

Effects of forest fragmentation and local habitat structure on densities of winter moth (*Operophtera brumata* L.)

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ABSTRACT. We study the effects of habitat fragmentation (habitat area, isolation, distance from forest edge) and local habitat structure (size and phenology of host tree and density of herb cover) on winter moth densities in oak forests near Antwerp, N. Belgium, focussing on both effects simultaneously and comparing males and females. In this way, we can study how adult dispersal strategies – active male flight vs. flightless females – affect the distribution of individuals. The analyses show that both the degree of fragmentation and local habitat structure affect moth densities and that the effects differ between males and females. Failing to correct for sex-differences and for various aspects of local habitat structure would have led to the conclusion that there were no effects of fragmentation on winter moth densities. Thus, structured populations in which dispersal rates vary between individuals need careful evaluation of the effects of fragmentation, separately for the different groups of individuals.

KEY WORDS: Habitat Fragmentation, Density, winter moth, dispersal, local adaptation.

INTRODUCTION

Habitat fragmentation – the process that reduces the area of natural habitats and thereby increases distances between suitable patches – is increasingly endangering many organisms and is one of the major threats to global biodiversity (e.g. SAUNDERS et al., 1991; STEFFAN-DEWENTER & TSCHARNTKE, 2000). Not surprisingly, habitat fragmentation has been a central theme in conservation biology since the field began (HARRISON & BRUNA, 1999). In spite of a very large body of literature studying the various effects of fragmentation, there are many obstacles relating to the design and replication of experiments that hamper the development of a solid general framework (HARRISON & BRUNA, 1999). Nevertheless, in their recent review HARRISON & BRUNA (1999) identified a number of general patterns. First, fragmented habitats often appear to be of impoverished quality, and second, physical and biological edge effects appear to be predominant in forest habitats as opposed to non-forest areas. Edge effects may render large natural habitats of hundreds of hectares equivalent to virtually all edge. These conclusions stand

in sharp contrast to many theoretical models, which put a lot of emphasis on the importance of dispersal among fragments (HARRISON & BRUNA, 1999).

In addition to these large scale fragmentation effects, subtle features of local habitat structure, such as habitat suitability or nutritional quality, can also influence the distribution of organisms in the landscape. Furthermore, behavioural traits, such as dispersal and habitat selection, need to be taken into account to understand variation in densities at any geographical scale. Finally, the scale of sampling and inference is of crucial importance (DIDHAM, 1997). Fragmentation takes place at the level of habitat patches, while many processes affecting densities and species distributions occur at a much smaller scale (e.g. host individuals). Therefore, local processes should be taken into account when studying regional patterns.

In this paper we investigate the distribution of winter moths (*Operophtera brumata* L.) in a highly fragmented landscape. We determine densities on individual host trees (pedunculate oak, *Quercus robur* L.) and study the effects of individual tree characteristics and their surrounding habitat, as well as the effects of habitat area and degree of isolation of the different woodlots. The winter moth is an interesting model system to investigate the effects of frag-

mentation and host characteristics for several reasons. First, winter moths show phenological adaptation to individual hosts within oak stands (VAN DONGEN et al., 1997). Therefore, local tree and habitat characteristics are likely to affect the distribution of this species. This is likely to occur at the level of the caterpillars, which feed upon the host and are affected directly by the degree of synchrony between egg hatching and leaf flush. Second, dispersal abilities differ markedly between adults and larvae, as well as between adult males and females. Adult females show almost no dispersal, which could predispose the species to be vulnerable to the effects of fragmentation. Nevertheless, larval wind dispersal can occur over several kilometres and could dilute effects. In addition effects on males and females could differ since males show active flight up to several hundreds of meters. These variations in dispersal abilities render the winter moth an interesting model species to study the effects of fragmentation at different geographic scales. We show that, unless the associations between densities on the one hand and both the effects of forest fragmentation and local habitat structure on the other hand are modelled carefully for males and females separately, patterns may be overlooked.

