

Host plants as islands: Resource quality and spatial setting as determinants of insect distribution

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Both the quality and spatial configuration of a habitat can affect the distribution of its inhabitants. However, few studies have directly compared the relative effects of the two. In this paper, we focus on spatial patterns in the distribution of an oak-specific moth, *Tischeria ekebladella*. At the landscape level, the species was more often present on well-connected trees than on isolated trees. Experimental transplants revealed pronounced variation in larval survival among individual leaves within trees. In fact, survival on a “good” and a “bad” leaf within a tree differed almost as much as survival between a “good” and a “bad” leaf chosen randomly on two different trees. Qualitative differences among trees did not explain the distribution of the species across the landscape, as average larval performance did not differ between trees naturally occupied and unoccupied by the species. Hence, spatial effects seem to dominate over host tree quality in determining the regional distribution of *Tischeria ekebladella*.

Introduction

Over the last few decades, population biology has witnessed a shift of emphasis from local processes to regional processes with a spatial component (e.g. Tilman & Kareiva 1997, Hanski & Gaggiotti 2004, Tschamntke & Brandl 2004). In studies of herbivorous insects, this can be caricatured as a contrast between studies of two types: a long tradition focussing on the local, chemical interplay between insect herbivores and their host plant (e.g. Dolinger *et al.* 1973, Feeny 1976, Louda *et al.* 1987, Zangerl & Berenbaum 1990, Forkner *et al.* 2004), and novel studies portraying all habitat as essentially equal in quality and focussing on the key processes of local colonization and extinction (e.g. Harrison *et al.*

1988, Harrison 1994, Hanski 1999, Doak 2000, Gutierrez *et al.* 2001, Biedermann 2004).

While this dichotomy is partly artificial (Hanski 2005), it serves to illustrate a central line of development in studies of the population dynamics of herbivorous insects: In many classical studies, the local abundance of insects is assumed to closely map local conditions. To this, the recent metapopulation approach adds a key insight. When host plants are patchily distributed at a spatial scale that restricts the dispersal of insects, spatial patterns of insect distribution and abundance could arise primarily from processes operating at the metapopulation level (e.g. Hanski 1999, Tschamntke & Brandl 2004). As a result, a species may be lacking from units of suitable habitat, or even be present in units of

unsuitable habitat (Pulliam 1988, Hanski 1999). The relative roles of space and quality will hence vary with the scale of variation in habitat quality as compared with the scale of insect dispersal (Hanski 2005, van Nouhuys 2005), and the relevant question about herbivorous insects becomes — how does the relative importance of host plant quality and the spatial configuration of available habitat compare to each other for any particular study system at any particular spatial scale?

Among host plants, trees form an interesting special case. They are long-lived, discrete units in space. They also support a diverse fauna of specialist insects (e.g. Feeny 1970, Novotny *et al.* 2002a, 2002b). From the perspective of such insects, individual crowns of the host-tree species will hence resemble islands of suitable habitat in a sea of other, largely unsuitable habitats. We can then refine the question above: how similar are conspecific trees as islands — at what scale do they vary in quality as compared with the dispersal capacity of insect herbivores, and how is this reflected in the regional distribution of the insects?

In trees, variation in quality is well documented at several spatial scales. At the scale of the full distributional range of host tree species (or major parts of it; e.g. Krischik & Denno 1983, Gaston *et al.* 2004) and at the level of separate tree populations (e.g. Cates & Zou 1990, Schultz *et al.* 1990, Neeman 1993) trees have been found to vary in a wealth of characteristics, including the chemical contents of leaves and phenology — traits with a likely impact on insect performance (Hartley & Jones 1997, Hunter 1997, Mopper & Simberloff 1995, Klemola *et al.* 2003, Tikkanen & Julkunen-Tiitto 2003). Nevertheless, these spatial scales are probably much larger than the typical movement range of most herbivorous insects. From the perspective of an individual insect, qualitative variation at a local scale within a limited area would appear to be more relevant (cf. McGeoch & Price 2004). In addition to substantial variation among host tree individuals observed at this scale (e.g. Hemming & Lindroth 1995, Hunter 1997, Kause *et al.* 1999, Whitham *et al.* 2003, Riipi *et al.* 2004), much variation has also been detected within individual trees (e.g. Suomela & Ayres 1994, Suomela & Nilson 1994, Suomela

et al. 1995, Wallin & Raffa 1998, Yamasaki & Kikuzawa 2003). In cases where variation within trees is large and variation among trees small, we would expect metapopulation dynamics among local insect populations to result in a clear-cut relationship between the spatial configuration of host trees and the regional distribution of insect herbivores.

