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Spatial abundance structures in an assemblage of gall-forming sawflies

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Summary

1. Examination of the fine-scale internal structure of species geographical ranges, and interspecific variation therein across landscapes, contributes to a more comprehensive understanding of the structure of geographical ranges. Two components of this internal structure that require further examination are the occurrence, extent and position of spatial autocorrelation, and relationships between the spatial abundance structures of closely related, ecologically similar species.

2. Here we compare the abundance structures of an assemblage of gall-forming sawflies (Tenthredinidae) across a landscape. We identify the relative roles of spatial and non-spatial factors in explaining their abundance structures and test the hypothesis that sawfly density is explained by host plant quality, as has been demonstrated repeatedly at finer scales. We use these results to distinguish between alternative sets of mechanisms that may be operating at the landscape scale.

3. Species densities were mainly multimodal across the landscape and significantly spatially structured, with patch, periodic and trend components. The abundance structures thus mimic those found generally for species across the full extent of their geographical ranges.

4. Many abundance structure characteristics were unique to species, with differences in their correlogram profiles, distances over which densities were positively autocorrelated, and the absence of significant spatial structure in one species.

5. In contrast to previous, fine-scale studies, host plant quality explained little of the variation in sawfly gall density across the landscape, whereas unexplained spatial structure contributed between 30% and 50%. Based on knowledge of the biology of these species and the absence of competitive interactions, species dispersal characteristics and the Moran effect are suggested as probable alternative hypotheses at this scale.

6. Therefore, a spatial approach has identified the hierarchical nature of mechanisms underlying the population dynamics of this sawfly assemblage for the first time. Furthermore, it has highlighted the importance of spatial processes in explaining the densities of species at the landscape scale, as well as the individualistic nature of their abundance structures.

Key-words: Moran effect, population dynamics, SADIE, *Salix lasiolepis*, spatial autocorrelation.

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Introduction

Species tend not to be distributed randomly or evenly across their ranges, either at local or regional scales. They are absent from some sites, common or aggregated at others, and may vary in abundance along environmental gradients (Brown 1984; Hengeveld 1990; Gaston 2003). Knowledge of this component, fine-scale structure of species distributions, i.e. the pattern and extent of spatial variation in the population abundance of species, or 'abundance structure' (Gaston 2003), is an important step towards a more comprehensive understanding of the structure of geographical ranges.

One apparently robust pattern in the abundance structures of species is positive spatial autocorrelation

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(Legendre & Legendre 1998). This pattern has been documented for a wide range of taxa over distances of centimetres to hundreds of kilometres (Kendall *et al.* 2000; Brewer & Gaston 2002). Although spatial autocorrelation is now generally considered a null expectation (Bell 2001), its occurrence, extent and position within geographical ranges is variable (Brown, Stevens & Kaufman 1996; Brewer & Gaston 2002). Evidence also suggests that species have unique abundance structures (Brown *et al.* 1996). However, few comparisons of the abundance structures of assemblages of co-occurring, ecologically similar species across landscapes have been made (Roslin & Koivunen 2001; Winder *et al.* 2001; Sagarin & Gaines 2002), and understanding of the relative roles of spatial factors and the mechanisms by which the spatial environment affects population and community dynamics is generally poor (Koenig 2002; Legendre *et al.* 2002; Plotkin, Chave & Ashton 2002). Therefore, although positive autocorrelation of abundances is prevalent, less information is available on the spatial extents and positions at which it occurs, and on how such patterns compare between ecologically similar, co-occurring (particularly animal) species (Austin *et al.* 1985; Plotkin *et al.* 2002; Gaston 2003). Such comparisons may identify potential mechanistic explanations for the variability found within and between species' distributions (Liebhold & Gurevitch 2002), which has potential value to both pest management and conservation (Hengeveld 1990).

The abundance structure of a species is clearly the composite outcome of the interaction of several processes, including the effects of climate, weather, history, resource quality, interspecific interactions and stochastic temporal variation on species population parameters and, ultimately, on their abundances (Hengeveld 1990; Ives & Klopfer 1997; Gaston 2003). The abundance structure of a species at the landscape scale (defined here as the scale across which individuals are potentially able to move freely between areas of suitable habitat) is thus likely to be determined at least partly by the species-specific, key population dynamics factors across the landscape (Brewer & Gaston 2003). When dispersal of individuals across a heterogeneous landscape is not limited by physical barriers or poor dispersal abilities, then the abundance structure may reflect the relative quality of habitat at different points on the landscape (Tregenza 1995; Logerwell, Hewitt & Denmer 1998; although see Ives & Klopfer 1997). For example, in species that have population dynamics driven strongly by resource factors, abundance structures are likely to be determined by the distribution and quality of resources across the landscape (Roininen, Price & Tahvanainen 1996; Bevers & Flather 1999; Williams, Jones & Hartley 2001).

