

Intraspecific variations in dispersal ability of saproxylic beetles in fragmented forest patches

C. Bouget · A. Brin · D. Tellez · F. Archaux

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Abstract The extrapolation of metapopulation concepts to saproxylic insects suggests that the occupancy of forest patches and the colonization of ephemeral deadwood substrates are driven by micro-evolutionary processes that are related to adaptive plasticity and intraspecific sex-dependent polymorphism of dispersal traits. We hypothesized that forest fragmentation could favor more mobile individuals within populations, but little empirical data have been published on the potentially sex-biased response of insect populations to habitat availability. We selected 88 fragmented woodlots in two European agricultural landscapes to cover different degrees of spatio-temporal fragmentation, from small, isolated and recently established woodlots to large, inter-connected ancient woodlots. In line with our hypothesis, the average wing loading (WL), used as a proxy for dispersal ability, for each of nine flight-dispersing saproxylic

beetle species should be lower in recent, small, isolated woodlots than in ancient, large, inter-connected woodlots, respectively (i.e. ancient vs. recent, small vs. large, isolated vs. connected). Forest patch size did not significantly influence the average dispersal ability of beetle colonizers. However, WL of one-third of the tested species did significantly respond to forest ancientness or connectivity. Significant patterns were sex-biased, probably due to the contrasting role of males and females in species colonization dynamics. WL was lower in recent than in ancient forest plots for *Melandrya barbata* males, and it was lower in isolated than in connected woodlots for *Tetratoma ancora* and *Phymatodes testaceus* males. Contrary to expectations, we did not observe any decrease in polymorphism of dispersal abilities with decreasing woodlot size or increasing isolation. Our findings give support to the usefulness of gender consideration in insect conservation ecology studies.

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C. Bouget (✉) · D. Tellez · F. Archaux
‘Forest Ecosystems’ Research Unit, National Research Institute of Science and Technology for Environment and Agriculture (Irstea), Domaine des Barres, 45290 Nogent-Sur-Vernisson, France
e-mail: christophe.bouget@irstea.fr

F. Archaux
e-mail: frederic.archaux@irstea.fr

A. Brin
UMR Dynafor 1201, Ecole d’Ingénieurs de Purpan, L’institut national polytechnique de Toulouse (INPT)–Université de Toulouse, 75 voie du Toec, BP 57611, 31076 Toulouse Cedex 03, France
e-mail: antoine.brin@purpan.fr

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Introduction

A species’ ability to disperse among patches is central to its population dynamics in fragmented landscapes (Clobert et al. 2012). The distribution of a given species may be limited by its dispersal ability or by its habitat requirements (“recruitment or habitat limitation”), and these features will in turn affect the species composition of communities. Results from empirical studies do not unanimously support the notion that dispersal is a major limiting element for many taxa (Hanski and Gaggiotti 2004). Prugh et al. (2008) concluded that the degree of isolation and the surface area of habitat patches are unsatisfactory predictors

of habitat occupancy for the majority of taxa (birds, mammals, reptiles, amphibians and invertebrates). In contrast, the authors of some studies claim that site history and current landscape structure are more important than local site conditions (Cousins et al. 2009). Finally, yet another set of studies have shown that, in some cases, the isolation of populations induce transient micro-evolutionary responses to fragmentation which promote greater dispersal ability (for insects as an example, see Simmons and Thomas 2004). At this point it should be emphasized that the adjustment of dispersal capacity to landscape heterogeneity may be species-specific and may vary in an opposite way between sexes (Turlure et al. 2011).

In flying insects, the level of habitat fragmentation may affect flight performance (Taylor and Merriam 1995), which is correlated with morphology, especially wing morphology (e.g. Berwaerts et al. 2002; Sekar 2012). Combinations of simple morphological measurements, such as wing loading (WL; i.e. the ratio between body mass/weight and wing area), have been used as proxies for dispersal ability (Wainright 1994). WL refers to the pressure exerted by the wings on the air to support the body mass, with low WL indicating better energy efficiency and accounting for better flight performance. WL metrics have also been used for other taxa (bats: Norberg and Rayner 1987; birds: Alexander 2002) and as the response variable along different gradients at the meso- and macro- scales (Starmer and Wolf 1989; Arribas et al. 2012). However, intra-specific differences in dispersal ability have been little explored to date. Maximum dispersal distances are species-specific, but individual dispersal ability depends on individual morphology (Bowler and Benton 2005). Within species, sex-biased behaviors have been considered the primary forces driving the polymorphism, but little quantitative information is available on sex-biased dispersal (Gros et al. 2008). In most species, males and females have different dispersal strategies due to the differential allocation of resources between the sexes and sex-specific costs of dispersal, such as sexual dimorphism, territorial behavior in males, inbreeding avoidance and investment of resources in eggs by reproducing adult females (“oogenesis–flight syndrome”; Clobert et al. 2012). For example, females may become more likely to disperse when they are seeking oviposition sites, while males may disperse less if they are territorial. Non-territorial males may be more likely to disperse to increase their access to “new” females that they have not yet mated with.

