

Pre-dispersal seed predation of gorse (*Ulex europaeus*) along gradients of light and plant density

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Abstract: Common gorse (*Ulex europaeus*) is one of the most invasive species worldwide. Biological control of gorse by two pre-dispersal seed predators (the weevil *Exapion ulicis* and the moth *Cydia succedana*) is used in New Zealand. Gorse shrubs are distributed along wide natural gradients, and this could influence seed predation. The aim of this study was to identify factors that influence seed predation along two natural gradients, of light availability and gorse density. Seed predation was studied in the native range of the species, in south-west France. A total of 140 shrubs in stands with different irradiance and population densities were monitored. The number of seeds damaged was determined at different scales: the pod, the shrub and the gorse stand. The multi-scale analysis revealed that weevil activity increased with the quantity of gorse seeds produced, mainly at the pod and plot scales. The moth appeared satiated by abundant seed production at the bush and plot scales. In addition, moth activity was maintained in shady plots where weevil activity decreased. On the whole predation intensity was high and varied little along the density gradient (about 60–80% of seeds destroyed). Conversely, predation intensity decreased significantly with shade (from about 80% in full-light plots to 25% of seeds destroyed in the shadiest plots). These results could help predict the impact of pre-dispersal seed predation on the dynamics of gorse populations along environmental gradients. The activity of the moth appeared to be complementary to that of the weevil because it was maintained where the weevil was rare (i.e. in shady environments). Thus, the joint presence of the two predators may be helpful in the context of biological control of gorse.

Keywords: biological control; gorse seed weevil (*Exapion ulicis*); gorse pod moth (*Cydia succedana*); limit of habitat; multiple predators; multi-scale analysis; predator attraction; predator satiation

Introduction

Common gorse (*Ulex europaeus* L.) is an evergreen leguminous shrub native to the European Atlantic coast. It is considered one of the most invasive plant species in the world (Lowe et al. 2000). It alters native biodiversity (Sullivan et al. 2007), increases fire hazard (Anderson & Anderson 2010), invades pasture lands and competes with trees in planted forests (Clements et al. 2001). It has colonised approximately 3.6% of New Zealand ($\approx 900\,000$ ha) (Magesan et al. 2012).

Pre-dispersal seed predation can have strong ecological consequences by limiting seed production and plant fecundity. It determines individual reproductive performance, and can impact plant abundance, distribution and the assemblage of plant communities (e.g. Kolb et al. 2007a; Espelta et al. 2009). In the case of gorse, the larvae of two pre-dispersal seed predators, the gorse seed weevil (*Exapion ulicis* Förster) and the gorse pod moth (*Cydia succedana* Denis & Schiffermüller), feed on gorse seeds inside pods. The number of seeds dispersed in the environment by gorse plants can dramatically increase in the absence of the two seed predators (see table 1 in Rees & Hill 2001) and, for this reason, these two predators have been introduced as biocontrol agents in New Zealand (Hill et al. 2000). However, gorse shows an important variability of its fruiting phenology in both native and invasive contexts and some gorse seeds are produced out of the main period of predators' larval development (Hill et al. 1991; Atlan et al. 2010). Consequently, the annual percentage of pods infested

rarely reaches more than 60% (e.g. Tarayre et al. 2007; Davies et al. 2008).

Intensity of seed production of plants and their seed predation vary along natural gradients, such as light availability (Kolb et al. 2007b) or plant population density (Jones & Comita 2010). In turn, these variations can impact the number of seeds dispersed and plant population growth rates (Kelly & Dyer 2002). Gorse shrubs are distributed along wide environmental gradients since (1) the species commonly forms dense monospecific thickets in high light conditions and (2) its habitat range includes the understorey of evergreen forest systems, in its native area (Augusto et al. 2005). Thus, in addition to the impact of the fruiting phenology, seed predation intensity also depends on the position of gorse plants along these environmental gradients.

The outcome of the interactions between plants and seed predators not only depends on the effect of environmental variations, but also on the scale at which they are analysed. For example, at coarse scales, the size of *plant populations* can influence the presence or absence of the predators (Kéry et al. 2001). At finer scales, predators may be more attracted by patches of seeds borne by the *host plant* and its close neighbourhood and may aggregate more on highly fecund individuals (Jones & Comita 2010), or on the contrary be satiated by a surfeit of seeds to eat (e.g. Silander 1978). In addition, the outcome of seed predation on a given host plant could depend on predator satiation at the *fruit level* (i.e. larger fruits or seeds resulted in more satiation) (Bonal et al. 2007).

Thus, to understand the relative importance and strength of plant–insect interactions, analyses need to be conducted in a spatially explicit framework (Gripengberg & Roslin 2007).

In this study, our main aim was to characterise the intensity of seed predation and the response of seed predators to the variation of gorse seed production in the native range of the host plant. To this end, seed production and seed predation were studied along two gradients of light and population density of gorse, and at different nested scales: the pod (within the shrub), the shrub (within the sampled plot), and the plot scales (Fig. 1). This characterisation could have important implications for predicting the outcomes of biological control of gorse in an invasive context.

Materials and methods

Region of study and host plant (*Ulex europaeus*)

The study was conducted in 2010 and 2011 in the central part of the ‘Landes de Gascogne’ forest, in south-west France (44.5–44.8° N, 0.8–1.0° W). This forest is composed of even-aged stands of planted maritime pine (*Pinus pinaster* Ait). Soils in the region are poor acidic sandy soils (Augusto et al. 2010). Gorse is well adapted to this oligotrophic environment and naturally occurs in the understorey of the maritime pine forest. Gorse commonly forms dense monospecific thickets in very young stands under high light conditions because it is a light-demanding species. However, its distribution range also includes older forest stands.

Two main reproductive phenologies have been described for the species. This study focused on the phenology that is by far the most frequent in our study region, where flowering occurs only in early spring (Barat et al. 2007). In full-light conditions, a tall individual shrub can produce up to 1500 pods, but only a few pods in understoreys that receive less than 40% of photosynthetic active radiation (Delerue et al. 2013). The mean number of seeds per pod ranges from 2.5

to 5.0 seeds in the least and most suitable environments for gorse, respectively (Delerue et al. 2013). Gorse seeds are small (6-mg fresh mass and 2-mm diameter, on average), and this trait shows low variability (Hornoy et al. 2011).