In this paper, we assess the importance of host plant quality *versus* spatial configuration on the distribution of *Tischeria ekebladella* Bjerkaner (Lepidoptera: Tischeriidae); a specialist leafminer of the pedunculate oak, *Quercus robur*. We describe spatial patterns in the regional distribution and local performance of the herbivore across an island of five km², and present an experiment aimed at disentangling the relative roles of host plant quality and spatial context in creating the observed patterns. More specifically, we ask: (1) how does the regional distribution of *T. ekebladella* relate to the spatial connectivity of individual host trees, (2) can these patterns be explained by local variation in host plant quality, and (3) how much qualitative variation actually occurs within and between host trees?

Material and methods

Spatial patterns in the regional distribution of *T. ekebladella*

To assess patterns and processes in oak–insect interactions in a spatial context, we mapped every individual of *Quercus robur* within a discrete area of five km² — the island of Wattkast in Korpo, south-western Finland. In 2003 and 2004, the location of each of 1868 oak trees with a height of at least 50 cm was measured with a precision of about 2–7 m using a hand-held GPS navigator. We also measured the diameter of the trunk of each tree. When a tree was big enough, we measured its diameter at breast height, in other cases we used the basal diameter.

To establish the effect of connectivity on the distribution of *Tischeria ekebladella* in this system, the concept was first operationalised as follows. The potential local population of moths on an individual oak tree was assumed to vary with the total amount of foliage, and hence with

tree size. Therefore, the diameter of the tree trunk was used as a proxy for local population size, N_j (hereafter simply referred to as the “size” of a tree).

The connectivity (the opposite of isolation) of each tree i was measured by a simple index, proportional to the expected numbers of moths immigrating from populations in surrounding trees at maximum patch occupancy:

$$S_i = \sum [\exp(\alpha d_{ij}) \times N_j], j \neq i \quad (1)$$

where d_{ij} is the distance between tree i and its neighbouring tree j , N_j is the size of tree j and α is a parameter describing how fast the number of migrants from tree j declines with increasing distance (index modified from Hanski 1994, 1997, 1999).

A rough estimate of $\alpha = -0.02$ was adopted from an independent study of dispersal distances in oak-specific insects (T. Roslin & S. Gripenberg unpubl. data). In brief, we placed 40 potted oak trees at fixed distances (37.5–300 metres) outside an isolated oak plantation in Inkoo, south-western Finland. As the surrounding region was known to be free of oaks for a radius of at least one kilometre, we assumed that every oak-specific insect found on our experimental trees emanated from the oak plantation. Hence, the distribution of eggs laid on the leaves of our experimental trees should closely reflect the distribution of dispersal distances for ovipositing females. Based on this approach, we fitted a generalised linear model to the data, where the number of larvae, u (and hence the number of dispersing females) encountered at a certain distance d from the source population is given by

$$u = ce^{\alpha d} \quad (2)$$

Here, c and α are constants, with $1/\alpha$ describing the average dispersal distance. For *T. ekebladella*, we obtained an α value of -0.02 (Wald confidence limits $[-0.03, -0.01]$, S.E. = 0.004).

To test whether the spatial location of each oak in relation to other oak trees affected the incidence of *Tischeria ekebladella*, we sampled 113 small-sized oaks representing the full range of connectivity values present in the system. The trees selected for this survey were 1–3 m high,

and small enough for each part to be inspected. Between 8 and 11 September 2003, we visited each of the selected oaks. On each tree, we examined all leaves, and hence confirmed the local presence or absence of *Tischeria ekebladella*.

Host plant-quality versus spatial location

To assess the relative roles of host-plant quality and spatial context in determining regional patterns in the distribution of *Tischeria ekebladella*, we transplanted moths to trees that were either naturally unoccupied or naturally occupied by the species. The performance of the leaf-mining larvae was then compared between the two tree categories.

