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Positive cascade effects of forest fragmentation on acorn weevils mediated by seed size enlargement

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Abstract. 1. Today, forest fragmentation is one of the major threats to biodiversity worldwide. In this context, fragmented populations of specialised forest organisms face an increasing risk of extinction because of factors such as local food scarcity. Nonetheless, the role of food availability may differ depending on organism size, which is expected to determine the energy requirements and mobility between fragments.

2. A field study was carried out on *Curculio elephas*, a forest beetle with low dispersal potential, whose larval development takes place in oak *Quercus* spp. acorns.

3. For a similar seed crop per tree, acorn size was larger in isolated oaks than in trees located in forest patches. Thus, fragmentation increased local food availability for *C. elephas*. Larger acorns enabled larval size to increase, a key fitness proxy associated with individual survival, adult size, and potential female fecundity. Indeed, the number of both adults and larvae was higher in isolated trees than in forest patches.

4. In the current scenario of increasing forest fragmentation, the survival likelihood of specialist insects may strongly depend on their ability to adapt to altered environmental conditions. To the best of our knowledge, this is the first study to report on how some forest insects may take advantage of fragmentation-mediated changes to survive in isolated trees.

5. From a conservation perspective, management policies should preserve isolated trees as a source of seeds and fauna for the natural regeneration of forest ecosystems after unproductive farmlands have been abandoned.

Key words. Acorn size, *Curculio*, forest fragmentation, forest insects, global change, individual fitness, larval size.

Introduction

The consequences of habitat fragmentation on species distribution and diversity have been a hot topic in ecology for years (Scheffer *et al*., 2001). By definition, habitat fragmentation is the division of an originally continuous habitat into several isolated patches with more or less distance between them (Turner, 1996; Telleria & Santos, 1999; Radford & Bennett, 2007). This can be particularly important for forest-specialist organisms, as basic resources become divided into a series of discrete smaller areas (Bender *et al*., 1998; Connor *et al*., 2000). The consequences of such partition can be more dramatic if movement between patches is impeded, either by long distances between fragments or by poor dispersal abilities (Turner, 1996; Lees & Peres, 2009). If so, resident species will depend solely on the resources available in the fragment and could become locally extinct if these resources become scarce (Telleria & Santos, 1999; Schmidt & Roland, 2006). On the other hand, spatial isolation will hamper the recolonization of the patch by curbing the arrival of post-extinction immigrants.

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Forest fragmentation is a prime concern for ecologists and conservation biologists, as many forests are extremely diverse habitats currently subjected to worldwide anthropogenic destruction (e.g. Telleria & Santos, 1999; Guevara *et al*., 2005; Manning *et al*., 2006). Some studies on different taxa have reported lower species richness and diversity in fragments than in continuous forests (Sekercioglu *et al*., 2002; Schmidt & Roland, 2006; Fujita *et al*., 2008). Other studies have tried to identify the traits that make some species more sensitive to fragmentation than others (e.g. body size, food habit, dispersal abilities; Laurance, 1991; Fujita *et al*., 2008). This lower diversity in fragments is often regarded as a consequence of the impoverished environmental conditions after fragmentation, which can ultimately reduce fitness and lead to the local extinction of certain species.

Lower food availability is considered to be one of the main reasons underlying local fauna extinctions in fragments (Burke & Nol, 1998). However, the so-called food scarcity hypothesis has rarely been tested in the field (although see Sekercioglu *et al*., 2002). Some studies have tested this hypothesis only indirectly by using correlated variables such as body condition (e.g. Suorsa *et al*., 2003), and only very few times have both food availability and the fitness consequences of reduced food availability been simultaneously estimated (but see Zanette *et al*., 2000), despite the need to test the 'food scarcity hypothesis' properly.

In insects, there is a particularly large gap with regard to population level analyses of the fitness consequences of fragmentation (Turner, 1996). Whereas large-scale biodiversity comparisons between continuous forest and fragments have been carried out (e.g. Brosi *et al*., 2008; Fujita *et al*., 2008), the consequences of fragmentation on key fitness proxies such as body size, survival, or fecundity have often been left aside. Some studies have reported less abundant and/or diverse communities in fragments (Brosi *et al*., 2008; Fujita *et al*., 2008; Silva & Simonetti, 2009), while others have found the effects on insect abundance or diversity to be either too few or too insignificant (Davies, 2002; Chust *et al*., 2007; Arellano *et al*., 2008). Simultaneous analyses of the consequences of fragmentation on food availability and fitness proxies may help to shed light on this issue.

