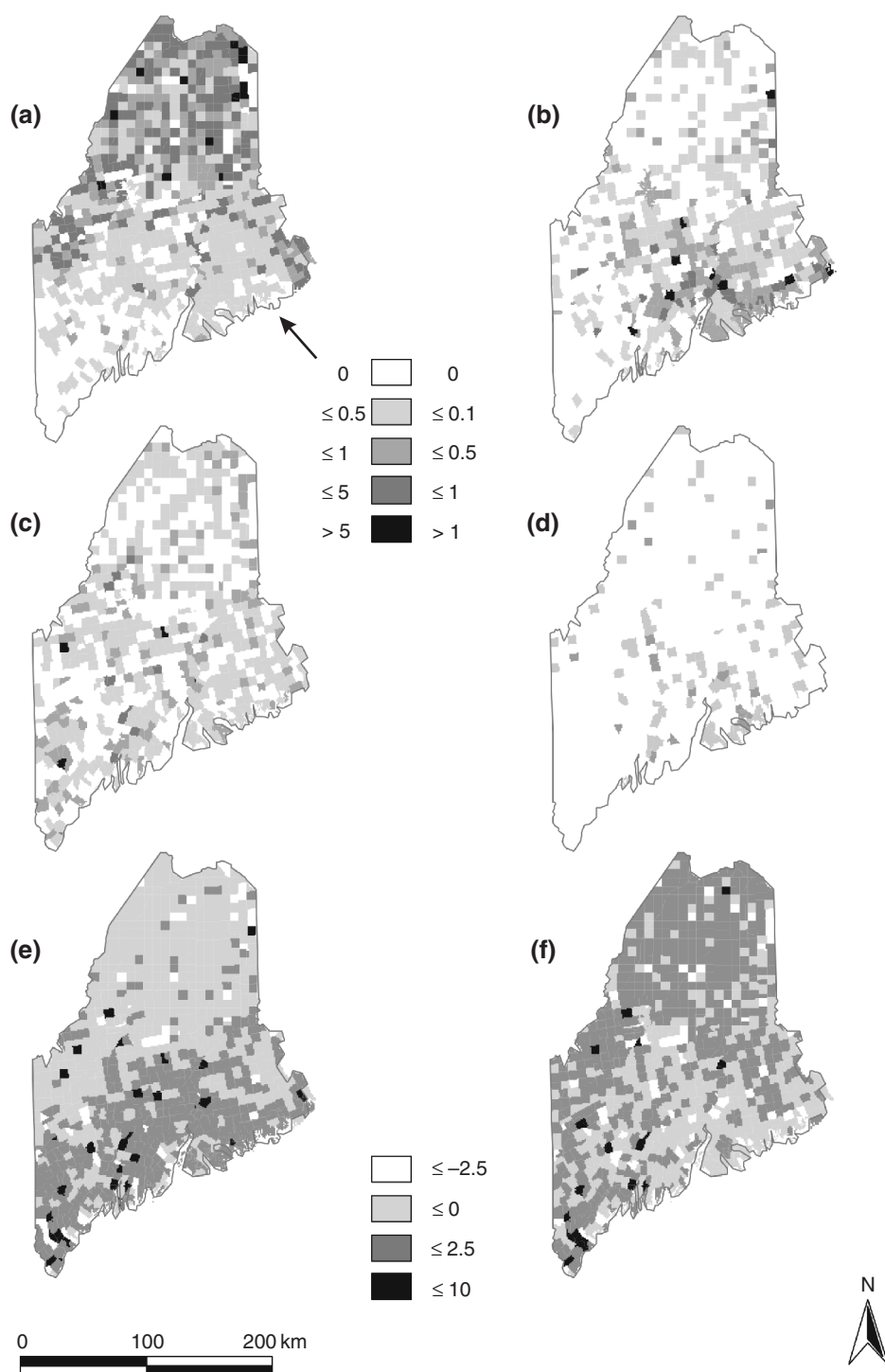


Fig. 3. The four top maps show the densities (number per tree) for the insect species contributing most to factors 1 and 2 in the principal components analysis of the insect data: (a) *Choristoneura fumiferana*, (b) *Gilpinia hercyniae*, (c) *Semiothisa* sp., (d) *Pikonema alaskensis*. The bottom maps show the values of the first two principal components for Maine's townships: (e) F1, (f) F2. The arrow links the left-hand numbers of the top scale to map a. The right-hand numbers of the scale apply to maps b, c, and d. The bottom scale applies to maps e and f.