Pre-dispersal seed predators

The gorse seed weevil (*Exapion ulicis* Förster, Apionidae) is specific to *Ulex europaeus*. It can fly from a temperature threshold of approximately 20°C (Hornoy 2012) but its dispersal ability is unknown. In spring, females lay batches of eggs in young pods, with an approximate total of 150 eggs in 30 ovipositions (Hornoy 2012). Adults are released at pod dehiscence. One cause of mortality of the larvae inside the pod is parasitism by a wasp (*Pteromalus sequester* Walker) (Barat et al. 2007).

The gorse pod moth (*Cydia succedana* Denis & Schiffmüller, Tortricidae) is bivoltine and infests gorse in spring. In autumn, it infests other *Ulex* species in Europe. How far female moths can fly is not known. Each female deposits a mean of 30 individual eggs on or close to a pod. Each larva chews a hole in the pod, feeds on the seeds, exits and then looks for another pod to feed on. It has been observed to feed on up to three different pods (Hill & Gourlay 2002). When a fruit that has been infested by the moth is opened, often only residual pieces of seeds and larval droppings are observed.

Distribution of plots along natural gradients

Dense gorse thickets are common in full-light conditions but not in old forest stands, since light availability decreases. Therefore, the experimental design was not factorial and was composed of two gradients, of light and density, analysed independently.

The light gradient

A total of 92 shrubs were sampled and shared between eight plots of at least 400 m² (Li-1 to Li-8) at seven sites along the range of light availability in the forest understorey (Table 1).

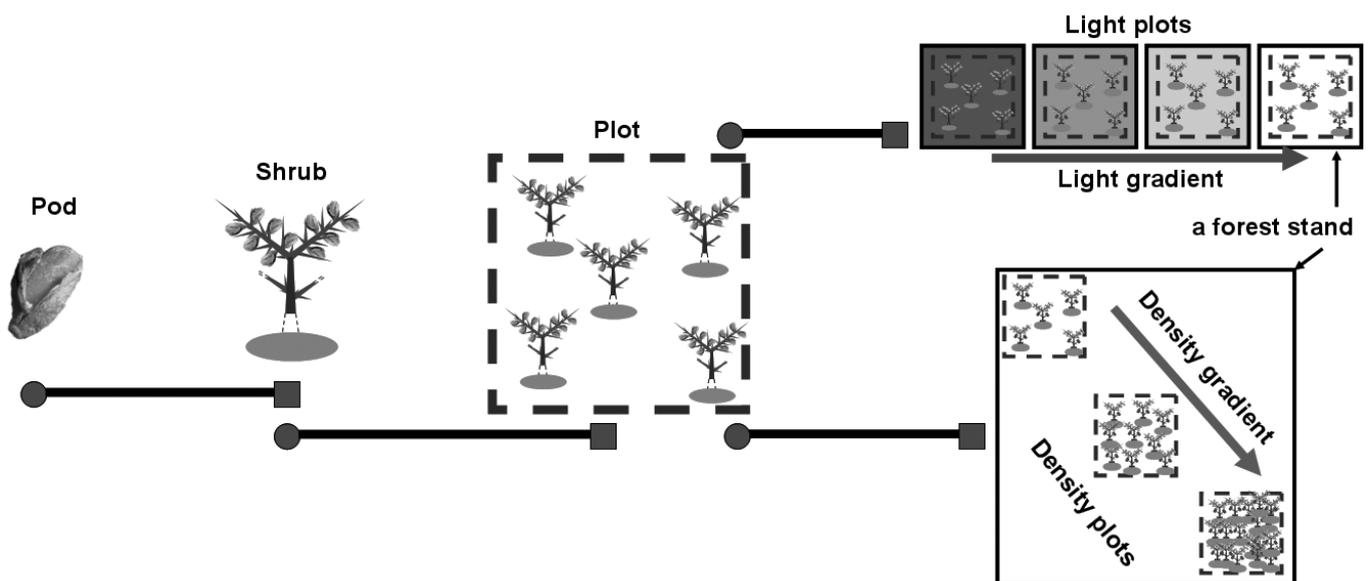


Figure 1. Nested scales of seed predation and data analysis along the light and density gradients. The different objects analysed are indicated by grey circles. Their corresponding level of nesting is indicated by grey squares and had to be taken into account during analyses. For example, to determine what makes a pod attractive to predators (the smallest scale), one must consider that pods were harvested on different gorse shrubs and that the predation of pods depends on their nesting scale on the same shrub.

Table 1. Description of experimental sites and main reproductive performance of gorse shrubs.

	Plot position on the natural gradient	Variable related to the natural gradient	Sampling year	Min – Max diameter (D ₁₀ in mm) ^c	Min – Max number of pods per gorse shrub	Mean number of seeds per pod (±SE)
		Mean light index (%) (±SD) ^a				
Light sample	Li-1	19 ± 4	2011	15.4 – 33.8	0–21	3.00 ± 0.38
	Li-2	29 ± 3	2010	10.5 – 36.8	0–69	2.72 ± 0.11
	Li-3	37 ± 5	2010	8.3 – 35.7	0–106	2.91 ± 0.12
	Li-4	46 ± 2	2011	9.9 – 28.0	4–111	1.80 ± 0.09
	Li-5	63 ± 4	2011	13.8 – 47.8	6–182	2.39 ± 0.11
	Li-6	87 ± 3	2010	8.8 – 57.3	6–544	3.15 ± 0.11
	Li-7	Full light	2010	11.0 – 41.3	76–923	3.72 ± 0.12
	Li-8	Full light	2011	15.3 – 43.1	30–1399	3.64 ± 0.10
		Mean density (indiv. m ⁻²) (±SD) ^b				
Density sample	De-1	0.2 ± 0.2	2010	11.0 – 41.3	76–923	3.72 ± 0.12
	De-2	0.3 ± 0.2	2011	15.3 – 43.1	30–1399	3.64 ± 0.10
	De-3	2.1 ± 0.8	2011	14.5 – 34.4	40–945	3.68 ± 0.09
	De-4	4.2 ± 1.7	2010	7.0 – 20.3	23–311	3.73 ± 0.10
	De-5	8.0 ± 1.9	2011	10.5 – 46.6	10–1067	4.30 ± 0.11
	De-6	9.8 ± 1.4	2010	9.3 – 29.0	54–660	4.67 ± 0.10

^a Given for the 12 individuals sampled per plot.

