








Phenotypic similarity between fruits of *Gevuina avellana* (Proteaceae) and wasp-induced galls of *Nothofagus dombeyi* (Nothofagaceae) does not protect fruits from predation by rodents

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ABSTRACT

Fruits of *Gevuina avellana* (Proteaceae) seem to mimic wasp-induced galls of *Nothofagus dombeyi* (Nothofagaceae) to escape predation by rodents, which may change both spatially and temporarily. The objective of this study was to evaluate the similarity between the fruits of *G. avellana* and the galls of *N. dombeyi* and to determine if this similarity protects fruits from predation by rodents in a disturbed temperate forest. We evaluated: i) the similarity between fruits and galls by measuring length, diameter, weight and color; and ii) the effects of galls on fruit predation by offering them to rodents in varying proportions, in a forest and a meadow, over two years. Fruits and galls showed similar phenotypes but fruits were more consumed than galls, even at low fruit frequencies, suggesting that their similarities are not due to mimicry. Fruits escaped predation more in the meadow than in the forest, particularly during the second year, thus indicating spatio-temporal variability in the phenomenon. The similarity between fruits and galls seems to be the result of phylogenetic and/or developmental constraints, rather than the result of a Darwinian coevolutionary pathway mediated by rodents. However, mimicry may happen with other dry-fruited plants inhabiting deforested habitats, which encourages further studies.

Keywords: Batesian mimicry, *Aditrochus coihuensis*, granivory, austral temperate forests, Chile

Introduction

Mimicry is a complex biological phenomenon that has attracted the attention of scientists for a long period of time (Ruxton *et al.* 2004). This is an evolutionary adaptation, defined as the “adaptive similarity” between species, in which three organisms, or groups of them, are involved: mimetics, models and operators (Ruxton *et al.* 2004). In the case of Batesian mimicry by antagonisms, a highly palatable organism (mimetic) gets protection from predators

(operators) because it resembles a poorly palatable species (model). This happens because the mimetic deceives the operator who is unable to discriminate between the mimetic and models (Wiens 1978; Ruxton *et al.* 2004). Therefore, the mimetic increases its fitness when it is in the vicinity of the model, because models reduce the antagonistic pressures exerted by operators (Wiens 1978; Ruxton *et al.* 2004). These tripartite interactions, where the operator is antagonist, have been studied mainly from the perspective of predation among animals (Ruxton *et al.* 2004).

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From the perspective of plant-animal interactions there are numerous cases of Batesian mimicry reported, where operators are mutualistic animals to plants. In fact, many pollinators (operators) are attracted to flowers of nectarless species (mimetic) due to their similarity and proximity to nectar-producing plants (models) (Dafni 1983; 1984; Nilsson 1983; Ackerman 1986; Bearsell *et al.* 1986; Johnson 1994; Roy & Widmer 1999). However, much less frequent are the cases of Batesian mimicry by antagonistic operators. An example of this situation is the mimicry by the vine *Boquila trifoliolata* in the temperate rainforests of South America (Gianoli & Carrasco-Urra 2014). The leaves of this plant in its adult stage (mimetic) bear a resemblance to the leaves of the trees that it climbs (models), in terms of size, shape, color, orientation, length of the petiole and thorns on the edges, which allows it to avoid attack by herbivores (operators) (Gianoli & Carrasco-Urra 2014). Unfortunately, cases of Batesian mimicry by antagonistic operators in other stages of the ontogeny of plants, such as when they are seeds and are eaten by granivorous animals, are still unknown.

The temperate forests of South America are inhabited by numerous species of rodents, which have a mixed diet with some degree of granivory (Meserve *et al.* 1988). These forests are also inhabited by the hazelnut tree *Gevuina avellana* (Proteaceae), which produces abundant fruits (Donoso *et al.* 2007). Sympatrically it inhabits the tree *Nothofagus dombeyi* (Nothofagaceae), which bears numerous globular galls on its branches induced by the wasp *Aditrochus coihuensis* (Hymenoptera, Pteromalidae) (Nilsson *et al.* 2011; Quintero *et al.* 2014). In early autumn, *G. avellana* disperses its fruits, which accumulate on the ground, mostly in the vicinity of the parental plants (Donoso *et al.* 2007). During this period, adults of *A. coihuensis* have already taken flight and the galls present in *N. dombeyi* begin to fall, accumulating in the vicinity of host plants (Nilsson *et al.* 2011). Consequently, during the fall, a mixture of fruits and galls are accumulated on the ground, but with variable frequencies, until the seeds germinate. At the same time, the abundance of rodents begins to increase, exerting a strong predation upon seeds (Murúa *et al.* 1986).

