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Scale-dependent mechanisms in the population dynamics of an insect herbivore

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Abstract A multiscale approach has led to significant advances in the understanding of species population dynamics. The scale-dependent nature of population processes has been particularly clearly illustrated for insect herbivores. However, one of the most well-studied insect herbivores, the galling sawfly *Euura lasiolepis*, has to date been examined almost exclusively at fine spatial scales. The preference-performance, plant vigour and larval survival hypotheses are well supported by this species. Here, we test these hypotheses at a spatial scale larger than that previously considered, i.e. across a landscape in northern Arizona represented by an altitudinal gradient encompassing a series of drainages. We also develop a qualitative model for understanding the population dynamics of *E. lasiolepis* based on patterns of survival and mortality found in this study and previous ones. Gall density was highly variable across the altitudinal gradient, not explained by host plant variables, and thus a poor surrogate for population abundance. These findings for the first time fail to support the plant vigour and preference hierarchy hypotheses for *E. lasiolepis*. Dispersal limitation most likely explains the lack of support for these hypotheses at this scale. By contrast, sawfly survival, gall abortion, parasitism and larval mortality were well explained by host plant quality variables and altitude. The larval survival hypothesis was well supported and is thus comparatively scale-invariant. A qualitative model developed here highlighted the importance of both willow water status and disturbance in determining host plant quality, as

well as an apparent trade off between shoot length and plant moisture status in determining vital rates across the altitudinal gradient. This study thus demonstrated for the first time the scale-dependent nature of mechanisms underlying the population dynamics *E. lasiolepis*, and identified the interaction between parasitism and altitude as a novel mechanism underlying spatial patterns in the survival and mortality patterns of this species.

Keywords Abundance structure · Gall · Preference-performance hypothesis · Preference-hierarchy hypothesis · Plant vigour hypothesis

Introduction

The importance of a multiscale approach to understanding population dynamics has long been highlighted (Legendre and Fortin 1989; Wiens 1989; Levin 1992). Populations are not only limited by multiple factors, but also the roles of various mortality and natality factors, emigration and immigration, and their dynamics change from one spatial scale to the next (Hanski 1994; Cappuccino and Price 1995; Tilman et al. 1997; Winder et al. 2001). For example, for a single species resources such as food or nesting sites may be limiting at different spatial scales (Cole and Syms 1999; Thomas and Kunin 1999). Patterns of aggregation also change with the scale of observation (Inouye 1999), and host–natural enemy relationships differ depending on the scale at which the natural enemy perceives and responds to its environment (Heads and Lawton 1983; Thomas and Kunin 1999; Williams et al. 2001). Studies conducted at different scales thus often provide very different answers to the same question (Blackburn and Gaston 2002; McGeoch and Gaston 2002). While the most appropriate scale of observation may be dictated by the biology of the focal species and the question posed, conclusions drawn from

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any single spatial scale may change when considered in the context of processes operating at coarser or finer scales (Cornell and Lawton 1992; Palmer and White 1994; Palmer et al. 1996; Fauchald 1999). Therefore, the adoption of a spatial perspective in population ecology has resulted in significant advances in the field, and also in the generation of novel hypotheses (e.g. Thomson et al. 1996; Logerwell et al. 1998; Hanski 1999; Stoll and Prati 2001; Brewer and Gaston 2003; Veldtman and McGeoch 2004).

The scale-dependent nature of population processes has been well illustrated for herbivorous insects (Walde and Murdoch 1988; Godfay and Hassell 1997; Hunter 1997; Hunter et al. 2000). For example, extinction probability has been shown to be related to butterfly metapopulation structure, i.e. the size, distance and physical arrangement of populations (Hanski et al. 1995), and the spatial synchrony of aphid and moth populations shown to decline with the distance between them (Hanski and Woiwod 1993; Sutcliffe et al. 1996). Furthermore, the detection of density dependence in host–parasitoid relationships has been clearly demonstrated to change with the spatial scale of observation (Hails and Lawton 1983; Freeman and Smith 1990; Hails and Crawley 1992; Ray and Hastings 1996; Williams and Liebhold 2000). Limits to foraging and search distances by natural enemies as well as differences in foraging behaviour, result in different patterns of host mortality at different spatial scales, and these vary both within populations and across species geographic ranges (Hails and Lawton 1983; Walde and Murdoch 1988; Norowi et al. 2000; Brewer and Gaston 2003). Therefore, species dispersal characteristics, direct responses to abiotic and biotic environmental heterogeneity, and interactions with conspecifics, competitors and natural enemies have all been demonstrated to contribute to scale dependence in the demographic rates of insect herbivores (Borcard and Legendre 1994; Bevers and Flather 1999; Brewer and Gaston 2003).

