

Dispersal and dormancy strategies among insect species competing for a pulsed resource

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Abstract. 1. Dormancy and dispersal are thought to be major adaptive mechanisms that enable short-lived organisms to cope with environmental stochasticity. The few empirical investigations that have explored the relationship between these two strategies in disturbed environments have focused mainly on communities of annual desert plants and suggest that dispersal plays a negligible role, as compared with dormancy, in reducing the risk of genotype extinction.

2. We predict that the relative advantage of dormancy *versus* dispersal is likely to be more balanced in species that disperse actively to select their reproductive locality.

3. To examine this prediction, we explored the dormancy and dispersal capacities of four actively dispersing sibling weevil species (*Curculio* spp.) that exploit the same, highly variable resource (oak acorns). The ability of each species to spread risks over time was estimated from the variability of dormancy duration within cohorts, while their ability to disperse spatially was quantified by flight performance.

4. We show that a first species, *C. elephas*, which was able to spread risk over time through dormancy, exhibited only medium flight capacities. In contrast, a second species, *C. glandium*, was able to fly over very long distances, but was hardly capable of spreading risk over time. Surprisingly, the two remaining species (*C. venosus* and *C. pellitus*) proved inefficient in spreading risk either in space or in time and seem to exhibit risk avoidance rather than risk-spreading strategy. We conclude that this strong diversification of dispersal–dormancy strategies observed among these four sibling species might contribute to stabilising their coexistence.

Key words. Bet-hedging, Dispersal–dormancy, flight mill.

Introduction

Environmental stochasticity, which is characterised by unpredictable temporal and spatial variations, probably have a significant effect on the growth rate of populations and influence the organisation of biodiversity (Chesson, 2000; Ostfeld & Keesing, 2000; Chesson *et al.*, 2004). Major and unpredictable environmental changes can reduce the size of populations, which might increase the impact of demographic stochasticity

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on the dynamics of populations and thus precipitate their local extinction (Connell, 1978; Pimm, 1991; Yang *et al.*, 2008). Spatial dispersal ability or variable dormancy duration among individuals carrying the same genotype are considered two of the main strategies exhibited by short-lived organisms for coping with environmental stochasticity, as both of them reduce the risk of local extinction of such a genotype (Venable & Lawlor, 1980; Venable & Brown, 1988). Several investigations have suggested that spatial dispersal may evolve as an alternative to dormancy in that it releases selective pressure exerted on variable dormancy duration or vice versa (Gadgil, 1971; Venable & Lawlor, 1980; Klinkhamer *et al.*, 1987; Venable & Brown, 1988; Snyder, 2006; Rajon *et al.*, 2009; Siewert & Tielbörger, 2010).

The relationship between these two strategies has so far been investigated empirically most exclusively in annual desert plants whose growth is limited by water availability, which is considered as a pulsed resource. The few studies available suggest that these two strategies are not interchangeable (Snyder, 2006), and that dispersal has a negligible impact on buffering the environmental variations compared to dormancy (e.g. Venable *et al.*, 2008; Siewert & Tielbörger, 2010). Even though the spatial range of fluctuations is affordable and allows seeds to reach distant resources, the passive nature of seed dispersal introduces an important random component into the direction and distance travelled by seeds (Snyder, 2010), which means that seeds are likely to land in unsuitable habitats for germination and growth (Snyder, 2006). This might explain why spatial dispersal plays only a negligible role in these plant communities, compared to dormancy.

In this study, we suggest that active dispersal (i.e. the ability of organisms to select their habitat on the basis of quality criteria; Pulliam, 1988) may promote the spatial dispersal of organisms living in environments that vary over time and space, thereby reducing the advantage of dormancy as a risk-spreading strategy. To explore this possibility, we investigated the relationship between dispersal and dormancy in four closely related weevil species [*Curculio glandium* (Marsham), *C. elephas* (Gyllenhal), *C. pellitus* (Boheman) and *C. venosus* (Gravenhorst), Coleoptera, Curculionidae] whose adults are able to disperse actively over space by means of flying. The four weevil species co-occur on the same individual oak trees (*Quercus* spp.), while competing for oak acorns that constitute the sole food resource for larval development (Coutin, 1992; Hughes & Vogler, 2004; Péliesson *et al.*, 2011;

Venner *et al.*, 2011). Oak acorns are a highly fluctuating resource, as their production varies considerably from year to year and across space, in a partly unpredictable manner, owing to mast seeding (e.g. Sork *et al.*, 1993; Koenig *et al.*, 1994b; Kelly & Sork, 2002). This production pattern also generates spatial heterogeneity in acorn availability, because oak trees are only partly synchronised at the population level (Crawley & Long, 1995; Liebhold *et al.*, 2004).