MATERIAL AND METHODS

Study species and density estimation

The winter moth is a univoltine moth species with adults active mainly in November in Northern Belgium. Adults emerge after pupation in the soil with the winged males flying towards trees while the brachypterous non-flying females crawl towards the nearest vertical object. Shortly after dusk, females emit pheromones to attract males and copulation takes place on the tree trunk. Adults crawl into the canopy where they lay eggs in bark crevices and on lichens. Males return to the ground and hide until the next evening. Eggs overwinter and hatch in early spring, in synchrony with host budburst. This synchrony has important fitness consequences, as early hatching results in starvation or wind dispersal of first instar caterpillars, while late hatching presents developing larvae with leaves of lower quality. We studied winter moths in oak forests, the primary host of this species. Within each forest patch, individual oaks show high variation in budburst dates, a pattern that is consistent across years (CRAWLEY & AKTERUZAMANN, 1988; VAN DONGEN, 1997; VAN DONGEN et al., 1997; and unpublished results). Consequently, optimal hatching dates for caterpillars vary on a very small geographical scale, resulting in some degree of local adaptation to the phenology of individual oak trees (VAN DONGEN et al., 1997).

Winter moth densities were determined in November 2000. We chose 12 oak forest patches that differed in size and degree of isolation. Degree of isolation was defined as the distance to a forest larger than 10 ha (VAN DONGEN et al., 1994, 1998). Forests larger than 10 ha were automati-

cally assigned a degree of isolation of zero. In each area, five to 15 trees were randomly selected four weeks prior to density determination. Afterwards, for each tree its size (trunk diameter at breast height and canopy radius, i.e. average distance from the trunk to the edge of the canopy), distance from the forest edge (in meters), budburst date (date when 50% of the buds had burst open with small leaves occasionally becoming visible; VAN DONGEN et al., 1997) and degree of herb-cover (proportion of the soil covered by small herbaceous plants; VAN DONGEN et al., 1994) were determined. Because trunk diameter and canopy radius were highly correlated, both were combined in a single measure of tree size. This measure was calculated as the average of trunk diameter and canopy radius after standardisation (i.e. subtraction of the mean, and division by the standard deviation). Thus, this tree size measure will have mean zero.

Each forest fragment was visited seven times between the 8th of November and the 12th of December, from 18.00-20.00 hours (the peak of adult activity). The numbers of male and female winter moths were counted by inspecting each tree trunk up to a height of 2.5 meters for about 1 minute. Details of the 12 forest fragments and the number of trees and visits are given in Table 1. The sequence of visits to the different forest fragments was randomised to avoid confounding the data with temporal variation in densities.

Statistical analysis

Because forest fragments larger than 10 ha were assigned a degree of isolation of zero, isolation and surface area were correlated ($r_s = -0.72$, $p = 0.008$). Effects of area and isolation are therefore difficult to disentangle statistically. To avoid multicollinearity problems in our analyses, we grouped the areas into three categories (further called isol-area): LARGE fragments greater than 10 ha, SMALL-CLOSE fragments smaller than 10 ha with a degree of isolation less than 300 meters, and SMALL-DISTANT fragments of which the degree of isolation was higher (Table 1, Fig. 1). This choice was arbitrarily made ensuring a reasonably balanced dataset – three, four and five forest fragments in each category respectively (Table 1) – and the criteria were not changed during the analyses.

Prior to the analysis of winter moth densities, we compared the degree of herb cover, the budburst date and tree size between the three area-classes (isol-area) and among the different fragments using a two-way mixed model nested ANOVA (fragment nested within isol-area). In addition, correlations between these three characteristics were investigated (after correction for plot effects) to avoid multicollinearity problems in the linear model described below. Next, male and female densities were analysed in relation to fragment-specific and tree-specific explanatory variables in a mixed-effects linear model. Male and female densities were calculated for each tree by averaging the counts over the seven visits, and were

TABLE 1

Summary of forest fragment characteristics and the number of trees that were sampled. Fragments were grouped into three isol-area classes reflecting a combined effect of surface area and isolation (see text for details).