One of the most intensively investigated herbivore–plant interactions is the monophagous, gall-forming sawfly, *Euura lasiolepis* (Hymenoptera: Tenthredinidae), and its association with its willow host, *Salix lasiolepis* (Salicaceae) (Price et al. 1995; Price 2003). Based on over 20 years of research, the life history, population dynamics, female oviposition preference (and its mechanistic basis), larval performance, interspecific interactions and adult dispersal behaviour of this species are well understood (Price 2003). Adult females preferentially attack long, vigorously growing shoots in populations of available shoot lengths, both within and between willow plants. This has been shown repeatedly in natural populations and under experimental conditions (Price et al. 1993, 1995). The survival of sawfly larvae (again in both natural and experimental populations) is higher on these longer shoots (Price et al. 1993, 1995). Furthermore, natural enemy-induced mortality does not change the general pattern of population dynamics in the species (Price et al. 1993, 1995; Hunter

and Price 1998). Therefore, the overriding influence on the population dynamics of *E. lasiolepis* demonstrated to date is the bottom-up effect of resource quality and the influence of plant water status on the supply of the resource (Price et al. 1993, 1995; Hunter and Price 1998). Indeed, knowledge of this species contributed significantly to a re-evaluation of the relative importance of bottom-up resource supply factors versus top-down mortality in the regulation of herbivore insect populations (Hunter and Price 1992; Price 2003). However, the wealth of information on *E. lasiolepis* has been gathered almost exclusively from studies conducted at fine spatial scales, across few localities and on clusters of few individual willows (although encompassing long time series). Based on the scale-dependent nature of relationships in herbivore insect populations outlined above, the relationships demonstrated for populations of *E. lasiolepis* to date may well be expected to change when considered over a larger scale (McGeoch and Price 2004).

The objective of this study was thus to assess the scale dependence of hypotheses well supported by this plant–insect interaction, by testing them at a spatial scale larger than that previously considered, i.e. across the landscape encompassing its population within the vicinity of Flagstaff, AZ, USA. Specifically, we test (1) the plant vigour hypothesis that gall abundance is higher on high quality willows (assessed using several variables previously shown to be good measures of willow quality (Price et al. 1995; Price 1991), (2) the preference hierarchy hypothesis that gall abundance is higher on willows with longer shoots (in this case, shoot length is the primary determinant of gall abundance rather than other measures of willow quality) (Craig et al. 1989), and (3) the larval survival hypothesis that survival to adulthood is higher on plants with long shoots (Craig et al. 1989). We also examine in more detail patterns of survival, natural-enemy and host-plant induced mortality in *E. lasiolepis* across the landscape with the aim of developing a spatially scaled understanding of its populations dynamics.

Materials and methods

Life history

E. lasiolepis adults emerge in late May and early June and oviposition occurs shortly thereafter, initiating gall development on young, rapidly growing shoots (Price and Craig 1984). Oviposition occurs in response to stimulation by the phenolic glucoside, tremulacin, emitted by growing shoots (Roininen et al. 1999). There is one largely synchronous generation per year and emergence coincides with the growth of new shoots on arroyo willow. Sawfly mortality can be partitioned into predation [by mountain chickadees (*Parus gambeli*) and grasshoppers (Orthoptera)], parasitism [predominantly *Pteromalus* sp. (Hymenoptera: Pteromalidae)] and host-plant factors (aborted galls, egg and larval mortality)

(Price and Craig 1984; Price and Clancy 1986a). Galls with no evident larval development (aborted galls) occur as a result of either (1) the sawfly retaining the egg during oviposition when willow water status is low (Preszler and Price 1988), or (2) the egg or young larva dies leaving no or little evidence of its existence in the gall (Price and Clancy 1986a). Larval mortality, particularly in early instars, is considered to be host-plant related and high first instar mortality is a result of inadequate plant resources and plant resistance (Waring and Price 1988; Price 2003).

Study area and field sampling

S. lasiolepis clones (distinct genotypes represented by individual plants that have spread vegetatively, Price 2003) were sampled along the ephemeral Schultz Creek and Rio de Flag streams in the vicinity of Flagstaff, AZ, 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. Sampling was conducted between April–May 2000 (i.e. on the 1999 *E. lasiolepis* generation, the previous generation to those reported in McGeoch and Price 2004), and coincided with the end of the 1999 generation for *E. lasiolepis* before emergence from galls. Seventy galled willow clones were selected along the gradient starting from the highest clone on Schultz Creek (2,449 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 sawfly species. The lowest clone in the Rio de Flag drainage, at 2,028 m a.s.l., was also included. Furthermore, *S. lasiolepis* is close to the southern edge of its geographic range in Arizona and its distribution is strongly limited by water availability (Price et al. 1995). The distribution of *S. lasiolepis* closely follows the distribution of major drainages in the study area, and is largely limited to a narrow band along these temporary streams. Therefore, we refer to the approximately linear distribution of this species along the elevational gradient represented by these drainages as the ‘landscape scale’, i.e. a scale between a local population and the geographic range of the species. The sampling design employed thus provided representative coverage of populations of *S. lasiolepis* and *E. lasiolepis* in the Flagstaff vicinity. Clones were chosen by blindly selecting individuals, 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 on it was encountered. Only clones with galls were considered because, whereas clones with galls represent potentially ‘suitable’ hosts, clones with no galls may either be ‘unsuitable’ or unoccupied by chance (see also rationale in McGeoch and Price 2004), and results are interpreted accordingly.