^b Mean and SD of the number of individuals in a 2-m radius around the 12 individuals sampled per plot.

^c D₁₀: Basal diameter measured 10 cm from the ground.

The full-light site was monitored in 2010 and 2011 (plots Li-7 and Li-8). Twelve gorse bushes per plot were selected in winter before the beginning of reproduction (except in the shadiest plot (Li-1) where there were only eight individuals growing). Individual plants were selected to represent a wide range of sizes (i.e. potentially producing a highly variable quantity of pods). For each shrub we used photosynthetically active radiation sensors to measure the fraction of incident light that it received, to create a light index of between 0% and 100% as in Delerue et al. (2013). The mean light index of all the shrubs sampled per plot was used to rank the plots along the light gradient (Table 1).

The density gradient

All 72 gorse plants studied along the density gradient were located at the same full-light site used in the light gradient. Each year, 36 shrubs were studied, which were shared equally between three plots of different densities (low, intermediate and high; see Table 1). ‘Low density plots’, where shrubs had no or few conspecific neighbours within a radius of 2.5 m (De-1 and De-2), correspond to the same plots used for light analyses (Li-7 and Li-8). Each year in winter, two additional 64-m² (8 × 8 m) plots with an intermediate density (De-3 and De-4) and high density of gorse shrubs (De-5 and De-6) were identified. By the end of summer, all the gorse plants in the density plots were cut to measure the mean number of conspecific neighbours in a 2-m radius around the individual shrubs sampled. This variable was used to rank the position of the different plots along the density gradient (Table 1).

Variable measurements

Production and predation rate of pods

All sites were visited every 2 weeks from complete maturation of the first pods (end of May) until the end of the reproductive period (beginning of July). At each visit, all the ripe pods were counted on each sampled gorse bush, and harvested before their opening. At each harvest date, 20 pods (when available) per individual shrub were opened randomly, giving a total of 4169 opened pods. In the case of predation by *Cydia succedana*, larvae were not always observed directly; however, the frass and exit hole were reliable signs of its presence. From these observations, we estimated (1) the predation rate of pods per shrub (0–100%), which was calculated from the percentage of pods that had been infested at each harvest date, weighted by the number of mature pods counted at this date, and (2) the number of pods infested per shrub (the predation rate of pods multiplied by the number of pods (pods plant⁻¹) produced).

Total number and percentage of seeds destroyed in pods

Inside ripe pods, at the end of their development, each weevil generally emerges from one seed and is well established in one seed chamber (Barat et al. 2007). In addition, each wasp generally feeds on one weevil. Thus, the number of weevils observed when the pods were opened plus the number of wasps provided a first raw estimation of the number of seeds damaged. This estimation was then corrected by examining the imprint of seed chambers in the pod endocarp and the residues of seed teguments and elaiosomes. In the case of predation by the moth larva, the determination of the number of damaged seeds was often impossible.

From these observations, two variables were calculated: (1) the sum of undamaged and damaged seeds gave the initial number of seeds in the pods opened; and (2) the percentage of seeds damaged inside the pods (the number of seeds damaged / initial number of seeds produced; 0–100%).

Multi-scale data analysis

All data analyses were performed using R software (R Development Core Team 2010). When performing an analysis at a given scale, we filtered out higher level effects due to our nested design (Fig. 1). Nested ANOVA, mixed modelling with random intercept, and standardisation were used for this purpose (see below). When regressions were fitted, we estimated their goodness of fit using the Modelling Efficiency (ME) as follows:

$$ME = 1 - \sum (y_i - \hat{y}_i)^2 / \sum (y_i - \bar{y})^2,$$

where y_i are the observations, \hat{y}_i the predictions of the regressions, and \bar{y} the mean of the observed values. ME ranges from 0 (model not better than \bar{y}) to 1 (perfect relationship).

For the graphical presentation of the results, the shrubs were split into three light classes (shady, medium- and full-light classes) according to the distribution of the tertiles of their light index. Three density classes were also created, by aggregating shrubs belonging to the De-1 and De-2 (low density) plots; De-3 and De-4 (medium density) plots; De-5 and De-6 (high density) plots. Individuals for which we had not been able to collect data from at least 15 pods were not used for analysis.

Predation at the pod scale

The percentages of seeds damaged inside pods between predators and plots were transformed following Warton & Hui (2011). Then, we used a nested ANOVA to test for the effect of the kind of predator on the explained variable, and performed pairwise multiple comparisons between pairs of plots. In addition, the initial number of seeds inside pods was compared between weevil-infested and not-infested pods (this could not be done for the moth). This was done with a mixed general linear regression model with Poisson distribution, log-link function, and a random intercept for each gorse shrub.

Predation at the shrub scale

To study the overall influence of the number of pods produced by the host plant on the number of pods infested by the predators, these variables were standardised given their mean and standard deviation at the plot scale. These standardised numbers of pods will be referred to hereafter as *relative in-plots number of pods*. Then, non-linear power relationships were fitted, between the number of pods infested and the total number of pods borne by the plant. Least-squares regression (*nls* function in R software) was used to fit these relationships following eqn (1):

$$At_i = a \times Pod_i^b + \varepsilon_i. \quad (1)$$

For the i^{th} shrub, At is the number of attacks, Pod is the number of pods, and ε is the residual error of the model. a and b are the model parameters. Values of b close to 1 indicate a linear relationship. If predators aggregate more (or conversely if they are satiated) on host plants with higher numbers of pods, the number of pods infested on the plant will show a convex (value of b higher than 1) or concave (values of b lower than

1) relationship with the number of pods borne by the plant.

Finally, the predation rates of pods of the two predators on the same shrub were also standardised to enable comparison with each other.

Difference in predation between plots

For each plot, we calculated the mean pod predation rates of shrubs for each predator. Then, we adjusted linear or non-linear (polynomial or exponential) relationships between these predation rates and the light index or mean density of gorse plants of the plots. Non-linear relationships were used to represent the possible non-linear activity of the predators along the gradients studied.