Area code	area (ha)	isolation (m)	# trees	Isol-area
KB	12	0	15	large
LO	17.6	0	15	large
ZZ	16.7	0	15	large
KL	1.8	90	8	small-close
LW	1.0	200	8	small-close
ZW	0.4	200	7	small-close
ZN	1.7	100	8	small-close
LS	0.5	900	8	small-distant
VS	1.7	350	8	small-distant
HM	0.8	400	5	small-distant
HN	3.2	450	9	small-distant
LI	0.7	1150	7	small-distant

log-transformed ($\log(\text{density}+0.1)$) to achieve approximate normality (as tested by the Shapiro-Wilks test, see results section). As we aimed to compare the effects of the explanatory variables between both sexes – i.e. to measure the impact of the different dispersal behaviour of males and females on their distribution – male and female density was analysed in a single model and interactions with sex were tested. A significant interaction of a factor with sex indicates that the effect of this explanatory variable is different for males and females. However, considering male and female densities simultaneously complicates the method since repeated measures on individual trees are analysed. We corrected for this statistical dependency by adding tree as a random effect to our model. Furthermore, fragment is also added as a random effect to account for the fact that data from individual trees within a forest fragment do not represent independent data for tests of fragment-specific effects (i.e. the Isol-area effect). Degrees of freedom of the fixed effect were approximated using Satterthwaite's procedure (VERBEKE & MOLENBERGHS, 2000). Effects of individual explanatory variables are visualised using residual plots. Additionally, for comparison,

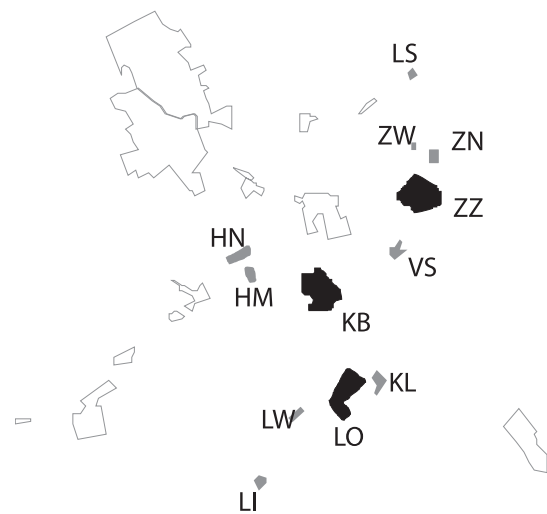


Fig. 1. – Map of forest patches in the study area. Fragments larger than 10 ha are indicated in black (i.e. Isol-area=LARGE), smaller areas located nearby a larger plot are indicated in dark grey (i.e. Isol-area=SMALL-CLOSE), and small and more isolated plots are indicated in light grey (i.e. Isol-area=SMALL-DISTANT). White forest fragments were not monitored.

the effect isol-area was tested ignoring all tree-specific variables using a one-way ANOVA model.

RESULTS

The one-way ANOVA model did not show a significant isol-area effect ($F_{2,112}=1.81$, $p=0.17$). Before starting with the more elaborate mixed model analysis of winter moth densities, we first compared variation in herb cover, tree size and tree budburst among forest fragments. Neither herb cover, nor tree size nor budburst date differed between the three area-classes (Table 2). Only herb cover showed significant variation among fragments within area-classes (Table 2). In addition, a plot of the mean values and standard deviations (Fig. 2) suggests that most variability can be found within the individual forest fragments. Herb cover, tree size and budburst date were not significantly correlated (all $p>0.05$). These three explana-

TABLE 2

Two-way nested ANOVA's models analysing variation in herb cover, tree size and tree budburst between the three groups of fragments (for details see Table 1) and among fragments nested within these three groups. The fixed isol-area effect was tested using a traditional F-test, while the random nested fragment effect was tested using a likelihood ratio test. Among fragment variation is given as a variance component with the residual variance between brackets.

Variable	isol-area	fragment (nested within isol-area)
Herb cover	$F_{2,9}=0.34$, $p=0.72$	$\sigma^2=0.036$ ($\sigma^2_{\text{residual}}=0.07$) ($\chi^2_1=19.3$, $p<0.0001$)
Tree size	$F_{2,9}=1.61$, $p=0.25$	$\sigma^2=0.10$ ($\sigma^2_{\text{residual}}=0.79$) ($\chi^2_1=2.5$, $p=0.11$)
Tree budburst	$F_{2,9}=2.61$, $p=0.13$	$\sigma^2=0.78$ ($\sigma^2_{\text{residual}}=58$) ($\chi^2_1=0.07$, $p=0.80$)

tory variables can therefore be added simultaneously in a statistical model without causing multicollinearity problems.