Many insects are small-sized organisms with reduced dispersal abilities (e.g. Debouzie *et al*., 1996; Hedin *et al*., 2008), and thus very susceptible to local changes resulting from forest fragmentation. Fragmentation provokes strong disruptions in crucial environmental variables for insects (e.g. insulation, temperature, humidity, etc.; Davies, 2002; McDonald & Urban, 2004; Savilaakso *et al*., 2009), which can affect their physiology and activity either directly (Gullan & Cranston, 2005) or indirectly through changes in the quantity/quality of their food sources. In this sense, some studies have reported fragmentation-induced changes in leaf morphology, suggesting potential cascade effects on local caterpillar populations, although it must be said that fitness consequences have not been directly assessed (Silva & Simonetti, 2009).

The main aim of this study is to analyse the effects of fragmentation on fitness proxies of forest insects, using the weevil *Curculio elephas* (Coleoptera: Curculionidae; Gyllenhal, 1836) as a study model. *C. elephas* is the most common pre-dispersal predator of holm oak, *Quercus ilex,* acorns in the Iberian Peninsula (Bonal *et al*., 2007). Many *Q. ilex* forests have been cleared for centuries, and only a few oaks have often remained scattered across farmlands (Terradas, 1999). Local environmental conditions can change because of isolation, altering oak physiology, and productivity (Moreno & Cubera, 2008). Fragmentation can increase local resource availability for isolated oaks and influence the number and size of the acorns produced. In turn, such changes could affect the larval size of *C. elephas*, which is an important fitness proxy strongly correlated with larval survival probability, adult size, and potential fecundity (Desouhant *et al*., 2000).The precise objectives of the study are as follows: (i) to test whether isolated oaks produce larger acorns and/or crops than trees located in forest plots; (ii) to assess whether an increased acorn size in isolated oaks can promote increased larval size in isolated trees as opposed to oaks located in forest patches; (iii) to investigate the consequences of larger larval size in terms of adult size, larval survival probability, and local population size in isolated trees in comparison with forest patches.

Materials and methods

Study area

The study was carried out in three different areas of central Spain: Pueblo Nuevo del Bullaque (Province of Ciudad Real; 39°20′N, 04°15′W), Bargas (Province of Toledo; 39°56′N, 04°01′W), and Huecas (Province of Toledo; 40°00′N, 04°11′W). In the three localities, the landscape is a combination of wide open grasslands and cereal fields with scattered oaks (from 5 to < 1 tree per ha) and forest plots with higher density (from 70 to 100 oaks per ha). In the open areas, tree density is not uniform, although, and the distance between oaks can range from 40 m to more than 2 km (see Ortego *et al*., 2010 for a detailed description).

Study species

Quercus ilex is an evergreen oak that is widespread in the Iberian Peninsula. Seed production can be very high, with up to 37 000 acorns per tree (Bonal *et al*., 2007). However, seed production is subject to strong inter-annual fluctuations (Espelta *et al*., 2009a,b; Muñoz *et al*., 2009). Acorn size is extremely variable from one tree to another (between 1 and 10 g), but very repeatable at the intra-individual level (Bonal *et al*., 2007; Espelta *et al*., 2009a).

The chestnut weevil *Curculio elephas* (Coleoptera: Curculionidae) is the most prevalent specialist acorn parasite in Iberian *Q. ilex* forests (Bonal *et al*., 2007). During the course of this study, all of the weevils trapped in the study area were *C. elephas,* and *Q. ilex* is the only species capable of being exploited by *C. elephas* in the study area. Adult *C. elephas* emerge in late summer, after an underground overwintering diapause, and climb up the oak trunks. Movement between trees is infrequent, especially if trees are scattered (see Debouzie *et al*., 1996 and references therein). Oviposition takes place between late August and mid-October, and infested acorns are dropped prematurely

(Bonal *et al.*, 2010). Larval development takes place in a single acorn and the cotyledons are the only food available (Bonal & Muñoz, 2009). Hence, larval size can be constrained if cotyledon reserves are depleted (Bonal & Muñoz, 2008, 2009). In turn, larval size is an important fitness proxy as it is strongly correlated with larval survival probability, adult size, or potential female fecundity (Desouhant *et al.*, 2000).

