

# Habitat fragmentation alters predator satiation of acorns

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## Abstract

### Aims

Acorn weevils (*Curculio* spp.), endoparasitic granivorous insects, impede recruitment of fagaceous trees, and in turn affect community structure and ecosystem functioning. Previous studies have made considerable progress in elucidating local factors that contribute to seed predation by acorn weevils, but it is still not clear how habitat configurations interplay with local factors in influencing *Curculio* predation. In this study, we assessed the roles of crop size, landscape configurations (area and isolation) and their interactions on the predation rate of seeds by acorn weevils.

### Methods

We studied acorn weevils feeding on the seeds of *Castanopsis sclerophylla* (Fagaceae) on two peninsulas and nine islands with varying areas and isolation levels in the Thousand-island Lake in Chun'an County, Zhejiang Province of China. Overall, crop size was estimated for 130 trees and predation status was assessed for 26 207 seeds from these trees during two years. Generalized linear mixed models were performed to clarify how island area and

isolation interplayed with crop size to determine predation rate on a single tree.

### Important Findings

A negative relationship was detected between crop size and seed predation rate, indicating predator satiation at the tree level. This suggests that acorn weevils tend to stay sedentary once they have arrived at a suitable habitat. Habitat fragmentation had significant effects on seed predation such that predation rate was higher on larger, less isolated islands. Furthermore, the relationship between crop size and predation rate was significantly changed by both island area and isolation. This finding highlighted that the effects of habitat isolation might be overlooked relative to those of habitat loss.

**Keywords:** *Castanopsis sclerophylla*, *Curculio*, isolation, limited dispersal, predator satiation

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## INTRODUCTION

Before germinating, seeds usually have to face the risk of being devoured by various animals including insects, rodents and others (Janzen 1971). As a response, plants have evolved at least two strategies to cope with seed predation. On one hand, plants may resist seed predators by physical or chemical defenses. For example, a thicker pericarp helps Japanese camellia (*Camellia japonica*) resist adult camellia weevils (*Curculio camellia*), which use their long rostrum to pierce the pericarp for oviposition (Toju and Sota 2006). In some *Quercus* species, acorns with high contents of secondary compounds, such as tannins, show lower predation by insects (Weckerly *et al.* 1989).

An alternative strategy for plants to cope with seed predators is by satiating the predators. Predator satiation, which was initially proposed in the study of periodical cicadas (Insecta: Homoptera; Lloyd and Dybas 1966), describes a pattern where the number of preys far exceeds the potential number that can be eaten by the predators, and thereby most preys escape predation. Thus, an inverse relationship between predation rate and prey availability can be predicted when predator satiation occurs (O'Dowd and Gill 1984). For seeds and seed predators, satiation and such inverse relationships have been reported, especially in mast seeding, i.e. when the synchronous production of seeds over long intervals by a plant population, is observed (see Kelly and Sork 2002 and references therein). However, seed predators are mostly found to be satiated at or

above the population level, whereas relatively little is known about seed predator satiation on a single tree (Romañach and Levey 2000). Furthermore, the only prerequisite for seeds to satiate predators is a crop size above the threshold which can be potentially taken by all local seed predators. Thus, predator satiation does not necessarily involve masting, although predators are more likely to be satiated in masting years (Kelly 1994).

Habitat fragmentation, which breaks a continuous habitat into several spatially isolated small fragments (Fahrig 2003), has been reported to adversely affect several interacting species (Hadley and Betts 2012; Magrath *et al.* 2014). This process can have nontrivial effects on the local predator populations (Terborgh *et al.* 2001; Laurance *et al.* 2011; Brezzi *et al.* 2017; Staab *et al.* 2017). However, to what extent and how the interactions between seeds and their predators will be influenced by habitat fragmentation are still far from understood.