Although saproxylic (i.e. deadwood-associated) insects do inhabit extremely fragmented forest ecosystems and even comprise a significant proportion of the biodiversity therein, few studies have focused on their dispersal mechanisms (Jackson et al. 2009). With the exception the dispersal studies of bark and ambrosia beetles (e.g. Sauvard 2004) in the context of forest protection, few empirical data

have been published on the response of saproxylic insects to habitat fragmentation or to past disruptions in the availability of their habitat. The extension of island biogeography and metapopulation concepts to saproxylic organisms suggests that the occupancy of fragmented forest patches in agricultural landscapes and the colonization of ephemeral deadwood substrates by insect specialist species (Vandekerkhove et al. 2013) are driven by micro-evolutionary processes related to adaptive plasticity and intraspecific (e.g. sex-dependent) polymorphism of dispersal traits. Among saproxylic beetle species, no univocal sex-biased pattern on dispersal behavior has been demonstrated in terms of the higher flight capacity in females than males (e.g. Dubois et al. 2010), or in males than females (e.g. Watson 2003).

From a theoretical perspective, recurring extinction and re-colonization by good dispersers may dominate population dynamics in small isolated patches (Gandon and Rousset 1999). If a morphological trait related to dispersal ability (e.g. WL) is genetically inherited, variations in its mean values in populations from small isolated patches should reflect these re-colonization events. Due to stronger selection pressures on individuals able to colonize, population assembly in small, isolated and recently established patches may be less dominated by random colonization events than that in large, inter-connected ancient forest patches, respectively. Increased dispersal ability in small isolated patches may be transient due to this trade-off between dispersal and subsequent selection for high reproductive output (Simmons and Thomas 2004). Moreover, we should find larger variations in WL in old and more connected woodlots than in recent and more isolated woodlots. Similarly, Painter et al. (2007) demonstrated that the current genetically depauperate lineages of the saproxylic beetle specialist *Pytho kolwensis* may be partly attributed to the small size and low number of its glacial refugia areas, in addition to auto-ecological parameters. Such micro-evolutionary processes related to adaptive plasticity should be manifest in intraspecific polymorphism. In other words, the quality and history of habitat used by saproxylic beetles should affect the intraspecific polymorphism of the dispersal trait. Moreover, asymmetrical selection pressures may be exerted on each sex for colonization of isolated patches (Julliard 2000).

Most forests in European agricultural landscapes have been fragmented into poorly connected woodlots (Estreguil et al. 2013) due to past deforestation for crops and pastures, recent reforestation of agricultural land and expanding transportation infrastructure (roads, railways, among others). In the study reported here, we assessed two typical French agricultural landscapes for the relative effect of several features characterizing forest spatio-temporal isolation/continuity: forest connectivity (i.e. percentage of forest cover in the surrounding landscape), woodlot surface area and woodlot ancientness. Ancientness

actually indicates continuity over time, whereas recentness shows temporal isolation. We defined a sampling design to cover a complete gradient from small, isolated and recently established woodlots to large, inter-connected ancient woodlots, respectively. The effect of isolation variables on individual WL was evaluated for nine common and uncommon flight-dispersing species which had been selected from the pool of trapped species for practical and ecological reasons (see section "[Beetle sampling and species selection](#)"). In our study, we sought to verify the following hypotheses:

- For a given species, due to a high selection pressure on individuals able to colonize, small, isolated and recently established woodlots would mainly be colonized by more mobile individuals (i.e. with a lower WL value). Mean WL for individuals living in the recently established woodlots should be lower, and variations in their WL narrower than for individuals living in ancient woodlots. This same pattern should also be found in small rather than large woodlots, and in isolated rather than inter-connected woodlots.
- Due to sex-biased patterns, the significance of species response to isolation features may be sex-dependent.