Field sampling

The effect of fragmentation on acorn size was studied in 2008 in three localities (Huecas, Pueblo Nuevo, and Bargas). In each locality, we randomly selected 12 isolated holm oaks and another 12 trees in adjacent continuous forested areas. The mean acorn mass was calculated for each tree from a sample of 15 non-infested full-grown acorns dried for 48 h at 80 °C. That sample size was enough because within-tree variance stabilises after weighting 6–8 acorns (Bonal *et al.*, 2007). In Huecas and Bargas, seed traps (plastic containers with a surface of 0.12 m^2 and 50-cm deep) were randomly situated (following Skalski, 1987) under the canopies to assess acorn production. The number of traps differed between trees to cover the same proportion of canopy surface in all of them (between 1.5% and 2%). Tree surfaces were calculated on the basis of three random measures of the diameter of their canopy, considering trees to be roughly circular (see Pulido & Díaz, 2005 for a similar procedure). These acorn crop estimates are reliable, as differences between the seed traps of each tree are very small compared with between-tree variability (see Bonal *et al.*, 2007). We assessed the possibility of unsuspected subtractions from the traps by placing 100 marked acorns in them; none were removed by the end of the study (see also Pulido & Díaz, 2005; Bonal *et al.*, 2007 for details). In both years, the traps were first checked on September 15, when the first infested acorns dropped, and from then on, every 15 days until December 30, when sound acorns stopped falling. During each check, the content of the traps was taken to the laboratory, where the acorns were classified as aborted, infested, or sound. From these data, we calculated the total number of grown acorns (infested plus sound ones) produced by each tree per square metre and in total (calculated as the production per square metre by the canopy surface).

In Huecas, all larvae emerging in 2008 and 2009 were collected to assess the effects of acorn size on larval size. Infested acorns were easily identified by the female oviposition scar on the seed coat (Bonal & Muñoz, 2007), and most infested acorns were collected in the seed traps before the larvae emerged (see Bonal & Muñoz, 2007 for a similar procedure). These acorns were placed outdoors in individual plastic vials opened above and covered with a plastic mesh to prevent predation by birds or rodents. The emerging larvae were checked on a daily basis and immediately weighted with a precision balance to the nearest 0.1 mg. One month after the last larvae emerged, infested acorns were dried and measured to the nearest 0.01 mm using a digital calliper. Then, they were opened to check whether the cotyledons had been depleted or not (see Bonal & Muñoz, 2008, 2009 for the same methodology) and to look for any dead larvae inside. The total number of larvae for each tree was estimated by multiplying the number of infested acorns per square metre by the canopy surface and then by the mean number of larvae per acorn recorded in that tree.

In Huecas, we also trapped adult weevils using emergence traps. Each of these consisted of a mosquito net attached to the tree trunk with an inverted cone with a closed bottle on the top. The weevils climbed up the trunk after leaving their underground cells and eventually marched into the net, which led them directly to the top bottle, where they were trapped. The traps partially covered the tree trunk, and the number under each tree ranged from 1 to 3, in proportion to the tree canopy. In both years, traps were opened before the onset of *C. elephas* adult emergence (August 15) and were definitively closed on December 15, covering the entire period of adult weevil activity. Traps were attached to the trunk very close to the ground ensuring that the captured adults came from that tree as opposed to others, as the scarce immigrants were far more likely to come flying or marching onto the canopies. The traps were checked every 3 days, and the insects were mostly collected alive. They were then taken to the laboratory and weighted to the nearest 0.1 mg using a precision balance.

Data analyses

The relationship between the proportion of acorns, whose cotyledon reserves had been depleted, and the mean acorn size was analysed by means of a generalised linear model, GLZ (Wald Statistic used for probability calculations) for a variable with a binomial distribution – cotyledon depleted or not depleted – and a logit link function; the year and the habitat (forest or isolated oaks) were also included as fixed factors. The effects of acorn size on larval and adult size were analysed using general linear models (ANCOVAS), in which mean acorn size was the covariate, and year and habitat the fixed factors.

