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Seeds and seedlings of oaks suffer from mammals and mollusks

close to phylogenetically isolated, old adults

Running head: Mammals and mollusks attacking oaks

Maud Deniau¹, Mickael Pihain^{1,2}, Benoît Béchade³, Vincent Jung¹, Margot Brunellière¹,
Valérie Gouesbet¹, Andreas Prinzing^{1*}

* correspondence author: andreas.prinzing@univ-rennes1.fr; + 33 06 06 65 13 87

¹ *Université de Rennes 1, Centre National de la Recherche Scientifique, Research Unit UMR 6553 'Ecosystems, Biodiversity, Evolution', Campus Beaulieu, Bâtiment 14A, 263 Av. du Général Leclerc, 35042 Rennes cedex, France*

² *Institute of Ecology and Earth Sciences, University of Tartu, 51014 Tartu, Estonia*

³ *Department of Biology, Drexel University, Philadelphia, PA, 19104, USA*

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Abstract

Background and Aims. Mammals and mollusks (MaM) are abundant herbivores of tree seeds and seedlings, but how the trees and their environment affect MaM herbivory has been little studied. MaM tend to move much larger distances during feeding stage than the more frequently studied insect herbivores. We hypothesize that MaM (i) select and stay within the patches that promise to be relatively the richest in seeds and seedlings, i.e. patches around adult trees that are old and within a distantly related, less productive neighborhood; and (ii) try to remain sheltered from predators while foraging, i.e. mammals remain close to adult trees or to cover by herbs while foraging, and might force their mollusk prey to show the opposite distribution.

Methods. We exposed oak acorns and seedlings in a temperate forest along transects from adult conspecifics in different neighborhoods. We followed acorn removal and leaf herbivory. We used exclusion experiments to separate acorn removal by ungulates vs. rodents and leaf-herbivory by insects vs. mollusks. We measured the size of the closest conspecific adult tree, its phylogenetic isolation from the neighborhood and the herbaceous ground cover.

Key Results. Consistent with our hypothesis, rodents removed seeds around adult trees surrounded by phylogenetically distant trees and by a dense herb cover. Mollusks grazed seedlings surrounding large conspecific adults and where herb cover is scarce. Contrary to hypothesis, impact of MaM did not change from 1 to 5m distance from adult trees.

Conclusions. We suggest that foraging decisions of MaM repulse seedlings from old adults, and mediate the negative effects of herbaceous vegetation on tree recruitment. Also, increase in mammalian seed predation might prevent trees from establishing in the niches of phylogenetically distantly related species, contrary to what is known from insect enemies.

Keywords: forest ecology; insects, mollusks and rodents; landscape of fear; leaf herbivory; optimal foraging; phylogenetic Janzen-Connell hypothesis; pathogens; phylogenetic diversity; *Quercus*; seed and seedling predation

Introduction

The seed and seedling phase is essential for successful tree recruitment, and seed and seedling herbivory by insects has been suggested to control the establishment and coexistence of tree species (Hanley & Sykes, 2009; Terborgh, 2012; Bagchi *et al.*, 2014). Insect herbivory on seeds and seedlings may be strongly influenced by the spatial distance to the adult tree or the phylogenetic distance of the neighborhood, according to the Janzen-Connell hypothesis (Janzen, 1970; Connell, 1971) and the phylogenetic Janzen-Connell hypothesis (Liu *et al.*, 2012), respectively: pressure by such insect herbivores on seeds/seedlings decreases with spatial distance to a conspecific adult tree or with phylogenetic distance to an adult tree (Schupp, 1988; Deniau *et al.*, 2018). Seeds are also often consumed by rodents and ungulates (Gonzalez-Rodriguez and Villar, 2012; Schnurr *et al.*, 2004), and seedlings are consumed by mollusks (Jennings and Barkham, 1975; Pigot and Leather, 2008). Slugs in particular, may be major causes of mortality of seedlings (Pigot and Leather, 2008). Despite this established importance of mammals and mollusks (MaM from here on) herbivory on seeds and seedlings, little is known on how this phenomenon is affected by trees and their environment.

MaM differ from insect herbivores by the fact that they travel across dozens to thousands of host seeds/plants while feeding (Grimm and Paill, 2001), whereas most insect herbivores stay on a single or few host plants during their feeding stage (van Asch and Visser, 2007).

Foraging across such an amount of host seeds/plants may have two consequences. First, MaM must frequently select and leave patches of seeds and seedlings depending on the

perceived quality of these patches relative to the matrix. Numbers of seeds and seedlings within a patch or matrix may be difficult to perceive while being inside the matrix or the patch, but adult trees might be used as proxy: as seed production of adult trees increases with adult age the patch surrounding an old adult might be richer in seeds and seedlings than a patch surrounding a young adult. Adult age, in turn, can be assessed from trunk size. Even terrestrial mollusks might be able to perceive trunk size as they orient themselves towards larger dark zones (Zieger et al. 2009), i.e. should approach an older tree. Also, some plant lineages produce more and larger and more nutritious seeds and seedlings than others. A patch surrounding an adult of the lineage preferred by given MaM is likely particularly rich in preferred seeds and seedlings and might attract MaM foraging across a matrix of adults belonging to phylogenetically distant lineages. Once MaM reached such a patch of the preferred lineage in a non-preferred matrix, MaM will likely exploit it down to a low giving-up density of resources (Charnow 1976, Kotler & Brown 2003). In contrast, in patches in a matrix composed of adults of the same, preferred lineage, MaM might be less attracted to an individual patch, be readier to leave it, and might become temporally satiated during peak periods of seed availability (Silvertown, 1980 for satiation mechanisms in general).

The second consequence of MaM herbivores being mobile and travelling long distances while feeding is that predators might spot and attack them. MaM need shelter where predators cannot see or attack them. Small mammals are major herbivores of seeds, and are attacked by aerial predators, notably owls. Visual or acoustic orientation of such an aerial predator, as well as attempts of attack, can be obstructed by a dense herb layer hiding the small mammal (Gill and Marks, 1991; Ostfeld and Canham, 1993; George and Bazzaz, 1999). Even trunks of standing trees may provide partial shelter to small mammals up to a few meters, leading to higher seed-removal activity of small mammals close to the trunks (Iida, 2006; Ribeiro et al., 2016). In a “landscape of fear” (Bleicher, 2017), such small-scale

shelters are essential. Mollusks are major herbivores of seedlings, and exposed to a diverse range of predators, including small mammals. It can be speculated that mollusks are sheltered from their predators where these predators are not, i.e. where herbaceous cover is sparse or tree trunks relatively far. Alternatively, climbing tree trunks might be a strategy to escape ground-dwelling predators such as carabid beetles. We hence hypothesize that mammals prefer to choose to forage on seeds in direct vicinity of a tree trunk and where cover by herbaceous vegetation is most dense. We hypothesize that mollusks might either take the opposite foraging choices to avoid predation by mammals, or similarly prefer proximity to adult trees to hide close to their trunks.

In most late-successional temperate forests, oaks (*Quercus* sp.) are abundant and constitute one of the main food sources for herbivores (Gurnell, 1993; Ouden et al., 2005): seeds (*i.e.* acorns) are very nutritious and often produced in high quantities, and are preferred by the dominant rodent species such as *Apodemus sylvaticus* over other tree species, in particular those of gymnosperm trees (Jennings, 1976). Also, leaves of oak seedlings are frequently consumed by herbivores (Deniau et al., 2017). Many temperate forests are highly spatiotemporally heterogeneous where the home range of a given rodent or ungulate acorn-predator likely spans zones of different tree-species composition (Abramson et al., 2006) providing seeds during different seasons. Within zones dominated by lineages distantly related to oaks, rodents might concentrate foraging activity on patches surrounding adult oaks.