Like annual desert plants, weevils are short-lived organisms able to spread risk over time through variable dormancy duration. Unlike annual plants, however, they can also actively disperse over space via adult flight, and seek out more favourable breeding sites (i.e. trees full of acorns). The four oak weevil species studied are already known to differ markedly in their ability to spread risk over time by means of distinct diapause strategies (Venner *et al.*, 2011). We predict that these species also have distinct spatial dispersal capacities offsetting their uneven ability to spread risk over time. In *C. elephas*, adults belonging to the same larval cohort commonly emerge over several years (see Fig. 1, adapted from Venner *et al.*, 2011). Such variable dormancy duration, interpreted as a diversified bet-hedging strategy [illustrated by the adage ‘don’t put all your eggs in one basket’ (Seger & Brockmann, 1987; Philippi & Seger, 1989; Gourbière & Menu, 2009)], should efficiently buffer the unpredictable fluctuations of acorn availability over consecutive years. Consequently, we predicted that *C. elephas* females would have poor dispersal ability. In contrast, adults of the other three species (*C. venosus*, *C. pellitus*, *C. glandium*) emerge, almost exclusively, a fixed number of years after larval development (in the second year for *C. glandium*, and the third year for *C. venosus* and

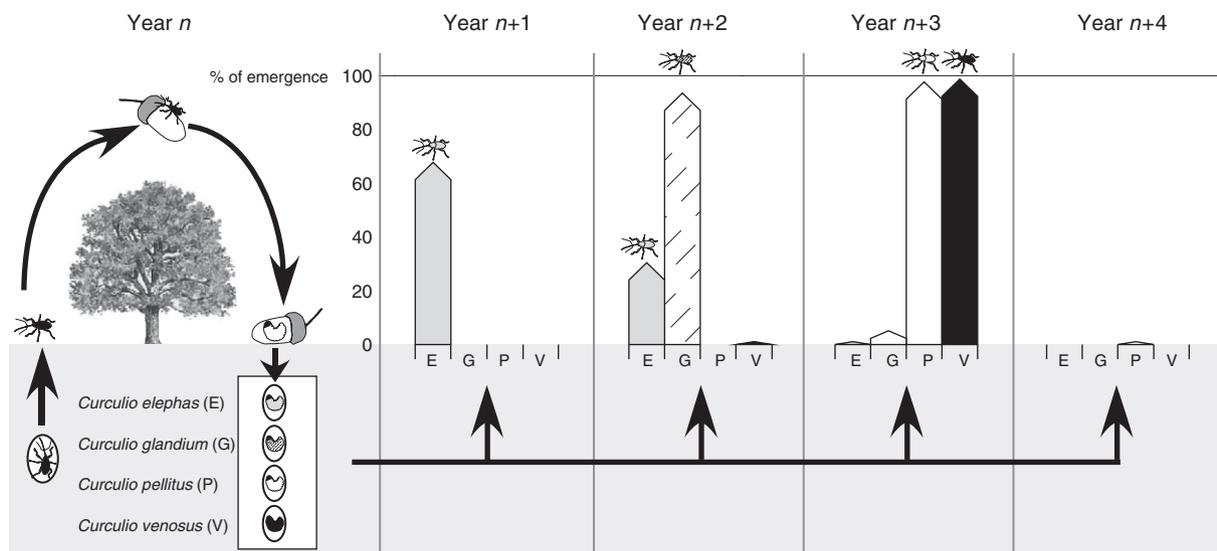


Fig. 1. Spreading of adult emergence over years by the four oak weevil species (adapted from Venner *et al.*, 2011). With regard to egg laying followed by larval development for a given year (Year n), *Curculio elephas* displays the ability to spread the emergence of adults over several years (66% emerging the first year, 30% during the second and 4% during the third year, respectively). In contrast, adults of the other three species (*C. venosus*, *C. pellitus*, *C. glandium*) emerge almost exclusively a fixed number of years after their larval development (the second year for *C. glandium*, with only 6% emerging during the third year, and the third year for both *C. venosus* and *C. pellitus*, with only 3% emerging the second and fourth years, respectively, on average).