In the spring of 2004, 51 small oak trees of variable connectivity were selected within the northwest corner of the island of Wattkast. As above, the trees were chosen to be small enough (1–3 m in height) for each part to be inspected from the ground. On 4–6 May 2004, close to budbreak but well in time before the emergence of adult moths, one branch tip per tree was enclosed in a large muslin bag (50 × 60 cm). The average number of shoots (i.e. clusters of leaves grown from a single bud in the current year) per bag was 11.9 (S.D. = 5.7), with an average 5.1 leaves (S.D. = 2.0) per shoot.

Tischeria ekebladella individuals to be experimentally introduced in the bags were collected in hibernated leaf-mines in May 2004. The collections were made in mixed leaf material in the densest oak stands of Wattkast (cf. Fig. 1). The mines were then reared outdoors in small cylindrical muslin cages, and a male and a female moth transferred to each experimental bag upon emergence between 5 and 19 June. The introductions were made in random order.

As we specifically wanted to examine direct effects of host-plant quality on the survival of the larvae, the bags were left on the trees during the whole course of the experiment, thereby excluding both parasites and predators. Between 14 and 20 September, all trees were revisited, the bags removed and the leaf-mines inspected. For every leaf within a bag, we recorded the total number of mines initiated on that leaf (in the form of leaf

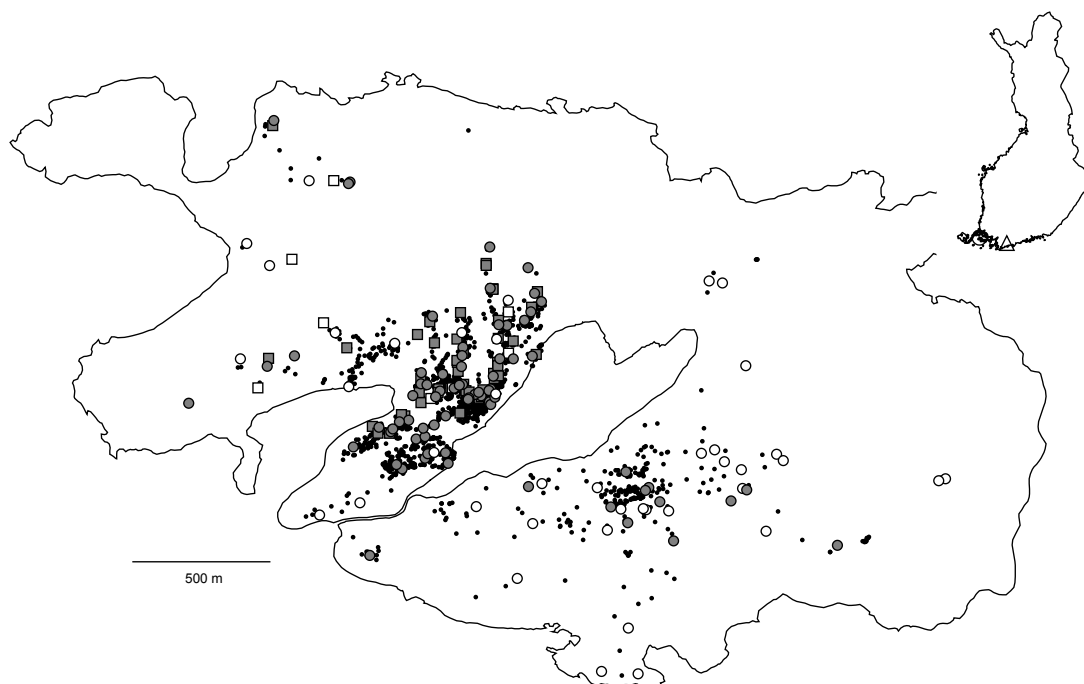


Fig. 1. Spatial distribution of oaks and of *Tischeria ekebladella* within the island of Wattkast. Each small black dot shows the location of an individual oak tree. Larger circles correspond to the set of 113 trees sampled in 2003; larger squares the 51 trees included in the transplant experiment of 2004. Of the latter two sets of trees, natural populations of *Tischeria ekebladella* were present on trees shown in grey and absent from trees shown in white. On the inset map of Finland, the circle shows the location of Wattkast, whereas the triangle shows the site of the Inkoo experiment (see text).

scars and active mines), the number of larvae still alive, and the identity of the shoot to which the leaf was attached. *Tischeria ekebladella* excavates its mine right under the upper epidermis of the leaf, and both mines and leaf scars are therefore whitish and easy to score — even in cases where the larva itself has died at an early stage. To establish the local presence or absence of a wild population of *Tischeria ekebladella* on the tree, we then examined every leaf outside the bags for active mines or scars.