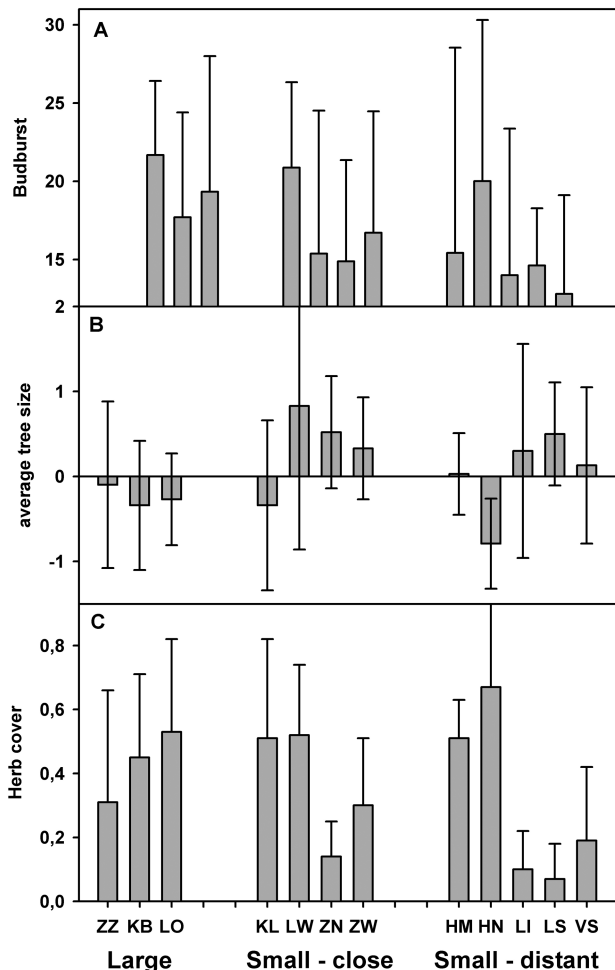


Fig. 2. – Between fragment variation in average budburst (A), tree size (B) and degree of herb cover (C). Error bars indicate standard deviations of the fragment-specific distributions.

Table 3 summarises the significance tests of the linear model relating winter moth densities to the different explanatory variables of interest. Graphical representations of the different associations are given in Figs 3 and 4. With the exception of tree size, which showed a positive association with density (Fig. 3), the effects of all other explanatory variables differed between the two sexes (Table 3). Densities decreased with date of budburst for females ($t_{107}=-2.76$, $p=0.007$) but not for males ($t_{107}=0.70$, $p=0.49$) (Fig. 3). Winter moth densities decreased with distance from the forest edge for both sexes, but the effect was significantly stronger for females as shown by the significant $\text{sex} \times \text{edge}$ interaction (Table 3) (females: $t_{107}=-4.74$, $p<0.0001$; males $t_{107}=-2.69$, $p=0.008$; Fig. 3). It is also worth noting that graphical inspection of this relationship revealed that the edge effect was only present in large areas because variation in distances to the edge were much smaller in the small fragments (Fig. 3). Densities decreased with herb cover, but only signifi-

TABLE 3

Summary of tests of the fixed effects relating winter moth density to a suite of explanatory variables (significant results in bold).

Source	F-value	num. d.f.	den. d.f.	p-value
Sex	63.0	1	107	<0.0001
Herb-cover	5.27	1	102	0.02
Tree size	17.4	1	98	<0.0001
Budburst	3.95	1	98	0.05
Edge	17.6	1	99	<0.0001
Isol-area	3.92	2	9	0.06
Herb-cover\timessex	6.43	1	107	0.01
Budburst\timessex	4.38	1	107	0.04
Edge\timessex	4.90	1	107	0.03
Isol-area\timessex	6.30	2	107	0.003
Tree size \times sex	2.43	1	106	0.12
Edge \times isol-area	0.90	2	104	0.41
Edge \times isol-area \times sex	1.05	2	102	0.35

cantly so in males (females: $t_{107}=-0.94$, $p=0.34$; males: $t_{107}=-3.18$, $p=0.002$). Finally, the effect of isol-area differed between males and females as well (Table 3, Fig. 4). For males, there was only a significant difference between large and small-distant fragments, while for females all small fragments showed a lower density relative to the larger ones (Fig. 4).