C. pellitus; Fig. 1 adapted from Venner *et al.*, 2011). These three species seem to be far less efficient than *C. elephas* in spreading risks over time, and might thus be more vulnerable if the tree on which the larvae developed were to produce no acorns in several successive years. We suggest that this poor ability to spread risk over time may be accompanied by an expanded capacity to actively disperse in space: adults of these three species would be able to escape adverse local conditions in a given year by dispersing toward more suitable localities.

In this study, we conducted a 6-year field survey in two localities to find out whether between-year fluctuations and spatial synchronisation of oak acorn crops were consistent with the patterns described in the literature, and we investigated whether the four insect competing species balanced temporal and spatial skills by assessing the flight capacity of wild-caught adult females.

Materials and methods

Between-year variations in the availability of oak acorns

During six consecutive years, from 2006 to 2011, we estimated the yearly acorn production of 23 oak trees located in two localities located 40 km apart near Lyon [France: 11 trees at site A (N45°35'; E5°01') and 12 at site B (N45°45'; E5°16')]. The oak trees were randomly chosen within a 500 m radius in each locality, and were mainly pedunculate (*Quercus robur*) and sessile (*Q. petraea*) oak trees at sites A and B, respectively. We used the classical visual count method consisting of two observers counting independently the maximum number of oak acorns at a given zone of the tree during 15 s (Koenig *et al.*, 1994a). The four distinct zones previously delimited in the canopy of each tree, corresponding to the four cardinal points were individually counted. These counts were then averaged to estimate the yearly acorn production of each tree. The amount of fruits produced by mast-seeding plants is best characterised by the between-year variation of individual oak trees and by the synchrony level occurring among oak trees from the same population (Herrera *et al.*, 1998; Buonaccorsi, 2003; Koenig *et al.*, 2003; Liebhold *et al.*, 2004).

Experimental design for quantifying flying performance

Insect sampling. To estimate the flying ability of adult females of each of the four weevil species, we caught females in six oak trees (three per site) throughout one breeding season (i.e. from May to September 2010). For that purpose, each week we beat the branches of trees with a wooden stick within 1 h after sunrise (see details in Schauff *et al.*, 1986; Venner *et al.*, 2011). Insects that fell on a white sheet laid under the tree were immediately collected and stored in a cold box before being brought back to the laboratory where their species was morphologically identified (Hoffmann, 1954). All live-trapped adults were weighed to the nearest 0.1 mg (balance Scaltec SBA 32, Goettingen, Germany) and sized for their maximum width and body length to the nearest

0.1 mm (binocular microscope Zeiss stemi-C; Zeiss, Illkirch, France).

Each female (23 *C. elephas*, 125 *C. glandium*, 15 *C. pellitus* and 66 *C. venosus*) was then stored for 24 h in individual Plexiglas boxes (5.8 × 4.4 × 5 cm) at constant temperature (22 ± 1 °C) and hygrometry (60 ± 5% relative humidity), and under natural photoperiod (± 15 min) before the test.

Flight mills. To quantify flying ability, adult females were individually introduced into a flight mill adapted from the device of Schumacher *et al.* (Schumacher *et al.*, 1997; Bruzzone *et al.*, 2009). Data recorded from such experimental devices are known to overestimate the total distance and total time an insect does usually travel by flight (Bruzzone *et al.*, 2009) as compared with mark–release–recapture data (Botero-Garcés & Isaacs, 2004). It nevertheless corroborates trends found in the field and is efficient at detecting the differences possibly existing between several species (Chen *et al.*, 2006) or between individuals of the same species (e.g. Hughes & Dorn, 2002).

The dispersal capacity of females was tested in an air-conditioned chamber provided with the same environmental conditions as those of the rearing room. Seven identical and independent devices were used simultaneously. The diurnal flying activity of each weevil female was monitored the day after its capture, starting at 11.00 hours and ending 7 h later. A nylon thread was glued to the dorsal side of the thorax of each female (we used a quick-drying glue, Loctite Super Glue-3). In the flying device, the nylon thread was then attached perpendicularly to the flight rod so as to set a 9.5 cm distance between the rotation axis and the point where the insect was attached, resulting in a 59.66 cm travelled distance per revolution. A reflector located on the flight arm and a computer-linked infra-red transmitter/receiver put on the mill enabled us to automatically record every revolution made by the insect. The revolution bouts could be interpreted in terms of continuous flights interspersed with breaks (Schumacher *et al.*, 1997). We considered that a break occurred whenever more than 4 s elapsed between two successive revolutions and that a single flight bout occurred between two successive breaks. The total duration and distance flown by each tested insect (the summed distance travelled by the insect) were recorded. These measures allowed us to compare the flying performance of the four weevil species and to test, within each species, whether the flying ability of insects varied throughout the season.