Materials and methods

Study area and sampling design

Fragmented woodlots were selected in a 30 × 40-km agricultural landscape located in the Gatinais-Puisaye ($n = 43$ woodlots) and Gascogne ($n = 45$ woodlots) regions of France [Electronic Supplementary Material (ESM) A]. The Gatinais-Puisaye landscape is located about 100 km south of Paris in Northern France, whereas the Gascogne region is near Toulouse in South-Western France. In each region, the sampling design included 15 woodlot triplets, with each triplet composed of one large (>10 ha) ancient, one small (<5 ha) ancient and one small recent woodlot (for a total of 45 woodlots). No large recent woodlot could be found in the selected landscapes. In the Gatinais-Puisaye region, two large ancient woodlots were included in two triplets each, so that the regional design included only 43 woodlots in total. The woodlots were also selected according to the percentage of forest cover in the surrounding landscape, and a wide range of cover densities were included to reflect different degrees of isolation. The isolation gradient combined with size and age resulted in six categories of woodlots: (1) large, ancient, connected; (2) large, ancient, isolated; (3) small, ancient, connected; (4) small, ancient, isolated; (5) small, recent, connected; (6) small, recent, isolated woodlots.

The percentage of forest cover in a buffer zone around each trap was calculated using ArcGIS® software ver. 2010 [Esri (Environmental Systems Research Institute), Redlands, CA] and French vegetation maps (BD TOPO®; l'Institut national de l'information géographique et forestière, Saint-Mandé, France) at two spatial scales [radius 500 m (78 ha); radius 2,000 m (1,256 ha)]. These spatial scales were considered adequate to differentiate beetle species with different dispersal ability (ranging from ten to several hundreds of meters; e.g. Sauvard 2004; Ranius 2006) and to demonstrate possible isolation effects between connected [high surrounding landscape forest cover (LFC)] and isolated (low LFC) woodlots. Within each landscape buffer zone, only woodland areas with a size of >0.05 ha were taken into account for forest cover calculations. LFC was taken as a continuous predictor and varied from 3 to 81 % (mean 24 %) in Gatinais-Puisaye and from 6 to 38 % (mean 21 %) in Gascogne at the 78-ha scale, and from 11 to 36 % (mean 20 %) in Gatinais-Puisaye and from 6 to 51 % (mean 19) in Gascogne at the 1,256-ha scale.

Woodlot surface area was assessed with ArcGIS® and varied from 1 to 373 (average 36) ha in Gatinais-Puisaye and from 1 to 82 (average 11) ha in Gascogne.

Forest ancientness was defined based on military maps drawn in the middle of the 19th century (Dupouey et al. 2007) at the moment when forest cover in France had reached its lowest value in the last two millennia. By definition, ancient forests are those which have been established for at least 200 years, i.e. their existence was already attested in the middle of the 19th century on state maps. Recent forests were defined as those created on former agricultural land, i.e. these sites had not yet been transformed into forests in the middle of the 19th century. In our two study regions, the only recent forests were small woodlots (average size 2.5 and 1.6 ha in Gatinais-Puisaye and Gascogne, respectively), whereas ancient forests included both small (average size 3.5 and 1.9 ha, respectively) and large (see preceding paragraphs) woodlots.

Beetle sampling and species selection

Flying saproxylic beetles were captured in alcohol-baited cross-vane flight interception traps (polytrap™). Three such traps were set out in each woodland at least 30 m apart. The traps were suspended roughly 1.5 m above the ground, and specimens were collected from April to July in 2012.

Species were selected based on the following criteria: occurrence in all woodlot types (small recent; small ancient; large ancient), minimum number of individuals (species represented by at least 40 individuals) and fragility to handling. The set of selected species should also be along a gradient of feeding ecology, size and rarity

according to their status in the Frisbee database (<http://frisbee.nogent.cemagref.fr/index.php/en/>). Overall, nine were retained for analysis, all of which are associated to deciduous trees, mainly oak and hornbeam (see ESM C for pictures):

- In Gatinais-Puisaye: two uncommon (not abundant and only locally distributed) species, i.e. *Melandrya barbata* (Melandryidae, saproxylophagous, 10 mm in length, in snags and logs) and *Tetratoma ancora* (Tetratomidae, xylomycetophagous, 3 mm, in wood-decay fungi), and three common species, i.e. *Trypodendron signatum* (Curculionidae Scolytinae, monogamous and xylophagous, 3 mm, in logs), *Melanotus villosus* (Elateridae, predator, 15 mm, in logs) and *Orchesia undulata* (Melandryidae, xylomycetophagous, 4 mm, in wood-decay fungi).
- In Gascogne: four common species, i.e. *Mycetophagus quadripustulatus* (Mycetophagidae, xylomycetophagous, 5 mm, in wood-decay fungi), *Melasis buprestoides* (Eucnemidae, saproxylophagous, 7 mm, in snags and logs), *Phymatodes testaceus* (Cerambycidae, saproxylophagous, 12 mm, in logs) and *Salpingus planirostris* (Salpingidae, predator, 3 mm, in snags and attached dead branches). For each selected species, about 30 individuals were sampled in ancient/recent, small/large, connected/isolated woodlots.