A model system for contrasting species abundance structures, and examining the relative importance of mechanisms underlying them, is the assemblage of gall-forming sawflies (Hymenoptera: Tenthredinidae) associated with *Salix lasiolepis* Bentham (Salicaceae) (Arroyo willow) (Price 2003). These species are closely related taxonomically, their biologies well understood, and in northern Arizona they are monophagous on Arroyo willow (Nyman, Widmer & Roininen 2000; Price 2003). The four species in the assemblage include *Euura lasiolepis* Smith (a stem galler), *Euura* sp. (petiole galler), *Pontania* sp. nr. *pacifica* (see Clancy, Price & Craig (1986) (leaf galler) and *Phyllocolpa* sp. (leaf folder) (Price 2003). The fine-scale population dynamics of these species is in most instances determined predominantly by host plant quality (Price 2003). The adults of all four species oviposit preferentially on long willow shoots, or on the leaves of long shoots (Craig, Itami & Price 1989; Stein & Price 1995). Shoot length is related closely to the age of the clone, water availability and the disturbance of ramets (which promote shoot growth; Preszler & Price 1988), and is thus indicative of host plant quality (Price 2003). It may thus be expected that the abundance structures of these species would be similar and related closely to that of their host at the landscape level. However, this prediction has not been tested, and indeed the strong relationship between host quality and sawfly abundance have generally been documented at fine scales of few individual willow clones (Price 2003).

Here we compare the abundance structures of this assemblage of galling sawflies across a landscape (where all species are exposed to the same resource pool distributed along the system of drainages in Flagstaff, Arizona) to identify the relative roles of spatial and nonspatial factors in explaining their abundance structures. We use this approach to distinguish between alternative sets of mechanisms that may be operating at this scale (Legendre & Fortin 1989; Hengeveld 1990). First, we predicted that the abundance structures of the four species are spatially structured (e.g. autocorrelated) across the landscape. We then tested the hypothesis that variability in gall density (both spatially structured and not) is explained significantly by host plant quality. If resource quality (represented by the growth vigour of willow clones) is the primary determinant of gall abundance at the landscape level, as it is within patches, then the density peaks of the four species should be spatially concordant and explained by measures of resource quality. Finally, we tested the idea that interspecific competition has a minimal effect on abundances at this scale, in accordance with previous, within-patch findings.

Methods

DATA COLLECTION

Salix lasiolepis clones were sampled along the ephemeral Schultz Creek and Rio de Flag streams in Flagstaff, Arizona, the first of which flows into the second. Willows were sampled along an extent of approximately 10·5 km spanning an altitudinal range of 421 m (Fig. 1). Sampling was conducted between June and July 2000, and coincided with the end of the summer gall development season for the four sawfly species. Seventy-three galled

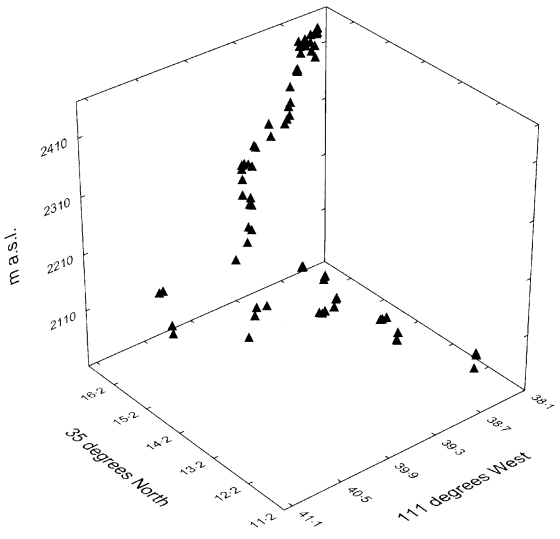

Fig. 1. The position and altitude of *Salix lasiolepis* clones sampled along Schultz Creek and the Rio de Flag, Flagstaff, Arizona.

willow clones were selected along the gradient starting from the highest clone on Schultz Creek (2449 m a.s.l.). This clone is the upper elevational limit of *S. lasiolepis* in the area, and thus represented a local distributional edge for the four species. The lowest clone in the Rio de Flag drainage, at 2028 m a.s.l., was also included. Furthermore, *S. lasiolepis* is close to the southern edge of its geographical range in Arizona and its distribution is strongly limited by water availability (Price, Craig & Roininen 1995). The distribution of *S. lasiolepis* follows closely the distribution of major drainages in the study area, and is limited largely to a narrow band along these temporary streams. The sampling design employed thus provided representative coverage of populations of *S. lasiolepis* and the four sawfly species in the Flagstaff vicinity. Clones were chosen randomly, approximately one every 55 m change in altitude, while walking the extent of the gradient. The selected clone was examined for galls. If it did not have any galls on it, the clone adjacent to that was examined until a clone with at least one gall (of any species) on it was encountered. Only clones with galls were considered because it is not possible from observation only to distinguish between clones that are unoccupied by chance vs. those that are unoccupied because they are not suitable (see also Price *et al.* 1995). This approach minimized the chance of a type I error (based on the null hypothesis that host plant quality is significant and equally important to explaining gall abundance across spatial scales).

The locality (using a Garmin 12MAP GPS) and altitude of each clone was measured. Direct and indirect host plant quality measures were taken, i.e. total number of ramets on the clone, mean ramet age (10 randomly selected ramets), the number of new (1 year old) ramets, new shoot density (mean number of new shoots from five randomly chosen ramets) and mean shoot length (n = 50 randomly chosen shoots). These variables have been shown to be good measures of host quality for these sawflies (Price *et al.* 1995). Clone height (m) and the mean distance of the five nearest neighbouring clones were also measured. The number of individuals of each sawfly species was estimated by counting the number of galls of each species on the same 200 randomly selected shoots from each clone.