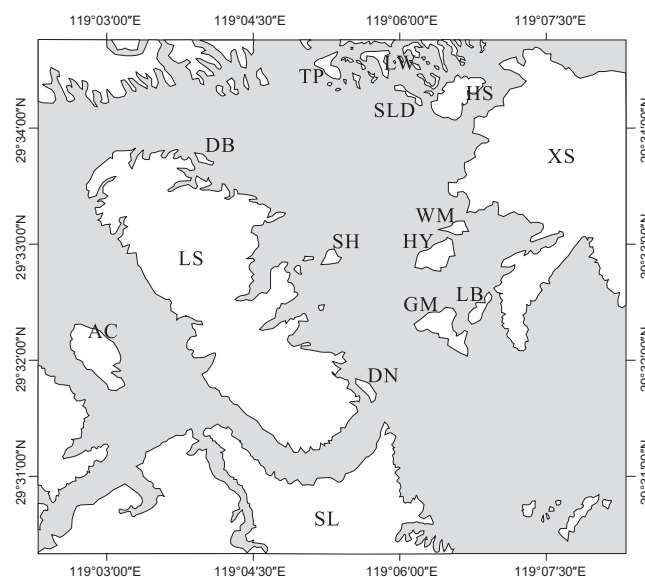
Habitat loss and breaking apart of habitats, the direct consequences of habitat fragmentation, could depress local predator populations (Laurance *et al.* 2011). The smaller a habitat is, the smaller the predator populations that could be sustained by it (Fahrig 2003). However, immigration can bring about an increase in predator populations and a decrease in the probability of local extinction for predators, i.e. the rescue effect (Stouffer *et al.* 2009). A small population which is more isolated and has lower immigration rates may suffer a higher risk to local extinction. Therefore, it may be expected that predators in larger habitats will exert higher predation pressures and are more likely to act as source populations for immigration. Sink populations that are farther from the source populations will show lower predation pressures. Alternatively, in smaller and isolated habitats, the predators may find refuge from their own enemies and impose stronger predation pressure on their rather limited food sources. Whether these differences in predation pressures that are caused by habitat fragmentation can in turn affect predator satiation remains an open question.

In this study, we tested these hypotheses *via* investigating how predation of *Castanopsis sclerophylla* (Fagaceae) seeds by acorn weevils (*Curculio* spp., Curculionidae) was shaped by crop size and landscape configurations on an archipelago of China. A total of 26 207 seeds were collected from both the mainland and nine islands as examples of isolated environments. By checking each seed for weevil predation, we addressed two specific questions: (i) Could large seed crops satiate predators on a single tree? If so, (ii) Did landscape configurations (here specified as island area and level of isolation) have significant effects on predator satiation?

## METHODS

### Study sites

This study was conducted at the southeastern region of the Thousand-island Lake (29°30'00"–29°35'00"N, 119°00'00"–119°07'30"E) in Chun'an County, Zhejiang Province, China (Fig. 1). This inundation was created in 1959 after the establishment of Xin'anjiang Dam. The mean annual precipitation



**Figure 1:** sampling localities for *C. sclerophylla* seeds in our study. XS and SL are peninsulas while others are islands.

is 1429.9 mm and the mean annual temperature is 17.0 °C. The zonal vegetation is evergreen broad-leaved forests with *C. sclerophylla* being the most common Fagaceae species. This region was selected since it contains islands with varying landscape configurations (island area and isolation) and is therefore appropriate for testing effects of habitat fragmentation (Table 1).

Island area and isolation were calculated using Google Earth (Google, Inc. Mountain View, CA, USA) images and software ArcGIS 9.3 (ESRI 1999–2008). There are two common measures for quantifying patch isolation (Fahrig 2003). The first is the distance to the nearest neighbor patch (Delin and Andrén 1999; Hargis *et al.* 1999). Alternatively, one can measure patch isolation as the distance of this patch to the mainland (Haila 2002). This measure emerged from the theory of island biogeography (MacArthur and Wilson 1967). To understand the difference between the two measures, one can imagine two small islands far from the mainland but adjacent to each other (islands TP and LW, e.g. in this study). If one took the first measure, he would conclude that each island face a small degree of isolation. In contrast, the second measure would inform us that both islands were highly isolated. Since there would be little rescue effect among small islands, the latter was more reasonable, at least in our case. Therefore, island isolation was measured as the minimum distance of this island to the peninsulas (XS and SL) or to the largest island LS. Island LS was a very large habitat for acorn weevils, and thus we set its isolation to 0.