No species was common to both regions

Morphometric measurements

The WL for each individual was calculated after measuring wing area and dry body weight. For each individual, one of the two hind wings was detached, placed on a graduated reticule and observed under a SMZ-745T Trinocular stereomicroscope (Nikon, Tokyo, Japan). Clear pictures of each wing were taken with a Nikon camera coupled to the NIS-Elements software (Nikon), and the wing area was measured with the open access software ImageJ ($\pm 0.001 \text{ mm}^2$; National Institutes of Health, Bethesda, MD). The wing area measurement error was estimated by repeating each measurement and comparing the two resulting standard deviations, species by species, in order to calculate its potential influence (but only for specimens from the Gatinais region).

After dissection, all individuals were lyophilized for 6 h in an ALPHA 1-6 laboratory freeze dryer (Martin Christ Gefriertrocknungsanlagen GmbH; Osterode am Harz, Germany) before being weighed on a Mettler Toledo[®] MX5 digital microbalance (Mettler-Toledo Int., Greifensee, Switzerland) to $\pm 0.001 \text{ mg}$.

The gender of each individual was identified by dissection after weighing, or by genitalia extraction when sexual characteristics were not externally visible.

Data analysis

We used one discrete (ancientness) and several continuous variables (woodlot surface area and LFC at the 78- and 1,256-ha scale) as predictors to describe woodlot isolation. Individual WL within each species was the response variable.

The effects of the isolation features on individual WL were analyzed using linear mixed-effects models, built using the “gamm” function in the “mgcv” package, with a Gaussian error distribution and triplet (the spatial cluster of three close woodlots) as random effects. Multi-model averaging (Burnham and Anderson 2002) provided estimates for effects of isolation features on WL. The null model and generalized mixed-models with all of the valid combinations of two explanatory variables were generated. All models with a difference in the Akaike information criterion of < 2 from the best model were used to calculate the model-averaged estimates weighted by the model weights (MuMIn, arm; R-packages). Relative importance is the weight of evidence for each parameter across all the best models combining several variables. Since co-linearity among predictor variables may lead to unreliable parameter estimates, we followed the strategy suggested by Zuur et al. (2010) to address the multi-collinearity problem before model averaging. We sequentially dropped the covariate with the highest variance inflation factor (VIF), then recalculated the VIFs and repeated this process until all VIFs were below a pre-selected cut-off of 3 (Zuur et al. 2010).

Between-gender comparisons may be meaningless due to complex allometric interferences. However, to account for potential sex-biased patterns of WL response to isolation, we searched for interaction effects on WL between gender and isolation features. We ran multiplicative generalized linear mixed models, with the isolation features and gender as fixed effects and woodlot as a spatial random factor. This interaction was analyzed for *O. undulata*, *T. ancora* and *T. signatum* in the Gatinais dataset (too few females of *M. villosus* and *M. barbata* were caught) and for three of the four species in the Gascogne dataset (the distinction between male and female for *S. planirostris* was too difficult with dried specimens).

Only significant responses ($p < 0.05$), with a relative importance of > 0.05 , were displayed. Gamm models were checked with residual plots, and residual versus fitted plots. Due to homoscedasticity in the residuals, the error variance was not modeled.

We used *F* tests to compare variance values of WL among individuals for all selected species in the different woodlot isolation classes based on woodlot surface area [small ($< 8 \text{ ha}$) vs. large ($> 15 \text{ ha}$)], ancientness [ancient (before < 1850) vs. recent (later than 1850)] and spatial isolation [isolated

Table 1 Effects of isolation features and interaction with gender on wing loading of individual species and species groups

Region	Species	Ancientness	LFC500 ^a	LFC2000 ^a	Woodlot area	Interaction gender:isolation
Gatinais	<i>Melandrya barbata</i> (n = 22)	WL (recent) < WL (old)*	∅ ^b	ns	ns	∅
	<i>Melanotus villosus</i> (n = 36)	ns	ns	ns	ns	∅
	<i>Orchesia undulata</i> (n = 28)	ns	∅	ns	ns	ns
	<i>Tetratoma ancora</i> (n = 31)	ns	ns	ns	ns	Gender: LFC2000**
	<i>Trypodendron signatum</i> (n = 34)	ns	ns	ns	ns	ns
Gascogne	<i>Mycetophagus quadripustulatus</i> (n = 30)	ns	ns	ns	ns	ns
	<i>Melasis buprestoides</i> (n = 50)	ns	ns	ns	ns	Gender: LFC2000***
	<i>Phymatodes testaceus</i> (n = 30)	ns	ns	ns	ns	Gender: LFC2000**
	<i>Salpingus planirostris</i> (n = 30)	ns	ns	ns	ns	ns