The above hypotheses on choices made by foraging MaM predict under which conditions MaM herbivory on seeds or seedlings should be highest: around adults with a large trunk being surrounded by phylogenetically distant adults and by a dense (mammals) or sparse (mollusks) herbaceous layer, and in direct vicinity of these trees. We tested these predictions for oaks (*Quercus petraea* or *Q. robur* or hybrids) by comparing acorn and seedling

herbivory with each of these conditions. We followed acorn removal, separating ungulates and rodents by exclusion experiments. We followed seedling herbivory, separating herbivory by vertebrates, insects and mollusks using exclusion experiments. We also discriminated plant attacks by different insect feeding guilds or airborne pathogens by observation. In a phylogenetically proximate neighborhood, oaks are often separated by 10m or less, which is why we restricted the spatial distances to maximum of 5 meters. Moreover, the possible shelter effect of a trunk from attack by aerial predators is likely only operating across shortest distances (Iida, 2006).

Materials and methods

STUDY SITE

We carried out the study in the forest of Rennes, Brittany, France (48°12' N, 1°33' W; ca. 90 m altitude; 3,000 ha) between 2013 and 2015. This area is characterized by an oceanic climate, a mean annual temperature of 11.3 °C and a cumulative annual rainfall of 836 mm. The forest is composed of two parcel types dominated by either oak (*Q. petraea* or *Q. robur* or hybrids) and beech (*Fagus sylvatica*), or by Scots pine (*Pinus sylvestris*) interspersed with oaks and other Angiosperms, all typical for European temperate oceanic lowland forests (Yguel et al 2011, Deniau et al., 2017). In total 10 tree species were found as neighbors of our adult trees (details in Yguel et al., 2011). Understory vegetation is mostly composed of a fern species (*Pteridium aquilinum*), a grass species (*Molinia caerulea*) and some shrubs of common holly (*Ilex aquifolium*). This forest is inhabited by typical enemies of tree seeds and seedlings occurring in western-European temperate forests: vertebrates, notably ungulates (wild boar *Sus scrofa* and roe deer *Capreolus capreolus*), and rodents (*Apodemus sylvaticus*; see Appendix S1); invertebrates, notably insects (see Appendix S2 for Lepidopteran species

occurring on adult oak trees) and mollusks (notably *Arion* sp. and *Limax* sp.; see Appendix S3); and airborne pathogens like the mildew fungus *Erysiphe* sp. Note that the red deer *Cervus elaphus* is absent from this forest (Office National des Forêts, pers. comm.) and that bird predators of acorns were never observed on the ground.

Within the forest, we selected ten pairs of adult oak trees (*Q. petraea* or *Q. robur* or hybrids, used by Yguel et al., 2011; see Appendix S4 for geographic distribution of pairs and for distances among pairs, ranging from 0.2 to 5 km, with an average of 2.1 km). In each pair, oaks belonged to the same species. Each pair had one tree in a more oak-dominated zone and one in an adjacent more pine-dominated zone. Diameters at breast height of focal trees ranged from 14 to 32 cm (mean 22 cm SD 5.8 cm), a range corresponding to adult age (e.g. Steele et al. 2007). Larger trees were absent from the more pine-dominated zones and were hence not considered. Selecting adult oak trees in both types of zones ensured a large range of phylogenetic distances between adult oaks and their neighbors (precise quantification of phylogenetic distances is explained below). This spatially paired design was essential to control for variation among pairs due to different macroenvironments (Legendre et al., 2004). Trees within a pair were separated by distances of less than 150 m. Such distances are within the range covered by rodents (Abramson et al., 2006), and they hence have a chance of entering also in patches dominated by trees that are phylogenetically distant from oaks (confirmed by our observations). Within their respective patch, rodents then might take foraging decisions based on the local environment as outlined in the Introduction. Note that while within a pair of focal oaks the mean phylogenetic distances from the respective neighbors were contrasting, these mean phylogenetic distances from neighbors covered a continuous gradient across all focal oaks.

EXPERIMENTAL DESIGN: ACORN REMOVAL

Acorn harvesting -- In late October 2013, we selected 5 mature oak trees as sources (*Q. robur*; note that acorn removal was not oak-species dependent, Appendix S5) outside the forest on a grassland (as they produce more acorns than trees inside forests; Jones, 1959). We harvested acorns still attached in trees by shaking branches. Twenty-one percent of the harvested acorns were infested by insects (e.g. weevil larvae); which we identified as those that floated in water, or showed a covered hole in their seed coat, a mark left by female insects during oviposition (see Perea et al., 2012). We excluded these infested acorns as they are less preferred by rodents than viable acorns and generally more predated, hence less likely to survive (Ouden et al., 2005; Perea et al., 2012). Finally, for each of the 5 acorn sources, we selected viable acorns approximately similar in size and shape to avoid differences in defense/tolerance or attractiveness (Bogdziewicz et al., 2018; Moreira et al., 2020). We used the same acorn-source tree for the two trees of each pair, and across pairs we verified that source provenance did not relate to removal rate (ANOVA, $p > 0.4$).

Exposure of acorns in the field and identification of acorn removers -- We exposed 2,000 viable acorns in the field in late November 2013. We established a transect of 5 m length, starting from the trunk of each of the twenty focal adult oak trees, and avoiding to approach other trees (Fig. 1). Starting from 1 m, we installed every meter a tray (20 cm x 20 cm x 2 cm, wood-colored, hardly extending above litter surface) and fixed it in the soil with a staple. We placed 10 acorns on each tray that were hence accessible to all removers (*i.e.* control). To identify whether ungulates or rodents were the major responsible of acorn removal, we chose to exclude one type of enemy. We established a second transect, identical to the first one but oriented in another direction to avoid unnaturally high density of acorns and hence attraction of removers. Every meter along this transect, we again exposed acorns, but now

with a cage made of a 25 mm metal mesh (height = 5 cm) fixed with a staple, excluding the mouthparts of ungulates but not of rodents. We placed 10 acorns in each cage.

Measurement of acorn removal -- We followed acorn removal every week from the day of exposure in the field in late November 2013. We counted the number of remaining acorns on each tray and cage until all acorns had disappeared (after a maximum of 91 days). We also noted if acorns presented evidence of *in situ* predation. Then, for each tray and cage, we calculated the delay before acorn removal by averaging the number of days before removal of the 10 acorns. We use the term ‘removal’ instead of ‘predation’ as the fate of the removed acorns is unknown.

SEEDLING HERBIVORY

Seedling harvesting -- In early March 2015, we harvested 18 oak seedlings (*Q. petraea* or *Q. robur* or hybrids) for each pair of adult oak trees. We harvested seedlings in the more oak-dominated zone of a given parcel, as seedlings were too rare in pine-dominated parcels. We chose seedlings carefully, to be approximately of same height/age (ca 20 cm, ca. 1 year old), morphology, to be no longer dependent upon stored reserves (i.e. no acorn attached), to have no visible signs of pathologies or damage, and to have intact buds. Seedlings were gently washed to eliminate possible infestation by eggs of herbivores.