DATA ANALYSIS

Measures of aggregation and association

Spatially, as well as non-spatially, explicit indices of intra- and interspecific aggregation were calculated to identify the relative independence of sawfly distributions, possible competitive interactions between individuals and species and spatial concordance in densities (see Perry 1995). Schluter's (1984) variance-ratio tests were used to examine spatially non-explicit species association (at two levels, across clones and across shoots on each clone) and abundance covariation (between clones only). Here, observed variance in the number of species (or individuals) on clones (or shoots) was compared with the variance expected under the null hypothesis of the occurrence and density of species being independent of each other (Schluter 1984). The variance ratio (VR) is multiplied by the sample size to obtain the test statistic (W) with a χ^2 distribution (VR significantly > or < 1 = positive or negative association or abundance covariation of species, respectively) (Schluter 1984). Shoot-level species association was calculated for all species and each species pair.

Intraspecific aggregation patterns were examined with spatially explicit aggregation indices using spatial analysis by distance indices (SADIE) (Perry 1995). This method, developed specifically for the spatial analysis of biological count data, compares the spatial arrangement of the observed distance to regularity (the total number of moves which individuals in each sample must make so that all sample units have the same number of individuals) with the permuted distances to regularity derived from a randomization procedure (Perry 1995). The index of aggregation (I_a) and associated randomization test is calculated with $I_a = 1$, indicating a random distribution, and $I_a > 1$ an aggregated distribution of individuals across sample units (clones) (Perry *et al.* 1999). An additional index, v, provides a measure of clustering for each sample unit (clone), with subscript i for patches and j for gaps (see Perry *et al.* 1999). Significant positive mean v_i values for a species indicate spatial clustering of gall density into patches, whereas significant negative mean v_j values indicate the presence of gaps in the spatial distribution of the species. These indices are tested under the null hypothesis of random arrangement of observed densities using formal randomization tests (Perry *et al.* 1999). Interspecific spatial associations of density counts were then calculated by correlating the cluster indices (v_i) for each pair of species and again assessing the significance thereof using a randomization test (Perry & Dixon 2002).

Spatial pattern analysis and explanatory models

To estimate patch size for the four species, spatial autocorrelation analysis was conducted using SAAP (version 4·3). Moran's *I* and all-directional correlograms were used to quantify the spatial structure and to identify scales of variation in the density ($\log_{10}$ x) of the four species (Legendre & Legendre 1998) (directional correlograms were not used as they demand very large data sets; Dungan *et al.* 2002). Patch size is defined here as the midpoint distance between the last significantly positive and first non-significant or negative *I*-value in the correlogram (Legendre & Fortin 1989). Twelve distance classes (880 m each) were used following Sturge's rule (Legendre & Legendre 1998). The numbers of point pairs were high and relatively similar in the first eight distance classes (that is up to a distance of 7·04 km) for each species, and autocorrelation values were thus interpreted for these classes (Legendre & Legendre 1998). Cross-correlation was used to compare significant correlograms (Legendre & Legendre 1998).

To identify the proportion of variability in gall density explained by spatial and non-spatial environmental factors, trend surface analysis and partial regression approaches were used (methods outlined by Legendre & Legendre 1998). The only modification to the method was the use of generalized linear rather than ordinary least-square models because gall data were in the form of counts of number of galls per shoot. A Poisson error distribution for number of galls was assumed and this was linked to the predictor variables with a logarithmic link function (McCullagh & Nelder 1989). The goodness of fit was measured using the deviance statistic, the proportion of explained deviance calculated for each model, and the change in deviance tested with *F*-ratios (McCullagh & Nelder 1989).

Therefore, following Legendre & Legendre (1998), trend surface analysis was first applied to determine the best fit combination of spatial variables that contributed significantly to explaining the variability in the gall density ($\log_{10}$) of each species (significant terms from the third-order polynomial of longitude and latitude records for each clone). Thereafter, partial linear regression analyses were conducted in which independent variables included were the best fit trend surface model variables (spatial component), as well as altitude, clone height, clone distance to stream, total number of ramets, ratio of old to new ramets, clone density, ramet age and number of shoots per ramet (environmental component which, except altitude, are all clone characteristics). Only the significant environmental variables were included in the final model. Parameter significance was corrected for overdispersion in the residual deviance (Dobson 2002). The presence of each species, excluding zero counts, was used in the above models, i.e. only clones with galls of the species in question were included (as $\log_{10}$ gall density) in the autocorrelation, trend surface and partial regression analyses.

Variation in gall density was then partitioned into fractions representing the proportion of variation explained by spatial structure common to both gall density and the environmental variables, i.e. the proportion explained by host plant variables (not spatially structured) on their own (A), the spatially structured host plant effect (i.e. spatial structure shared by the host plant variables and gall density) (B), spatial structure in gall density not explained by the measured environmental variables (C) and remaining unexplained variation (D) (Legendre & Legendre 1998). Components A and B were used to test the hypothesis that host plant quality is responsible for explaining the variability and spatial structure in gall density. Component C was used to identify the relative importance of spatial mechanisms (such as dispersal and fine-scale climatic factors) in the distribution of sawfly abundance across the landscape (see rationale by Legendre & Legendre 1998). The explanatory power of the host plant (environmental) variables was calculated using the change in deviance resulting from exclusion of the host plant variables (A) from the generalized linear model (McCullagh & Nelder 1989). This was tested using an *F*-ratio test (Dobson 2002). The explanatory power of components B and C (above) were calculated in the same way.