### Study species

*C. sclerophylla* (Lindley and Paxton) Schottky, a monoecious and self-compatible nut-bearing tree, is one of the most common plant species in subtropical evergreen broad-leaved forests (Shi

**Table 1:** seed predation by acorn weevils in different habitats in the Thousand-island Lake region

| Sites | Landscape type | Area (ha) | Isolation (m) | Number of studied trees | Crop size (mean $\pm$ SE; seeds per branch) |               | Predation rate (%; mean $\pm$ SE) |            |
|-------|----------------|-----------|---------------|-------------------------|---------------------------------------------|---------------|-----------------------------------|------------|
|       |                |           |               |                         | Year 2011                                   | Year 2012     | Year 2011                         | Year 2012  |
| SL    | Peninsula      | —         | 0             | 18                      | 303.3 (120.4)                               | 201.9 (73.1)  | 11.0 (3.4)                        | 6.7 (2.2)  |
| XS    | Peninsula      | —         | 0             | 23                      | 37.7 (7.4)                                  | 246.8 (46.2)  | 8.8 (3.2)                         | 13.9 (7.1) |
| AC    | Island         | 50.6      | 386           | 14                      | 62.2 (19.7)                                 | 134.3 (25.9)  | 5.4 (1.8)                         | 22.2 (9.0) |
| DN    | Island         | 1.1       | 106           | 10                      | 193.3 (57.7)                                | 199.6 (106.3) | 8.7 (5.3)                         | 7.5 (3.9)  |
| GM    | Island         | 15.6      | 689           | 5                       | NA                                          | 105.8 (24.2)  | NA                                | 6.9 (4.4)  |
| HY    | Island         | 13.0      | 559           | 14                      | 77.7 (47.4)                                 | 363.9 (87.7)  | 0.4 (0.4)                         | 1.1 (0.7)  |
| LS    | Island         | 874.9     | 0             | 28                      | 188.2 (39.2)                                | 279.4 (36.6)  | 12.7 (4.6)                        | 41.8 (7.3) |
| LW    | Island         | 7.1       | 120           | 5                       | 115.8 (48.1)                                | 254 (NA)      | 0.6 (0.6)                         | 7.9 (NA)   |
| SH    | Island         | 1.5       | 680           | 9                       | 185.0 (67.3)                                | 249.4 (80.6)  | 0.9 (0.9)                         | 2.2 (0.9)  |
| TP    | Island         | 3.9       | 202           | 2                       | 74.5 (41.5)                                 | NA            | 4.1 (1.1)                         | NA         |
| WM    | Island         | 3.2       | 302           | 2                       | NA                                          | 197.0 (155.0) | NA                                | 0.1 (0.1)  |
| Total |                |           |               | 130                     | 149.9 (25.5)                                | 238.4 (22.7)  | 7.9 (1.5)                         | 15.3 (2.7) |

Abbreviation: SE = standard error.

and Chen 2012). This species flowers from April to May, and its pollen dispersal is mediated mainly by wind, and therefore not substantially attenuated by habitat fragmentation (Wang et al. 2012). Seeds of *C. sclerophylla* become mature in October and November. The seeds are primarily dispersed by the gravity, and then eaten or secondarily dispersed by rodents.