Exposure of seedlings in the field and identification of seedling attackers -- Immediately after harvesting, we planted seedlings along a transect of 5 m length, perpendicular to the trunk of each focal adult oak (Fig. 1). We transplanted seedlings at 3 distances along this transect: 0.5 m, 2.5 m and 5 m. Per distance, three seedlings were placed, spaced by approximately 30 cm. We identified seedling attackers by traces of consumption as follows: Airborne pathogen was recognized by the white powdering mantle which covers leaves. Vertebrates entirely kill

seedlings by cutting stems and uprooting seedlings. Invertebrates induce different leaf damages that are specific to a feeding guild (Giffard et al., 2012; Castagneyrol et al., 2013; see Appendix S6 for pictures): ‘entire-leaf chewers’ eat entire parts of leaves; ‘leaf skeletonizers’ are partial-leaf chewers and leave the veins; ‘leaf rollers’ roll parts of leaves; ‘leaf suckers’ pierce very small holes into leaves; ‘leaf miners’ consume leaves internally and ‘gall makers’ induce new structures on leaves. Chewers may be mollusks or insect chewers. Feeding traces of mollusk and insect chewers are visually undistinguishable without large magnification (personal observation). To separate the respective effects of insect and mollusk chewer, we applied an exclusion experiment. We established 3 treatments for each position along the transects: (i) control; (ii) exclusion of insects, using a synthetic pyrethroid insecticide that kills insects by contact and if it is ingested (Mandarin® Pro 50 g/L esfenvalerate, PHILAGRO, France) used at a concentration of 12.5 mg/L, as recommended by the manufacturer. We sprayed the insecticide on seedling leaves every 2 weeks (note that control seedlings were sprayed with water at the same time, to avoid any potential bias due to watering). Esfenvalerate has no attractive or repulsive effect on slugs (comparisons to controls in Piechowicz et al., 2012) and only minor incidence on seedling functions or survival (Root, 1996; Carson and Root, 2000; Mitchell, 2003); (iii) exclusion of both insects (using insecticide as described above) and mollusks. To exclude mollusks, we placed a PVC pipe (10 cm diameter, 15 cm height) around each seedling and inserted this pipe into the soil on 5 cm, hence preventing mollusks to pass underneath. We covered the upper extremity of the PVC pipe by a 5 cm-wide strip of copper tape, as it repulses mollusks by contact (Lankau, 2007). Seedling leaves were above the PVC pipe, hence limiting the impact of the PVC pipe on seedling microenvironment.

Measurement of seedling leaf herbivory -- As leaf herbivory may accumulate with time, we began by recording the date of seedling budburst (*i.e.* leaves totally deployed) based on

controls at 3-day intervals. Most seedlings developed only one bud. We thus considered only the first bud that burst for each seedling. As leaf herbivory may accumulate with time, we quantified the age of the seedling leaves on which herbivory was measured. We calculated the leaf age of each seedling at the end of July 2015, when we measured herbivory.

We followed seedling herbivory weekly from the day of transplantation to the end of July 2015, when most damages by herbivores had occurred. We noted the number of leaves per seedling weekly from the end of May to the end of July (30 days). Such a high temporal resolution of the screening allowed us to identify cases where an entire leaf had disappeared due to chewer consumption. In late July, we noted the presence/absence of consumption by vertebrates. We also estimated for each seedling the percent of leaf area removed (LAR) by chewers, skeletonizers, suckers and attained by airborne pathogens, using a grid of points (0.25 cm²) (Yguel et al., 2011). The percent of LAR corresponds to the ratio between the number of points falling on area consumed by each herbivore, and the number of points forming the whole surface (including area consumed by chewers), multiplied by 100. Leaves which have been totally consumed had %LAR = 100 and we calculated the average value across all leaves for each plant. We also counted the number of rollers, miners and gall makers per leaf and then averaged for each seedling. If a seedling died (as happened in 8.9% of the seedlings developing leaves, 6.1% overall) it did not receive a LAR score.

CHARACTERIZATION OF CONSPECIFIC ADULTS AND GROUND COVER

First, we evaluated the spatial distance of seedlings to their closest conspecific adult (Fig. 1). Inevitably, when oaks were the dominant species, the focal adult oak was not always the closest conspecific; we thus measured the spatial distance of each transplanted seedling to the stem position of the closest conspecific adult (> 2 m height).

Second, we measured the circumference at breast height of the closest conspecific adult and used this measure as a proxy of tree size. We took the average distance and circumference ('size' from hereon) when two conspecific adults were equally close to a seedling. For acorns, these measures of closest conspecific adults were not available and we instead used distance to and size of the focal adult tree as proxies. These proxies might be poor far from the focal adult tree, but conclusions did not change when including only acorns at 1 m from focal adult conspecific (Tab. 1).

Third, we quantified the degree to which the canopy was dominated by species distantly related to oaks rendering the focal oak relatively more attractive for oak enemies. For a given focal adult oak, we determined phylogenetic isolation from the neighboring canopy, using average phylogenetic distances to each of its adult neighbors with which their crown was in contact, established by Vialatte et al. (2010) and Yguel et al. (2011) (ranging from 0 to 140 Million Years Before Present, MYBP, Appendix S7 for explanation of the procedure).

Finally, we quantified the ground cover around the seedlings in a 1 m² plot, noting the number of oak seedlings, and the percentage coverage by deadwood, mosses, "herbs" (the fern *Pteridium aquilinum* and the grass *Molinea caerulea*), and shrubs (*Rubus spec*, *Lonicera spec.* and *Ilex aquifolium*). The canopy cover was taken from Deniau et al. (2017) and measured at 0.5, 2.5 and 5 m distance from the focal oak, by taking hemispherical photographs prior to canopy closure, just before seedling bud burst. Photos were taken approximately 1 m above planted seedlings, using a Canon Eos 7D (Canon, Tokyo, Japan) with a circular fisheye lens (SIGMA 4.5 mm F 2.8 DC Circular Fisheye 180°; SIGMA, Kawasaki, Japan). All photographs were taken on a uniformly overcast day to ensure the best contrast between tree branches and sky and homogeneous lighting of the canopy (Rich 1990). Photos were then traced with Gap Light Analyzer software (Frazer, Canham & Lertzman 1999) to extract the percent of canopy openness.

DATA ANALYSIS

For all analyses focused on LAR, we used a logit transformation of LAR to enhance the fit of the models to data (Warton and Hui, 2011). Logit of 0 is not defined, hence we added 0.01 to all data points.

We determined which enemies induce the most important damage on acorns and seedlings. In order to identify if acorn removal was determined by ungulates or rodents, we tested the effect of cage (control, ungulate exclusion) on the delay before acorn removal, using an analysis of variance (ANOVA). Similarly, we tested the effect of treatment (control, insect exclusion, insect and mollusk exclusion) on LAR by chewers, using an ANOVA, followed by a Tukey HSD post-hoc. In both cases, we included *tree* nested in *pair* as random effect to account for the nested structure of the design.

We then evaluated how acorn removal and seedling herbivory were determined by the different characteristics of conspecific adult and ground cover. Each analysis used multiple explanatory variables. Overall, correlation coefficients among explanatory variables were low, on average $|0.14|$, and a maximum of 0.55 (between phylogenetic isolation and tree cover). One variable could thus not entirely replace another one and we entered them all into a single model explaining either acorn removal or seedling herbivory, partly followed by later variable selection.