To further check for any potentially confounding effect of spatial autocorrelation on the variables of interest, we also performed two Mantel tests. First, we tested whether acorn size differences among oaks were related to the Euclidean geographic distance between them. Second, we used a partial Mantel test to assess whether the differences in larval size between trees were correlated with acorn size differences, after checking the effect of spatial distance (Storfer *et al.*, 2007).

The relationship between the mean acorn size and the number of adults emerging under each oak (adults per trap) was assessed using a general linear model (ANCOVA). In this analysis, mean acorn size was included as a covariate, and habitat and year as fixed factors. In all parametric analyses, variables were log transformed when necessary to meet the normality assumptions.

We tested the effect of larval size on their survival in the field. As we had 2 years of data (2008 and 2009) and most larvae emerged after a 1-year diapause (Menu & Debouzie, 1993), we analysed the effects of the total number of larvae estimated for each oak in 2008 and their mean weight on the number of adults trapped at each tree the following year (2009). This was performed using a generalised linear model (GLZ) for a dependent variable with a Poisson distribution (count of the number of adults) and log link function; the type of habitat (forest or fragmented) was also included as a fixed factor. All statistical analyses were conducted using the Statistica 6.0 software package (Statsoft. Ltd, Sweden), except in the case of the Mantel tests, which were performed using XLStat (Addinsoft Inc., Brooklyn, NY, USA).

Results

Effects of forest fragmentation on acorn size and acorn production

The acorn crop (number of acorns m^{-2}) did not differ significantly, either among localities (random factor; $F_{1,45} = 1.88$, $P = 0.40$) or between forest and isolated trees (fixed factor habitat; $F_{1,45} = 2.63$, $P = 0.35$), or their interaction ($F_{1,45} = 0.41$, $P = 0.52$). Although acorn size did not differ among localities ($F_{2,61} = 7.51$; $P = 0.11$), acorns were significantly larger in isolated trees than in forest plots ($F_{1,61} = 37.50$, $P = 0.025$; Fig. 1). The interaction between locality and habitat was insignificant ($F_{2,61} = 0.71$, $P = 0.49$), indicating that the larger acorn size in isolated oaks compared with trees located in forest plots is consistent across all the localities studied.

In Huecas, the locality that was monitored intensively for two consecutive seeding seasons, acorn production did not differ between isolated and forest trees ($F_{1,44} = 1$, $P = 0.32$). With respect to inter-annual changes, acorn crops were larger in 2008 than in 2009, although differences were only marginally significant ($F_{1,44} = 4.03$, $P = 0.06$). The interaction between the factors year and habitat was also insignificant ($F_{1,44} = 0.38$, $P = 0.53$). By contrast, acorn size differed between forest and isolated trees; in both years, acorns were larger in isolated ones ($F_{1,40} = 6.65$, $P = 0.01$), although this effect did not change from 1 year to the next ($F_{1,40} = 2.17$, $P = 0.14$). Nor did we find a significant interaction between year and habitat ($F_{1,44} = 0.38$, $P = 0.53$). Finally, the Mantel test showed that the distance between trees was unrelated to differences in acorn size ($r = 0.03$, $P = 0.27$), indicating an absence of spatial autocorrelation for this variable.

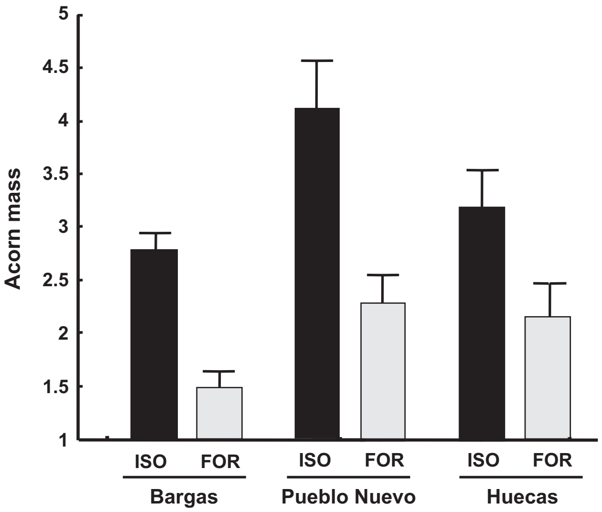

Fig. 1. Differences in acorn dry mass (mean ± SE, g) between isolated (ISO) and forest plot oaks (FOR) in the three study sites: Bargas, Pueblo Nuevo, and Huecas.