Statistical models

We used generalised linear models (McCullagh & Nelder 1989) and generalised linear mixed effects models (Breslow & Clayton 1993, Littell *et al.* 1996) to analyse the data. To test for an effect of landscape configuration on the incidence of *Tischeria ekebladella*, we used a gen-

eralised linear model where the local presence or absence of the species (0/1) was modelled as a function of the connectivity value of the target tree (Eq. 1). Given the binary response, we assumed a logit link function and binomially distributed errors. This model was fitted in SAS System for Windows 8.02, PROC GENMOD (SAS Institute 2001).

In order to assess whether host-plant quality differed between trees naturally unoccupied and trees naturally occupied by *Tischeria ekebladella*, we fitted a generalised linear mixed effects model to the data on the survival of individual larvae. Survival was modelled as a function of whether the tree was naturally occupied by the species or not (0/1, a fixed effect), of the total number of larvae initially present on the leaf (accounting for density-dependent survival; a fixed effect) and of the identity of the tree, the shoot nested under the tree and the leaf nested under the shoot (all three discrete, random

effects). As the response was binary (0/1, reflecting whether the larva survived until inspection in mid-September or not), we assumed a logit link function and binomially distributed errors. This model was fitted using the GLIMMIX macro implemented in SAS System for Windows 8.02, PROC MIXED (Littell *et al.* 1996, SAS Institute 2001).

To assess the relative amount of variation present at different hierarchical levels, we used analysis of variance components to split the total variance attributed to random effects in the model into variations among trees, among shoots within trees, among leaves within shoots, and residual variation. Confidence limits for relevant variance proportions were estimated by parametric bootstrap as implemented in S-PLUS 6.1 (Insightful Corp. 2002).

We also assessed the absolute amount of variation in larval survival at respective hierarchical levels. This was done by simulating data from the fitted model. We examined variation in probability of survival at each level (tree, shoot, leaf, and individual) by keeping all factors at higher hierarchical levels constant, and simulating a “good” observation (i.e. one standard deviation above the mean) and a “poor” observation (i.e. one standard deviation below the mean). For each hierarchical level, we simulated data sets of 10 000 observations.

Results

Spatial patterns in the regional distribution of *T. ekebladella*

Tischeria ekebladella was found on 73 out of the 113 examined trees (Fig. 1). The pattern of incidence was significantly related to the degree of isolation of the host tree: mines were more likely to be present on a tree of higher connectivity (logistic regression: $\chi^2 = 12.40$, $df = 1$, $P = 0.0004$; Fig. 2).

Host plant-quality versus spatial location

Of the 51 trees onto which we successfully transplanted *Tischeria ekebladella*, 43 trees were

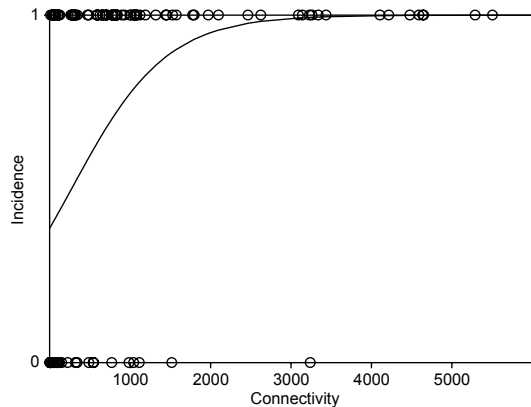


Fig. 2. The relationship between the connectivity of a tree and the incidence of *Tischeria ekebladella*. The circles show empirical values (incidence = 0 if species absent and incidence = 1 if species present) and the curve the relationship estimated by a generalised linear model.

occupied by a natural population, whereas eight trees were unoccupied by the species. In the experimental introductions, the fecundity of females was found to be very high: individual females laid up to 144 eggs. On very few of the trees did host tree quality inflict any significant mortality on the offspring: across all trees and leaves, 1795 out of 2037 larvae (88%) were still alive by the end of the summer, and the median tree-specific survival was 92%.