The fruits of *G. avellana* are very similar in shape and color to the galls of *N. dombeyi* and they would present greater palatability than the galls because of their higher nutritional content. As a result, consumption of *G. avellana* fruits by rodents might be modulated by the presence of galls in the neighborhood. Therefore, we hypothesized that *G. avellana* (mimetic) could be involved in a phenomenon of coevolution by Batesian mimicry with respect to the galls on *N. dombeyi* induced by *A. coihuensis* (model), to escape from consumption by rodents (operators). We also hypothesized that this putative coevolutionary interaction could change spatially and temporarily. The aim of this study was to evaluate a possible Batesian mimicry mediated by rodents between fruits and galls of *G. avellana* and *N. dombeyi*, respectively, and its putative variations between

sites and years. Specifically, the aims of this research were: i) to evaluate the phenotypic similarities between fruits and galls, and ii) to evaluate the effects of galls on the rodent-mediated removal of fruits, and their putative variations between sites (i.e., a forest and a meadow) that occurred over two consecutive years. It is worthwhile highlighting that we were not capable to separate removal from consumption due to logistic difficulties. With this caveat in mind, we assumed fruit removal as a proxy to consumption.

Materials and methods

Study site and species

Field work was conducted in the austral fall and winter (March to September) of 2014 and 2015, in the “Laboratorio Natural Las Cascadas, Universidad de Los Lagos” (47°07'10.29"S 72°37'00.65"W), Los Lagos District, Chile. The study site is located within the inland temperate laurifolious forest strata of *Nothofagus dombeyi* (Mirb.) Oerst. (Nothofagaceae) and *Eucryphia cordifolia* Cav. (Cunoniaceae), which originally covered an area of 10,204 km², but due to deforestation, currently covers an area of 5,589 km² (Luebert & Pliscoff 2006). Within the study site it is possible to find an area of continuous forest (hereafter the forest), which adjoins the Vicente Perez Rosales National Park, plus a deforested area on the shores of Lake Llanquihue (hereafter the meadow) inhabited, nonetheless, by groups of trees and isolated individuals of several species. Both sites, forest and meadow, are separated by ≥ 200 m. During April 2015, the study site was affected by the eruption of the volcano Calbuco, at a distance of approximately 22 km. The study site was on the border of the drop zone of pyroclastic material, so received a smooth rain of volcanic ash over 5 days between April and May 2015. There are no quantitative measures of the amount of fallen ash in the study site; however, local residents indicated that a 1 cm thick layer of ash was accumulated, which is a modest covering compared with many other localities inside the drop zone of pyroclastic material.

According to previous field samplings (data not shown), the native rodents *Abrothrix longipilis* (Waterhouse, 1837), *A. olivaceus* (Waterhouse, 1837), and *Oligoryzomys longicaudatus* (Bennett, 1832) inhabit the study site. Both species of *Abrothrix* (Waterhouse, 1837) inhabit the forest floor and are omnivores, although *A. olivaceus* prefers fruits and seeds and *A. longipilis* prefers mushrooms, probably according to their dissimilar bioenergetic requirements (Rau *et al.* 1981; Murúa 1995). *Oligoryzomys longicaudatus* is a granivorous rodent with terrestrial and scansorial food searching behaviour (Murúa 1995). The exotic rodents *Rattus rattus* (Linnaeus, 1758), and *Mus musculus* (Linnaeus, 1758) also enter in deforested areas, and can also consume the fruits and seeds of native plants (Ellis *et al.* 1998; Bilenca *et al.* 1992).