Sum of the effects of predation at all scales along the natural gradients

Finally, the total predation rate of seeds for each individual shrub was calculated as the ratio of seeds dispersed to seeds produced by a shrub expressed as a percentage. The number of seeds produced by each shrub was calculated as the number of pods produced by a shrub multiplied by the mean number of seeds produced per pod (intact + damaged seeds). The number of seeds dispersed was calculated according to eqn (2):

$$SeedDisp_i = Pod_i \cdot SeedPod_i \cdot (1 - [PropExap_i \cdot SeedExap_i]) \cdot (1 - [PropCyd_i \cdot SeedCyd_i]). \quad (2)$$

For the i^{th} individual in the j^{th} plot, $SeedDisp$ is the total number of seeds dispersed, Pod is the number of pods produced, $SeedPod$ is the mean number of seeds per pod, $PropExap$ and $PropCyd$ are the percentages of pods infested by the weevil and the moth respectively, $SeedExap$ and $SeedCyd$ are the percentages of seeds destroyed inside pods by the weevil and the moth respectively. The variation of this total predation rate of seeds was analysed with regards to the mean light index or density of gorse plants of the plots.

Results

Predation at the pod scale

Differences in the percentage of seeds damaged inside pods by the different predators on a given shrub were highly significant in both gradients ($P < 0.001$, nested ANOVA). However, the percentages of damaged seeds were always high, mainly between 75% and 90% in all plots for the weevil and higher than 90% for the moth (except Li-4). The portion damaged by the weevil consistently represented 85–90% of that of the moth (Table 2).

The predation damage by each predator showed significant differences between plots of the two gradients (Table 2). These differences did not appear to be structured along the natural gradients for the moth. Regarding the weevil, higher percentages of seeds were damaged in the plots in full-light conditions and low density (Li-7 and Li-8 plots, which are equivalent to De-1 and De-2 plots).

In addition, we found that pods infested by the weevil contained a higher number of seeds than uninfested pods in both the light sample (Fig. 2a) and density sample (Fig. 2b).

Predation at the shrub scale

In the light gradient (Fig. 3a), the number of pods infested by the moth increased less than the number of pods borne by the

Table 2. Differences in the percentage of seeds damaged inside pods by both predators along the light and density gradients.

Percentage of seeds damaged inside pods						
	Plot ^a	The weevil (Mean ± SE)		The moth (Mean ± SE)		Mean weevil / Mean moth
Light sample	Li-2	79.2 ± 1.4	ab	90.8 ± 2.8	ab	0.87
	Li-3	83.7 ± 6.0	ab	94.9 ± 1.2	bc	0.88
	Li-4	62.0 ± 10.3	a	85.5 ± 3.6	a	0.73
	Li-5	85.9 ± 3.3	ab	96.4 ± 1.3	bc	0.89
	Li-6	84.1 ± 2.7	ab	96.8 ± 0.9	bc	0.87
	Li-7	92.5 ± 1.2	b	98.1 ± 1.1	c	0.94
	Li-8	90.7 ± 1.3	b	97.5 ± 1.0	bc	0.93
	Average per gorse shrub in the whole sample		85.8 ± 6.8		95.8 ± 3.3	
Density sample	De-1	92.5 ± 1.2	c	98.1 ± 1.1	b	0.94
	De-2	90.7 ± 1.2	bc	97.5 ± 1.0	b	0.93
	De-3	77.9 ± 1.9	a	96.3 ± 1.3	ab	0.81
	De-4	83.8 ± 2.0	abc	98.1 ± 1.0	b	0.85
	De-5	86.1 ± 1.6	b	100.0 ± 0.0	b	0.86
	De-6	75.8 ± 1.8	a	92.0 ± 2.2	a	0.82
	Average per gorse shrub in the whole sample		82.9 ± 1.6		97.1 ± 2.5	

^a Plot Li-1 could not be represented because only one individual produced more than 15 pods and the percentage of seeds damaged could not be determined.

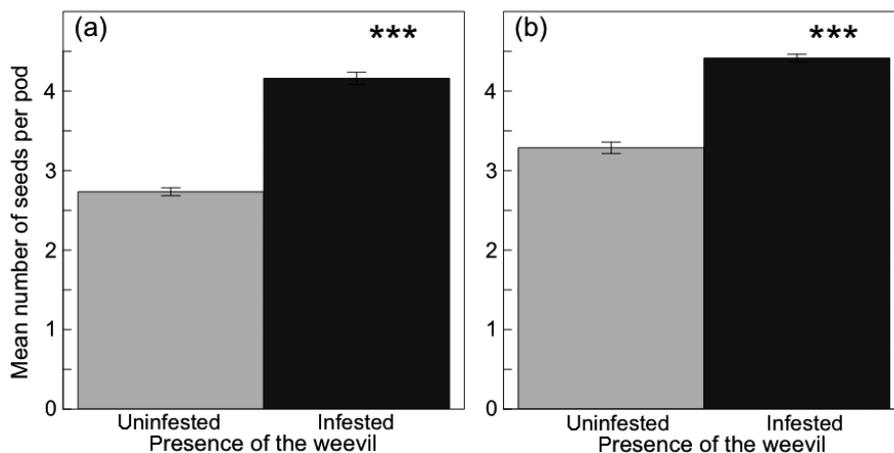


Figure 2. Relationship between the number of seeds per pod and the presence of weevil larvae along the light (a) and density (b) gradients. Bars indicate the mean (\pm SE) of the relative in-shrub number of seeds per pod. Asterisks indicate the significance of the mixed general linear modelling (***) $P < 0.001$.

host plant (b parameter value < 1). Regarding the activity of the weevil, we found the opposite trend ($b > 1$) but the 95% confidence interval of b contained 1 ($b \in [0.88 - 1.50]$). When considering the combined results of predation (weevil + moth), the number of attacks was proportional to the number of pods on the host plant ($b \approx 1$) with a very high goodness of fit of the relationship (Modelling Efficiency, ME = 0.97). Along the density gradient (Fig. 3b), the number of pods infested by the moth also tended to increase less than the number of pods borne by the host plant ($b < 1$; 95% confidence interval = 0.72–1.07). The total number of attacks was proportional to the number of pods on the host plant ($b \approx 1$, ME = 0.94).

Along both gradients, for a given shrub, there was a negative covariance of the predation rates of pods of the two predators (Fig. 4a,b). In addition, along the light gradient (Fig. 4a) high predation rates of pods by the moth were found more frequently on less-fecund shrubs, while host plants with many pods were subject to higher predation rates by the weevil.