Effects of acorn size on larval and adult size

The generalised linear model showed that larvae were more likely to suffer food shortage during development in small acorn oaks, as the proportion of acorns with cotyledon reserves completely depleted was inversely related with mean acorn size (Wald Stat. = 8.66; d.f. = 1; $P < 0.01$). Such a relationship was unaffected by either the year or the habitat ($P > 0.1$ for all main effects and interactions). Food shortage during development had further consequences on larval size, which on the average was 25% lower in forest oaks than in isolated trees for the two study years (isolated vs. forest trees, mean ± SE; 0.082 ± 0.06 g vs. 0.066 ± 0.05 g in 2008 and 0.09 ± 0.07 g vs. 0.07 ± 0.04 g in 2009). Such differences were a consequence of the larger acorn size in isolated oaks, as larval size was positively related with mean acorn size ($F_{1,26} = 4.88$, $P = 0.03$; Fig. 2a), while neither the year nor the habitat effects were significant ($P > 0.1$ for all main effects and interactions). This effect of acorn size on larval size was not because of spatial autocorrelation, as the partial Mantel test showed that acorn size and larval size were significantly related ($r = 0.26$, $P < 0.0001$), after controlling for the Euclidean geographical distance between trees. As with the results obtained for weevil larvae, the mean size of adult weevils was positively correlated with acorn size (general linear model: $F_{1,25} = 21.61$, $P < 0.001$; Fig. 2b), without any significant effect by the habitat and year factors ($P > 0.1$ for all main effects and interactions).

Weevil population numbers in isolated oaks versus forest plots

More adult weevils emerged beneath isolated trees than in trees located in forest patches in both study years (mean ± SE; 4.4 ± 1.8 vs. 2.4 ± 1.4 individuals per trap in 2008 and 2.1 ± 0.5 vs. 0.3 ± 0.2 in 2009). Such differences were significantly explained by acorn size, as it was positively related with the number of adults recorded per trap at each oak ($F_{1,39} = 4.16$; $P = 0.04$; Fig. 3), with no significant effect by the type of habitat ($F_{1,39} = 1.43$, $P = 0.23$). Although more adults emerged in 2008 than in 2009 ($F_{1,39} = 13.51$; $P < 0.001$), the relationship between acorn size and number of emerging adults was not affected by the year (interaction between acorn size and year; $F_{1,39} = 0.83$, $P = 0.36$; Fig. 3).

The positive relationship between the number of emerging adults and acorn size may be partly explained by the higher survival likelihood of the large larvae coming from large acorn oaks. In fact, the generalised linear model showed that, even though the number of adults trapped at each oak in 2009 depended on the total number of larvae estimated for that tree in the previous year (Wald. Stat = 23.45; d.f. = 1,