Besides the variability in winter moth densities among trees and forest fragments, there was still a significant amount of unexplained variation left. The random fragment effect explained 57% of the total variation ($\sigma^2=0.62$, $Z=1.97$, $p=0.02$) while the random tree effect explained 20% ($\sigma^2=0.22$, $Z=4.27$, $p<0.0001$). The amount of unexplained residual variance after correction for these fragment and tree effects was 0.25. The residual values of this full model were approximately normally distributed (Shapiro Wilks' $W=0.97$).

DISCUSSION

Our study shows that both habitat fragmentation and local habitat structure affect winter moth densities. In several cases, these effects appear to differ between males and females. The differences in dispersal abilities through the habitat are likely to explain the observed differences in associations. In contrast to the flightless females, males show active flight. Effects of local habitat structure that affect larval distribution could therefore persist in females but disappear in males. For example, the fact that the edge-effects as well as the effect of tree budburst were stronger for females could be due to the fact that the factors determining densities operate at the larval stage, which is still reflected in the distribution of females, but only to a lesser extent in the flying males. The fact that the association between herb cover and density is only significant for males could indicate that this factor did not affect larval densities and therefore did

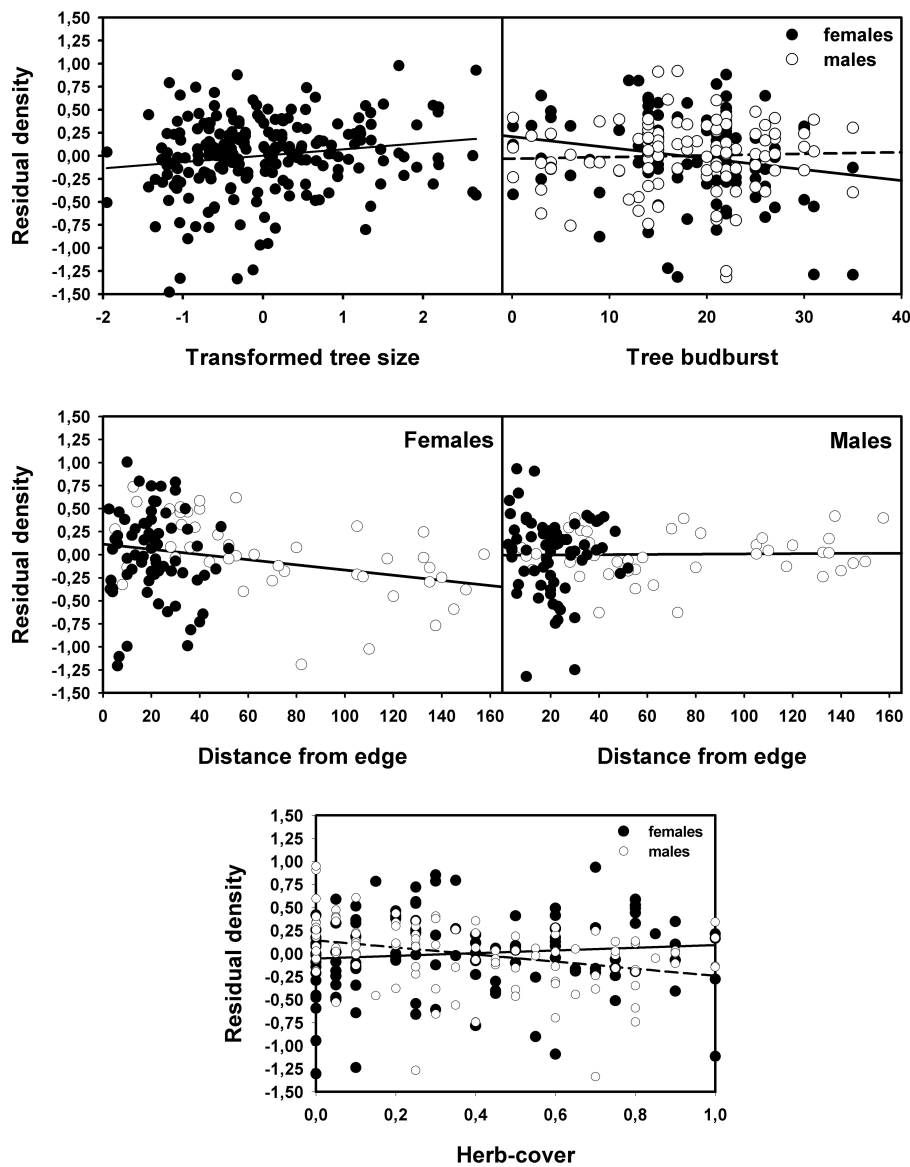


Fig. 3. – Relationship between winter moth density and tree size (A), tree budburst (B), distance from the edge (C1 & C2) and herb-cover (D). For explanatory variables that showed a significant interaction with sex, plots were constructed to highlight the importance of the interaction effect by splitting data by sex (females: solid line; males dashed line). For the association between density and distance from the edge, solid symbols represent data from small fragments, and open symbols observations from large fragments.

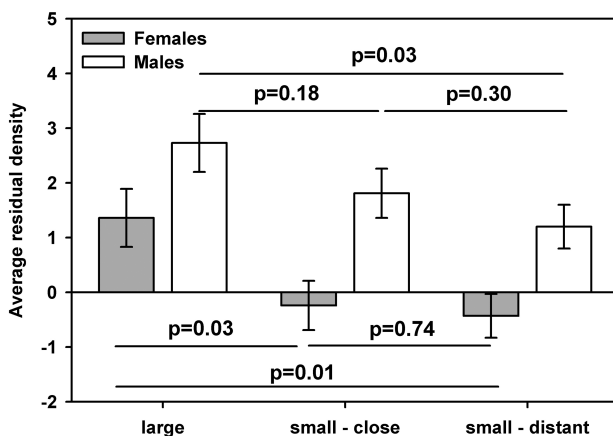


Fig. 4. – Differences in male and female winter moth densities between area-classes. P-values are corrected for multiple comparisons using Tukey’s method.

not affect the distribution of females. We can only speculate about why only male densities are lower with denser herb cover. Possibly, the lower male densities on those trees are the result of the fact that males also use the herb plants as substrate to wait for females. This behaviour has been observed (data not shown), but was not quantified because of practical difficulties in assigning particular herb