Only significant responses ($p < 0.05$; relative importance > 0.5) tested with linear mixed-effect models {with triplet [one large (> 10 ha) ancient (old); one small (< 5 ha) ancient; one small recent (recent) woodlot] as a random effect} are displayed

WL, Wing loading

Significant at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns, Not significant ($p > 0.05$)

^a LFC500 and LFC2000, Percentage of landscape forest cover (LFC) in a 500— or 2,000-m-radius landscape disk, respectively

^b ∅, Not tested

(LFC < 20 %) vs. connected (LFC > 20 %)]. We did not compare raw variance values but rather the variance of residuals from a simple mixed-effect model, with species as a fixed variable and triplet as a random effect.

All analyses were conducted with R v2.12.0. All R-packages used are available online (http://cran.r-project.org/web/packages/available_packages_by_name.html).

Results

The average difference between repeated measurements of wing area was lower than its standard deviation by a factor of 3–30, depending on the species. For *M. barbata*, for example, the average difference between two measurements (0.15 mm^2) was 30.1-fold lower than the standard deviation (4.67 mm^2). For *O. undulata*, the average difference between two measurements (0.26 mm^2) was only 3.5-fold lower than the standard deviation of wing area (0.92 mm^2). The error on WL measurements was therefore considered to be negligible compared with the natural variations of the measured variable.

Between-species comparisons of WL were not meaningful per se and are not discussed here since variations in WL among species mainly reflect differences in body size (the larger the species, the higher the mean WL).

Ancientness and landscape effects on intraspecific variations of WL

In accordance with our initial hypothesis, the mean WL of *M. barbata* individuals (mainly males) significantly

responded to one of the spatio-temporal isolation features, namely, woodlot ancientness (Table 1; ESM B), with the mean WL being lower in recent than in ancient woodlots. No other significant response of mean WL to isolation parameters was evidenced for four species in the Gatinais (*M. villosus*, *T. ancora*, *O. undulata*, *T. signatum*) or for four species in Gascogne (*M. buprestoides*, *P. testaceus*, *S. planirostris*, *M. quadripustulatus*).

Range of wing loading response

Contrary to expectations, no significant differences in the range of WL variance among individuals were observed for any of the selected species in the following comparisons: recent versus ancient woodlots, small versus large woodlots and isolated versus connected woodlots (Table 2).

Influence of gender on wing loading response to isolation

The gender–isolation interaction effect on wing polymorphism was not assessed for *Melandrya barbata* and *Melanotus villosus* in Gatinais (Table 1) because of a strongly unbalanced sex ratio in favor of males. The interaction effect on WL between gender and LFC at the 1,256 ha-scale was significant for *T. ancora* in Gatinais and for *P. testaceus* and *M. buprestoides* in Gascogne (Table 1). The response of WL to LFC for these three species differed between males and females (Fig. 1). Partly in agreement with our hypothesis, mean male WL for *T. ancora* in Gatinais and *P. testaceus* in Gascogne decreased slightly with LFC, whereas female WL did not vary significantly. Conversely, WL of *M. buprestoides* males in Gascogne did not vary with forest cover in the

Table 2 Variations in standard deviation of wing loading in woodlot categories based on spatio-temporal isolation features

Fitted wing loading standard deviation	Location of agricultural landscape	
	Gatinais	Gascogne
Woodlot ancientness		
Recent (>1850)	0.0435 ns	0.0794 ns
Ancient (<1850)	0.0418	0.0884
Woodlot area		
Small (<8 ha)	0.0431 ns	0.0851 ns
Large (>15 ha)	0.0424	0.0848
Landscape forest cover (LFC)		
Isolated (LFC <20 %)	0.0446 ns	0.0881 ns
Connected (LFC >20 %)	0.0411	0.0775

ns: $p > 0.05$

F tests were used to compare the variance values of residuals from a simple mixed-effect model, with species as a fixed variable and triplet as a random effect

surrounding landscape, whereas female WL significantly increased with forest isolation, contrary to our expectations.