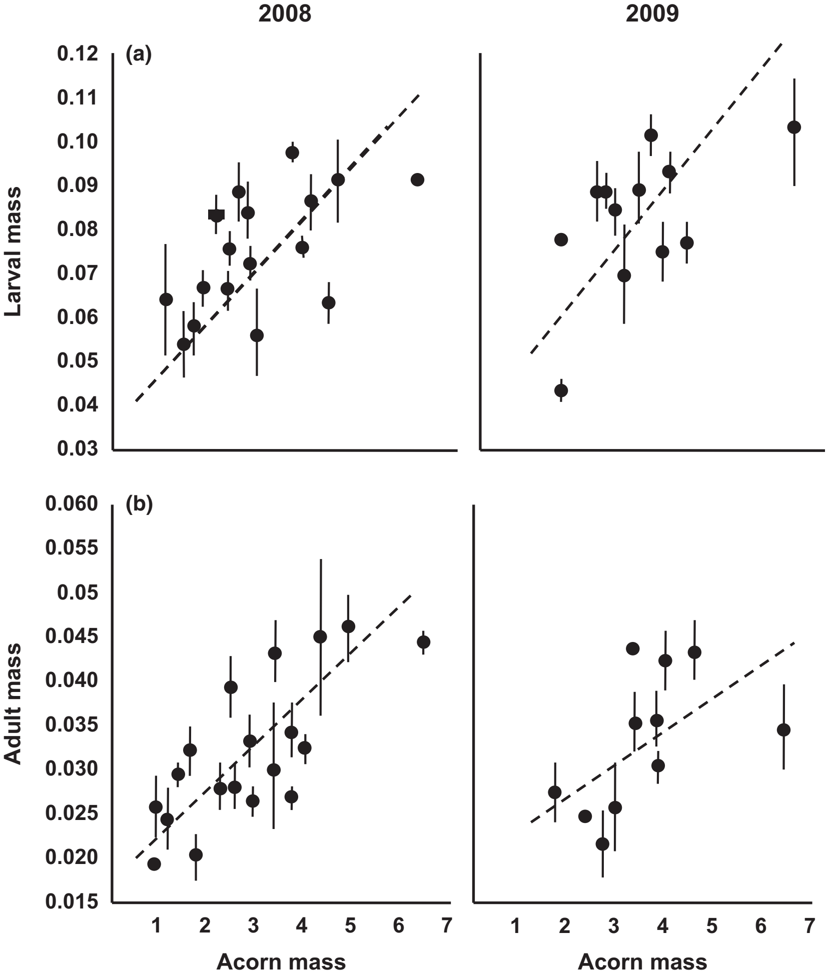

Fig. 2. Comparisons across trees. Figure 2a: Relationship between larval mass in grams (means shown as points and ±SE as vertical lines) and mean acorn dry mass (g) in the 2 years of the study. Figure 2b: Relationship between adult mass (mean ± SE, grams) and mean acorn dry mass (g) in the 2 years of the study. Dashed lines represent the significant regression slopes.

$P < 0.001$), mean larval mass had a significant positive effect as well (Wald. Stat = 5.52; d.f. = 1, $P = 0.01$) with no significant effect of habitat (Wald. Stat = 0.02; d.f. = 1, $P = 0.87$).

By last, a final general linear model demonstrated that local larval population size was associated with the number of adults that emerged under each tree ($F_{1,30} = 15.54$, $P < 0.001$). Once this covariate was included in the model, neither the year ($F_{1,30} = 1.16$, $P = 0.28$) nor the habitat ($F_{1,30} = 0.14$, $P = 0.7$) had any independent effect on the total number of larvae estimated for each tree.

Discussion

Despite fragmentation altering local environmental conditions and potentially affecting vegetation (Davies, 2002; McDonald & Urban, 2004; Silva & Simonetti, 2009), the consequences on phytophagous insects have usually been overlooked (but see Faveri *et al.*, 2008). In the case of the holm oak forests, tree thinning may increase resource availability, especially in dry Mediterranean areas (Gracia *et al.*, 1999; Moreno *et al.*, 2007). In fact, water availability in the soil, water potential, and CO_2 assimilation rates are all significantly higher in isolated holm oaks than in high-density stands (Moreno & Cubera, 2008). This may explain why isolated oaks produce larger acorns than those in forest plots, even if the mean number of acorns produced does not differ between habitats.

Previous studies have shown that acorn size can constrain larval size (Bonal & Muñoz, 2008, 2009) and, accordingly, larvae were larger at isolated oaks. Larval size is an important fitness proxy strongly correlated with survival likelihood, as it has been individually measured in chestnut-feeding *C. elephas* populations (Desouhant *et al.*, 2000). In our study area, more adults were trapped at isolated oaks than at forest ones, partly as a result of the larger larval size and survival in the former. Controlled experiments have also shown that adult body size is