The variation in survival that we encountered was more pronounced among and within individual trees than among occupied *versus* unoccupied trees. While the density of mines on an individual leaf had a strong effect on the survival of larvae within that leaf ($F_{1,691} = 11.11$, $P < 0.001$), there was no significant difference in larval survival among trees with and without a natural population of *T. ekebladella* ($F_{1,691} = 1.03$, $P = 0.31$). In fact, the average survival of larvae was slightly higher on unoccupied than on occupied trees, but the estimated effect was minimal as compared with variations among trees, among shoots within trees and among leaves within shoots (Fig. 3). On the logit scale, the difference in survival between occupied and unoccupied trees only amounted to 48% of the standard deviation associated with variation among trees, 88% of the standard deviation of variation among shoots within trees and 35%

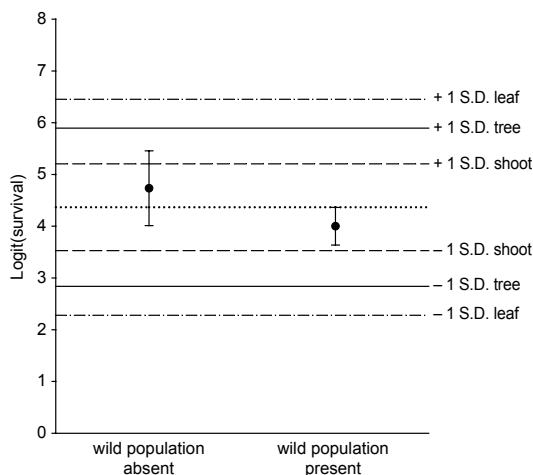


Fig. 3. Estimated effect of a tree being occupied or not on the local survival of *Tischeria ekebladella*. For comparison, the dotted horizontal line shows average survival (on a logit scale), continuous horizontal lines show tree-to-tree variation (average ± 1 S.D.), dashed horizontal lines show shoot-to-shoot variation within trees, and broken horizontal lines (— · —) indicate leaf-to-leaf variation within shoots within trees. Estimates from a generalised linear mixed model; see text for details.

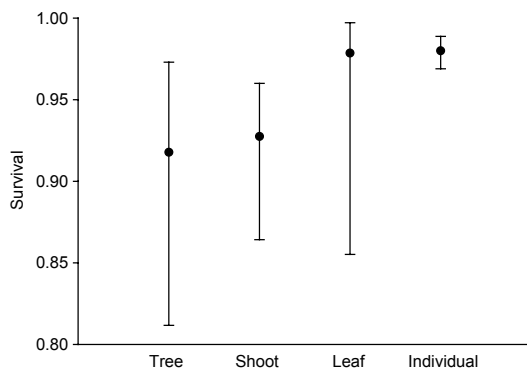


Fig. 5. Absolute variation in larval survival at different hierarchical levels. For each level, the error bars show the average amount of variation caused by adding or subtracting one standard deviation of the variation observed at this and lower levels.

of the standard deviation of variation among leaves within shoots. Hence, the lack of an effect cannot be ascribed to limited statistical power, as there was simply less variation between occupied and unoccupied trees than among trees as individuals or among different parts within trees.

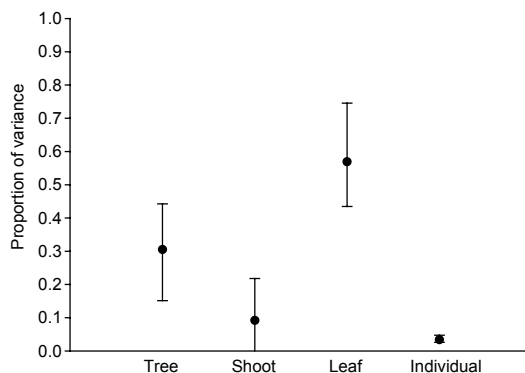


Fig. 4. Partitioning of variance in the survival of *T. ekebladella* among individual oak trees, shoots within trees and leaves within shoots. The error bars show approximate 95% confidence limits as derived by parametric bootstrap.