We first tested the effects of: *distance* and *size of to the conspecific adult*, *treatment*, and the interactions between *size* and *distance*, *treatment* and *size*, and *treatment* and *distance*. *Tree pair* was included as a random factor to account for the nested structure of the design. We tested the effects of these variables first on *delay before acorn removal*. In these tests, the conspecific adults were the focal trees, and hence *focal tree* could not be entered as an additional random factor given that *size of focal tree* did not vary within *focal tree*. P values

might hence be inflated, but were non-significant, anyway. Neither *treatment* nor interactions with *treatment* were significant, and we hence excluded them from the model and reduced the analysis to the control treatment to avoid pseudoreplication. Then, we tested the effects of *distance*, *size*, *treatment* and their interactions on LAR. In these tests, the conspecific adults were the closest adults including in cases non-focal trees (which could not always be avoided when planting seedlings). We could hence additionally account for the random factor *focal tree* (nested in *tree pair*). We also accounted for the *leaf age*, *density of oak seedlings*, *tree cover*, *shrub cover*, *herb cover*, and *moss cover* which had been recorded for all seedlings (but not for the seed trays at >1 m from the focal adult tree).

We then tested the effects of *phylogenetic isolation of the focal adult tree*. As phylogenetic isolation was a single information per focal tree we restricted the analysis to a single replicate of a treatment per focal tree, the one that is closest to, and hence most representative of, the focal tree. We accounted for the *size of the focal tree*, *density of oak seedlings*, *tree cover*, *shrub cover*, *herb cover*, *moss cover*, and *treatment*. *Tree pair* was included as random factor. To account for possible changes in the effects of each explanatory variable with *treatment*, we fitted separate models including one of the possible interaction terms, retained the significant ones and included them together in a final model (including all interaction terms together would have led to excessive multicollinearity). The final model was reduced by best subset selection to avoid overparameterization, using adjusted R^2 as selection criterion. We first tested the effects of these variables on *delay before acorn removal*. We found that neither *treatment* nor interactions with *treatment* were significant and we hence excluded them from the model and reduced the data set to control treatment to avoid pseudoreplication. We then tested the effects of these variables on *LAR*, including *leaf age* as covariate.

We always checked the adequacy of models to data with residuals-vs-fitted values plot and QQ-plot of the residuals. A maximum of 4 out of 179 data points were excluded (for acorn

removal across all trays), and results of analyses with and without outlier exclusion are reported throughout (at most, results differed between relationships being marginally significant at $p < 0.1$ rather than significant at $p < 0.05$, Appendix 8). Analyses were done using Statistica version 13 (TIBCO Software Inc. (2017, <http://statistica.io>), and R version 3.6.1 (R Core Team 2019) packages: lme4 (Bates et al., 2015), nlme (Pinheiro et al., 2020), multcomp (Hothorn et al., 2008) and MuMin (Barton, 2015).

Results

WHICH ENEMIES REMOVE ACORNS OR LEAF SURFACE?

All the acorns exposed were removed within 91 days. Mean removal times per tray varied between 7 and 66 days. During the survey, we found no trace of predation on the exposed acorns. Delay before acorn removal was not affected by the exclusion of ungulates ($F=2.17$; $P=0.143$, $df_{error}=179$, 4 outliers excluded $F=0.01$; $P=0.923$, $df_{error}=175$), rodents were hence the main removers.

Out of the 180 planted seedlings, 123 had developed leaves and were hence susceptible to attacks by herbivores (37 control, 41 insect exclusion and 45 insect and mollusk exclusion). Herbivory on control seedlings was largely the result of invertebrates (Fig. 2a): 76% of the seedlings were attacked by invertebrates, against 8% by vertebrates and 8% by airborne pathogens. Among seedlings attacked by invertebrates, 89% were damaged by entire-leaf chewers (*i.e.* insects or mollusks), 18% by skeletonizers and 4% by miners. We observed no damage due to suckers, rollers and gall makers. Damage by leaf chewers was mostly done by insects and mollusks. Excluding insects significantly reduced LAR by half, and excluding both insects and mollusks significantly reduced LAR by a further two thirds (ANOVA across

all treatments, $F=14.04$; $P<0.001$, df error = 95. 1 outlier excluded $F=13.60$; $P<0.001$, df error = 94; Fig. 2b).

WHAT AFFECTS REMOVAL OF ACORNS AND OF LEAF SURFACE?

Delay of acorn removal was not affected by spatial distance to focal conspecific adult tree or its size ($t = 0.38$, df error = 85, $p = 0.703$, $t = 1.50$, df error = 85, $p = 0.139$, Appendix 8). In contrast, acorns were removed faster next to focal conspecific adults that are phylogenetically isolated and that are surrounded by dense herb cover, many seedlings, and in tendency a dense shrub cover (Tab. 1). Univariate graphic exploration in Fig. 3 shows that the significant effects of phylogenetic isolation and herb cover in Tab.1 correspond to an acceleration of seed removal by approximately 19 and 15 days, respectively. As phylogenetic isolation decreases with the relative abundance of oaks we verified whether the effect of phylogenetic isolation on acorn removal reflects nothing more than an effect of relative abundance of oaks. We found that this is not the case: if both, phylogenetic isolation and relative abundance of oaks, are included into the model, they both score significant ($t = -2.92$, $p = 0.043$, and $t = -2.82$, $p = 0.048$).

Leaf herbivory was higher on seedlings close to large trees ($t = -1.90$, df error = 80, $p = 0.062$, Appendix S8), in particular when insects had been excluded from seedlings ($t = 2.25$, df error = 80, $p = 0.027$, Appendix S8). Univariate graphic exploration of this result in Fig. 4 shows that leaf herbivory increased strongest with tree size when only insects and not mollusks were excluded. Also, leaf herbivory was higher on seedlings next to focal adults that are phylogenetically isolated, and in the absence of herb cover (in the "all exclusion" treatment) (Tab. 1). Univariate graphic exploration of this result in Fig. 5 shows that herbivory decreased strongest with herb cover when only insects and not mollusks were

excluded. Finally, leaf herbivory was significantly increased with seedling density, especially under insect exclusion (Tab. 1).

Discussion

In our study system, mammals and mollusks play an important role for acorn/seedling predation: rodents removed 100% of the acorns within at most 91 days, and mollusks were responsible for roughly half of the leaf herbivory. We found no effect of spatial distance to adult conspecifics on removal of acorns or leaf area. We however found that acorn removal by rodents was faster around conspecific adults surrounded by phylogenetically distant neighbors, where the focal adult tree might appear comparatively more attractive for enemies. Moreover, acorn removal by rodents was faster around adult trees with a high ground cover where acorn predators are sheltered from their own enemies. Seedling herbivory by mollusks increased with size of the conspecific adult and tended to decrease with herb cover. These results are consistent with predictions of our hypothesis that enemy pressure on acorns/seedlings increases with the attractiveness of conspecific adult neighbors to foraging highly mobile enemies such as mammals and mollusks.

OBSERVED VARIATION IN ACORN REMOVAL MAY HAVE MAJOR CONSEQUENCES

Low phylogenetic isolation and scarcity of herbaceous cover delayed acorn removal by, on average, two weeks, with an even stronger effect after accounting for covariables. Across the thousands of acorns produced by a single oak in many years, an average tendency of two weeks delay likely corresponds to additional dozens of acorns surviving for several months. Moreover, even a removal delay of only two weeks may be essential for acorn survival,

especially if acorns lay on the ground, instead of on our wooden acorn trays. With time, acorns on the ground are covered by a litter layer and become less detectable by and accessible to rodents, strongly reducing acorn removal (Crawley & Long 1995). Moreover, acorns laying on the ground rather than on a tray, germinate within two weeks (Finch-Savage & Clay 1994) so that rodents cannot remove them anymore. Also, during two weeks the acorn stocks of rodents might become saturated.