Results

Willows with galls were found across the full extent of the sampled gradient (Fig. 1). Of the 73 sampled clones, 66 lay within 5 m of the Schultz Creek and Rio de Flag streams (the remaining seven clones grew between 10 m to 153 m from the drainage). The stem galler was three to seven times more abundant than the other species, followed by the leaf folder, leaf galler and petiole galler (Table 1).

Table 1. Density and distribution of the four sawfly species sampled. Values calculated only from clones on which the gall species was present

Gall former	Stem	Petiole	Leaf	Folder
No. galls/200 shoots (mean ± SE)	51·25 ± 6·89	7·45 ± 1·26	10·44 ± 2·30	19·17 ± 2·27
No. (%) clones galled (n = 73)	71 (97·26)	55 (75·34)	43 (58·90)	59 (80·82)
Total no. galls	3639	410	449	1131
Max. no. galls/clone	341	39	81	83
Altitudinal range (m)	421	416	356	421
Altitudinal max. (m a.s.l.)	2449	2444	2440	2449
Altitudinal min. (m a.s.l.)	2028	2028	2084	2028

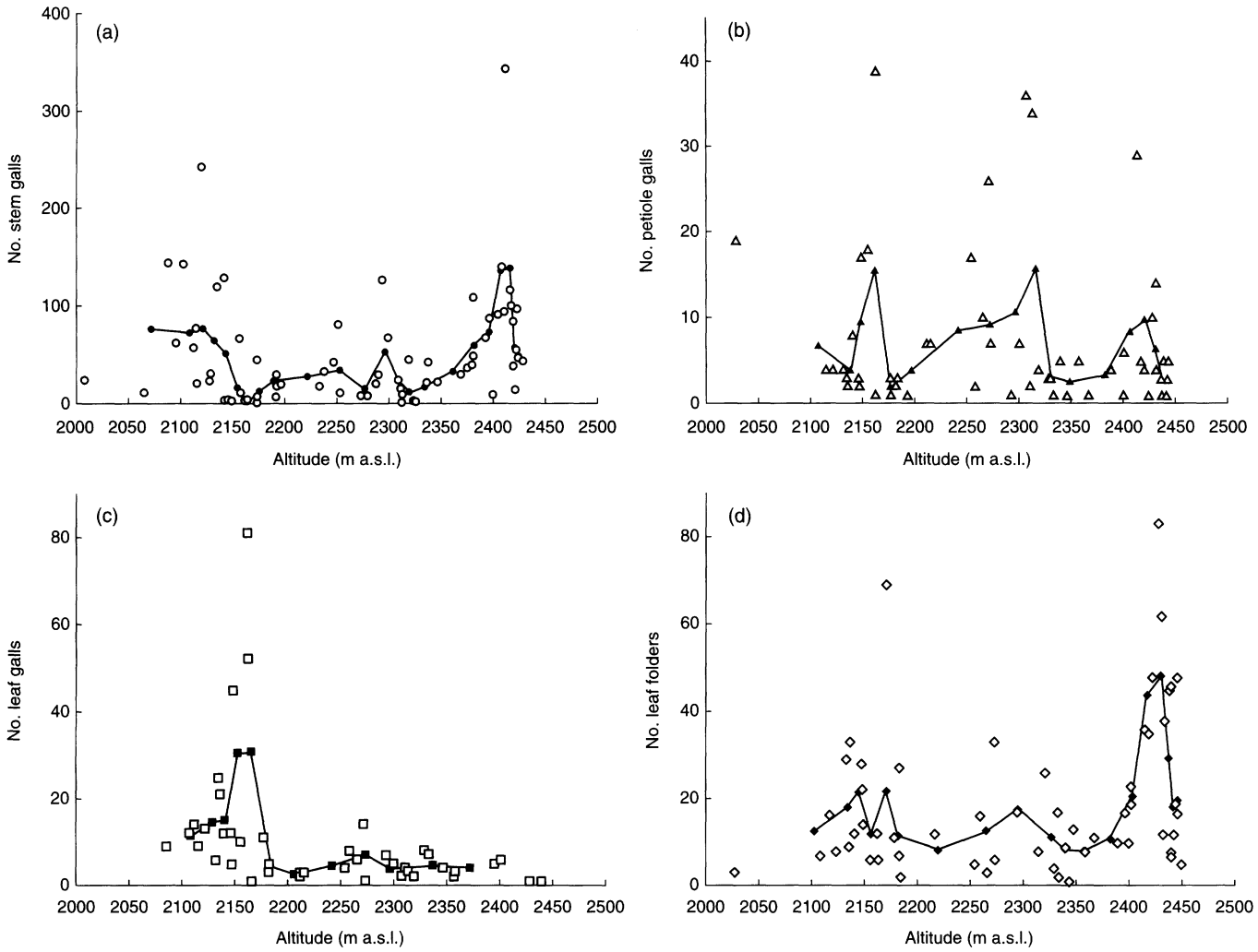

Fig. 2. Densities of stem galls, petiole galls, leaf galls and leaf folds on *Salix lasiolepis* clones across the altitudinal gradient. Filled symbols and line represent running mean totals (n = 5, window = 3) of altitude, and gall or folder density. Open symbols are raw data.