Gevuina avellana Molina (Proteaceae) is a tree found in southern South America, with ample distribution between 34°S and 43°S, from Colchagua to the Guaitecas Islands in Chile (Donoso *et al.* 2007). In its natural habitat it may be associated with other species, such as *N. dombeyi*, in woodlands and open areas (Donoso *et al.* 2007). It has a globose or slightly oval fruit, varying in color depending on the degree of maturity, from green to red, reaching purplish black at maturity. It presents an edible seed lodged in a woody fruit rich in tannins (Donoso *et al.* 2007). Its fruits are eaten by small mammals which, in some cases, can transport them to the galleries or burrows where they live (Murúa & Gonzalez 1981; Murúa 1984; Armesto 1987) (Fig. 1).

Nothofagus dombeyi (Nothofagaceae) is an evergreen tree with a latitudinal distribution range from 39°S to the Magellanic forests at 44°S (Premoli & Kitzberger 2005). *Nothofagus dombeyi* hosts a large number of galling species, with about 14 different species (Quintero *et al.* 2014). The main species that induces galls in *N. dombeyi* is the wasp *A. coihuensis* (Ovruski, 1993) (Pteromalidae), which attacks the growth buds (Quintero *et al.* 2014). The induced galls are globular and red to dark brown (Quintero *et al.* 2014) (Fig. 1).

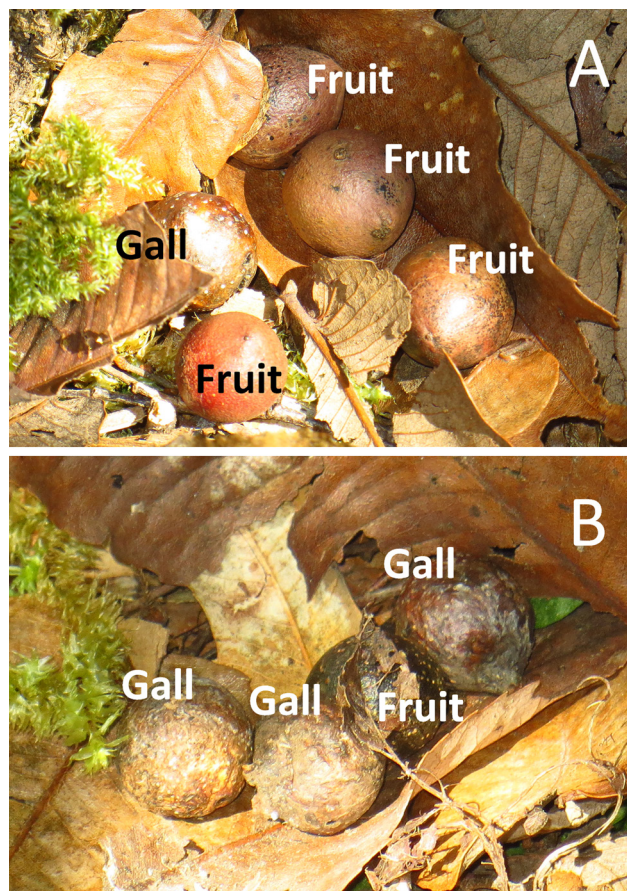


Figure 1. Fruits of hazelnut tree *Gevuina avellana* and galls of the tree *Nothofagus dombeyi* induced by the wasp *Aditrochus coihuensis* at low (A) and high (B) frequencies in a disturbed forest of Chile.

Phenotypic traits of fruits and galls

To evaluate the phenotypic similarity between fruits and galls, a sample of 500 fruits and 150 galls in the forest and 500 fruits and 500 galls on the meadow, were collected between March and April 2015, subsequent to falling from the trees. Each unit was identified in terms of its taxa (fruit or gall) and habitat (forest or meadow). Later, under laboratory conditions, the length, diameter, weight, and color of each fruit and gall, was determined. The length was measured as the maximum distance between the apex of the fruit or gall and the insertion point to the branch, using a digital caliper (0.01 mm precision). Similarly, the diameter of each fruit and gall was measured using a digital caliper. The weight was measured in fresh fruits and galls using a digital analytical balance (0.0001 g accuracy). The color was estimated by digital photographs obtained under standardized conditions; that is, under full darkness, with flash, and at a distance of 60 cm between the lens and the object. Subsequently, using the Adobe Photoshop Professional software, the RGB signal was decomposed from five randomly selected points in each fruit and gall. The red (R), green (G) and blue signal (B) was obtained from the average of these points, for each fruit and gall.