MAMMAL ACORN PREDATORS MIGHT INDUCE NICHE CONSERVATISM

In our study system, acorn removal by mammals was faster close to adult trees in a phylogenetically distant neighborhood. Our result is inconsistent with Ginkel et al. (2013) who found that acorn removal was higher in a deciduous forest (*i.e.* closely related species) than in a coniferous forest (*i.e.* distantly related species), due to a higher activity of wild boars in deciduous forests. Our result is also inconsistent with the phylogenetic Janzen-Connell effect (Liu et al., 2012) suggesting that under a phylogenetically distant adult tree, acorns/seedlings suffer little predation (a form of herd immunity effect, Webb et al., 2006). In our case, acorn removal was mostly due to rodents, as exclusion of ungulates had no effect on acorn removal (Fig. 2a). We suggest that a faster acorn removal below an oak surrounded by distant relatives may be due to a concentration of attacks by enemies: rodents who forage in a neighborhood dominated by distantly related species are attracted by the few oaks available in this environment, and may be reluctant to leave them (Jennings, 1976 for preference for oak acorns). This mechanism, however, requires that rodents enter the patches dominated by trees phylogenetically distant from oaks. This is likely to be the case in our study, conducted after a mast year and with resource patches being small and proximate (see Methods). The observed high acorn removal by rodents in a phylogenetically distant neighborhood suggests high acorn predation, which in turn may prevent oaks to spread into such neighborhoods, thus

restricting the access to novel abiotic and biotic niches (inversely to the adults which benefit from released enemy pressure, and increased support by mutualists; Yguel et al., 2011; Yguel et al., 2014a, albeit decreased support from parasitoids; Yguel et al. 2014b). On the contrary, under a closely related canopy, predation pressure by a given number of available rodents is diluted among abundant resources, and acorn predators might leave the patch around one adult already after a slight decrease in patch quality given the high quality of the surrounding patches. Overall, a neighborhood of closely related species of trees might provide a protection of focal acorns from rodent removal, hence possibly favouring the aggregation of closely related species in the same habitat patch and thereby the conservatism of the habitat niche. Possibly the contrary may be true for the more specialized, less mobile larval weevil pre-dispersal predators of acorns, but this has, to our knowledge, not been tested.

MAMMAL ACORN PREDATORS MIGHT ALLOW SEEDLING ESTABLISHMENT IN SUITABLE ENVIRONMENTS

Acorn removal by rodents also accelerated with cover by herbaceous layer, i.e. the fern *Pteridium aquilinum* and the grass *Molinia caerulea*. Increased acorn predation under fern cover has already been described by George and Bazzaz (1999). Ferns constitute a shelter under which rodents are protected from their predators. Hence, rodents forage frequently under cover (Ouden et al., 2005), hidden from predators. Grasses like *M. caerulea* have the same protecting effect as ferns (Gill and Marks, 1991) as they produce dense tufts of vegetation (Taylor et al., 2001), providing many hideouts for rodents on the ground. Inversely, a reduced acorn removal in understory-free areas may contribute to the establishment of seedlings. The observed reduction of acorn removal in open conditions suggests reduced predation – in precisely those conditions that are required for seedling growth: seedlings tolerate only little shade (Ellenberg et al., 1992) and suffer from *M.*

caerulea neighbors (Deniau et al., unpublished results). Overall, understory-free areas protect acorns from removal by rodents, hence optimizing the living conditions of the forthcoming seedlings. These very seedlings, however, might suffer from increased herbivory by a potential prey of rodents, i.e. mollusks, as suggested by one of our analyses.

HERBIVOROUS MOLLUSKS REPULSE SEEDLINGS FROM LARGE ADULTS

Seedling herbivory by chewers increased with the size of conspecific adult trees, an effect that appeared only when insects were excluded, reflecting the activity of mollusks. Mollusks are generalists (Hunter, 1978), can consume green leaves of trees (Jennings and Barkham, 1975) and may be the main enemies of tree seedlings in temperate forests (Pigot and Leather, 2008, for *Acer pseudoplatanus*). Such an accumulation of mollusks around large adult trees has not been demonstrated before, but is plausible because larger trees are more productive and more seedlings might be available at its proximity. We note that the insecticide application and the copper tubes might not have permanently excluded insects and mollusks. Instead, these treatments might have triggered recolonizations by insects and mollusks from the adjacent conspecific adult tree, in particular if that tree is large. In that case, the explanation of the observed patterns would not be foraging mechanisms, but mechanisms of a micro-island biogeography – but the implications would be the same: Overall, large adults might prevent conspecific seedlings from establishing in their surrounding due to the impact of mollusk herbivores.

LIMITATIONS OF THE STUDY

First, we considered a very limited gradient of spatial distances of only 5m. Earlier studies have demonstrated changes in enemy pressure by specialist enemies along such gradients

(Schupp, 1988; Deniau et al., 2018), albeit here we did not find such changes. Theoretically, enemy pressure might change across larger distances, although such larger distances may be absent in many temperate forest stands in which conspecific adults are less than 10m apart (Ellenberg, 1992). Also, larger distances might not provide shelter from attack by aerial predators of oak enemies.

Second, rodents might have been satiated and forgotten acorns in caches, so that removal did not equal predation. This scenario is unlikely given that acorn production was extremely low the year of study and, after a year of masting, rodent density was likely very high, a situation in which rodents are predators rather than dispersers (Silvertown, 1980; Koenig and Knops, 2000; Clotfelter et al., 2007; Nopp-Mayr et al., 2012). Even if some acorns are forgotten, this might not change our conclusions as forgetting might happen equally frequently in phylogenetically proximate and distant neighborhoods. Also, acorns that are forgotten might eventually die as they have been caged too deep or as they do not stand the competition among the many seedlings emerging from a forgotten cache.

Third, we did not account for the density of autochthonous acorns or for soil pathogens, which may influence foraging decisions. We did, however, account for the density of autochthonous seedlings, which may be representative of densities of acorns. Moreover, above-ground pathogens were rare on leaves (Fig. 2) and below-ground pathogens do not induce increased herbivory close to large adults (Deniau et al., 2018). Additionally, we studied only a single year, one of low acorn production. The observed decline of acorn removal in phylogenetically proximate neighborhoods might be even more pronounced in high acorn production years when such neighborhoods are swamped with acorns.

Finally, our interpretation centers around mechanisms related to the movement and patch use of MaM since they utilize many more seeds or seedlings during their life than do insect herbivores. However, MaM may also be more generalist in their host range than many insect

herbivores (e.g. Hunter 1978). The mechanisms we suggest actually imply an intermediate degree of specialization, where MaM may prefer using oak acorns or seedlings, but may survive on other food while traversing a matrix dominated by distantly related species.

CONCLUSION

We found that mammal and mollusk enemies of acorns and seedlings, respectively, respond to properties of individual adult trees and thereby potentially contribute to structuring forest communities at a very fine scale. Rodents are relatively mobile acorn predators which seem to attack acorns mainly where seedlings would have difficulties to establish, and acorn predators might contribute to niche conservatism by selecting against acorns in a distantly related neighborhood. Seedling herbivores operate around large adult trees and might prevent recruitment of seedlings as large adults accumulate generalist mollusk herbivores. These results may have additional implications for forest management. Management practices often recommend to keep old and large trees, and to mix tree species, but without considering the effect on acorn/seedling predators. The present study shows that a mixture of distantly related tree species might be disadvantageous for acorn survival. Moreover, our results suggest that controlling understory vegetation may help to reduce acorn predation; and that regeneration should already start when adults are still small and hence attract little seedling herbivores.