Difference of predation between plots

The predation rate of pods by the weevil increased exponentially along the light gradient (Fig. 5a), while that of the moth was more variable, and neither increased nor decreased consistently along the light gradient (Fig. 5b). This resulted in an increase in the total predation rates of pods along the light gradient (Fig. 5c). In the density sample, the pod predation rate by the weevil was highest in the densest plots (Fig. 5d), whereas predation by the moth tended to decrease along the density gradient (Fig. 5e). On the whole, no significant variation in the total predation rate of pods was observed along the density gradient (Fig. 5f).

Sum of the effects of predation at all scales along the natural gradients

Both seed production by individual shrubs before predation and the number of seeds finally dispersed showed exponential

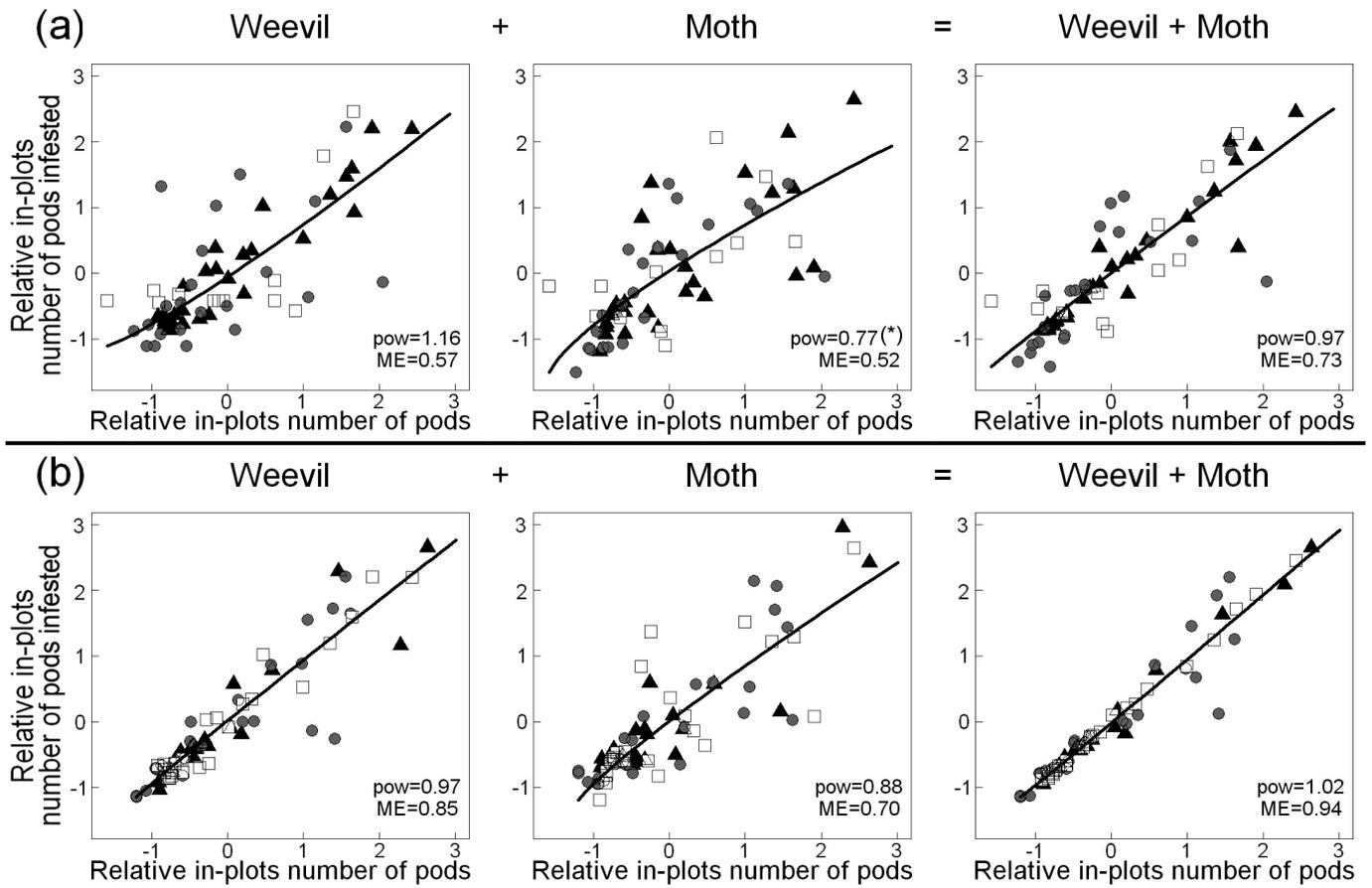


Figure 3. Relationships between the number of pods infested by each predator or by both predators and the number of pods borne by the host plant along the light (a) and density (b) gradients. In the bottom right-hand corner of the plots, ‘pow’ (for power) indicates the value of parameter b of the models fitted according to eqn (1) (*, the 95% confidence interval of b does not include 1). The goodness of fit of the relationships (Modelling Efficiency, ME) is also given. The fitted relationships are represented by solid black lines.

In (a) □ is the shady class ($N = 12$ (30 minus 2 operator errors and 16 shrubs that produced fewer than 15 pods)), ⊙ is the medium-light class ($N = 22$ (31 minus 1 operator error and 8 shrubs that produced fewer than 15 pods)), ▲ is the full-light class ($N = 29$ (31 minus 2 shrubs that produced fewer than 15 pods)). In (b) □ represents low-density plots ($N = 24$), ● represents medium-density plots ($N = 24$), ▲ represents high-density plots ($N = 23$ (24 minus 1 operator error))