Before primary dispersal, seeds of *C. sclerophylla* may be consumed by acorn weevils (*Curculio* spp., Curculionidae). Adult acorn weevils emerge between late summer and mid-autumn after pupation, and feed on leaves. After mating on the trees, the females bore a tiny hole through the testa with their snouts and oviposit into the seeds from August to mid-October (Bonal et al. 2012; Bonal and Muñoz 2008). Generally, there is only one larva in a seed, perhaps to avoid intraspecific competition, though sometimes different females may lay eggs in a single seed (Bonal and Muñoz 2009). The larvae developing inside the seeds feed on the cotyledons, and the embryo is likely to be intact if a seed is large enough, i.e. seed-level satiation (Bonal and Muñoz 2008). The infested seeds therefore may still germinate. After development inside the seeds, acorn weevil larvae leave the seeds and burrow underground, and diapause over winter until next summer (Espelta et al. 2009). However, some individuals have a prolonged diapause for several years to reduce the impacts of unfavorable environments (Menu 1993).

Acorn weevils are usually weak fliers, and even a few hundred meters would be considered as a significant dispersal barrier (Bonal et al. 2012; St Pierre and Hendrix 2003). For example, flight distances of *C. elephas* usually do not exceed 100 m (Bonal et al. 2012).

### Sampling design

Trees of *C. sclerophylla* were distributed on XS and SL, both of which were peninsulas, and on 13 islands within this region (see abbreviations in Fig. 1). After an extensive survey, we did not find any seed on *C. sclerophylla* trees on four islands (DB,

SLD, HS and LB). Thus, all seeds were sampled from the two peninsulas and nine remaining islands.

During 2011 and 2012, all seed-bearing *C. sclerophylla* trees on the islands, except the largest island LS, were tagged. Three plots (6 ha) were set up, respectively, on the largest island LS and the peninsula XS with a minimum distance of 2 km. Only one plot was set up on the peninsula SL, because *C. sclerophylla* trees covered a relatively small area there. We tagged all seed-bearing *C. sclerophylla* trees within each plot on LS, XS and SL. A total of 130 trees were tagged in this study. On several islands, sample sizes were small due to limited seed-bearing trees (Table 1).

To reduce the damage to the plant, we collected seeds from the branches with the largest crop size on each given tree. A total of 26 207 seeds were collected in early November and then stored in valve bags. Larvae of acorn weevils were checked daily until no larvae was found for 10 consecutive days. All sampled seeds were dissected to check for the presence of *Curculio* larvae. In total, 2746 acorn weevils and 76 Lepidopteran caterpillars were found inside these seeds. Further analyses with *COI* sequences showed that the acorn weevils consisted of two *Curculio* species, the dominant one being *C. bimaculatus* Faust and the other not yet identified (Hu X.H. et al., unpublished data).

### Data analyses

In this study, we focused on predation rate of seeds at the tree level. The differences of predation rates among sites were examined by Kruskal–Wallis rank sum test. The explanatory variables used to model predation rate were as follows.

- (i) Crop size of a single branch. This variable was centered and scaled before further analyses to reduce heteroscedasticity. The differences of crop size among sample sites and between peninsulas and islands were tested by analysis of covariance with year as a covariate.

- (ii) Landscape configurations: island area and isolation. The minimum distance from an island to the peninsulas (XS and SL) or to the largest island LS was used to evaluate isolation. Island area and isolation were also centered and scaled to reduce heteroscedasticity.
- (iii) Year. Seeds were collected in 2011 and 2012. Although the seed crop sizes were significantly larger in 2012 than in 2011 ( $F_{1,118} = 6.33$ ,  $P = 0.013$ ), there was no evidence for a mast year in 2012 from the raw data. Therefore, year was included in the analyses as a random factor, to account for temporal variation.

We used generalized linear mixed models (GLMMs) with a logistic link function to model predation rate as a function of crop size, landscape configurations (island area or isolation) and year, assuming a binomial distribution of residuals. Crop size and landscape configurations were treated as fixed effects and year as random effect. Overdispersion test for binomial data accomplished by the function “qcc.overdispersion.test” in the R package qcc (Scrucca 2004) showed that there was some overdispersion in our data ( $P < 0.0001$ ). To address this problem, we included island as an additional random effect in the models. Since island area and isolation were highly correlated ( $r = -0.577$ ,  $P < 0.0001$ ), it was difficult to disentangle the effects of each unambiguously in a single model. Thus, island area and isolation were included in separate models (hereafter as area model and isolation model respectively), and their effect will be discussed separately.