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Author contributions. MD, VJ and AP conceived the ideas and methods, MD led the field work, with the main support of VG, MB and BB; MD, MP, AP, MB and VJ analyzed the data and wrote the manuscript, with the support of MP.

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1 **Tables and Figure**

2

3 **Tab. 1.** Phylogenetic isolation affecting delay of removal of acorns (left) and of leaf area of seedlings (right), accounting for ground cover and treatment. *Treatment* is the
 4 exclusion of particular groups of enemies. *Treatment* was dropped out from analyses of acorn removal (Methods) but significantly affected seedling herbivory (Fig. 2).
 5 Analyses limited to acorns and seedlings closest to focal conspecific adult. Covariates were the random effect *tree pair*, and (in models of seedling herbivory) the *age of*
 6 *leaves*. Covariates are not shown. Best subset search was applied and excluded variables are noted "Excl".

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	Acorn-removal delay		Leaf area removed	
	t	p	t	p
Phylogen. isolation of focal conspecific adult	-2.84	0.012	2.73	0.014
Treatment	NA	NA	F=1.79	0.196
Size of conspecific adult	Excl	Excl	Excl	Excl
Seedling density	-2.69	0.017	3.65	0.002
Moss cover	Excl	Excl	Excl	Excl
Tree cover	Excl	Excl	-2.98	0.008
Shrub cover	-1.94	0.072	1.31	0.207
Herb cover	-2.35	0.033	0.88	0.392
Treatment*Seedling density	NA	NA	F=8.77	0.002
Exclusion all*Seedling density	NA	NA	-4.16	0.001
Exclusion insects*Seedling density	NA	NA	2.67	0.016
Treatment*Herb cover	NA	NA	F=2.58	0.105
Exclusion all*Herb cover	NA	NA	-2.18	0.044
Exclusion insects*Herb cover	NA	NA	-1.54	0.142
adj R ²	0.45		0.48	
df error	15		17	

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1 **Fig. 1. Design of study of acorn removal and seedling herbivory**, established for 20 focal oaks. See
2 Methods for details

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4 **Fig. 2. Identification of the main seedling herbivores.** (a) Control oak seedlings were
5 mostly attacked by invertebrates notably chewers. (b) Leaf area removed (LAR, means
6 \pm standard errors) was significantly reduced by exclusion of insect chewers and exclusion of
7 both insect and mollusk chewers. See text for statistical tests.

8

9 **Fig. 3. Delay of removal of acorns decreases with phylogenetic isolation of focal**
10 **conspecific adult from its neighborhood (a) and with herb cover (b).** See Table 1 for
11 statistical analysis accounting for multiple explanatory variables.

12

13 **Fig. 4. Leaf herbivory on seedlings depending on size of the closest conspecific adult for**
14 **different herbivore exclusion treatments.** DBH: diameter at breast height. Full analyses
15 (Appendix 8) accounting for multiple explanatory variables show that under exclusion of
16 insects (or insects and mollusks), herbivory is largest closest to large conspecifics.

17

18 **Fig. 5. Leaf herbivory on seedlings depending on herb cover for different herbivore**
19 **exclusion treatments.** Full analyses (Tab. 1) accounting for multiple explanatory variables
20 show that under exclusion of herbivores, herbivory is largest in the absence of herb cover.