Variation within and between trees

Moth survival varied both among different parts of one and the same tree and among trees as individuals. Of the total variation in $\text{logit}(\text{survival})$ attributable to random effects, less than a third (30%) occurred among individual trees (Fig. 4). In particular, variation among individual leaves within shoots was substantial, and significantly larger than variation among trees (Fig. 4; average estimate for leaf outside 95% confidence limits for tree-level variation). This effect emerged despite the fact that we had explicitly accounted for any density dependence in survival, by including leaf-specific densities of mines in the model. The residual variation was extremely small (Figs. 4 and 5), indicating that multiple larvae mining on the same leaf almost always had the same fate.

From a biological perspective, absolute variation in survival was substantial at all levels examined: adding one standard deviation in tree-to-tree variation to average survival among occupied trees corresponds to an increase in survival of 5.5%, subtracting one standard deviation to a reduction of 10.6% (Fig. 5). For shoots within trees, the corresponding figures were 3.3% and 6.3%, respectively, for leaves within shoots 1.9% vs. 12.3%. Hence, survival on a “good” and a “bad” leaf randomly chosen on two shoots within a tree differed almost as much as survival between a “good” and a “bad”

leaf chosen randomly on two different trees. Within leaves, residual variation among mines was small enough to be biologically negligible, with an increase or decrease in mine quality by one standard deviation corresponding to an increase or decrease in survival of 0.9% and 1.1%, respectively.

Discussion

The relative roles of the quality and configuration of host trees in creating patterns in the distribution of specialist insects can only be resolved case-by-case for particular species at particular spatial scales. In this study, we showed that the local presence or absence of the leaf-miner *Tischeria ekebladella* within an area of five km² is closely related to the spatial configuration of the habitat, as reflected by the connectivity of host tree individuals. In principle, this pattern lends itself to two alternative interpretations: Host quality could covary with host quantity, in which case the observed relationship could be merely an artefact of increasing resource quality in denser stands of oaks. Alternatively, the incidence of *Tischeria ekebladella* could be determined by processes at the metapopulation level, with an increasing rate of local colonization as compared with local extinction for more well-connected trees, and hence a higher local incidence (Hanski 1994, 1999).

Our experimental transplants of *T. ekebladella* to different parts of the landscape, and to trees naturally occupied and unoccupied by the species, provide evidence against the first alternative. Since the moth larvae survived equally well on both types of trees, patterns in host plant quality were not consistent with patterns in the regional distribution of *T. ekebladella*. Moreover, over 88% of all larvae survived when sheltered from predators and parasites, which also suggests a weak and subordinate role of plant defence in regulating the local density of the target species within a single season. Hence, we feel safe in excluding host-plant quality *per se* as a causal factor in creating the observed patterns. Of course, this does not exclude spatial variation in other factors with a potential impact on the distribution of the species. Factors to be experi-

mentally addressed in the near future are spatial variation in abiotic factors with an impact on over-wintering mortality, and spatial variation in biotic factors such as shared predators and parasites between oak-specific insects and taxa in the surrounding landscape (Holt & Lawton 1994, Östman & Ives 2003, Morris *et al.* 2004).

That tree-to-tree variation in the average quality of foliage is of secondary importance in this system is also illustrated by our findings on the hierarchical distribution of variation in larval performance among different trees and different parts of one and the same tree. As shown in Fig. 5, the survival of *T. ekebladella* varied as much between different parts of one and the same tree as between different trees, and we can envisage the trees as habitat “islands” of more or less equal average quality. This finding has profound ramifications for several other aspects of the system, including not only how we should sample it, but also what type of microevolutionary processes we are likely to observe in it.

From the perspective of ecological sampling designs, the observed pattern implies that the commonly used method of inferring overall plant quality from the quality of a few haphazardly collected leaves is unlikely to provide very accurate results in systems like ours. Given similar levels of variation within and between trees, heavy replication within individual trees will inevitably be needed to resolve minor differences among tree individuals (Suomela & Ayres 1994, *see* Markham 2002 for a similar argument). To overcome a part of this problem in bioassays attempting to link the chemical contents of foliage to herbivore performance, leaves from a single shoot should be used to reduce variation among replicates.