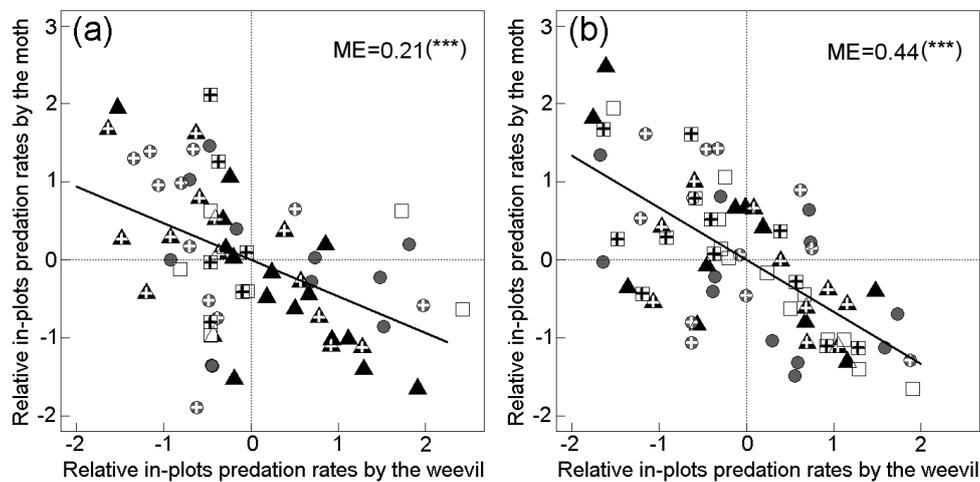


Figure 4. Covariance between the predation rates of pods of the two predators on the same shrubs along the light (a) and density (b) gradients. At the top of the panels, the goodness of fit of the relationships (Modelling Efficiency, ME) and their significance (***) are given. Within a plot, the higher the relative predation rate of a given predator, the higher this rate compared with the mean of the plot, while negative values indicate rates below the plot mean. The symbols indicate the light or density classes as in Fig. 3. For each plot, shrubs with low fecundity (pod-set below the median of the plot, symbols with patterns) are distinguished from shrubs with high fecundity (pod-set equal to or above the median, plain symbols).

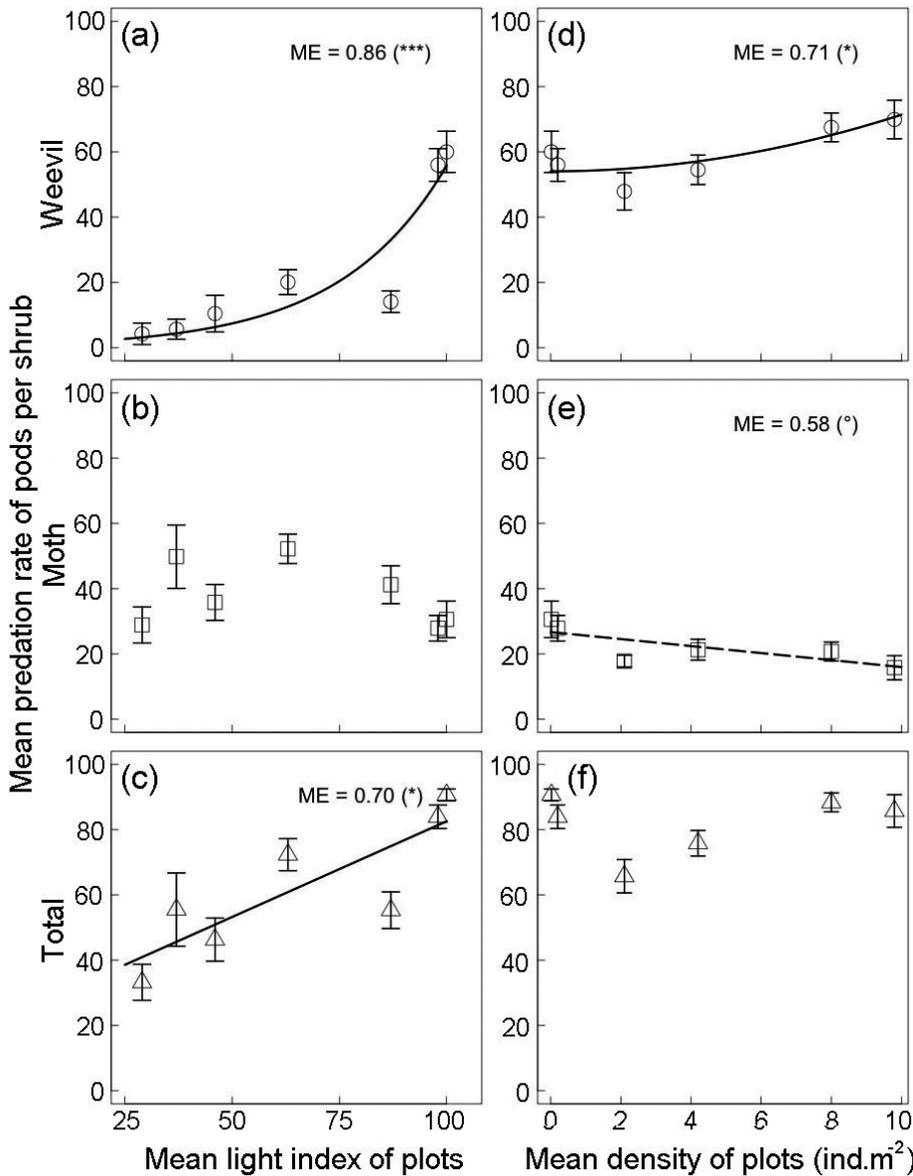


Figure 5. Variations in the predation rates of pods of the two predators and in the total predation rates of pods among plots distributed along the light (a, b, c) and density (d, e, f) gradients. At the top of the panels, the goodness of fit (Modelling Efficiency, ME) of the significant relationships (*** $P < 0.001$; * $P < 0.05$; ° $P < 0.1$) is given. These relationships are shown with solid lines (dashed line if $P < 0.1$). Non-linear relationships are shown in (a) (exponential) and (d) (polynomial of order 2, a linear relationship is not significant here). Standard errors are shown with vertical lines on the symbols.

$N = 8, 5, 7, 10, 9, 12$ and 12 individuals for plots Li-2 to Li-8 respectively (Li-1 could not be represented because only one individual produced more than 15 pods). $N = 12, 12, 12, 12, 9$ and 12 individuals for plots De-1 to De-6 respectively.

relationships with light availability along the light gradients (Fig. 6a). However, the total predation rate of seeds also increased along the light gradient (Fig. 6c), thus the difference in the number of seeds finally dispersed between the lightest and shadiest plots was lower than when predation was not taken into account (Fig. 6a).

The mean seed production per individual tended to decrease slightly with an increase in the number of neighbours along the density gradient (Fig. 6b), but the total predation rate of seeds remained constant along the entire density gradient (Fig. 6d) and the number of seeds produced and dispersed per individual shrub responded in parallel (Fig. 6b). In low-, medium- and high-density plots (in the same forest stand) the values observed in 2011 were close to the values observed in 2010.