The locality (using a Garmin 12MAP GPS) and altitude (GPS and altimeter in combination) of each

clone were measured. Host-plant quality measures were taken, i.e. total number of ramets on the clone, mean ramet age (ten randomly selected ramets), the number of new (1-year old) ramets, and mean shoot length ($n = 50$ randomly chosen shoots). These variables have been shown to be good measures of willow clone quality for *E. lasiolepis* (Price et al. 1995). Clone height (m) and the mean distance of the five nearest neighbouring clones (clone density) were also measured. Disturbance to clones was estimated qualitatively as the percentage of ramets showing signs of mammal browsing or Sapsucker (*Sphyrapicus*) damage. The number of individual *E. lasiolepis* galls was estimated by counting the number of galls on 200 randomly selected shoots from each clone. In addition, 50 galls were collected from each of the above clones and dissected (eight clones had fewer than 50 galls and a minimum of 24 galls was collected from these). From these galls it was possible to determine the number of individual *E. lasiolepis* per gall (an alternative to gall density as a measure of sawfly abundance), the number of galls in which no oviposition or development took place (aborted galls), the number of galls in which larvae died after eclosion, the number of parasitised *E. lasiolepis*, and the number of *E. lasiolepis* that emerged successfully (survival), as well as maximum gall diameter (mm) (Price and Craig 1984). Gall density estimates were repeated for the same willow clones in July 2000 (representing the 2000 generation). Unless stated otherwise all calculations of survival and mortality factors were done excluding aborted galls, i.e. representing ‘interval’ survival and mortality (see also Price and Clancy 1986a; Price 1988).

Analyses

To identify the proportion of variability in gall density, the number of individuals per gall, gall wasp survival, parasitism, larval mortality, and gall abortion explained by spatial and host-plant factors, trend surface analysis, and partial regression approaches to the analysis of spatially explicit biological data were used (methods outlined by Legendre and Legendre 1998 and applied in, for example, Brewer and Gaston 2003). The only modification to the method was the use of generalised linear, rather than ordinary least square, models because gall data were in the form of counts of number of galls, or proportions of wasps surviving or dying (see also McGeoch and Price 2004). A Poisson error distribution for gall density was assumed and this was linked to the predictor variables with a logarithmic link function (McCullagh and Nelder 1989). The relationship between gall density in the 1999 generation and that in the 2000 generation was similarly tested. A binomial distribution was assumed for survival, parasitism, larval mortality, and gall abortion and these were linked to the predictor variables with a linear logistic link function (Collett 1991). The number of individuals per gall was analysed assuming a normal

error distribution with a logarithmic link function (McCullagh and 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 and Nelder 1989; see also Brewer and Gaston 2002 for similar application of these methods).

Following Legendre and Legendre (1998), trend surface analysis was first applied and the best subset of spatial variables contributing to explaining the variability in the dependent variables was selected (trend surface terms from the third order polynomial of longitude and latitude records for each willow clone). Best subsets were selected as the significant model with the fewest terms and lowest deviance (significant differences between models were determined using the critical χ^2 value on the difference in degrees of freedom and deviance between the two models, McCullagh and Nelder 1989). The best subset of environmental predictor variables (altitude, clone height, clone density, total number of ramets, number of new ramets, ramet age, new shoot density, shoot length, and number of galls per shoot) was similarly determined. Mean gall diameter per clone was also included as a predictor variable in the parasitism model (Price and Clancy 1986b). Spatial and environmental terms from the above models were combined and the best subset of terms selected from these as the final model (not all terms in these best subset models were necessarily significant, but were retained if their contribution significantly reduced the model deviance). Parameter significance was corrected for overdispersion in the residual deviance (Dobson 2002). Colinearity was assessed by calculating tolerance values for each predictor variable in each model, and tolerances of >0.1 were regarded as acceptable (Quinn and Keough 2002).

Variation in the dependent variables (gall density, survival, parasitism, and aborted galls) was then partitioned into fractions representing (a) the proportion of deviance explained by altitude and host-plant variables on their own (environmental component, *Env.*), (b) the spatially structured environmental effect (i.e. spatial structure shared by the environmental

component and dependent variable; interactive component, *S×E*), and (c) spatial structure in gall density not explained by the measured environmental variables (spatial component, *Space*) (Legendre and Legendre 1998; McGeoch and Price 2004). These components were used to assess the relative importance of measured environmental variables and spatial mechanisms (such as dispersal and fine-scale climatic factors) in explaining the variability in the dependent variable in question (see rationale by Legendre and Legendre 1998).