From the perspective of microevolutionary processes, the small-scale variability in foliar quality in our system will probably preclude the type of adaptations at the tree level envisaged by the adaptive deme formation hypothesis (cf. Edmunds & Alstad 1978, Mopper & Strauss 1998, Mopper 2005). On the contrary, high heterogeneity within individual oak trees may effectively prevent local adaptations at the level of individual trees (e.g. Cobb & Whitham 1993) and favour behavioural responses to fine-scale variation in resource quality (S. Gripenberg

et al. unpubl. data). To assess the generality of our findings, we urge our colleagues to describe hierarchical patterns in herbivore performance for the systems where local adaptations have already been found (e.g. Hanks & Denno 1994, Komatsu & Akimoto 1995, Mopper *et al.* 1995, Mopper 2005).

The exact mechanisms giving rise to large variation within trees may be manifold. Trees are hierarchically structured, and some of the variation that occurs among different units of hierarchical levels (among branches, shoots and leaves) can stem from variation in the amount and type of resources allocated to different units (Orians & Jones 2001). Genetic differences due to somatic mutations have been suggested to create part of the heterogeneity (Whitham & Slobodchikoff 1981, Edwards 1990), but their influence on herbivore fitness remains unclear (e.g. Hutchings & Booth 2004). Several studies showing large variation within individual tree clones also suggest that variation may stem from highly different factors than genotypic effects (e.g. Keinänen *et al.* 1999, Laitinen *et al.* 2004). For instance, different environmental and microclimatic conditions (e.g. light availability) can create heterogeneity at different spatial scales within the canopy, resulting in patterns such as vertical stratification or more local differences in leaf quality (e.g. Maiorana 1981, Nichols-Orians 1991, Fortin & Mauffette 2002, Yamasaki & Kikuzawa 2003). Localized herbivory may also cause induced responses unevenly spread across the canopy (e.g. Ryan 1983, Tuomi *et al.* 1988, Wold & Marquis 1997, Arnold & Schultz 2002). Moreover, leaves of different age or developmental stage may be of different quality from the perspective of herbivorous insects (Raupp & Denno 1983, Lawrence *et al.* 2003, Nahrung & Allen 2003).

In our particular study system, somatic mutations do not seem like a credible explanation for the high variability in larval survival observed within trees. The trees were small, and repetitive mutations at the scale of individual shoots appear unlikely. Neither do differences in age among leaves account for the pattern: the oak leaves are produced by a single flush of leaves in the late spring and will hence all be of similar age (Niemelä & Haukioja 1982). Moreover, we excluded herbivory by species other than *T.*

ekebladella by bagging the branches, and we also included the exact density of *T. ekebladella* in our statistical models, thereby compensating for responses due to variable herbivory by this particular species. Hence, we find the most plausible mechanism for the patterns of variation to be slight differences in the exact resource allocation to and biosynthetic activity of individual leaves, but still lack direct evidence in support of this view.

To conclude, regardless of the exact mechanism(s) giving rise to large variation within trees, the moth *Tischeria ekebladella* apparently perceives individual tree crowns as internally variable islands of rather similar average quality. In our particular study system of few km², the spatial configuration of these islands appears to override variation in their quality in determining patterns in the spatial distribution of the moth. As a result, the interplay between the trees and the insects will be strongly affected by where in the landscape a tree grows. From the perspective of the moth, the spatial distribution of the trees will strongly affect both distributional and micro-evolutionary dynamics. From the perspective of the tree, growing in a well-connected part of the landscape will increase its probability of being colonised by *T. ekebladella*, whereas more isolated trees may escape herbivory by this species. We do not expect *T. ekebladella* to cause much damage to its host tree, but if the pattern extends across herbivore species, the location of a tree in the landscape may have profound effects on its fitness (cf. Crawley 1985, Herms & Mattson 1992, Cornelissen & Fernandes 2001) and on the structure of the local insect community (cf. Janzen 1973, Kruess 2003, van Nouhuys 2005). Both perspectives deserve substantial attention in future studies. The extent to which the current findings extend to other taxa is still an open question, and one which can only be answered by comparative work in other systems.

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