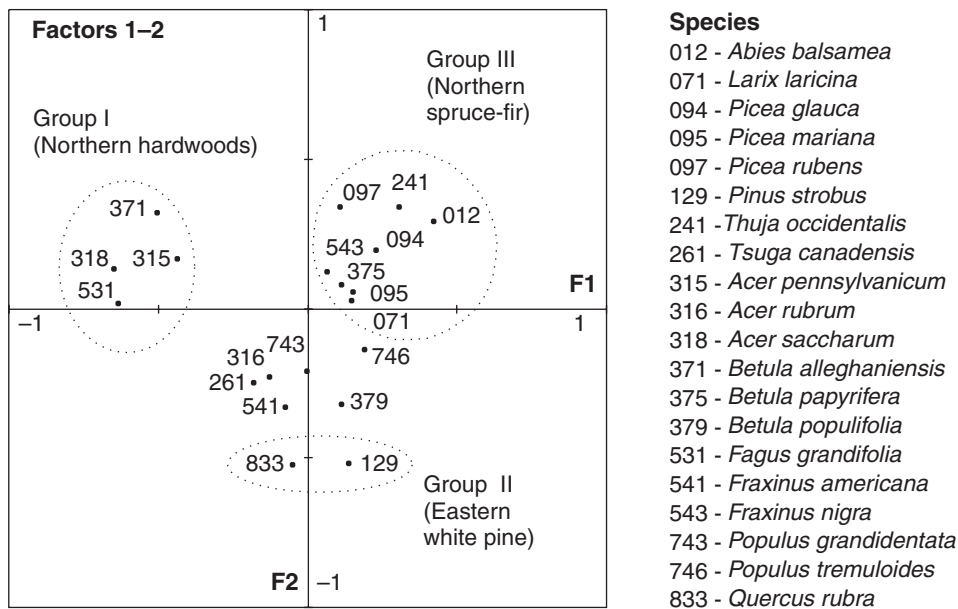


Fig. 4. Projection of the tree species from the Forest Inventory and Analysis on the plane defined by the first two main factors of the principal components analysis. Group I, composed of species in the northern hardwoods and beech–birch–maple forest types (Eyre, 1980), was highly negatively correlated with the first principal component. Group II consisted of two species components of the eastern white pine forest type and was the main contributor to the second principal component. Group III was composed of northern spruce–fir forest type species and was correlated positively with both components. Other species, mostly hardwood species, are representative of the mixed northern hardwoods and aspen–birch forest types.

showed complementary distributions and a strong north–south trend: pines were abundant in the south and absent in the north, while spruces were distributed mostly in the north.

The relationship between insect occurrence and forest type proximity is described by the cross-correlograms in Fig. 7. The best defined spatial structure is observed in the cross-correlations between factor 1 of the insect data and factor 2 of the forest data (Fig. 7b): a negative correlation can be observed between the two factors up to distances of 120 km. The plots of Figs 3e and 5f reveal the reason for this tendency; the insect factor 1 values showed a decreasing south–north trend, while the forest factor 2 values showed the opposite trend. Other cross-correlations were less strong. The insect factor 1 was only weakly positively correlated with the forest factor 1 (Fig. 7a); the insect factor 2 was slightly negatively correlated with the forest factor 1 (Fig. 7c) and correlated positively with forest factor 2 (Fig. 7d).

Discussion

The Maine insect survey data analysed here were not taken in an entirely random fashion and it is conceivable that observers introduced some systematic bias in the selection of sampling locations. Different herbivore species also vary in their tendency to be sampled by the branch beating method (Lowman & Wittman, 1996). Not all townships

were sampled each year, which caused gaps in the data. In order to address this problem, all samples from a single township were averaged over the entire 1971–1996 study period, however this prevented any fine-grained spatial characterisation or any type of analysis of spatial dynamics.