Data analysis. We used the individual coefficient of variation to reflect between-year variability in the acorn production of a given tree. This coefficient was computed using the mean temporal variation in the fruits counted on each individual tree ($\overline{CV_i}$, calculated by averaging the individual coefficients of variation obtained in a given locality). To quantify the synchrony level of fruit production among oak trees located at a given site, we computed the mean Pearson correlation coefficient (\overline{r}) considering the acorn crop of all possible pairs of oak trees (Buonaccorsi, 2003).

Flight distances

We analysed the flight distance (total distance, TD) travelled by insect females during the experiment using a linear model with log-transformed data (logTD). First, we considered only the species effect (SP) on this variable using a contrast procedure. In a second step, we analysed for each species the seasonal dynamics of the flight distance travelled. Three explanatory variables were included in our statistical models to account for the effect on flight distance: (i) of body weight variations existing between individuals of the same species ('Weight'); (ii) of differences existing in the amount of oak acorns produced by the tree where insects were collected ('Fruit prod.');

Results

Between-year variation, periodicity and synchronicity in oak acorn production

From a 6-year field survey in two localities sited 40 km apart from each other, we found high between-year variability in acorn production (Fig. 2) as attested by the high values of individual coefficients of variation (\overline{CV} : 0.74 at site A; 0.81 at site B). Neighbouring trees experienced intermediate and weak synchrony at site A ($\overline{r} = 0.61$) and at site B ($\overline{r} = 0.28$), respectively. Furthermore, acorn production is characterised by

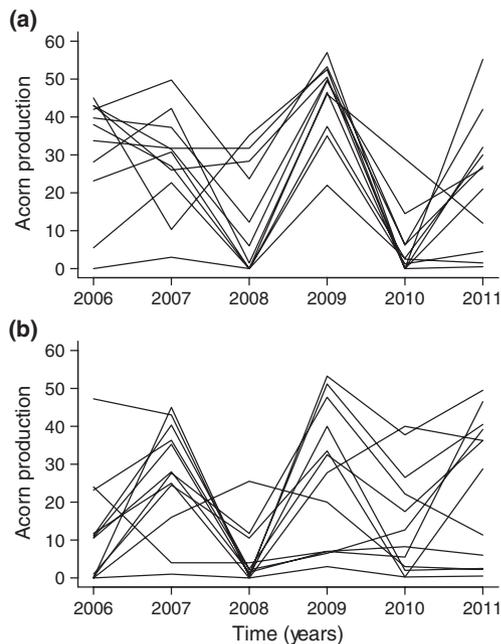


Fig. 2. Between-year variation in the oak acorn production at the two study sites. Yearly production of oak acorns estimated by visual counts at each site (site A and B shown in panels a and b, respectively) between 2006 and 2011. Each line corresponds to the observed values of an individual oak tree.

strong spatial heterogeneity, as each year some trees are desynchronised (Fig. 2). Overall the between-year fluctuations and spatial synchronisation of oak acorn crops were consistent with the patterns commonly described in the literature on oak trees.

Flight distance. We observed a marked overall difference between the four weevil species in the total flight distance travelled by wild-caught females ($F_{3,225} = 22.46$, $P < 0.001$; Fig. 3). Two species (*C. pellitus* $n = 5$ and *C. venosus* $n = 66$) indiscriminately showed poor dispersal ability (contrast method: $t_{df=228} = -0.033$, $P = 0.97$). While *C. elephas* females ($n = 23$) showed intermediate ability for flying over a longer distance than that of *C. pellitus* and *C. venosus* (contrast method: $t_{df=228} = 2.84$, $P = 0.004$), *C. glandium* females ($n = 125$) could fly the longest distance of all the four weevil species (contrast method: $t_{df=228} = 6.29$, $P < 0.001$).