From six phenotypic measurements (length, diameter, mass, R, G, B), obtained for each fruit and gall, a Principal Component Analysis (PCA) was performed taking into account the taxa (fruit or gall) and habitat (forest or meadow). Then, to evaluate whether there were significant differences between taxa (fruit or gall) and its habitat (forest or meadow), a two-way ANOVA was performed on the values of each phenotypic trait and values of PC1 and PC2 scores obtained from PCA, using the Statistica v. 10 statistical package.

Removal of fruits and galls

To evaluate the effects of the frequency of fruits and galls in the environment on their removal by rodents, a field experiment was set up by offering fruits and galls to rodents at varying frequencies, over two consecutive years in two dissimilar habitats (i.e. a forest and a meadow). Fruits and galls from the forest and meadow were pooled to perform this experiment in July 2014 and July 2015. Varying mixes of the supply of fruits and galls were placed on plastic plates fixed to the ground, but open to animals. Fruits and galls were offered in five different frequencies (0.1, 0.25, 0.50, 0.75 and 0.9), considering a total of 50 units in each case. Four replicates of each of the five frequencies were performed, which were arranged in 40 sampling stations with a distance of ca. 20 m between each station. Thus, twenty sampling stations were located in the forest and twenty in the meadow. At each station the proportion of fruits and galls were randomly arranged. This procedure aimed to offer fruits and galls over the entire time lapse

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in which seeds remain dormant (from March to August, when seeds germinate; C.E. Valdivia & G.A.E. López-Colin, unpubl. res.); that is, when seeds are exposed to predation by granivores. Nevertheless, in the present case, the fruits and galls were only exposed to removal by rodents for one night each year, due to the extremely high rates of removal observed. This situation suggests that fruits of *G. avellana* are highly sought after and consumed by rodents, which strongly differs from the granivory rates of other plants from these forests (e.g. Donoso *et al.* 2003; Celis-Diez *et al.* 2004). Therefore, variations in the proportions of fruits and galls offered to rodents allowed us to evaluate the effects of their frequencies on the prey selection exerted by rodents for one night; that is, over a very short time lapse, which could, eventually, hinder our understanding of the predation patterns on fruits (Greenwood & Elton 1979). Nevertheless, a previous study did not find changes in the pattern of frequency-dependent predation by the same species of rodents preying on fruits of other plants, but performed during different time lapses, which suggests that experiments performed during short or long time lapses may reach very similar results (see Celis-Diez *et al.* 2004). With this caveat in mind, the frequency-dependent selection model of Greenwood & Elton (1979) was used by assuming that seeds removed actually corresponded to seeds consumed:

$$e_{fruit} / e_{gall} = (VA_{fruit} / A_{gall})^b$$

where e_{fruit} / e_{gall} is the ratio of the number of fruits and galls consumed by predators and A_{fruit} / A_{gall} is the ratio between the number of fruits and galls in the environment. The parameter b is a measure of frequency-dependence. If $b > 1$, then the selection is pro-apostatic; that is, rodents disproportionately select the most frequent prey in the environment. If $b < 1$ the selection is anti-apostatic; that is, rodents disproportionately select the most infrequent prey in the environment. If $b = 1$ the selection is independent of the frequency of the alternative prey in the environment. Furthermore, the parameter V indicates the trend or bias toward a specific prey. In this case, if $V > 1$, there is a bias towards the fruit consumption. If $V < 1$ there is a bias towards gall consumption, and if $V = 1$ there is no bias in the consumption. The values of b and V were obtained from the analysis of log-log regressions. Subsequently, to determine whether V and b differ significantly from 1, their average values and confidence intervals at 95% were determined. Thus, it was considered that b or V significantly differed from 1 if both parameters did not include the value 1 inside the confidence interval.