Despite the limitations of the sample data, they appear to have been adequate for the purposes of quantifying the large-scale geographical distribution of herbivore communities. For example, Fig. 1 shows that the spruce budworm *C. fumiferana* was the most abundant herbivore species and that abundance peaked in 1979. This corresponds with historical records of defoliation, which indicate that this species caused the most extensive defoliation during the period and that 1979 was also the year of maximum defoliation (Blais, 1983; Williams & Liebhold, 2000). The data are also consistent with studies showing that forest canopies tend to be dominated by one or two species of herbivore (Hunter, 1992; Barbosa *et al.*, 2000). The vast majority of insect species sampled in the Maine insect survey existed at low densities. A few species were more abundant, *C. fumiferana* being the most dominant numerically, with a massive 67% of all specimens collected.

Herbivore community structure

Principal components analysis was used to identify associations among insect species (Fig. 2). Despite the relatively small proportion of total variation explained by factors

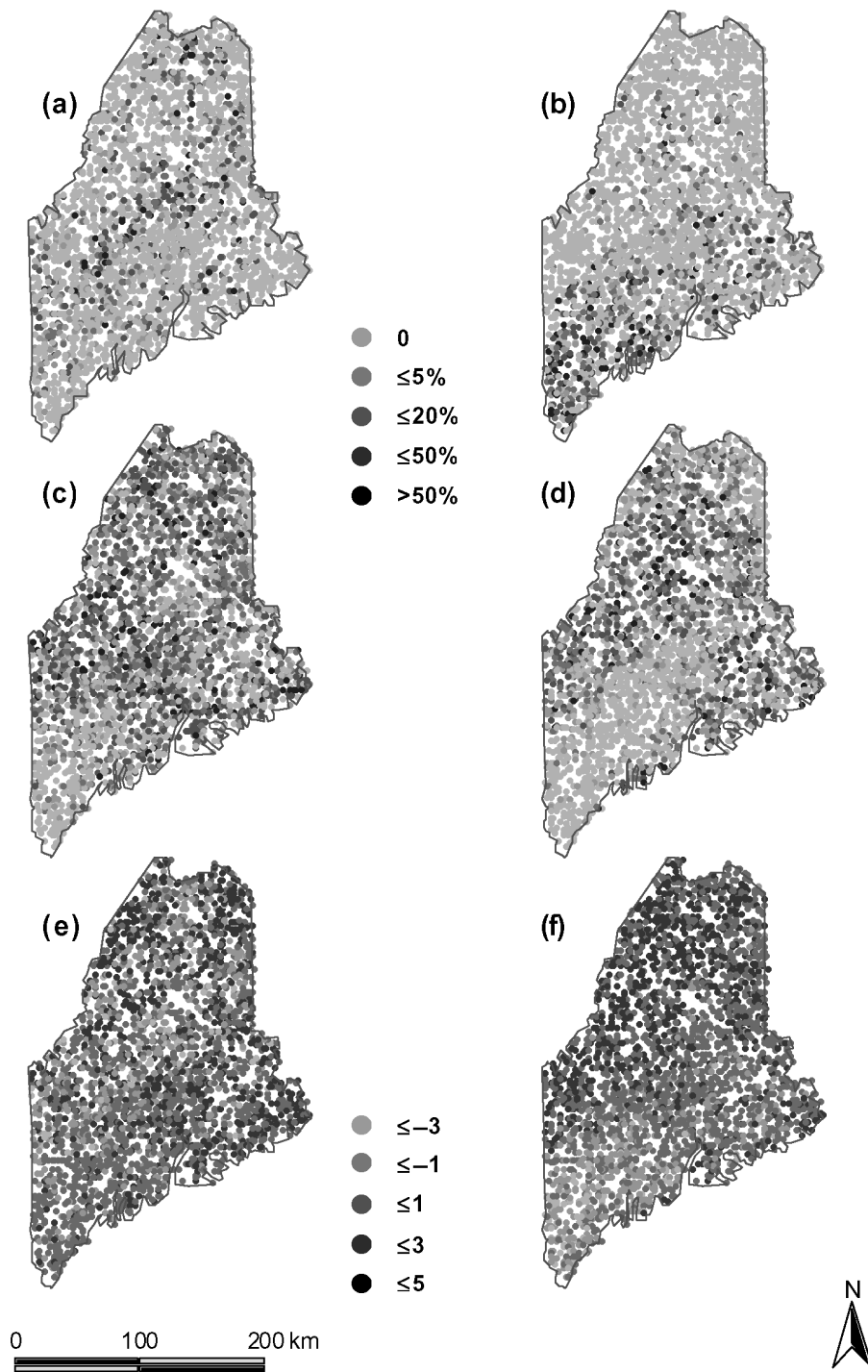


Fig. 5. The four top maps show the percentage basal area for the tree species contributing most to factors 1 and 2 in the principal components analysis of the forest inventory data: (a) *Fagus grandifolia*, (b) *Pinus strobus*, (c) *Abies balsamea*, (d) *Picea rubens*. The bottom maps show the values of the first two principal components for the 3001 sampling locations: (e) F1, (f) F2. The top scale applies to maps a, b, c, and d; the bottom scale applies to maps e and f.