plants to the area around a tree. Finally, the effects of fragmentation also appeared to differ between males and females. For females, densities were significantly lower in smaller forest fragments, irrespective of their degree of isolation. In males, densities were only lower in the more remote fragments. Thus, we provide evidence that both surface area and isolation affect densities, but that male dispersal could help to prevent or lower these effects in fragments located close to larger forests. Winter moth males do not appear to fly over

distances large enough to reach other areas when measured within a forest (VAN DONGEN et al., 1996). However, dispersal behaviour in open areas has never been studied in detail. In addition, hedgerows and linear tree-rows could act as corridors increasing connectivity, but their importance has never been investigated.

What mechanistic processes lie beneath the effects of surface area, isolation and distance from the edge are difficult to determine and require an experimental approach. With regard to the positive edge effect, it has been argued that this could be due to the larger sizes of host trees at the edge of forests (MURCIA, 1995). However, we still find this edge effect after controlling for the effect of tree size. In more isolated fragments, winter moths have been shown to exhibit lower degrees of genetic variability and lower fecundity (VAN DONGEN et al., 1994, 1998) which could have led to lower densities. In addition, it has been hypothesised that in more isolated forest fragments, winter moths would have problems synchronising their egg hatching with oak budburst (VAN DONGEN et al., 1997), which could further reduce fitness and densities. Since synchrony appears to be a major factor determining mortality of caterpillars and fecundity, we suggest that minute investigation of synchrony and of its spatial and temporal variation could lead to better insights into how fragmentation affects the population structure of the winter moth (VAN DONGEN, 1997).

Winter moth densities are affected by both regional fragmentation as well as local processes (habitat structure). The scale of sampling and analysis is very important in such situations. When all tree-specific variables were ignored, the effect of fragmentation was insignificant. Thus, controlling for various other effects at a local scale increases the statistical power and accuracy of pattern detection at a regional scale. In spite of the fact that several covariates were included in the model, there was still a large amount of unexplained variation in densities at both the level of the tree and of the habitat patches.

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