All four species occurred across the extent of the gradient, although the leaf galler was not found on the single lowest clone at 2028 m a.s.l. (Table 1, Fig. 2). No monotonic change in gall density across the altitudinal gradient was apparent for any of the species, although leaf gall density was consistently low at higher altitudes (Fig. 2). Stem gall and leaf folder density by contrast were highest above 2400 m a.s.l., and petiole gall density was most variable across the gradient (Fig. 2).

AGGREGATION AND ASSOCIATION

Only the leaf galler and leaf folder were significantly intraspecifically aggregated on clones (significant I_a indices, Table 2). However, these two species and the stem galler were significantly clustered into patches of high gall density clones over the sampled area (mean v_i values, Table 2). Only leaf gall density was clustered into both patches and gaps (Table 2). Petiole gall density was neither aggregated on clones or spatially clustered.

The four species were associated positively on clones (VR = 1·30, W = 94·98, P < 0·05, n = 73), and thus occurred together on the same clone more frequently than expected by chance. However, their densities did not covary (VR = 0·0002, W = 0·015, P >> 0·05, n = 73), and clones with high densities of one species did not necessarily support large numbers of the remaining species. The stem gall and leaf folder densities were also significantly positively spatially associated on clones, i.e. forming significantly spatially concordant patches between 2420–2451 and 2240–2320 m a.s.l. (Table 2, Fig. 2). By contrast, leaf folder and leaf gall densities were significantly negatively associated (spatially discordant), particularly between 2420 and 2440 m a.s.l. (Table 2, Fig. 2).

Within clones, on individual shoots, the four species were sometimes significantly positively associated (on 40 clones) and sometimes independent (on 33 clones) [(although few remain significant after Bonferroni correction for multiple testing (Rice 1989)]. The percentage of shoots on which pairs of species co-occurred was extremely low, and less than 1% for most species pairs (Table 2). The only species pair that was significantly associated on shoots on any of the clones was the stem galler and leaf folder (significantly positively associated on the shoots of 14 of the 73 clones, i.e. VR > 1·21, W > 233·71, n = 200 in each case).

Table 2. Intraspecific and interspecific spatial analysis by distance indices and associated probability values for gall density of the four sawfly species (represented by their gall types). I_a, overall index of aggregation; mean v_i and mean v_j, indices of clustering identifying presence of gaps and patches, respectively, in the physical distribution of galls

	Gall former			
	Stem	Petiole	Leaf	Folder
Intraspecific indices				
I_a	1·624	1·027	2·959	2·225
(P-value)	(0·061)	(0·390)	(0·001)	(0·006)
mean v_i (patch clones)	3·033	1·560	2·892	4·173
(P-value)	(0·005)	(0·095)	(0·005)	(0·002)
mean v_j (gap clones)	−1·463	−0·922	−3·725	−1·651
(P-value)	(0·118)	(0·449)	(0·001)	(0·082)
Interspecific association				
Petiole	−0·187			
% co-occurrence on shoots	0·77 ± 1·46			
Leaf	−0·192	0·126		
% co-occurrence on shoots	0·55 ± 1·00	0·12 ± 0·38		
Folder	0·517*	−0·194	−0·468*	
% co-occurrence on shoots	1·86 ± 2·76	0·21 ± 0·46	0·08 ± 0·28	

*Interspecific association significant at $P < 0·05$;% co-occurrence on shoots given as mean ± SD (n = 73).

SPATIAL ABUNDANCE STRUCTURE

Gall density was significantly spatially structured for three of the four sawfly species; petiole gall density showed no spatial structure at the scale examined in this study (Fig. 3). These results concur with the mean patch indices (v_i) calculated using SADIE (Table 2). Leaf gall density was positively autocorrelated over greater distances than the other species, i.e. up to 2·64 km with a patch diameter of approximately 3·08 km (Fig. 3). Stem gall and leaf folder densities were positively spatially autocorrelated at distances of 0·88 km and thus both had patch diameters of approximately 1·32 km (Fig. 3). The presence of periodicity in the stem gall and leaf folder correlograms (re-occurrence of positive autocorrelation in larger distance classes) suggests that the average distance between adjacent patches for these two species are 8·80 km and 9·68 km, respectively (Radeloff *et al.* 2000). However, the spatial structure in gall density was different for the four species (with no significant lag correlations in the cross-correlation functions for any of the pairwise comparisons of significant correlograms; $P > 0·05$ and all lag correlations < 0·46 for three pairwise comparisons).

EXPLANATORY MODELS

Significant trend surface equations were obtained for stem gall, leaf gall and leaf fold density, with between 30% and 54% of the variability explained by a combination of polynomial X (longitude) and Y (latitude) terms (Table 3). These trend surface models successfully removed the spatial structure in gall density (correlogram P-values of residuals were not significant). No spatial terms were significant in the petiole gall density model.

Of the environmental variables, altitude was correlated strongly and significantly with latitude (Pearson's correlation coefficient: $r > 0·9$, $P < 0·05$ for all species). Altitude was thus not included as an independent environmental variable in any of the models, and the contribution of the spatial term Y was considered to account for any altitudinal effect (on its own, altitude contributed significantly to explaining the variation in stem gall, leaf gall and lead fold density). However, additional variation in stem gall density was explained by three of the measured environmental variables, including shoot length (Table 3). Clone height was the only significant environmental variable in the leaf folder model, and clone height and shoot length were in the leaf gall model (Table 3). In addition to the lack of spatial structure found for petiole gall density, none of the environmental (clone) variables explained variation in the density of this species.