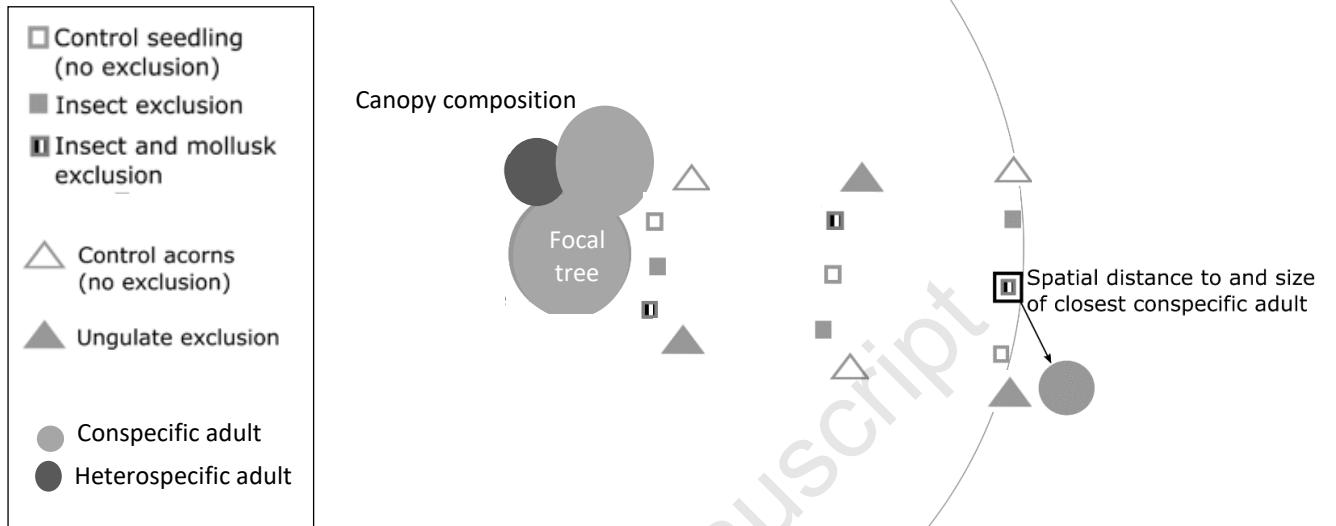
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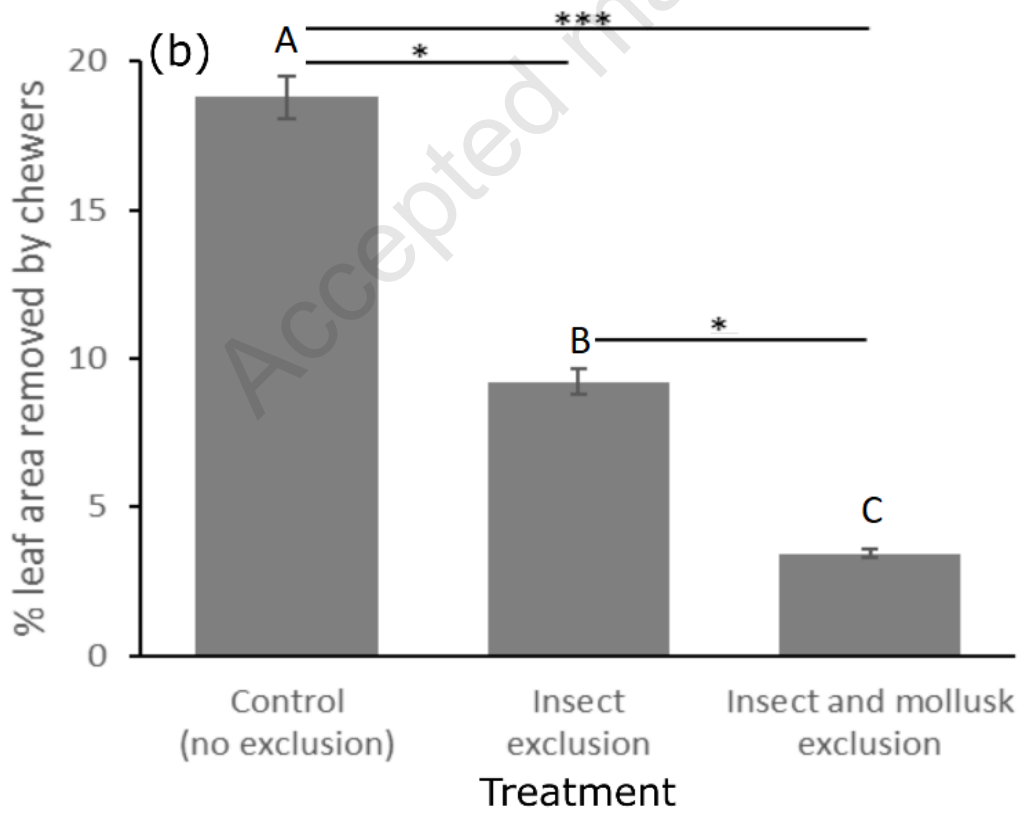
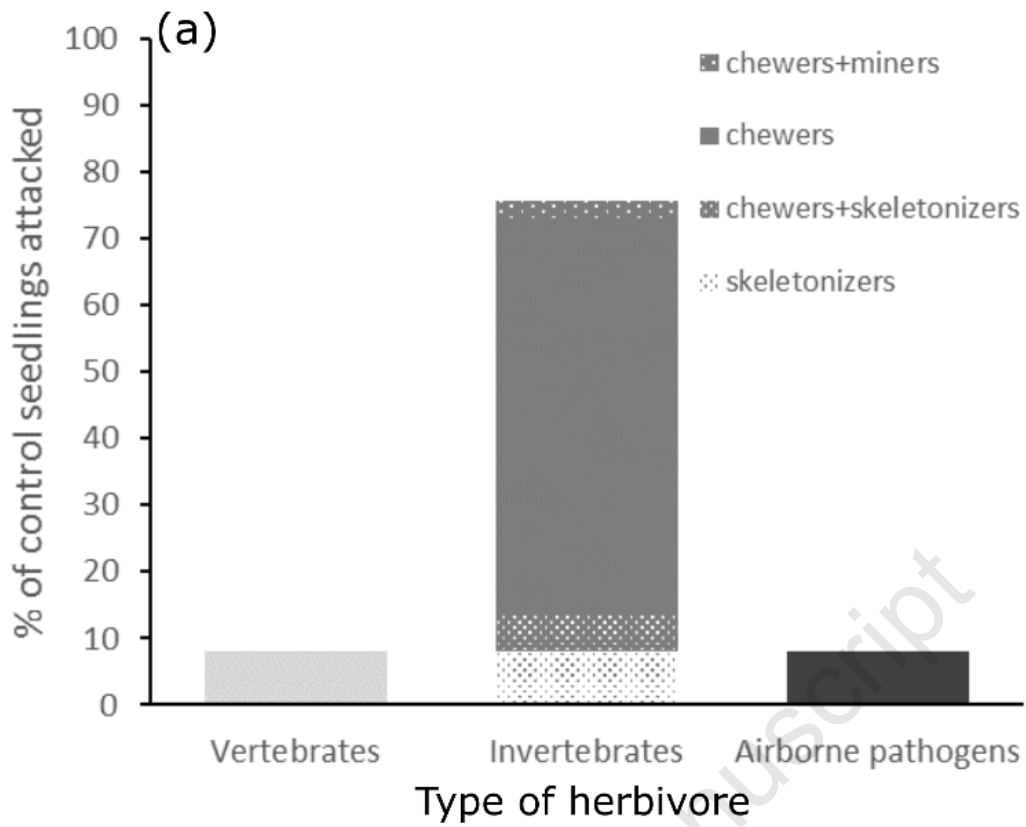
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25 **Fig. 1.**

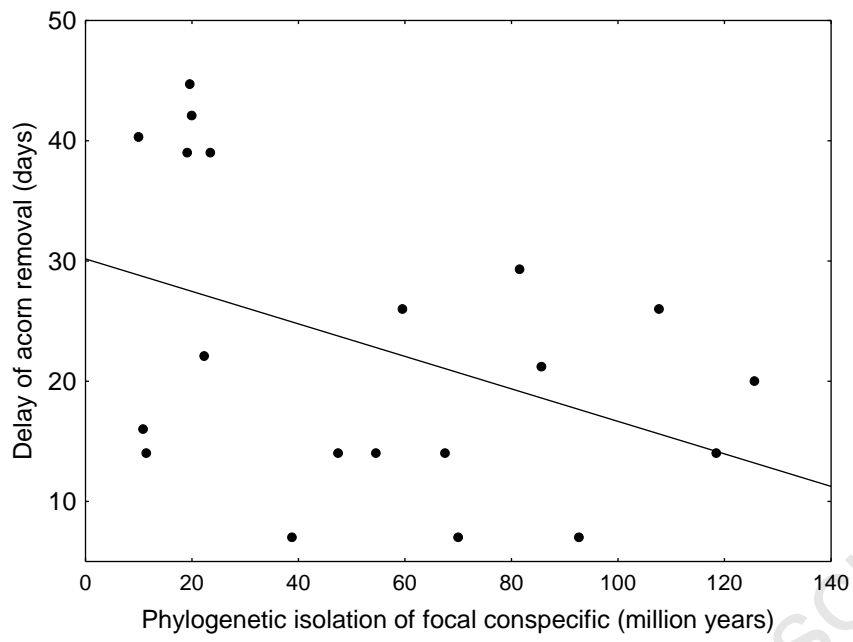




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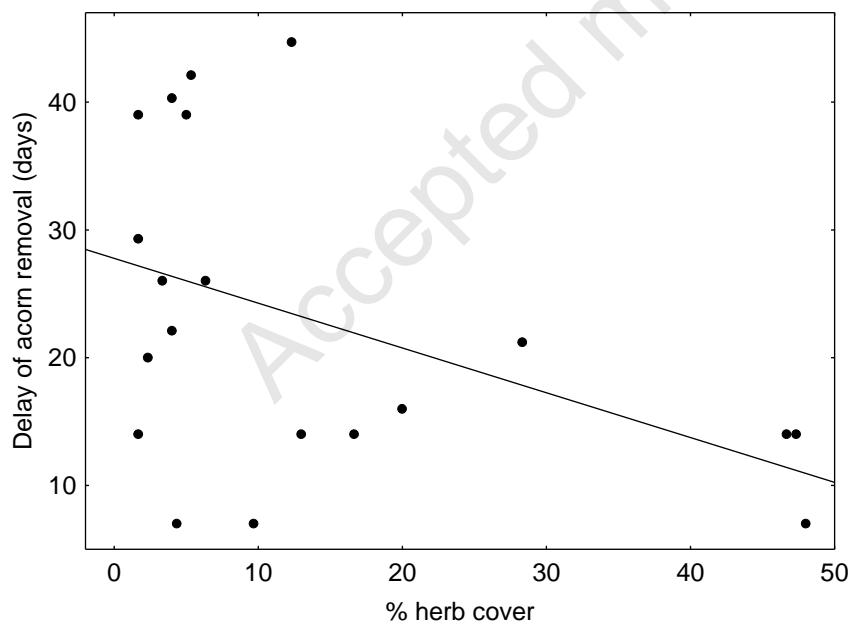
27 **Fig. 2.**