Discussion

From the pod to the plot scale, we found evidence that gorse seed predation is ubiquitous but not uniform along the light and density gradients studied.

Predation at the pod scale

The percentage of seeds damaged by the weevil inside pods was lower than that damaged by the moth in both gradients. However, the ratio of the percentage of seeds destroyed inside pods by the weevil to that destroyed inside pods by the moth was approximately 90% in all plots. In addition we found that the damage by the weevil was higher in full-light conditions and low gorse plant density. Hoddle (1991) showed that female weevils preferred to oviposit in pods free of other conspecific larvae. However, because weevils were much more abundant in corresponding plots compared with other shaded plots (see Fig. 5a), and because other gorse plants (and oviposition sites) were distant from the sampled host plants, several ovipositions on one single pod may have occurred more often, leading to more weevil larvae in pods and a higher percentage of seed damaged. Even so, the observed differences among plots were small. On the whole, the percentages of seeds destroyed inside pods by both predators are comparable. These percentages are also comparable between the different plots. Therefore the direct comparison of the predation rate of pods of both predators and between shrubs or plots at coarser scale seems rational.

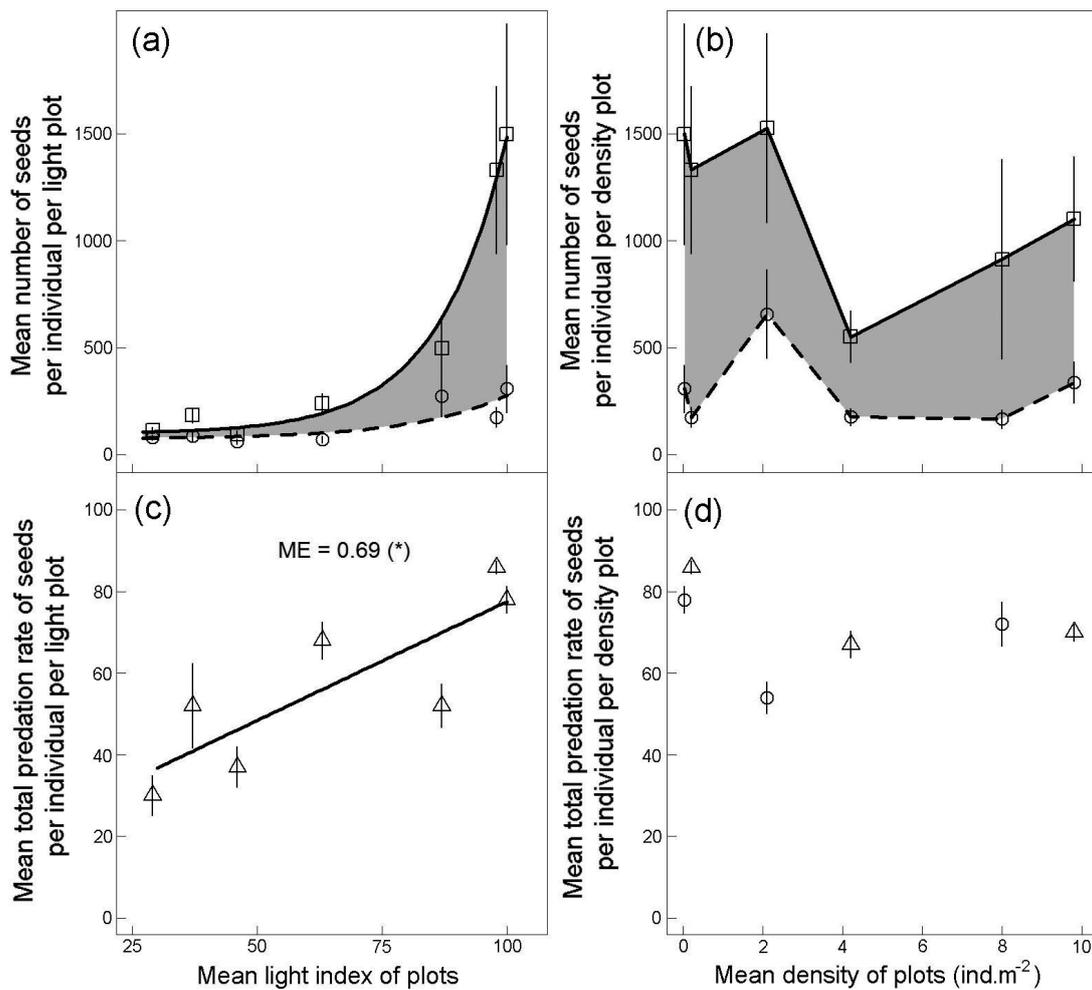


Figure 6. Sum of all the effects of predation on seed production along the light (a) & (c) and density (b) & (d) gradients. In (a) and (b) the mean number of seeds produced by individual bushes (before predation) is indicated by squares; the mean number of seeds dispersed (see eqn (2)) is indicated by circles. The grey areas represent the effect of predation on seed production. In (a) exponential relationships are fitted between the number of seeds produced (solid line) or dispersed (dotted line) and the mean light index of the plots. In (b) the numbers of seeds produced and dispersed are linked respectively by solid and dotted lines but no relationships were fitted. In (c), the significant linear relationship between the mean proportion of seeds destroyed per plot and the mean light index of the plot is shown (the ME is given at the top of the panel). In (d) predation rates in the first year of the study (triangles) are distinguished from those in the second year (circles). Standard errors are shown with vertical lines on the symbols. Li-1 is not represented, as in Fig. 4. The number of individuals in all plots is given in Fig. 5.

The results showing that pods infested by the weevil contained more seeds than uninfested pods is consistent with the preference-performance hypothesis (Jaenike 1978; Gripenberg et al. 2010), assuming that females choose the most suitable sites for the optimum development of their larvae. Indeed, since gorse seeds have a constant size, a pod that contains more seeds could ensure the complete development of more weevil larvae. The size of the pod, which is linked to the number of seeds it contains, could play a determining role in the female’s choice to oviposit (Hornoy 2012).

Predation at the shrub scale

The weevils and the moth responded differently to the increase in number of pods borne by the host plant. Considering predation by the *weevil*, in the *light plots* the number of pods infested tended to increase more than the number of pods borne by the host plant (Fig. 3a) but the non-linear (convex) relationship was not statistically confirmed. In fact, higher predation rates of pods were often found on more fecund

individuals (Fig. 4a). In the *density plots*, no departure from linearity appeared. On the whole, at the shrub scale, the activity of the weevil was not strongly modified by the set of pods borne by the host plant, even if this activity tended to increase in the light plots.