The best explanatory power was thus achieved for leaf gall density (69·9%; $\chi^2 = 383·39$, d.f. = 9, $P < 0·001$), with lower total percentage deviances for stem gall (54·2%; $\chi^2 = 1956·14$, d.f. = 8, $P < 0·001$) and leaf fold (52·5%; $\chi^2 = 405·20$, d.f. = 5, $P < 0·001$) density (Table 3). The contribution of non-spatially structured environmental variables (A, Table 3), although low (6–9%), was significant for all species. The contribution of spatially structured environmental variation (B, Table 3) was similarly low for leaf fold and leaf gall density, and comparatively higher for stem gall density (Table 3). Fraction B (Table 3) represents the spatial structure common to both gall density and the environmental variables, i.e. there may be a causal relationship between the host plant variables and gall density. However, the spatial structure that is common to both of them may also be the result of a common response to an additional, unknown factor (Legendre & Legendre 1998).

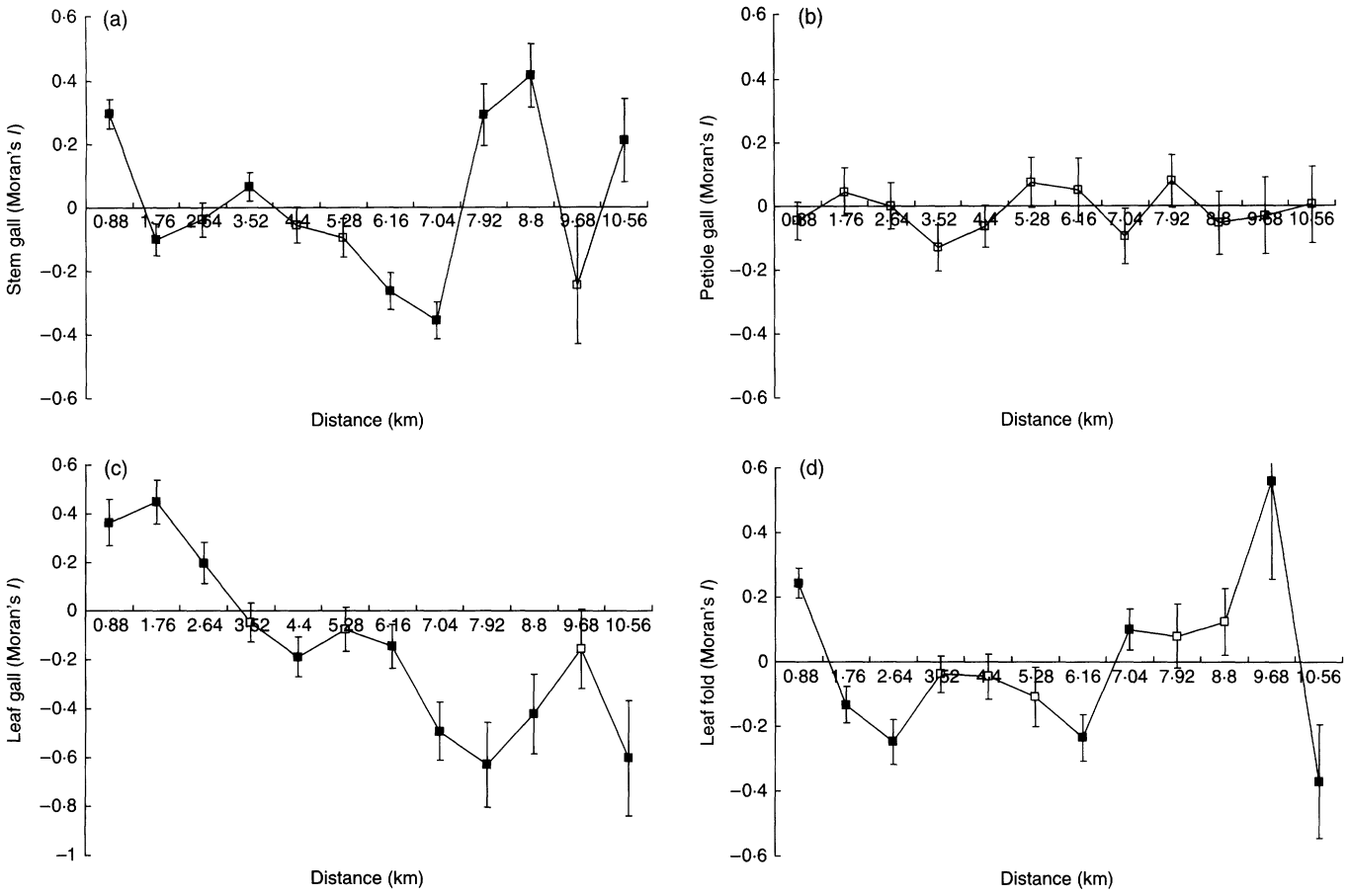

Fig. 3. Correlograms of the density ($\log_{10}$ x) of the four sawfly species. Global probabilities are significant at $P < 0{\cdot}05$ (closed symbols) when several *I*-values (± SD) in the correlogram are significant after progressive Bonferroni correction (alpha = 0·05); stem gall $P < 0{\cdot}0001$, petiole gall $P = 0{\cdot}721$, leaf gall $P < 0{\cdot}0001$, leaf fold $P < 0{\cdot}0001$. Number of point pairs in the first eight, interpreted distance classes (see Methods) range from 232 to 365 (stem galls), 87–211 (petiole galls), 58–125 (leaf galls) and 104–310 (leaf folds).