Discussion

Overall, we observed several significant effects of fragmentation and historical factors on species WL. In our study, the landscape and historical effects on species WL occurred in both regions despite a number of strong region-specific differences in terms of current landscape composition (higher density of hedges in Gascogne, closer large potential source forests in Gatinais) and landscape dynamics (higher increase in LFC during the last two centuries in Gascogne). Despite small sample sizes, WL analyses reflected wide intraspecific variations in dispersal ability and demonstrated significant isolation-driven variations in WL values for one-third of the tested species; these results allow potential random results to be discarded. Between-gender comparisons were not computed, since their significance is strongly weakened by complex allometric interferences. With both genders combined, the average dispersal ability of the nine selected species was not significantly affected by forest connectivity, ancientness and/or area.

Sex-dependent response of dispersal abilities of saproxylic beetle colonizers to spatio-temporal isolation

Influence of forest ancientness

In accordance with our initial hypothesis, the WL of the *Melandrya barbata* male individuals which had colonized

recent woodlots was lower than that of males in both small and large ancient woodlots. In other words, the individuals which had successfully colonized recent woodlots were on average better dispersers than those caught in ancient woodlots. *M. barbata* is associated to moist decaying oak and beech wood (Alexander 2002) and is not considered to be associated with and to track ephemeral deadwood. No demographic trend, such as a higher abundance of *M. barbata* in ancient woodlots, was observed in addition to this morphological response (unpublished data).

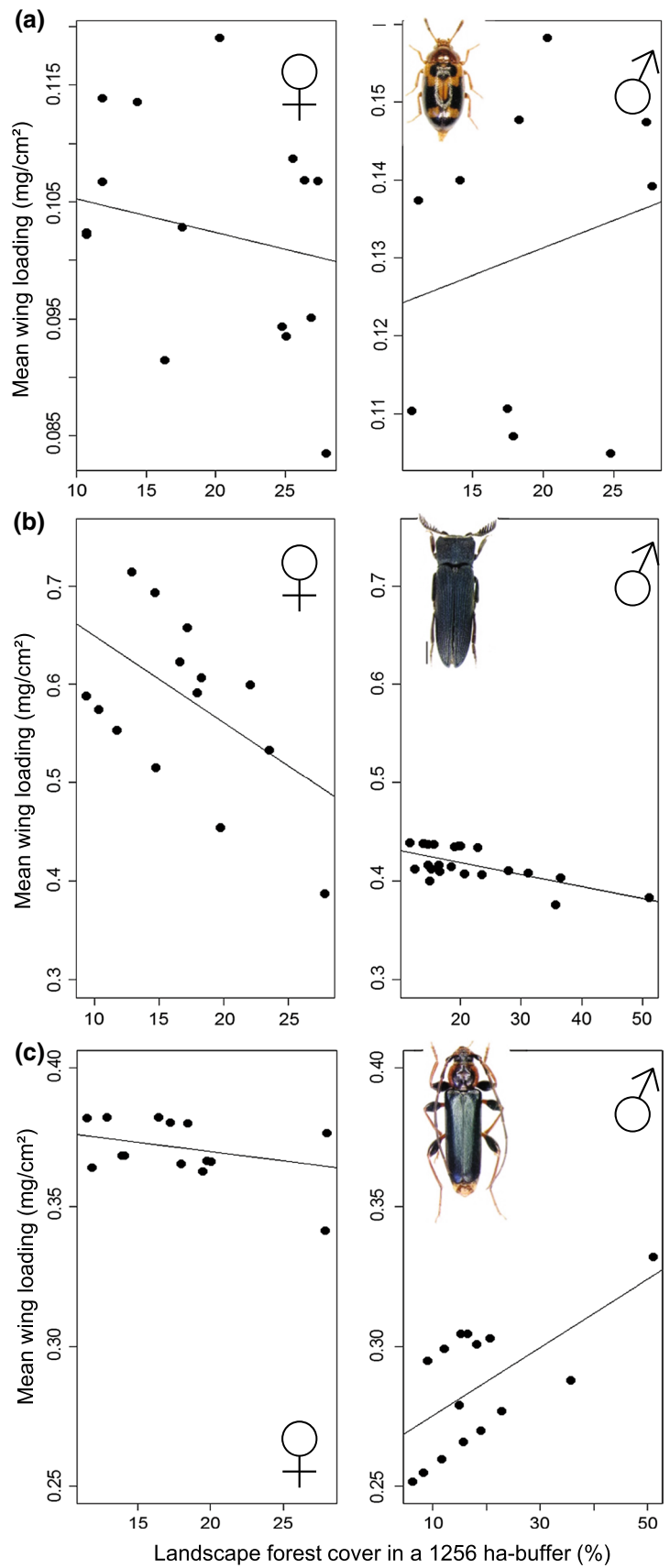
These contrasted morphological characteristics between populations in ancient versus recent woodlots are related to dispersal abilities and confirm that forest (and deadwood) continuity is important for the dynamics of some saproxylic species populations (Nordén and Appelqvist 2001). Only a few studies have previously highlighted distinct saproxylic beetle assemblages in recent forests and ancient forests where agriculture has not interrupted deadwood input (Goßner et al. 2008; Irmeler et al. 2010; Buse 2012). Even the effects of forest continuity on habitat availability have rarely been described (but see Lohmus and Lohmus 2005). More studies are required at the population level on the colonization of reforested areas by insect groups with limited dispersal, such as saproxylic species (DeKoninck et al. 2008). Analogous studies of butterfly (Hill et al. 1999) and winged-dimorphic cricket (Simmons and Thomas 2004) species with expanding ranges have shown that recently colonized populations exhibit increased dispersal ability or changes in flight morphology at the range margin as compared with longer established populations in the core range.