Results

Gall density and the percentage of surviving *E. lasiolepis* individuals varied widely across the altitudinal gradient with, for example, survival of individuals on willow clones ranging between 5% and 100% (Table 1). Gall densities in the 1999 and 2000 generations were very similar (Fig. 1a), and gall densities across generations were positively related ($F_{1,68}=66.42$, $P<0.0001$, deviance explained=49.41%). However, gall density was neither higher on high-quality willow clones, nor on clones with longer shoots (Table 2a). Indeed, the gall density model including the best subset of terms was not significant and variation in gall density across the gradient was thus not explained by any of the measured host-plant variables (Table 2a). Mean shoot length of galled clones was also highly variable across the gradient (Fig. 2). Nonetheless, shoot length was highest on the highest altitude clones (Fig. 2). Disturbance to clones was largely sporadic, with 14% showing signs of Sapsucker damage and 46% browsing damage. However, the degree of browsing on clones was low (64% of damaged clones with less than 10% of ramets damaged). Browsing damage was distributed across the extent of the gradient, whereas Sapsucker damage was almost exclusively confined to the upper 20 clones. Because of the low frequency and severe skew in these data, disturbance was not included in the explanatory models.

Table 1 *Euura lasiolepis* gall density (on 200 shoots per clone), survival, and mortality on Arroyo willow clones ($n=70$) across the landscape, *nc* number of clones on which demographic variable was >0

Demographic variable	Nc	Mean \pm SE	Median	Minimum	Maximum
Gall density ^a	70	55.83 \pm 5.25		3	186
Surviving individuals ₁ ^a (%)	70	59.25 \pm 3.24	64.22	5.41	100.00
Successful galls ₂ (%)	70	41.08 \pm 2.87	38.64	2.00	84.00
No. of individuals per gall ₁ ^a	70	1.28 \pm 0.03		1.00	1.95
No. of individuals per gall ₂	70	0.83 \pm 0.04		0.10	1.50
Aborted galls ^a (%)	70	36.55 \pm 2.12	33.00	10.00	92.00
Dead larvae ₁ ^a (%)	62	12.56 \pm 1.53	8.00	0	60.00
Predation of galls ₂ (%)	25	5.37 \pm 0.01	0	0	48.00
Parasitised individuals ₁ ^a (%)	63	21.05 \pm 2.05	18.09	0	65.00

Calculation excluding₁ and including₂ aborted galls. Successful galls were those from which at least one adult sawfly emerged

^aExplanatory models presented in Table 2

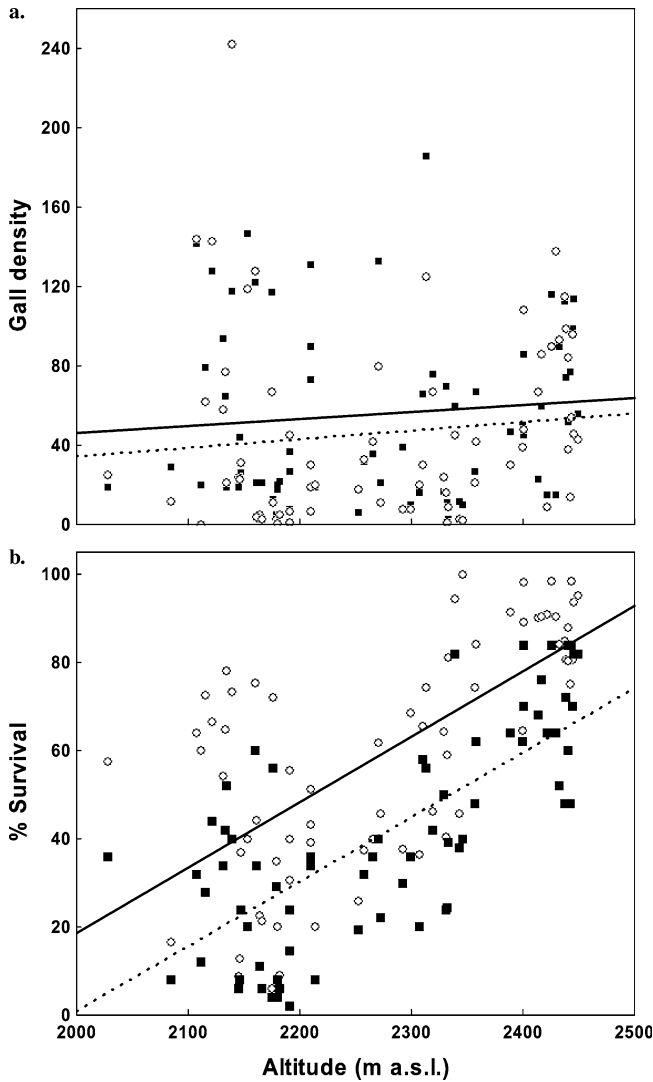


Fig. 1 *Euura lasiolepis* gall density per 200 shoots (a) (filled square = 1999 and open circle = 2000 generation, maximum outlier of 346 in 2000 generation excluded here) and percentage of *Euura lasiolepis* individuals surviving (b) (filled square = % galls with emerging sawflies and open circle = % emerging sawfly individuals excluding aborted galls) on willow clones across the altitudinal (m a.s.l.) gradient (lines fitted to data points for illustration only, appropriate model results provided in Table 2)

By contrast, 75% of the deviance in *E. lasiolepis* survival was explained by a range of spatial terms, altitude, and plant quality variables, including shoot length (Table 2b). Survival increased with altitude and was higher on longer shoots and clones with more young ramets (Table 2b, Fig. 1b). Spatial structure in the environmental variables ($S \times E$) contributed most to explaining *E. lasiolepis* survival (50%), although environmental variability on its own was also important (13%) (Table 2c). The relationship between survival and altitude remained similar regardless of the inclusion of aborted galls in the percentage calculation (Fig. 1b). Therefore, survival of sawflies to adulthood was significantly positively associated with shoot length on willow clones.