1–3 (20.9%), the analysis highlighted major characteristics in the structure of the herbivore community. The first principal component underlined the influence of *C. fumiferana* on the analysis, reflecting its importance in herbivore commu-

nities. The second and third principal components illustrated common host associations among conifer-feeding species. Species associated with hardwoods were not correlated strongly with either axis and were mixed in the

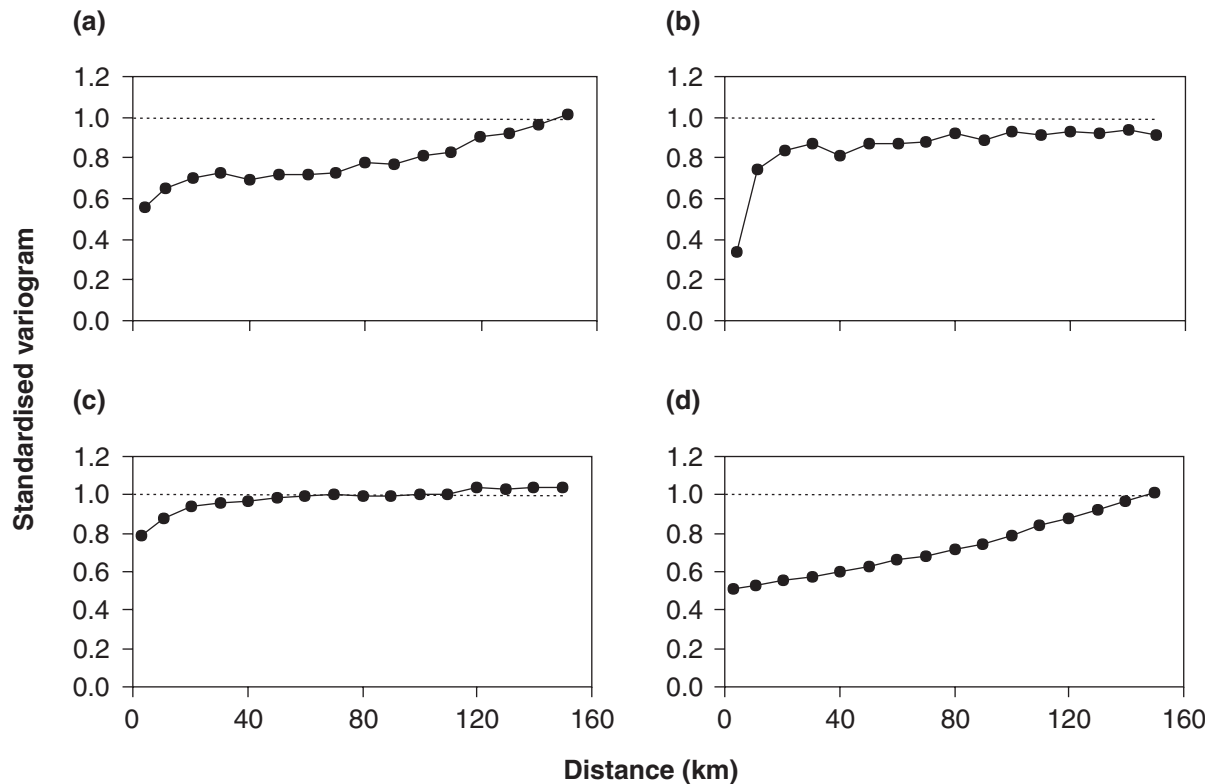


Fig. 6. Omni-directional semi-variograms, standardised by the sample variance, for principal components analysis values at sampling locations: (a) F1 of insect survey, (b) F2 of insect survey, (c) F1 of forest inventory, (d) F2 of forest inventory.

centre of the multivariate space along with other conifer feeders (Fig. 2).