In terms of rodent-mediated consumption, it was considered that there was Batesian mimicry if the consumption pattern was pro-apostatic ($b > 1$). Then, to evaluate the variation between sites over two consecutive years (i.e. categorical predictors) on the removal of fruits and

galls (i.e. a dependent variable), a two-way ANCOVA, where the frequency of fruits and galls in the environment was considered as a covariate, was performed. Both the ANCOVA analyses and the log-log regressions were performed using the statistical package Statistica v. 10.

Results

Phenotypic traits of fruits and galls

The fruits and galls from the forest and meadow differed significantly in terms of their length (ANOVA: $F_{origin} = 83.14$; $P < 0.001$; $F_{taxa} = 48.87$; $P < 0.001$; $F_{origin \times taxa} = 7.87$; $P < 0.001$), diameter ($F_{origin} = 4.55$; $P < 0.001$; $F_{taxa} = 6.96$; $P < 0.001$; $F_{origin \times taxa} = 2.26$; $P = 0.132$) and weight ($F_{origin} = 318.86$; $P < 0.001$; $F_{taxa} = 4803.37$, $P < 0.001$; $F_{origin \times taxa} = 374.85$; $P < 0.001$). They also showed significant differences in coloration, either in the red signal ($F_{origin} = 85.14$; $P < 0.001$; $F_{taxa} = 631.43$; $P < 0.001$; $F_{origin \times taxa} = 16.09$; $P < 0.001$), green signal ($F_{origin} = 5.71$; $P < 0.001$; $F_{taxa} = 115.84$; $P < 0.001$; $F_{origin \times taxa} = 4.72$; $P < 0.001$) or blue signal ($F_{origin} = 4.04$; $P < 0.001$; $F_{taxa} = 358.56$; $P < 0.001$; $F_{origin \times taxa} = 2.96$; $P = 0.085$) (Tab. 1).

Considering the six traits as a whole (ACP), there were partial differences according to origin, and total differences by taxa (PC1: $F_{origin} = 3.47$; $P = 0.062$; $F_{taxa} = 1310.36$, $P < 0.001$; $F_{origin \times taxa} = 0.07$, $P = 0.795$; PC2: $F_{origin} = 100.65$; $P < 0.001$; $F_{taxa} = 58.42$; $P < 0.001$; $F_{origin \times taxa} = 30.89$; $P < 0.001$) (Tab. 1). Therefore, fruits and galls from the forest and meadow exhibited partial similarities according to total traits evaluated here (Fig. 2).

Removal of fruits and galls

During 2014, fruit removal was almost two times lower in the meadow than in the forest, with 52.6% and 100% of the fruits removed, respectively. During 2015, fruit removal was five times lower (meadow: 22.4% and forest: 96.4%).

Table 1. Phenotypic traits of fruits of *Gevuina avellana* and galls of *Nothofagus dombeyi* induced by the wasp *Aditrochus coihuensis* in forests and meadows of southern Chile. Mean \pm 1SE are reported. Different letters indicate significant differences ($P < 0.05$) after Tukey HSD tests for unbalanced samples.

Traits	Forest		Meadow	
	Fruits (n = 500)	Galls (n = 150)	Fruits (n = 500)	Galls (n = 500)
Length (mm)	17.4 \pm 0.1 ^a	16.3 \pm 0.2 ^b	16.1 \pm 0.1 ^b	15.8 \pm 0.1 ^c
Diameter (mm)	16.2 \pm 0.1 ^a	15.4 \pm 0.2 ^{ab}	15.5 \pm 0.1 ^b	15.3 \pm 0.3 ^b
Weight (g)	2.1 \pm 0.0 ^a	0.4 \pm 0.0 ^b	1.4 \pm 0.0 ^c	0.4 \pm 0.0 ^b
Red signal (R)	68.9 \pm 1.0 ^a	92.5 \pm 1.5 ^b	54.1 \pm 0.9 ^c	86.7 \pm 1.0 ^b
Green signal (G)	49.8 \pm 2.9 ^a	67.2 \pm 1.0 ^b	40.2 \pm 0.4 ^c	66.7 \pm 2.9 ^b
Blue signal (B)	43.4 \pm 0.5 ^a	52.8 \pm 0.7 ^b	41.4 \pm 0.4 ^c	52.6 \pm 0.5 ^b
PC1	-0.8 \pm 0.0 ^a	0.9 \pm 0.1 ^b	-0.9 \pm 0.0 ^a	1.3 \pm 0.1 ^b
PC2	-0.7 \pm 0.0 ^a	1.3 \pm 0.1 ^b	0.3 \pm 0.0 ^b	0.4 \pm 0.1 ^b