Examining alternative measures of sawfly abundance and success across the gradient, the percentage of successful galls on a clone (galls with at least one emerging adult sawfly) ranged widely, although it was similar on average to the percentage of surviving sawfly individuals (Table 1). The mean number of individuals per gall reached a maximum of almost 2.0 (Table 1), and increased significantly with altitude (Fig. 3a, Table 2c). The total deviance in the number of individuals per gall explained was 36%, and this was constituted largely by the spatially structured environmental component (23%) (Table 2b). Host-plant quality variables, including shoot length, did therefore also not explain a significant proportion of the deviance in this alternative measure of sawfly abundance.

Amongst the mortality (or gall failure) factors, gall abortion and parasitism were most important (Table 1). The maximum number of aborted galls (92%) and parasitism (65%) recorded on single clones were also particularly high. Larval mortality was generally low, but some larval mortality occurred on most willow clones (Table 1). Predation by grasshoppers and mountain chickadees was sporadic and low (Table 1), and models of predation were thus not constructed. All three mortality factors declined significantly with an increase in altitude (Fig. 3b–d, Table 2d–f). Amongst the mortality factors, parasitism levels were best explained (72%), declined with a mean increase in gall diameter, and were also higher on sparser (fewer ramets) willow clones in high clone density patches (Table 2f). The spatially structured environmental component ($S \times E$) and environmental component ($Env.$) contributed most (42 and 24%, respectively) to explaining the deviance in parasitism across that gradient. By contrast, the environmental component ($Env.$) contributed most to explaining larval mortality (34%) and gall abortion (29%), with very low to negligible contributions by the spatial ($Space$) and spatially structured environmental ($S \times E$) components (Table 2d, e). The proportion of aborted galls was higher on tall willows, and lower on shoots with more galls per shoot (Table 2d). Larval mortality was lower on longer shoots, and also on shoots with more galls per shoot (Table 2e). In addition to independently declining with an increase in altitude, host-plant measures also contributed significantly to explaining the three mortality factors (Table 2d–f).

Discussion

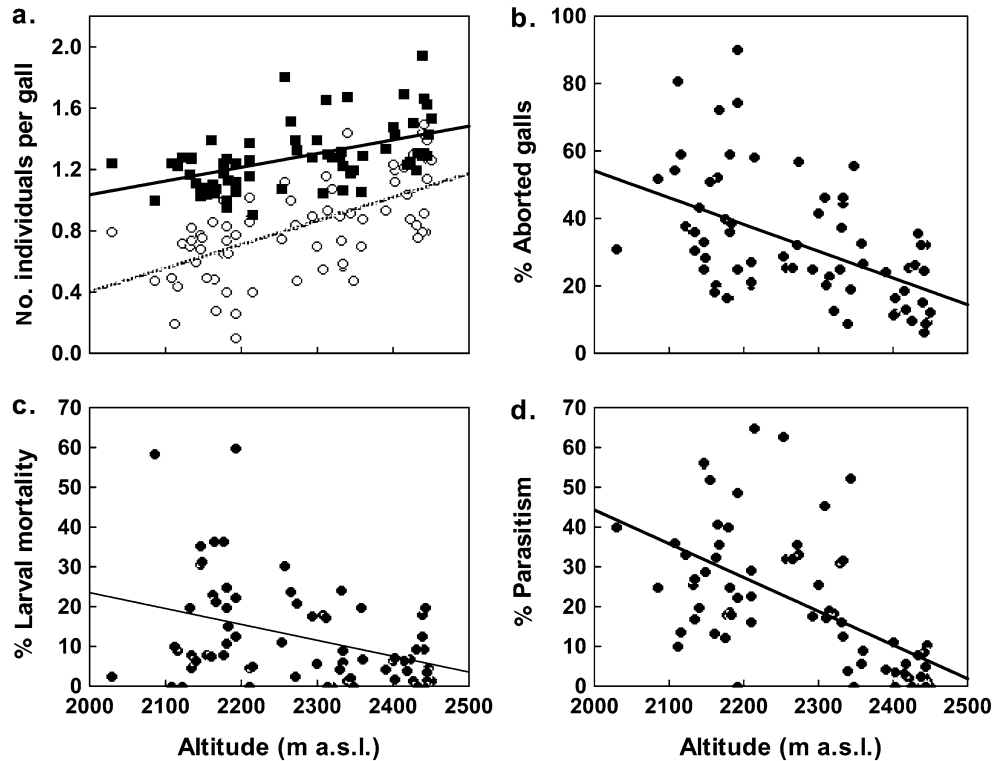
These findings are the first instance in which the plant vigour and preference hierarchy hypotheses are not supported for *E. lasiolepis*, as significant relationships between gall abundance, host-plant quality, and shoot length were not found. Indeed, gall abundance was uniformly variable across the gradient. The mechanistic basis of the relationship between gall abundance and shoot length is oviposition site selection by the