Geostatistical analyses quantified the spatial structure of caterpillar assemblages (Fig. 6). The variogram for axis 1 reflects a clear north to south spatial trend across the sampling domain indicative of the dominance of *C. fumiferana* in the north (Fig. 3). The spatial distribution of values for axis 2 also appears to have a slight trend, though there was more localised spatial structure (indicated by low variogram values at short distances). The strongly negative values in the south-central portion of the state represent a higher abundance of group C insects, *G. hercyniae* and *P. alaskensis*, which are associated with *Picea* (Fig. 3).

Forest community structure

Application of principal components analysis to the forest inventory data also indicated associations among over-storey tree species (Fig. 4). This analysis suggested the existence of three groups of associated species: group I consisted of representatives of the northern hardwoods forest type, group II of the eastern white pine forest type, and group III of the northern spruce-fir type (Eyre, 1980).

Areas with northern hardwoods appeared to be dispersed widely throughout the region though they were slightly more numerous in central and northern areas (Fig. 5e).

The variogram for axis 1 (Fig. 6c) had a large nugget effect and short spatial range. This variogram indicates that there was relatively little spatial correlation and there was no evidence of a long-distance trend (Liebhold *et al.*, 1993). In contrast, the spatial distribution of axis 2 indicated a strong north-south trend. Strongly negative values should be associated with the white pine forest type (Fig. 4) and these occurred mostly in the southern portion of the region (Fig. 5f).

Relationship between herbivore community structure and forest composition

The cross-correlograms of Fig. 7 showed some variation in the extent to which insect assemblages were correlated spatially with forest community structure. By far the strongest cross-correlations were the inverse spatial correlation between factor 1 of the insect data and factor 2 of the forest data (Fig. 7b) that occurred for distances up to 120 km. This relationship is probably the result of the association of *C. fumiferana* with the northern spruce-fir forest type, and may also be due in part to associations of pine-feeding insects such as *Semiothisa* with the eastern white pine forest type. The negative spatial cross-correlation between these two factors thus reflects the spatial correspondence between the gradual north-south transition in abundance of spruce-