All statistical analyses in this study were conducted using R3.1.1 (R Development Core Team 2014). The function “glmer” in the package lme4 (Bates et al. 2015) was used to perform GLMMs.

## RESULTS

Seed crop size showed large variation among trees, ranging across four orders of magnitude (Table 1). Nevertheless, crop size did not show any significant difference either among sites ( $F_{10,118} = 1.38$ ,  $P = 0.20$ ), or between islands and peninsulas ( $F_{1,127} = 0.016$ ,  $P = 0.90$ ). Even when the largest island LS was excluded, islands did not show any significant deviation from peninsulas in crop size ( $F_{1,99} = 0.068$ ,  $P = 0.79$ ). Seed predation rate also displayed large variation among trees (Table 1). Furthermore, predation rate showed significant difference among sites (Kruskal–Wallis  $\chi^2_{(10)} = 32.98$ ,  $P = 0.0003$ ). There was no significant difference of predation rate between peninsulas and islands (Kruskal–Wallis  $\chi^2_{(1)} = 0.40$ ,  $P = 0.53$ ), but when LS was excluded, islands showed significant deviation from peninsulas in predation rate (Kruskal–Wallis  $\chi^2_{(1)} = 5.74$ ,  $P = 0.017$ ).

We found a significant negative relationship between predation rate and crop size, both in the area model and in the isolation model (Table 2, Fig. 2). In addition, predation rate significantly increased with island area, but marginally significant decreased with island isolation (Table 2). Furthermore,

**Table 2:** effects of crop size and habitat feature (area and isolation) on predation rate analyzed by the generalized linear mixed models

| Explanatory variables | $\hat{\beta}$ | SE     | $z$    | Pr(> z ) |
|-----------------------|---------------|--------|--------|----------|
| Area model            |               |        |        |          |
| Intercept             | -2.970        | 0.883  | -3.37  | 0.0008   |
| Crop size             | -0.779        | 0.046  | -16.79 | <2e-16   |
| Area                  | 1.366         | 0.540  | 2.53   | 0.0114   |
| Crop size:area        | -0.291        | 0.0377 | -7.71  | 1.29e-14 |
| Isolation model       |               |        |        |          |
| Intercept             | -3.429        | 0.876  | -3.91  | 9.07e-05 |
| Crop size             | -0.751        | 0.054  | -13.86 | <2e-16   |
| Isolation             | -0.868        | 0.453  | -1.92  | 0.055    |
| Crop size:isolation   | 0.370         | 0.052  | 7.18   | 6.80e-13 |

Abbreviations:  $\hat{\beta}$  = the estimate of regression coefficients; SE = standard error.

both island area and isolation altered the relationship between predation rate and crop size, as revealed by significant effects of interaction terms in both models (Table 2). Specifically, predation rate decayed with increasing crop size faster in larger islands (Fig. 2A), and faster in less isolated islands (Fig. 2B).