In both gradients, the number of pods infested by the *moth* appeared to increase less than the number of pods borne by the host plant. However, this observed non-linear (concave) relationship was only significant in the light plots (Fig. 3a). In that case, it could imply that the ability of the moth to oviposit was satiated when the number of pods on a given shrub increased.

Considering the total number of pods infested by the weevil and the moth, strong linear relationships ($b \approx 1$, $ME > 0.90$) were found with the number of pods of the shrubs (Fig. 3a,b). This was due to a negative covariance of the predation rates of pods by the two predators (Fig. 4a,b), i.e. their pod predation rates compensated each other at the shrub scale. However, the different responses of the two predators described above

are not sufficient to explain this compensation. Indeed, when several predators exploit the same resource, they can interact synergistically or antagonistically (Ives et al. 2005). In line with this, two non-exclusive explanations may account for the observed negative covariance. First, in the density plots (Fig. 4b), the total level of predation was high. It likely resulted in competition for oviposition sites between the predators. Indeed, a higher predation rate by one predator necessarily implied a lower rate by the other on the same plant; otherwise their sum would have exceeded 100%. Second, in cases where the percentage of pods that escaped predation was high (e.g. the medium-light plots, see Fig. 4a), both predation rates could be high (relative to those found in the plot) and uninfested pods could still be available. Thus the simultaneously higher or lower relative predation rate of the two predators was expected, at least in some cases. It did not occur in our study. This suggests that one predator forages preferentially where the other is absent. Allelochemical compounds produced by the seed predators (Hodde 1991) or by gorse plants (Hornoy et al. 2012) may be involved in this foraging behaviour. In any case, as a consequence of the negative covariance observed for both predators, the total number of pods infested finally matched the quantity of pods of the host plant.

Difference of predation between plots

Along the *light gradient*, the increase in pod predation rate by the weevil is consistent with the results of several other studies showing the preference of weevil species for high light conditions (e.g. Hough-Goldstein & LaCoss 2012). Indeed, Hornoy (2012) showed that the flight activity of the gorse seed weevil is influenced by warmer temperatures. However, a higher number of weevils in the light plots Li-7 and Li-8 could also result from their attraction to a large gorse population in the corresponding forest stand (the density gradient was set up in the same stand). It should be pointed out that both the pod predation rate by the weevils (Fig. 5a) and the production of seeds by gorse shrubs (Fig. 6a) showed a similar exponential relationship with the light index of the plots. These two explanations are not exclusive and may reinforce the phenomenon.

The distribution of the moth did not appear to be linked with light availability. As the moth flies at around dusk, it may not be sensitive to the variation of incident light. In addition, interactions with the weevil may also be involved. In particular, the presence of the moth could have been higher in full-light conditions without the presence and competition for oviposition sites with the weevil in the corresponding plots.

Along the *density gradient*, we found the highest predation rates of pods by the weevil in the densest plot, while the highest predation rates by the moth were found in the low-density plots. This is consistent with the negative covariance observed at the shrub scale. In addition, the results for the activity of the weevil are consistent with the study of Moravie et al. (2006), who showed an aggregation of another Apionidae (*Apion onoropodi*) with limited dispersal ability on high quality patches.

Sum of the effects of predation on seed production and ecological implications

At the pod scale, variation in the percentage of seeds damaged was small along both gradients. At the shrub scale, the rate of pod predation by each predator compensated for the other. Therefore the key determinant of the outcome of predation revealed by the multi-scale analysis is the plot in which the

gorse shrubs grew and the position of the plot along the natural light and density gradients.

Along the *light gradient*, both the reproductive output of gorse and the intensity of predation were low in the shade. Indeed gorse is a light-demanding species, and at the limit of the habitat of a species, its abundance and reproduction are known to decrease along with seed predation by granivorous species (e.g. Vaupel & Matthies 2012).

The *density gradient* was set up in a single forest stand that, on the whole, contained many gorse shrubs. Thus, the high intensity of predation all along the density gradient may reflect the effect of the size of the gorse population at larger scales than those of the study. However, locally in the studied forest stand, the total intensity of predation did not appear to be influenced by variation in gorse shrub (and seed) density.

Within the studied plots, at the shrub scale, the results suggest antagonistic interactions between the predators. However, the most determinant variation in predation intensity appeared at the plot scale, and these may reveal some differences in niche between the two predator species. The activity of the weevil was highest in the lightest plots and patches where gorse seeds were abundant, while the activity of the moth was maintained in a wider range of light environments. Even when Gourlay et al. (2003) found that the moth suppressed the activity of the weevil, the total predation of seeds when both predators were present increased compared with the predation by the weevil acting alone. Therefore, even if the impact of both predators is not strictly additive, seed predation may reach the highest level where both predators are present.

The weevil was introduced to New Zealand in 1931 and is now well established (Hill et al. 2000). The moth was introduced more recently in 1992 and its establishment throughout the country is also expected (Hill & Gourlay 2002). In that case, the joint presence of the two predators may be helpful for the biological control of gorse. However, for seed predation to have ecological consequences, it must impact the growth rate of the plant population (Ehrlén 2002). Previous work has estimated the potential impact of biocontrol agents of gorse (Rees & Hill 2001). The new results presented here could help more precise assessment of the impact of pre-dispersal seed predation on the dynamics of gorse populations along environmental gradients.

Conclusions

On the whole, predation intensity by the weevil was higher where the number of seeds was greatest (i.e. in pods with many seeds, on more fecund gorse shrubs in light plots, and where shrubs were at a high density). This may be because female weevils are attracted to abundant gorse seeds and because of aggregative behaviour. The moth appeared satiated by abundant pod production by gorse shrubs in the light plots, and its activity tended to decrease in the densest plot accordingly. However, the activity of the moth appeared to be complementary to that of the weevil because it was maintained in shady environments where the weevil was rare. Therefore, biological control against gorse may achieve highest seed destruction with both seed predators. To gain a better understanding of the ecological consequences of these results, and of their implications for biological control, further investigations must integrate these variations of intensity of predation into a larger view of the fitness of the species' populations along the same natural gradients.

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