Table 3. Partial regression analyses of gall densities. Significant environmental variables and spatial coordinate terms for the gall density model of each species are listed, as well as the significance of the contributions of environmental (env.) and spatial (space) components

			% Deviance in gall density accounted for				
Gall former	Environmental variables	Spatial coordinate terms	Total	A Env.	B Env. X Space	C Space	A Env. only C Space only
Stem	No. of ramets Clone density Shoot length	x, x^2, y^2, xy^2, y^3	54·2	8·6	15·0	30·6	A $F_{3,36} = 6{\cdot}93$, $P < 0{\cdot}01$ C $F_{5,65} = 15{\cdot}51$, $P < 0{\cdot}001$
Folder	Clone height	x, y^2, xy^2, y^3	52·5	6·4	5·7	40·4	A $F_{1,57} = 8{\cdot}87$, $P < 0{\cdot}01$ C $F_{4,54} = 15{\cdot}77$, $P < 0{\cdot}001$
Leaf	Clone height Shoot length	x, x^2, y^2, xy, xy^2, x^3, y^3	69·9	8·1	7·4	54·4	A $F_{2,40} = 3{\cdot}66$, $P < 0{\cdot}05$ C $F_{7,35} = 3{\cdot}09$, $P < 0{\cdot}02$

Discussion

Significant, but not pervasive, spatial structure was found in this assemblage of coexisting, monophagous species across the landscape. Indeed, patch, periodic and trend components were apparent in the abundance structures of the spatially structured sawfly species (Radeloff *et al.* 2000; Legendre *et al.* 2002). Positive spatial autocorrelation was characteristic of gall densities in closest proximity to each other. Patch structure of this form is typical of species abundances and the result of one or more dispersal, intra- or interspecific interaction, biotic or abiotic environmental factors (Legendre 1993; Lennon 2000). Its presence is in fact now widely expected and used to identify scales of species responses and interactions (Logerwell *et al.* 1998; Keitt *et al.* 2002).

Periodic components (repeated patchiness across space) in species abundance structures are also not uncommon, and are used to infer periodicity in landscape structure, distances between patches and similarities in species densities at opposite range boundaries (Brown *et al.* 1996; Radeloff *et al.* 2000). As maps of their density profiles showed, the densities of these sawfly species were multimodal (generating the periodicity in spatial autocorrelation), with density peaks (rather than troughs) towards the edges of the distributions in some cases. Contrary to the optimum response surfaces shown generally by species across the extent of their geographical ranges (Brown 1984; Hengeveld 1990; Gaston 2003), mean sawfly densities did not peak at the centre of their distribution across the landscape, but more commonly towards the edges of it. This is possibly a consequence of the 'partial' examination of these species ranges (Gaston 1994), but is also often characteristic of species densities at habitat edges (Malcolm 1994; McGeoch & Gaston 2000).

The final component of spatial structure identified was the trend in sawfly density. Trends are generally indicative of direct or indirect responses of species to environmental gradients that run across the full extent the examined area (Austin 1987; McCoy 1990; Hill, Hamer & Hodkinson 1998; Legendre & Legendre 1998). In this instance the measured gradient was indirect (i.e. altitude), although species responses to it were potentially direct [direct response of sawflies to changes in temperature and moisture availability along the altitudinal gradient (Merriam 1890)], and indirect [host plant quality changes along the gradient to which the sawflies respond (Price 2003)]. The combination of these three spatial components thus meant that the abundance structures of sawfly species across the landscape were complex, with multiple components of spatial structure, rather than either monotonic or hump-shaped abundance structures at this scale (Brown 1984; Hengeveld 1990). Similar results have also been found in other 'partial' range studies (Ives & Klopfer 1997). Moreover, this structure in some ways mimics that found for species across their full geographical ranges, where abundance structures are composed of multiple, irregularly spaced areas of hot and cold density spots (Brown 1984; Hengeveld 1990; Maurer & Taper 2002; Brewer & Gaston 2003; Gaston 2003).

While previous studies of this sawfly assemblage have concentrated largely on the local environment (8–15 clones within 100–200 m of each other) to explain sawfly densities (Price 2003), these results show that fairly extensive patches of high average gall density occur (over distances of 0·8–2·6 km), that these patches in some instances repeat themselves across the landscape, and that there is an underlying trend in gall densities. None the less, the detailed gall density structures for the four species were in many ways unique and thus in accord with the few comparisons of the abundance structures of co-occurring species in assemblages that have been undertaken (Austin *et al.* 1985; Brown & Maurer 1989).