Table 2 Generalised linear model results (parameter estimates and Type 3 likelihood tests) for gall density, sawfly survival, level of parasitism, number of aborted galls, and larval mortality

Model	Terms	df	Deviance (scaled) [explained]	Sign of coefficient	χ^2 (<i>F</i>)	<i>P</i> <
Gall density (minimum tolerance=0.34)						
Null		69	2376.38			
Final		64	1972.80 (58.80) [16.98%]			
Space		5,64			(2.62)	0.10
	y^2	1	[16.00%]	+	0.41	0.52
	x^2	1		+	3.00	0.08
	y^3	1		+	0.014	0.90
	x^2y	1		+	5.31	0.05
Env.	Altitude	1	[0.98%]	-	1.25	0.26
S×E			[0%]			
Survival (minimum tolerance=0.29)						
Null		69	952.08			
Final		62	238.33 (65.91) [74.96%]			
Space		7,62			(26.52)	0.0001
	y^2	1	[10.63%]	+	6.08	0.02
	Xy	1		+	46.65	0.001
	y^3	1		+	109.17	0.001
Env.	Altitude	1	[13.47%]	+	4.85	0.05
	No. of new ramets	1		+	20.79	0.001
	Shoot length	1		+	6.61	0.05
	No. of galls per shoot	1		+	3.21	0.08
S×E			[50.86%]			
No. of individuals per gall (minimum tolerance=0.52)						
Null		69	2.93			
Final		65	1.86 (70) [36.58%]			
Space		4,65			(9.38)	0.001
	Yx^2	1	[4.19%]	+	4.48	0.05
Env.	Altitude	1	[9.37%]	+	4.38	0.05
	No. of new ramets	1		+	3.47	0.07
	No. of galls per shoot	1		+	2.03	0.15
S×E			[23.02%]			
Aborted galls (minimum tolerance=0.70)						
Null		69	512.01			
Final		64	329.69 (64.60) [35.61%]			
Space		5,64			(7.08)	0.001
	Xy	1	[4.95%]	+	6.61	0.05
Env.	Altitude	1	[29.85%]	-	7.32	0.01
	Clone height	1		+	6.73	0.01
	No. of new ramets	1		-	0.39	0.60
	No. of galls per shoot	1		-	5.38	0.05
S×E			[0.81%]			
Larval mortality (minimum tolerance=0.50)						
Null		69	322.17			
Final		65	199.08 (66.37) [38.19%]			
Space		4,65			(10.05)	0.001
	X	1	[3.64%]	-	4.46	0.05
Env.	Altitude	1	[34.03%]	-	11.20	0.001
	Shoot length	1		-	17.76	0.001
	No. of galls per shoot	1		-	7.60	0.01
S×E			[0.52%]			
Parasitism (minimum tolerance=0.58)						
Null		69	534.98			
Final		62	144.60 (65.04) [72.97%]			
Space		7,62			(23.91)	0.0001
	x^2	1	[5.85%]	-	0.09	0.76
	x^3	1		+	97.29	0.0001
	x^2y	1		-	18.14	0.001
Env.	Altitude	1	[24.96%]	-	12.76	0.001
	Clone density	1		+	14.90	0.001
	Total no. of ramets	1		-	21.42	0.001
	Gall diameter	1		-	10.97	0.001
S×E			[42.16%]			

Proportion of deviance explained by spatial (Space), environmental (Env.), and spatially structured environmental (S×E) components

Fig. 2 Number of individuals per gall (a) (*filled square* = excluding aborted galls and *open circle* = including aborted galls) and percentage of aborted galls (b), percentage larval mortality (c) and percentage individuals parasitised (d) (both excluding aborted galls) and on willow clones across the altitudinal gradient (lines fitted to data points for illustration only, appropriate model results provided in Table 2



female sawfly (Price 2003). However, dispersal in *E. lasiolepis* has been shown to be limited, and females are highly phylopatric (Stein et al. 1994). In consequence, oviposition site selection generally occurs at the within-clone scale, not at the extent of the landscape (see also McGeoch and Price 2004). This is the most likely explanation for the absence or very weak relationship between host-plant quality or shoot length and gall abundance at this scale. Indeed, the majority