Influence of forest connectivity

Tetratoma ancora males in Gatinais and *Phymatodes testaceus* males in Gascogne which had colonized isolated woodlots were on average better dispersers than their counterparts in connected forests, in line with our expectations. The average dispersal ability of females of both species was not affected by forest isolation (i.e. by a decrease in the LFC). On the contrary, for *Melasis buprestoides* in Gascogne, the WL of females only was affected by woodlot isolation. Contrary to expectations, their WL increased with woodlot isolation.

The contrasted gender-influenced responses we found must be related to the differing drivers of male and female dispersal within the specific species' population dynamics (mating systems, female colonization of new oviposition sites, male territoriality, responsibility for foraging, genetic outbreeding, female investment in egg production, among others). From our results, forest fragmentation mainly affected the dispersal ability of males and also favored the more highly mobile individuals. These

Fig. 1 Male and female wing loading (WL) response to isolation features (percentage of landscape forest cover in the surrounding landscape (buffer radius 2,000 m, buffer area 1,256 ha). Only significant interaction effects ($p < 0.01$) are displayed here (mean WL values in mg/cm^2). A trend line of fitted values generated by a linear mixed model was added to the scatter plot. **a** *Tetratoma ancora* (Gatinais; $n = 31$), **b** *Melasis buprestoides* (Gascogne; $n = 50$), **c** *Phymatodes testaceus* (Gascogne; $n = 30$). Photographs of insects are copyright of Pierre Zagatti



sex-dependent variations were probably related to species colonization dynamics. Results from available studies show that males or females may have the higher dispersal ability and that either may have the responsibility for colonizing new habitat patches in a fragmented environment. The literature is rather poor in terms of quantitative studies on between-gender differences in dispersal among saproxylic beetles. Oleksa et al. (2013) reported that sex-specific costs of dispersal cause females to be the main sex responsible for effective dispersal in the genus *Osmoderma* (see Dubois et al. 2010; Hedin et al. 2008). Similarly, in a study on *Scapanus australis*, which bores in wood of coconut palms, Beaudoin-Ollivier et al. (2003) also argued that females possibly disperse greater distances to insure outbreeding with unrelated males because flight is less costly for females given their smaller body mass and lower WL. From theoretical models (Gros et al. 2008), a higher dispersal ability for females would be naturally selected to maximize successful colonization, whereas higher dispersal abilities for males would enable species to favor genetic outbreeding. It should be emphasized that the dispersal ability of female individuals is known to vary over their life cycle: flight muscles and body fat regress while ovarioles develop, with the reverse effect occurring at the end of oviposition (Lieutier et al. 2004).

For *Melandrya barbata* and *Melanotus villosus*, the lack of females among the trapped individuals may reflect a difference in dispersal behavior between genders. Males may be more abundant, more active fliers (see Watson 2003 about another similar deadwood-associated species) or may have a distinct dispersal mode which makes them easier to sample with window-flight traps. For stag beetles, for example, the species dispersal pattern consists almost exclusively of flights by males, while females fly very rarely and disperse over shorter distances, moving frequently along the ground (Sprecher-Uebersax and Durrer 2001; Rink and Sinsch 2007). Moreover, Drag et al. (2011) observed that males were recaptured more frequently than females despite no between-gender difference in cumulative dispersal distance.

Influence of forest area

In our study, forest patch size did not significantly influence the dispersal characteristics of the individuals caught. For any given species, average WL in small woodlots (ancient or recent) was no lower than that in large woodlots (ancient). Conversely, Irmeler et al. (2010) provided evidence that the contribution of the least mobile species to woodlot species richness increases with forest size in German agricultural landscapes.