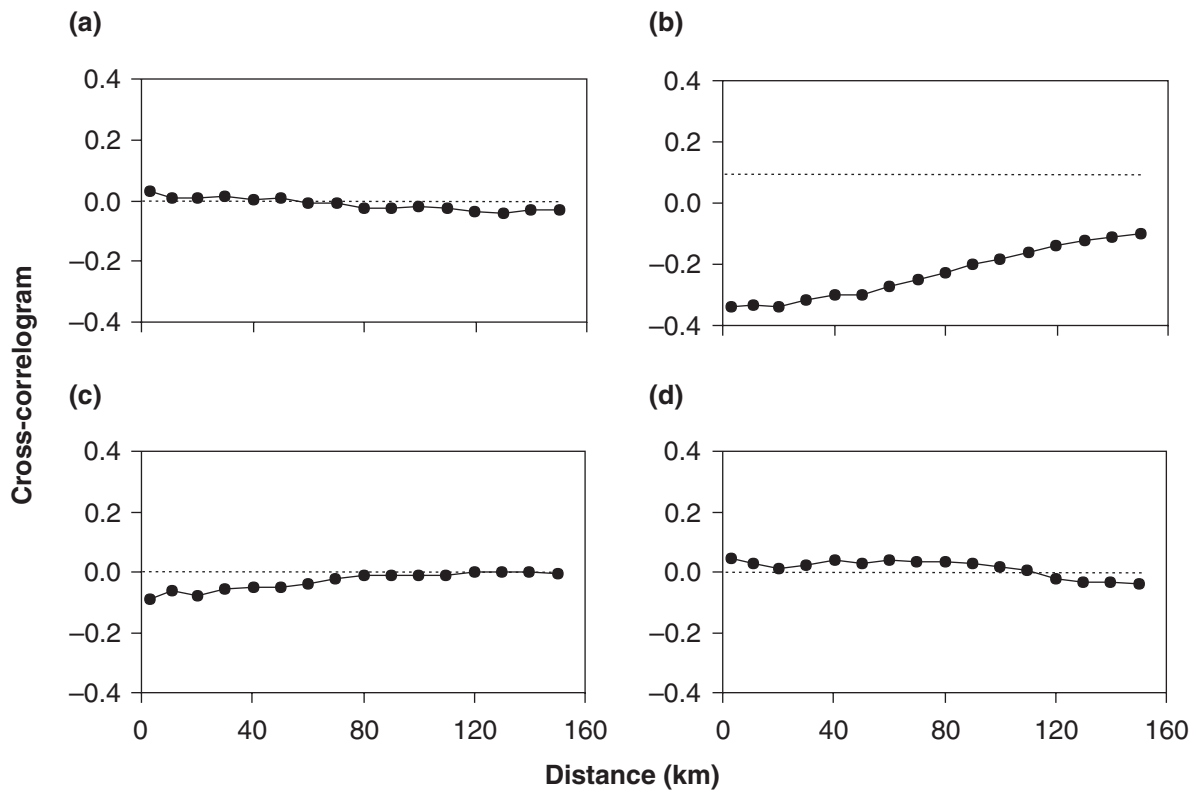


Fig. 7. Omni-directional pseudo-cross-correlograms computed between the values of the principal components analyses of the insect survey and of the Forest Inventory and Analysis: (a) F1 insect–F1 forest, (b) F1 insect–F2 forest, (c) F2 insect–F1 forest, (d) F2 insect–F2 forest.

fir feeders to pine feeders with the north–south transition in dominance by the northern spruce–fir type to dominance by the eastern white pine type.

The other cross-correlograms were less conclusive. There was little spatial correlation between known host associations; insect factor 2 was not associated statistically with the gradient from pine to spruce–fir as reflected by forest factor 2 (Fig. 7d). Forest factor 1 corresponded clearly to the continuum of hardwood to conifer forest types (Fig. 4) and it would be expected that there might be a corresponding continuum in insect communities associated with hardwoods and conifers. When insect principal components were plotted (Fig. 2), however, hardwood-feeding insects always fell in the middle of the graphs, indicating that their abundance did not explain much of the overall variation among samples. This probably resulted from hardwood-feeding insects being present in all or most samples (townships). One interpretation could be that the spatial association between hardwood-feeding insects and their host forest types may have occurred at a scale smaller than the sample size used in this study (township). This resulted in a failure of the principal components analysis to recognise the hardwood-feeding insects as a unique guild and is also a probable reason why the gradient from hardwood to conifer types observed in forest factor 1 was not correlated spatially with either of the insect factors (Fig. 7a,c).

In conclusion, the results indicate that the large-scale herbivore community structure was most distinct for conifer-associated species. The most abundant caterpillar, *C. fumiferana*, was also the most influential insect in the quantification of spatial patterns. Hardwood-feeding caterpillars did not form well-defined groups and showed varying geographical distributions that were not dependent on the distribution of hardwood forest communities, but this probably resulted from the relatively large spatial size of the sample unit (Maine townships vary in size but typically cover an area of 100 km²). If more survey data were collected using a more precise spatial reference system, it would be expected that hardwood-feeding insects would be identified in a principal components analysis as a distinct guild and that guild would be correlated geographically with the distribution of hardwood forest types.

Concern over the accelerating loss of biodiversity has stimulated renewed interest in relationships among species richness, species composition, and the functional properties of ecosystems. While the study illustrates clearly the limitations of the use of large-scale survey data for characterising forest insect communities, this type of analysis provides useful information on forest biodiversity. Geographical variation in community structure has important implications for the dynamics of species composition and abundance in both space and time (Brown *et al.*, 1995). Thus, long-term

management of biodiversity should concentrate on more than just numbers of species, focusing also on functional species guilds (Ehrlich, 1996; Knight, 1998). Knowledge of patterns and scale of spatial and temporal variation should be considered increasingly for conservation planning, particularly as habitats become highly fragmented.

The analysis presented here provides a limited characterisation of forest insect communities and their geographical association with habitat characteristics, but it illustrates how existing survey data can be used to identify the most important relationships. Future surveys can be improved by using global positioning systems for geo-referencing. Given more precise spatial locations of samples, associations between insect and forest communities could be characterised more extensively. As most canopy herbivores are neither economically important nor abundant (i.e. outbreak species), future studies could also focus on these low density species, yielding a better understanding of the ecology of herbivore communities in forest canopies.

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