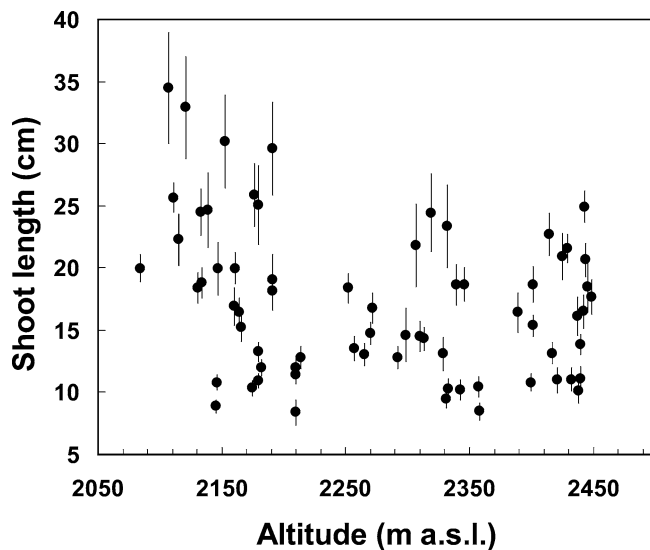


Fig. 3 Shoot length on galled *Salix lasiolepis* clones across the altitudinal (m a.s.l.) gradient. *open circle* = mean shoot length per willow clone \pm standard error

of studies on other plant–insect systems that support these hypotheses have been conducted at fine spatial scales (e.g. Larsson 1989; Bjorkman 2000; Cornelissen and Fernandes 2001; Faria and Fernandes 2001).

By contrast, the larval survival hypothesis was supported at the landscape scale and, as predicted, sawfly survival was significantly higher and larval death significantly lower on willow clones with longer shoots. Unlike gall abundance, the mechanisms underlying survival are thus apparently scale-invariant from the individual clone to the landscape. While female oviposition site selection may be dispersal limited, once the oviposition site has been selected larval survival remains greater on longer shoots. Larval performance is therefore dependent largely on host-plant quality (Price 2003), and its observation less scale dependent than abundance.

At the landscape scale, therefore, survival is a better predictor of sawfly performance than gall abundance. Although there was a fairly strong positive relationship between interannual local gall abundances, there was no straightforward relationship between gall abundance and sawfly survival. The relationship between environmental variables, including shoot length, and stem gall density reported in McGeoch and Price (2004) (for the generation following that reported here) was significant, albeit weak. While the relative importance of key factors are well known to change between generations (Southwood and Comins 1976; Royama 1992), the results of McGeoch and Price (2004) and those presented here agree that host-plant factors contribute much less to

explaining gall density at the landscape scale than the 47–92% of variation accounted for by this relationship at finer scales (Price 2003).

The use of gall abundance as a surrogate for population abundance is based on the assumption that the mean number of sawflies per gall is constant between willow clones and across the landscape. This was clearly not the case in this study, and indeed adult sawflies are known to form galls by ovipositor insertion without oviposition and this behaviour is negatively related to host-plant quality (Price and Clancy 1986a; Preszler and Price 1988). Female sawflies are also known to lay more than one egg per node (per gall) when host plant quality is high (Price 2003). The large proportion of aborted galls found at lower altitudes and high number of sawfly individuals at higher altitudes strongly suggest an altitudinal gradient in host-plant quality. Nonetheless, gall density was not a useful surrogate for population viability at the landscape scale. The absence of a positive relationship between abundance and survival in herbivore insects is not uncommon (see e.g. McGeoch and Gaston 2000; Brewer and Gaston 2003). However, it does limit the value of using merely the abundance of sedentary, persistent structures (such as galls and leaf mines) in understanding herbivore population dynamics.

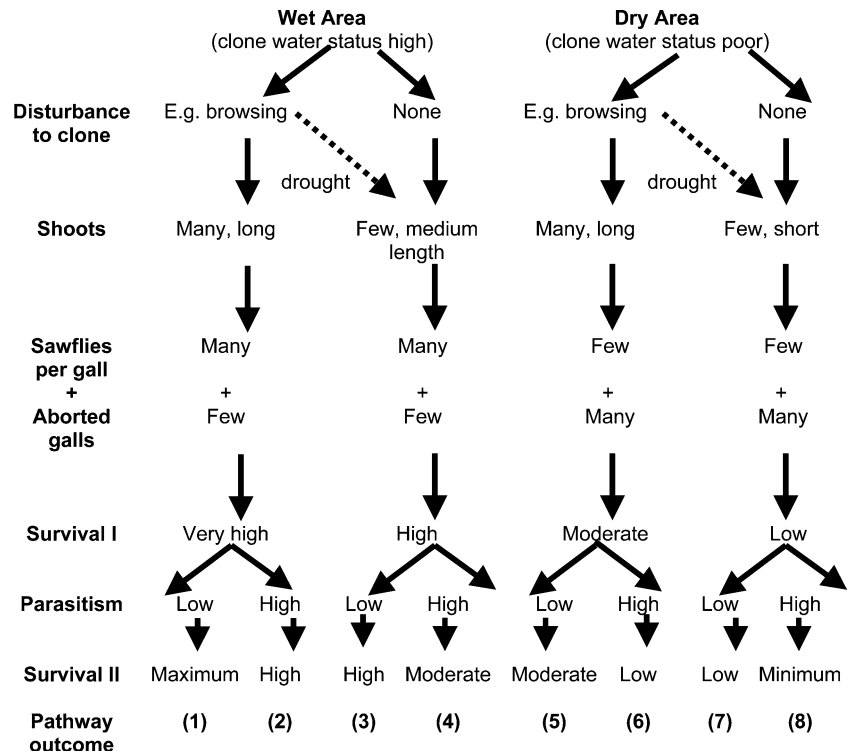
In this study, gall productivity (individuals per gall) and sawfly survival increased with altitude in the absence of an equivalent altitudinal gradient in gall abundance. Indeed, all the modelled demographic rates except gall abundance responded significantly to altitude. Altitude is clearly a surrogate for unmeasured environmental variables such as precipitation, relative humidity, willow clone water status, temperature, and sunlight. For example, the adiabatic cooling rate over the 421 m altitudinal gradient sampled is 4.08° C, equivalent to a 5.52 ° latitude north (see also Price et al. 1998). In addition, willows in the upper third of the gradient are all shaded by large pines and other conifers (*Abies* and *Pseudotsuga*), whereas they are generally unshaded at lower altitudes. Not only does shade reduce evapotranspiration, but snow and water flow are more persistent towards the top end of the gradient. Therefore, temperature and light intensity are lower and precipitation and evapotranspiration higher towards the upper compared with the lower end of the Schultz Creek gradient (Merriam 1890; McGeoch and Price 2004). Sawfly demographic rates were also not randomly distributed across the gradient, but both survival and mortality factors were consistently associated with altitude. Therefore, as predicted, an examination of the population dynamics of *E. lasiolepis* at the landscape scale has demonstrated a change in some relationships that hold consistently at fine scales, identified an environmental gradient to which demographic parameters respond, and highlighted the effect of interactions between different parameters of host-plant quality on local demographic rates. This once again emphasises the value of multiscale spatial studies in understanding species population