In particular, in this study, patches of high leaf gall density were not spatially concordant with stem gall and leaf fold densities, although areas of high gall density for these three species were coincident at low altitudes. Differences in between-species abundance structures were also apparent in their correlogram profiles and the distances over which gall densities were positively autocorrelated (i.e. patch sizes). In addition the density of one of the four species, the petiole galler, showed a complete absence of spatial structure. Because the presence of spatial structure, in particular positive autocorrelation in shorter distance classes, is considered the null expectation (Bell 2001), its absence in the petiole galler warrants further consideration (acknowledging that the species may be spatially structured at scales finer than those discernable in this study, McGeoch & Gaston 2002). The density of this species was comparatively low across the extent of the landscape, and indeed low aggregation by rare species is considered to be a characteristic that promotes persistence (Gaston 2003; Schiegg 2003). However, leaf fold and leaf gall densities were similarly low, with only a few willow clones (seven and three, respectively) exceeding the density recorded for petiole galls. The occupancy of petiole galls was also higher than leaf galls, and the latter was strongly spatially structured. Therefore, lack of spatial structure in the petiole galling species does not appear to be explained by its low mean abundance (Dessaint, Chadoeuf & Barralis 1991). Instead, it seems more likely that a set of mechanisms different to those of the other species is responsible for its abundance across the landscape. These findings are the first suggestion, in contrast to the often temporally extensive yet fine-scale studies on tenthredinid sawflies to date (Price *et al.* 1990; Price & Carr 2000; Price 2003), that bottom-up resource factors are not universally the dominant mechanism responsible for variability in sawfly population dynamics. Although the presence of similarities in the abundance structures of species does not necessarily reflect similarities in the mechanisms generating them, different abundance structures do point to different mechanisms (Legendre & Fortin 1989).

Competition was ruled out as a mechanism contributing significantly to the abundance structures of these species, at least at the gall density levels encountered in this study. Indeed, competitive interactions between herbivore insect species are generally considered to be rare, spatially and temporally variable, and present most commonly within species guilds (Denno, McClure & Ott 1995). The four species examined were found to be associated positively on clones across the gradient. Adult female sawflies of all species were thus either preferentially selecting the same clones on which to oviposit, or gall initiation and development was most successful on the same clones for all species (Stein & Price 1995). None the less, at fine spatial scales individuals and species are generally independently distributed, with occasional negative associations occurring between some pairs of species at high densities (Fritz *et al.* 1987; Craig, Itami & Price 1990). The only significant negative

association found across the landscape in this study was the spatially discordant distribution of the leaf folder and leaf galler. Because these two species share the same resource, i.e. the leaf, they might be expected to compete. However, their densities and co-occurrence on shoots was extremely low (0·08%), and they were not associated significantly (positively or negatively) on shoots. Evidence thus suggests that the mechanistic explanation for the spatial discordance in the abundance structures of leaf folder and leaf galler species is not interspecific competition.

In spite of their exposure to the same resource pool and the previous, repeated demonstrations of the importance of resource quality in the population dynamics of willow sawfly species (Price 2003), host plant characteristics explained only a small proportion (6–8%) of the abundance structures of three of the species. However, host plant quality is related largely to plant water status (Price & Clancy 1986), and spatial structure in host plant quality may itself be driven partly by spatially autocorrelated moisture gradients across the landscape (i.e. a Moran effect, Ranta, Kaitala & Lindstrom 1999). For example, temperature differences between the upper and lower ends of the sampled altitudinal gradient are approximately 3 °C (Merriam 1890) with cooler, more moist conditions at higher elevations. Local patchiness in water availability and disturbance could also occur, associated for example with fine-scale depressions or variation in drainage flow rate and exposure. While host plant water status may be spatially structured, only a small additional proportion of the variability in gall density (5–15%) was explained by spatially structured host plant quality (Legendre & Fortin 1989). At best, therefore, the host plant quality contribution to explaining gall density for the three species was in the order of 12–24% (components A + B in Table 3).

These percentages remain considerably lower than those recorded for the relationship between host plant quality and gall abundance in previous studies (47–92%, Price 2003). However, previous studies demonstrating this relationship were conducted at fine scales, i.e. on local patches of few individual clones, often examined over a series of galling seasons. The mechanisms underlying the abundance structure observed across the landscape in this study apparently do include some degree of similar selection for, and possibly performance on, particular clones. However, limited dispersal by species (at least *E. lasiolepis*, Stein *et al.* 1994) is likely to restrict the area within which such selection occurs, and selection of high quality hosts may thus be dispersal limited. As a result the host plant quality mechanism may be strong and identifiable only at fine, and not landscape, scales (Bevers & Flather 1999). Such changes in mechanistic explanations with spatial scale of observation are well documented (e.g. Wiens *et al.* 1986; McGeoch & Gaston 2002), but they have not been found previously for sawflies.

Although host plant quality explained little of the variability in gall density, spatial structure in gall density accounted for between 30 and 54% of this variation. In the absence of resource quality and competition as primary determinants of abundance structure, (i) species dispersal characteristics, (ii) the effects of natural enemies, (iii) the direct responses of species to spatially autocorrelated microclimatic variables (the Moran effect, Ranta *et al.* 1999) and/or (iv) historical factors and temporally stochastic variation, may explain the current spatial structure (Borcard & Legendre 1994; Ives & Klopfer 1997). A hierarchy of mechanisms structuring abundance in this assemblage may thus be proposed: host plant quality is responsible for gall density at fine, within-patch scales, with sawfly dispersal functions generating patch structure around these high quality willow clones (Stein *et al.* 1994; Price 2003). Abiotic environmental gradients then moderate average gall densities across the landscape.

The comparison of the abundance structures of these four taxonomically related, ecologically similar, co-occurring species has highlighted the importance of spatial processes in explaining the densities of species at the landscape scale and the individualistic nature of species abundance structures. Moreover, this approach has clarified further the hierarchical nature of the mechanisms underlying the population dynamics of this sawfly assemblage. Indeed, spatial approaches of this kind are providing considerable insight into the mechanisms underlying patterns in the distribution of diversity.

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