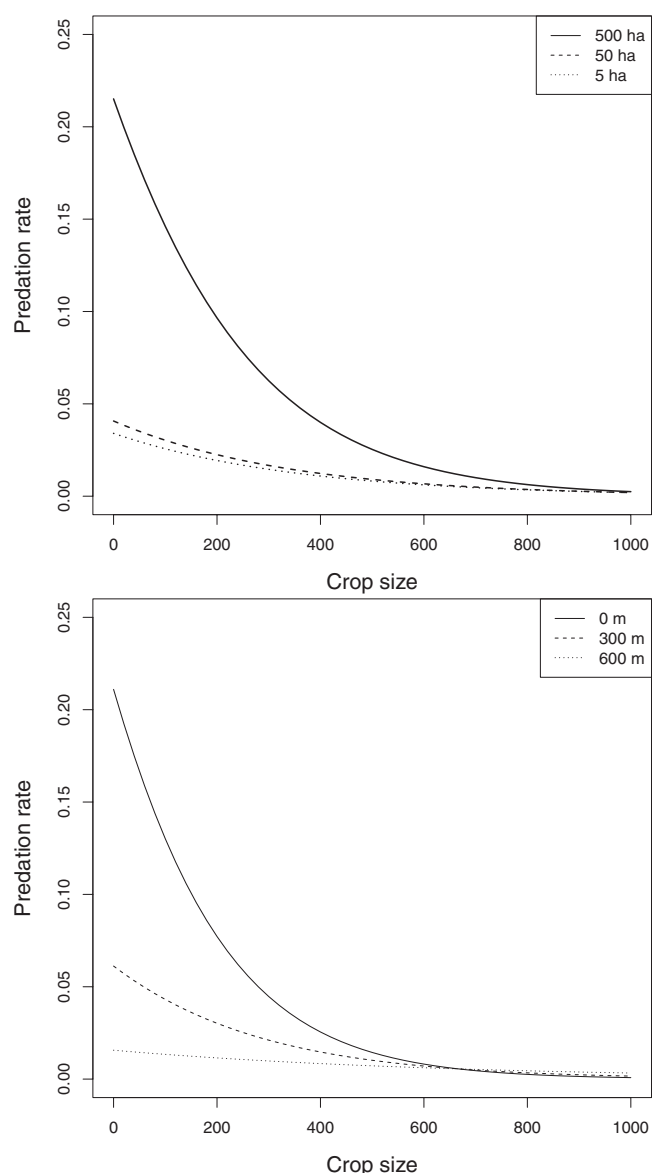
## DISCUSSION

Effects of plant traits (Batáry et al. 2007; Bonal et al. 2007; Brody 1992; Brody and Mitchell 1997) and landscape configurations (Batáry et al. 2007; Govindan et al. 2012; Su et al. 2011) on infestation rate by weevils had been extensively studied, but their interplay received much less attention (but see Bonal et al. 2012). In the present study, we found a significant, negative relationship between crop size and predation rate by granivorous insects, and such a relationship was affected by island area and isolation.

### Effects of seed production on predation rate

Lower seed predation rates observed on trees with larger seed crops suggested predator satiation, which is often hypothesized as a main selective advantage for mast seeding of perennial plants (Janzen 1976; Kelly 1994; Kelly and Sork 2002). Satiation may occur at or above the population level (Espelta et al. 2008; Koenig et al. 1994). However, among-tree variation of seed production has been overlooked so far. Our results show that satiation of acorn weevils can happen at the level of individual tree, suggesting that predator satiation can still be a selective driver underlying large seed crops even when they are not synchronous among trees. The most plausible explanation for seed predation satiation at the individual tree level is that an acorn weevil can dig and oviposit in a limited number of seeds and weevils may tend to be sedentary once they find a suitable tree. There is no report on the number of eggs that a female acorn weevil of the studied species can lay. A female chestnut weevil *C. elephas* lays in average 29





**Figure 2:** impact of island area (A) and island isolation (B) on the relationship between predation rate and crop size. For a given area (or isolation), regression curve is based on the estimates from the model. Area is set to 500, 50 and 5 ha, which represents the scale of large, medium and small islands in this study, respectively. Isolation is set to 0, 300 and 600 m, which represents the scale of low, medium and high isolation in this study.

eggs (Menu and Debouzic 1993). Acorn weevils, in general, are weak fliers, and they may prefer to oviposit in acorns of the same tree. Nevertheless, this preference needs to be tested in *Curculio* spp. As to seed predators with higher dispersal ability, such as birds or rodents, predator satiation can only be observed in the whole plant population or community (Janzen 1976; Nathan and Casagrandi 2004). Therefore, the two levels (tree and population/community) at which seed predators are satiated may result from their disparate activity preferences.