Seasonal dynamics of flight. After accounting for the potential effect of intrinsic differences in body weight of individuals on total flight distance they travelled (Table 1), we did not find any seasonal variation in flight activity, except for *C. glandium* whose flying capacity declined until the end of the breeding season (Fig. 3; Table 1). Furthermore, we detected a significant effect of seed production on the flying ability of *C. glandium* (Table 1): females tend to disperse more when the acorn availability decreases.

Discussion

Variable dormancy duration and spatial dispersal are both expected to evolve in short-lived organisms as an adaptive response to major fluctuations in their environment (e.g. Venable & Lawlor, 1980; Venable & Brown, 1988; Snyder, 2006). So far, however, there has been little empirical evidence of any interaction between these two strategies. In this study, we looked at the relationship between dispersal and dormancy in four closely related weevil species exploiting the same fluctuating resource. In agreement with the literature about mast seeding by oak trees (Sork *et al.*, 1993; Koenig *et al.*, 1994b), acorn availability in the sites studied largely fluctuated over time (Fig. 2). As oak trees were overall only partly synchronised, the acorn availability at weevil population level remained significantly heterogeneous. Consequently, both spatial dispersal capacity and risk spreading over time by dormancy might constitute efficient alternative strategies allowing the four insect species to cope with the variability of their limiting resources and reduce the risk of local extinction.

Curculio glandium, *C. venosus* and *C. pellitus* display little ability to spread risk over time. Adults from the same larval cohort almost exclusively emerge a fixed number of years following larval development (after 2 years for *C. glandium* and after 3 years for *C. pellitus* and *C. venosus*; Venner *et al.*, 2011). These three species can, therefore, be expected to be efficient spatial dispersers. In agreement with this prediction, we found that *C. glandium* showed a great propensity to disperse in space. Unlike *C. glandium*, however, *C. venosus*

Table 1. Modelling the seasonal dynamics of the flying ability of four weevil species.

Species	Variables	Estimated parameter	d.f.	F value	Pr(>F)	S
<i>Curculio glandium</i>	Intercept	3.099e+02				
	Weight	8.553e-02	1,121	7.31	0.007	**
	Fruit prod.	-1.043e-04	1,121	9.86	0.002	**
	Time	-2.074e-02	1,121	24.86	<0.0001	**
<i>C. elephas</i>	Intercept	6.933 e+02				
	Weight	7.777e-03	1,19	0.33	0.57	NS
	Fruit prod.	-5.236e-04	1,19	2.91	0.10	NS
<i>C. venosus</i>	Intercept	9.963e+01				
	Weight	2.899e-02	1,62	1.41	0.23	NS
	Fruit prod.	3.362e-05	1,62	0.013	0.90	NS
<i>C. pellitus</i>	Intercept	-8.132e+01				
	Weight	-7.759e-02	1,11	12.61	0.004	**
	Fruit prod.	5.551e-05	1,11	0.20	0.66	NS
	Time	5.942e-03	1,11	0.46	0.50	NS

For each weevil species, we used a linear model with log-transformed data to account for the effect on the insect body weight ('Weight') and the estimated amount of acorns produced by each tree ('Fruit prod.') and to test the effect of the season ('Time') on the total distance travelled by females. Significant *Pr*-values are given in bold. NS, not significant, **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