dynamics (Tilman et al. 1997; Bevers and Flather 1999; Cole and Syms 1999; Ribeiro et al. 2003).

By placing well-established local-scale relationships in a landscape context, using the patterns identified here, it is possible to build a qualitative, predictive model for the survival of *E. lasiolepis* (Fig. 4). This frame-based model is designed to explain conditions resulting in survival extremes and is thus simplified to contrast only 'wet' versus 'dry' areas. Across a landscape, maximum survival to adulthood in a sawfly generation is predicted to result from high moisture availability and high plant water status in combination with disturbance to willow clones (e.g. browsing that stimulates shoot growth) (Price and Clancy 1986a; Stein et al. 1992; Hjalten and Price 1996) (Fig. 4 (1)). High host-plant quality (vigorous growth and long shoots) then results in female sawflies laying more than a single egg per gall (or more than one oviposition per node) as well as low levels of gall abortion (gall formation without oviposition and egg mortality) and larval mortality (Craig et al. 1988, 1989; this study). Should parasitism (and predation) levels simultaneously be low, the number of individual sawflies surviving to adulthood attains a maximum (Fig. 4 (1)). By contrast, survival is lowest when moisture availability and clone water status are low, with no disturbance to clones (Fig. 4 (8)). Host-plant quality is low (only short shoots available), few eggs are laid per gall, and levels of gall abortion and larval mortality are high. This, combined with moderate parasitism levels (parasitism has never been recorded to exceed 65% in *E. lasiolepis* (Price 2003)), results in extremely low survival to adulthood (Fig. 4 (8)). Furthermore, drought conditions are likely to result in a switch in pathways, with a change in shoot formation and clone water status conditions (Price 2003) (Fig. 4).

This model highlights the importance of both clone water status and disturbance in determining host-plant quality. As previously shown, high gall densities are associated with long, vigorously growing shoots (Price 2003). However, although the number of galls produced may be high when shoots are long, unless plant water status is simultaneously high, fewer eggs will be laid per gall and the survival of these will be low. By contrast, in the absence of vigorously growing, long shoots, although gall density will be low, many eggs are laid per gall and the survival of individuals in these galls is higher when plant water status is high. Therefore, there is an apparent trade off between shoot length (stimulating oviposition and gall development) and clone moisture status (encouraging more oviposition events per galls and facilitating egg and larval survival). In addition, high parasitism may further moderate survival. An absence of disturbance to clones at wet sites, and low clone moisture status with high mortality at dry sites are thus factors predicted to limit *E. lasiolepis* populations across the landscape. Gall density may remain fairly constant across the landscape, and yet significant differences in population demographic rates may exist.

Fig. 4 Pathways of water availability, host-plant quality, and parasitism resulting in different levels of *E. lasiolepis* survival to adulthood on *S. lasiolepis* clones. Predicted relationships are supported by this study as well as Price et al. (1993), Hjalten and Price (1996), Price (2003) and outcomes are numbered for reference in the discussion



This study thus provides a clear example of the contribution of a multiscale approach to the study of population dynamics, and the change in mechanisms driving populations from local to landscape scale. The interaction between parasitism levels and altitude was also identified as a novel mechanism underlying spatial patterns in the survival and mortality of this galling sawfly species. Lastly, the study provides insight into mechanisms more likely to be scale-variant (those based on species dispersal characteristics) and those that are comparatively scale-invariant (resource-quality-based mortality).

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