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30 (b)

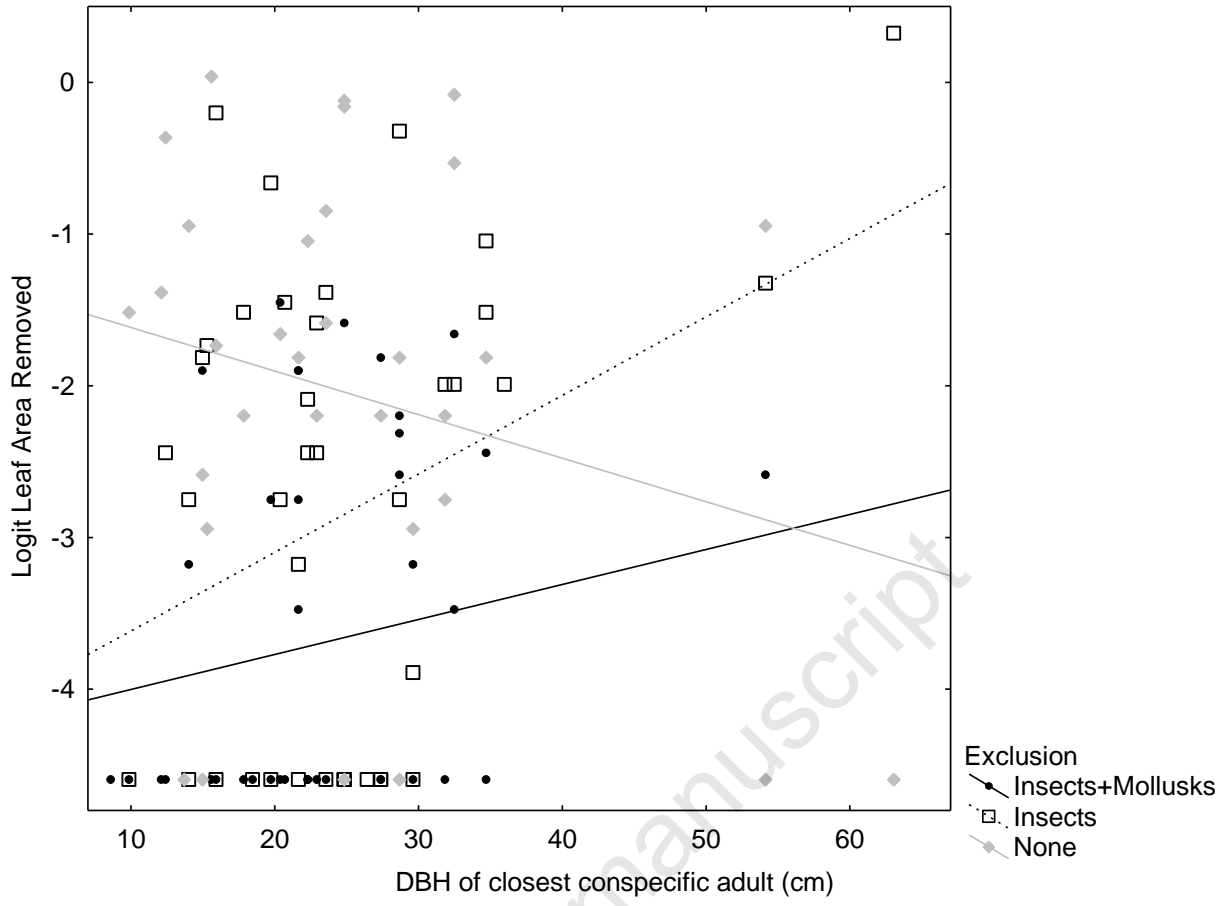


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33 **Fig. 3.**

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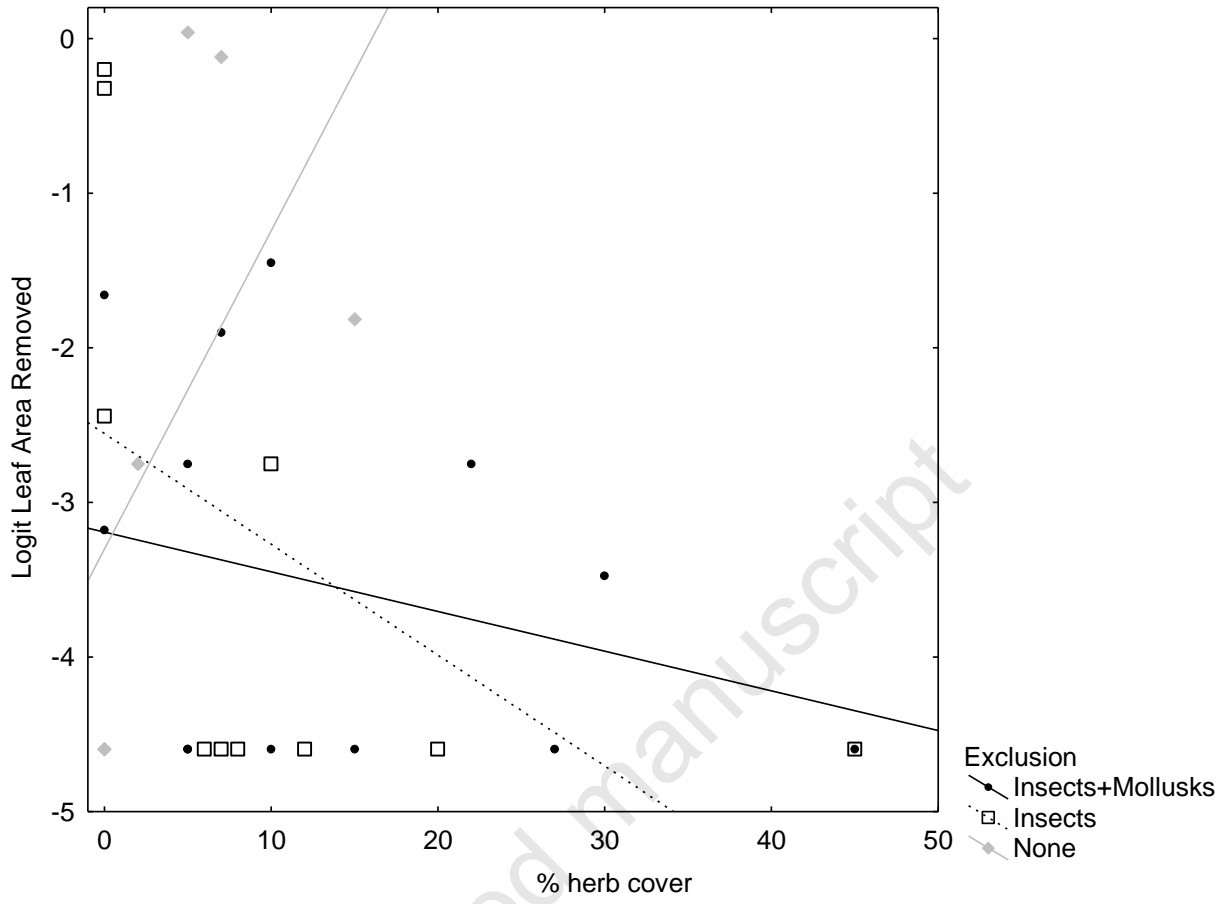


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37 **Fig. 4**

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43 **Fig. 5**