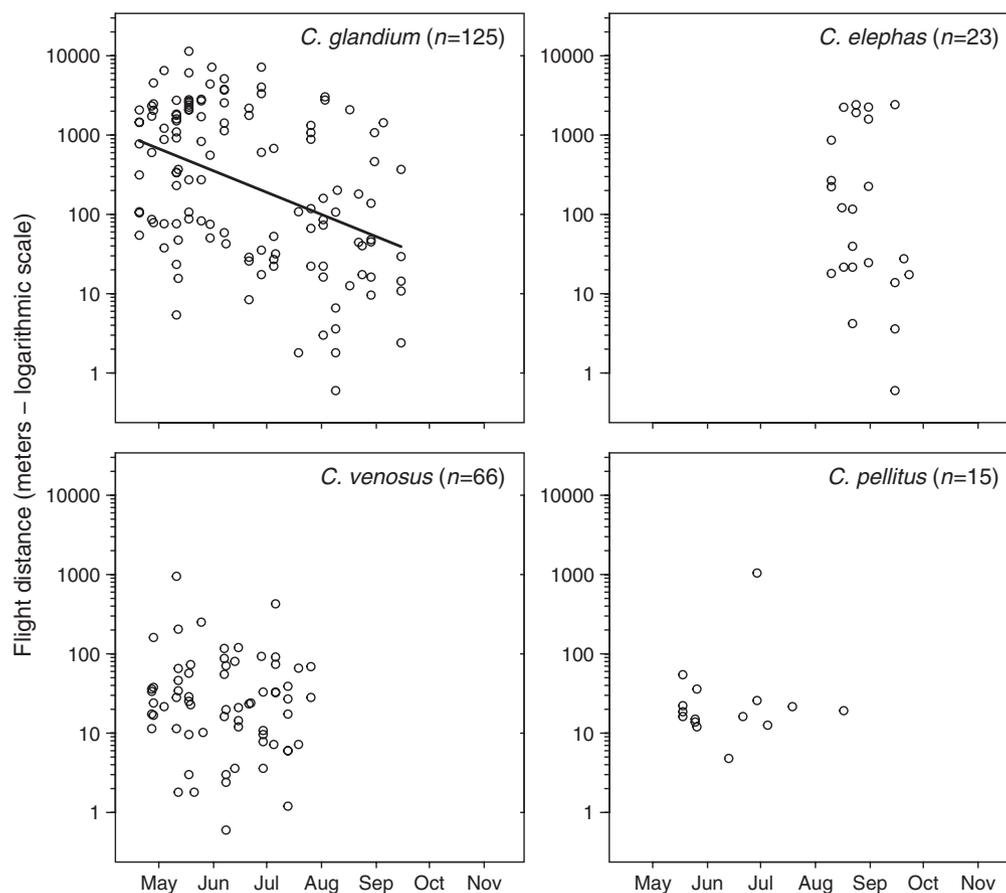


Fig. 3. Influence of the time during the breeding season on the flying ability (in log-transformed data) of wild-caught females of the four weevil species. *Curculio pellitus* and *C. venosus* show poor dispersal ability during the 7 h of the experiment. *Curculio elephas* females showed intermediate ability for flying and *C. glandium* females could fly the longest distance of all four weevil species.

and *C. pellitus* adult females seemed to be unable to fly over great distances, which together with their poor ability to spread risks over time, resembles a risk avoidance rather than risk-spreading strategy (see below).

In flight mill assays the longest flight was recorded for *C. glandium*, with some females travelling up to 12 km in a few hours. This intensive flight activity was accompanied by high interindividual variability within the population (Fig. 3). Weevils that travelled a long distance were therefore likely to be good dispersers whenever they emerged in a poor environment (i.e. when there are almost no acorns on the tree on which they hatched); this would make them likely to reach distant trees with larger acorn crops. Interestingly, some other *C. glandium* females travelled over a very short distance, and thus seem to be poor spatial dispersers. Such variable spatial dispersal ability could be due to either genetic variability or to some form of plasticity. It would for example coincide with spatial bet-hedging strategy, as already envisaged in other organisms (e.g. Krug, 2001; Toonen & Pawlik, 2001). In this sense, individuals belonging to the same cohort and dispersing at various distances are likely to encounter sharply contrasting environments, which overall might correspond to a spatial risk-spreading strategy within the same genotype. The variable dispersal ability observed within *C. glandium* population may also result from plasticity in the way energy is allocated toward dispersal as a response to environmental cues detected by newly emerging adults. For example, individuals emerging in a rich environment would allocate energy neither in wing muscles nor in flight metabolism but rather in their reproduction and then would become poor dispersers. In contrast some individuals could escape to unfavourable conditions by allocating resources in a way that increases their dispersal ability. In this sense, the distance travelled by females was found to be greater when the tree they came from produced a low amount of oak acorns. As a consequence, we could find both good and poor dispersers in a given locality. Whatever the mechanism underlying such variable dispersal ability within *C. glandium* populations, dispersal seems to play a decisive role to reduce the risk of local extinction in this species.