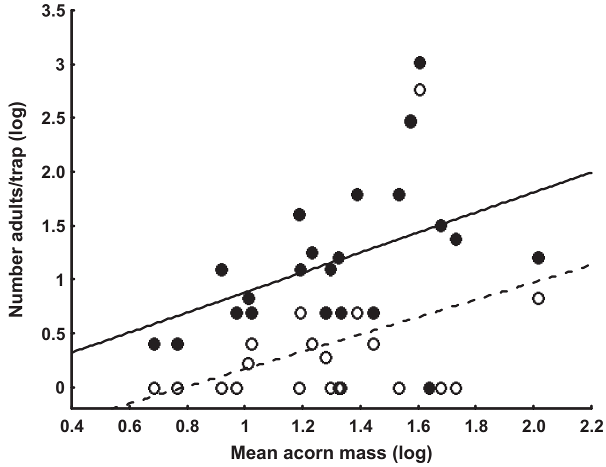

Fig. 3. Relationship between mean acorn dry mass (g) and the number of adults emerged under each tree (individuals per trap) in 2008 (filled circles, solid line) and 2009 (empty circles, dashed line).

strongly correlated with potential female fecundity (Desouhant *et al*., 2000). Thus, larger adults emerging under isolated oaks could also leave more descendents, although here caution is needed because such a positive relationship cannot always be extrapolated to field conditions (Kazmer & Luck, 1995; Ellers *et al*., 1998).

Capture–recapture data from chestnut trees indicate that dispersal distances are low, usually not exceeding 100 m (see Debouzie *et al*., 1996 and references therein). In the present study, the correlation at the tree level between the number of emerging adults and the total number of larvae suggests low immigration as well. In fact, the lower tree density, especially in the case of isolated oaks, probably decreases the chance of between-tree movement compared with the usually denser chestnut tree forests. Spatial isolation coupled with low mobility makes *C. elephas* scattered populations more susceptible to catastrophic events. Summer droughts, for example, may kill many of the local individuals if the soil is not moist enough to allow adult emergence (Menu & Debouzie, 1993; Bonal *et al*., 2010), as probably occurred in 2009, when far fewer adults were trapped compared with the more rainy 2008. In addition, isolation increases vulnerability to extreme local inter-annual fluctuations in acorn availability (Bonal & Muñoz, 2007; Espelta *et al*., 2009b) in comparison with oak forests, where there will always be at least some trees producing acorns (Espelta *et al*., 2008).Moreover, even if acorn availability is not limiting, scattered populations will be more vulnerable to low local acorn quality, as studies on chestnut trees have demonstrated that seed availability is not always correlated with suitability for oviposition (Debouzie *et al*., 2002).However, despite all these odds, we recorded *C. elephas* in all isolated trees and in large numbers in certain cases. Hence, it is clear that mechanisms which help reduce the risk of local extinction after catastrophic events must exist. For example, a variable length of the diapause duration – individuals of the same cohort can emerge as adults in 1, 2, or 3 years (Menu & Debouzie, 1993) – can promote long-term population persistence in stochastic or unpredictable environments (Menu *et al*., 2000; Menu & Desouhant, 2002).

The present study shows that the hypothesised food scarcity in forest fragments cannot be assumed as a general rule in the case of forest insects. This may explain why certain studies have found abundant and diverse arthropod communities within fragments (Davies, 2002; Chust *et al*., 2007; Arellano *et al*., 2008). To the best of our knowledge, this is the first study to report positive cascade effects on insect fitness proxies of fragmentation-induced changes in vegetation. In terms of management, such effects could support the decision of maintaining a heterogeneous landscape, with dense forest masses and gaps with isolated trees, to promote biodiversity. However, we must not be misled into thinking that an extreme fragmentation is intrinsically positive for these organisms, as tree clearing involves a global decrease in suitable habitat and overall population size. Moreover, we must be cautious before extrapolating these results to other areas, such as the tropics, where adverse edge effects may hamper the presence of some forest specialists in small fragments (Gove *et al*., 2009).The conclusion that can be drawn from the present work is that scattered trees can play a key role in ecosystems acting as reservoirs of healthy insect populations, meaning that they should be taken into account in environmental landscape management (Manning *et al*., 2006, 2009; Fischer *et al*., 2010). Oak trees usually appear in agricultural landscapes as scattered trees and should be preserved as a source of seeds and fauna for further natural forest regeneration on abandoned farmlands.

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