## Effects of habitat fragmentation on predation rate

Both habitat area and isolation extent have substantial influences on acorn weevil abundance. The fact that in our study these two variables have a strong negative correlation prevents us from completely disentangling their separate roles in affecting abundance, but it is highly plausible that both had an effect. Seeds of a *C. sclerophylla* tree are more likely to be damaged by acorn weevils on larger islands (Table 1). Normally, larger habitats can support large populations of both the host plant and weevils, whereas small habitats are only able to support much fewer individuals of the host plant, leading to small weevil populations that may suffer from detrimental genetic effects such as high levels of inbreeding (Frankham 2005). Those small populations of acorn weevils are likely to be further restricted by interannual fluctuation of crop size at local scale. Thus, low predation rate is expected in *C. sclerophylla* populations on small islands, and strong effects of habitat area on insect population dynamics have also been reported in many previous studies (Kruess 2003; Kruess and Tschamtko 2000).

However, if a small population is close to large populations, high immigration may help a population persist and reduce the extinction risk in the small habitat, i.e. rescue effects (Brown and Kodric-Brown 1977). Consistent with those previous studies, our present study also detected negative effects of isolation on predation rate, reflecting the critical role of migration in the maintenance of weevil populations on small habitats.

The detected isolation effects suggest that adult *C. bimaculatus* flights between islands is rather limited. In other words, c. 600 m is probably beyond the flight distance of this weevil. Similar patterns have been reported in other weevil species (Bonal et al. 2012; St Pierre and Hendrix 2003). It seems that *C. bimaculatus* can readily fly c. 100 m which is the nearest distance in this study, as otherwise there would not be any rescue effect. For example, islands DN and SH have similar areas (1.1 ha vs. 1.5 ha) but with contrasting isolation levels (106 m vs. 680 m). In 2011, crop sizes were similar on both islands. However, the predation rates were nearly nine times higher on DN than on SH (Table 1). It should be noted that this point is not inconsistent with predation satiation on the tree level. The point is related to flight ability, whereas predation satiation at the tree level is related to activity preference. Acorn weevils may fly 100 m, but once they find a suitable tree, acorn weevils tend to be sedentary. The mechanisms underlying this phenomenon are still poorly understood, but high-dispersal cost is likely to be one of most possible reasons (Forero et al. 2002; Nevoux et al. 2013).

## Effects of habitat fragmentation on predator satiation

Both tested factors, i.e. reduction in area size and increased isolations, are important components of habitat fragmentation. These two factors not only have direct effects on

predation rate of *C. sclerophylla* seeds by acorn weevils, but also influence the tree-level predator satiation in our study. The faster decay of predation rate with increasing crop size on larger islands and on less isolated islands suggested that producing large crops of acorns is perhaps a more effective reproductive strategy to cope with seed predators where predation pressure is high.

Most previous studies which compared effects of habitat loss and isolation found that effects of isolation were trivial relative to those of habitat loss (McGarigal and McComb 1995; Trzcinski *et al.* 1999; Villard *et al.* 1999), but see Bonin *et al.* (2011). The discrepancy is likely to result from the differences of activity ranges among studied species. Some previous works studied birds whose activity ranges are extremely large, and thus it could be expected that habitat isolation only had a weak effect (McGarigal and McComb 1995; Trzcinski *et al.* 1999; Villard *et al.* 1999). On the contrary, the acorn weevils studied here are weak fliers with small activity ranges, therefore habitat isolation may determine the strength of rescue effect.

Overall, habitat fragmentation not only affects weevil populations, but also changed the relationship between weevils and their hosts probably by influencing rescue effects. Our study highlights the necessity to integrate biotic processes with landscape configurations and the importance of meta-population dynamics when understanding spatial structure of organisms for conservation purpose.

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