Response of the dispersal trait breadth

In addition to mean values, we also analyzed the variation range of WL values (i.e. the “trait breadth”). Since small island populations are characterized by high turnover rates, poor dispersers are less common in a fragmented landscape, and isolated patches are dominated by individuals with high dispersal abilities (Tscharrntke et al. 2002). Contrary to our hypothesis, however, variations in WL values in small, isolated and recently established forests, where population assembly is presumably less dominated by random colonization events, were not narrower than those in large, inter-connected ancient woodlots due to stronger selection pressure on individuals able to colonize. Unlike Painter et al. (2007) who found that current levels of genetic variation are partly linked with current and past habitat isolation, we did not observe an increase in the polymorphism of dispersal ability with current woodlot isolation for each of the nine species studied.

Conclusion and perspectives

It should be emphasized that all the observed significant results (one-third of the tested species) were actually related to sex-biased patterns. Our findings provide support to the usefulness of gender identification for sampled individuals in population ecology studies of saproxylic beetles (Gros et al. 2008). The absence of significance in the WL response to isolation for two-thirds of the species tested or one of the genders may be discussed in the light of two major points: (1) the high ability of some saproxylic species to disperse, and (2) the suitability of the WL as a proxy of dispersal abilities.

First, the dispersal ability of saproxylic beetles is actually extremely diverse. Some species, often linked with highly ephemeral habitats (such as bark beetles), have a high dispersal capacity (Sauvard 2004) and are able to cross a several kilometer section of unfavorable habitat. In our study, the WL of males and females of the scolytid *Trypodendron signatum* was not affected by isolation features, possibly due to the dispersal ability of the species (Salom and McLean 1989). Species associated to intermediate, stable habitats, such as fungus-inhabiting species, are known to exhibit a range of dispersal distances between these extreme values (Jonsell et al. 1999). Among our selection of xylomycetophagous species to be tested, the response to isolation was significant (*M. barbata*, *T. ancora*) or not (*O. undulata* and *M. quadripustulatus*). The fact that some of our species were not limited in terms of dispersal in the studied forest landscapes could contribute to weak and non-significant isolation effects on WL variations.

Secondly, the use of WL as a proxy for dispersal ability may be questioned. The WL has been recently and

successfully used for saproxylic beetles (Gibb et al. 2006), water beetles (Arribas et al. 2012) and phytophagous leaf beetles (Naranjo 1990; Boiteau and Colpitts 2001). This index here provided new information about the colonization of fragmented woodlots in a European agricultural landscape by saproxylic beetles. In our data, the significant responses of WL to isolation features concerned both common (*P. testaceus*, *M. buprestoides*) and uncommon (*M. barbata*, *T. ancora*) species. The study of variations in WL and dispersal ability for common or rare species which are more or less sensitive to fragmentation deserved further attention. In Swedish forests, Gibb et al. (2006) have already demonstrated that rare saproxylic species have a lower mean WL, suggesting superior dispersal abilities, than more common congeneric species. Since WL is very influenced by variations in body size, its use is mainly relevant for congeneric (Gibb et al. 2006) or intraspecific approaches. For females, WL analyses may also be biased by variations in body conditions with physiological status, from teneral and immature to fully reproducing adult females. Other morphological variables affect the aerodynamics of insect flight: wing beat frequency, wing shape and the volume of wing muscles (thoracic mass and length, flight muscle ratio, i.e. thoracic mass/body mass) (Harrison 1980). These features are, however, far too difficult to measure to be included in another morphometric index of flight morphology.

It should be acknowledged that present-day occurrence patterns are the result of colonizations and extinctions and also reflect the situation historically. Nonetheless, studies of occupancy patterns reveal the consequences of real dispersals over larger spatial and temporal scales than direct methods (capture–recapture, electronic tags and telemetry, flight mills) (Ranius 2006). It should also be pointed out that colonization events include immigration and settling processes, where deterministic within-patch habitat-driven environmental effects may have a substantial influence. In addition to mobility (number of displacement events) and dispersal capabilities (flight or walking, distance), the sensitivity of a species to habitat fragmentation also depends on other ecological traits, such as demography (population size, reproduction rate) and stenoecy factors (ecological plasticity) (Nordén and Appelqvist 2001). The response of saproxylic beetles to forest fragmentation and to forest history should be further investigated in other forest landscapes using population genetic tools and comparing winged and wingless species colonization (Horak et al. 2013).

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