In contrast, *C. elephas* females showed much less spatial dispersal ability than *C. glandium* females (600 m versus 1200 m in 7 h, on average, for *C. elephas* and *C. glandium*, respectively). This species is known to be efficient at spreading the risk over time as adults of a given larval cohort are emerging over several years (Fig. 1). This is also supported by the fact that distinct genetic structures were found among populations of *C. elephas* located within 200 m from one another (F. Menu, pers. comm.). These two species (*C. glandium* and *C. elephas*) therefore cope with the spatial and temporal variability of acorn availability in distinct ways, and display markedly different combinations of dormancy and dispersal strategies. *Curculio glandium* is more likely to escape spatially when poor conditions are encountered locally (which occurred in 2008; Fig. 2) because of the ‘good dispersers’, which are able to reach distant, more productive oak trees. On rare occasions, however, oak tree populations (e.g. Liebhold *et al.*, 2004) might be short of acorns over a spatial range

that exceeds the flight distance of this species. Even though, *C. glandium* populations might still locally persist due to a residual ability to disperse over time (6% adults emerged later than 2 years after larval development; Venner *et al.*, 2011, Fig. 1). Similarly, *C. elephas* could also be able to cope with the spatial heterogeneity of the resource by means of moderate flying ability, although to a much lesser extent than *C. glandium*.

Unlike communities of annual desert plant species (e.g. Siewert & Tielbörger, 2010), which also compete for a pulsed resource, spatial dispersal might have an influential role in the dynamics of weevil communities. The relative advantages conferred by dormancy (via diapause) and dispersal could thus be more closely balanced than for annual desert plants. This can be explained by the active mode of dispersal in insects, where ‘good dispersers’ may actively seek out resource-rich sites, for example, by using information based on the amount of pollen produced by trees that may herald a forthcoming mast crop (Sork *et al.*, 1993). Thus, the cost of dispersal may be lower for weevils than for desert plants that disperse passively and hence, randomly. There might also be other differences between plants and insects that might hinder the efficiency of spatial dispersal in spreading the risk in plants. For example, the dormancy strategy is stable in the four insect species studied and independent of environmental conditions (fixed dormancy pattern; Venner *et al.*, 2011). In contrast, germination may be partly predictive in annual desert plants (Clauss & Venable, 2000) allowing them to emerge during favourable periods, which reduces the interest of spatial dispersal. In the same way, dormancy may be favoured in plants owing to the low energy cost involved throughout this period, whereas insects may have to invest much more energy during dormancy (Bel-Venner *et al.*, 2009). Future theoretical works should be able to elucidate how dispersal and dormancy act as risk-reducing strategies in disturbed environments, notably using models that take into account both the type of dispersal (active vs. passive); the mechanisms involved in the termination of dormancy (e.g. whether this depends on cues predicting favourable conditions) and the costs of energy needed for dormancy.

Unexpectedly, two of the four weevil species (*C. pellitus* and *C. venosus*) displayed very limited ability to disperse spatially (Fig. 3), as well as having poor ability to spread adult emergence over several years (Fig. 1). These two species may display traits other than spatial dispersal or risk spreading over time to buffer the marked fluctuations of the resource: for instance, they both emerge early (Pélisson *et al.*, 2012) and are the earliest weevil species to lay eggs in the season (Venner *et al.*, 2011). Such previous access to the food resource may enable them to find some egg-laying sites locally every year, even when acorn production is low because there are always some fruit products. This strategy could in turn prevent weevils from maximising their reproductive success when the resource is not limiting, as eggs laid early in the season might fail to develop due to the greater probability of fruit abortion (Venner *et al.*, 2011). This would have the effect of homogenising reproductive success among individual insects, which might be interpreted as a ‘conservative bet hedging strategy’ (‘a bird in the hand is worth two in the bush’) (Childs *et al.*, 2010). This

strategy has already been proposed in the case of semelparous perennial plants that, by initiating flowering either early in life or during the growth season are able to avoid high mortality risks and reproductive failure due to an occasional shortened season (Simons & Johnston, 2003; Rees *et al.*, 2004, 2006; Childs *et al.*, 2010).

Classically, diversified bet hedging is expected to evolve when individuals have an opportunity to skip unfavourable local conditions in a given year by traits such as dispersing or entering/pursuing dormancy (e.g. Seger & Brockmann, 1987). In contrast, conservative bet hedging is more likely when the adverse conditions are inescapable. Contrary to this conventional view, our results suggest that both conservative and diversified bet hedging might co-occur within communities of sibling species exploiting the same fluctuating resource. In the oak weevil communities studied, we found markedly diversified strategies among the four species (dispersal, dormancy and probably diversified or conservative bet-hedging strategies), which were likely to buffer environmental fluctuations. We suggest that such diversification could play a key role in stabilising the coexistence of these competing species, but theoretical investigations are required to investigate this issue in our biological system or in closely related ones (e.g. Annala, 1981) and in any species competing with each other and coexisting in variable environments.

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