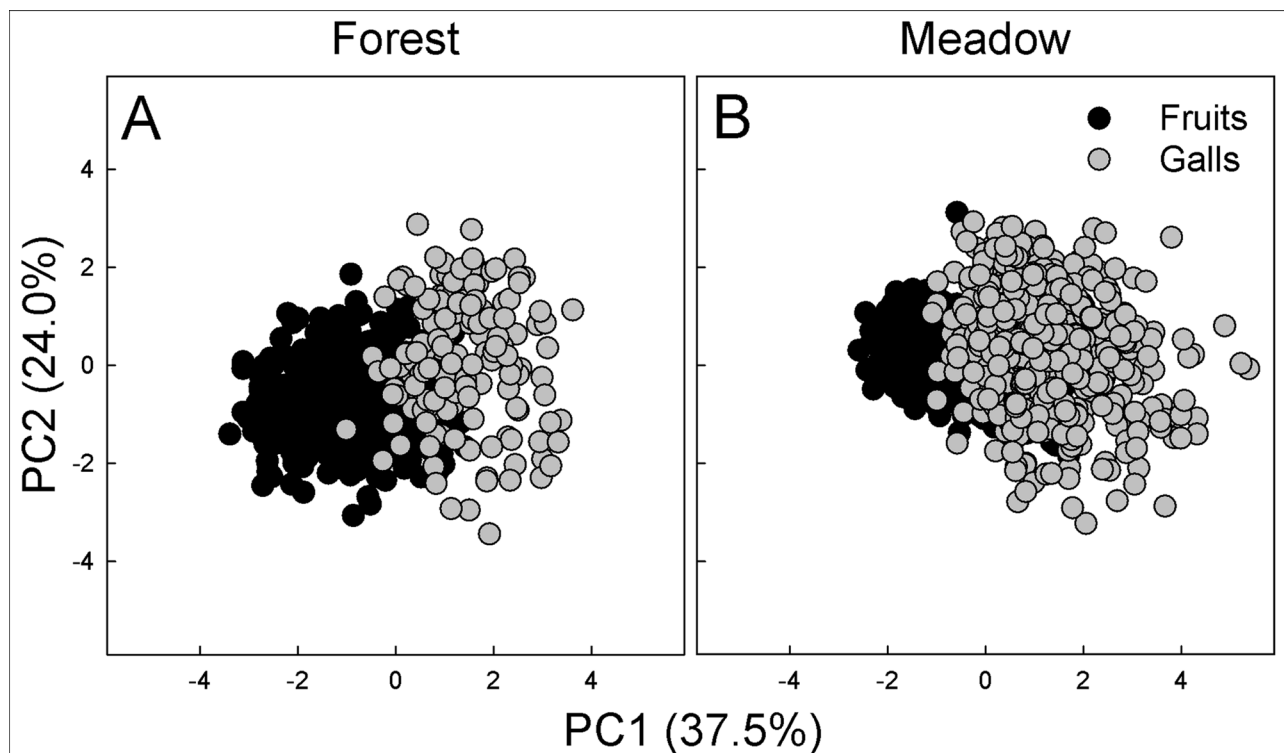


Figure 2. Results of a Principal Component Analysis on phenotypic traits of fruits and galls (length, diameter, weight, and RGB signals from the colorimetric decomposition) from the forest and meadow. PC1 and PC2 from forest and meadow are shown separately for easy reading. All traits were evaluated in mature fruits and galls scattered on the soil, in 2015.

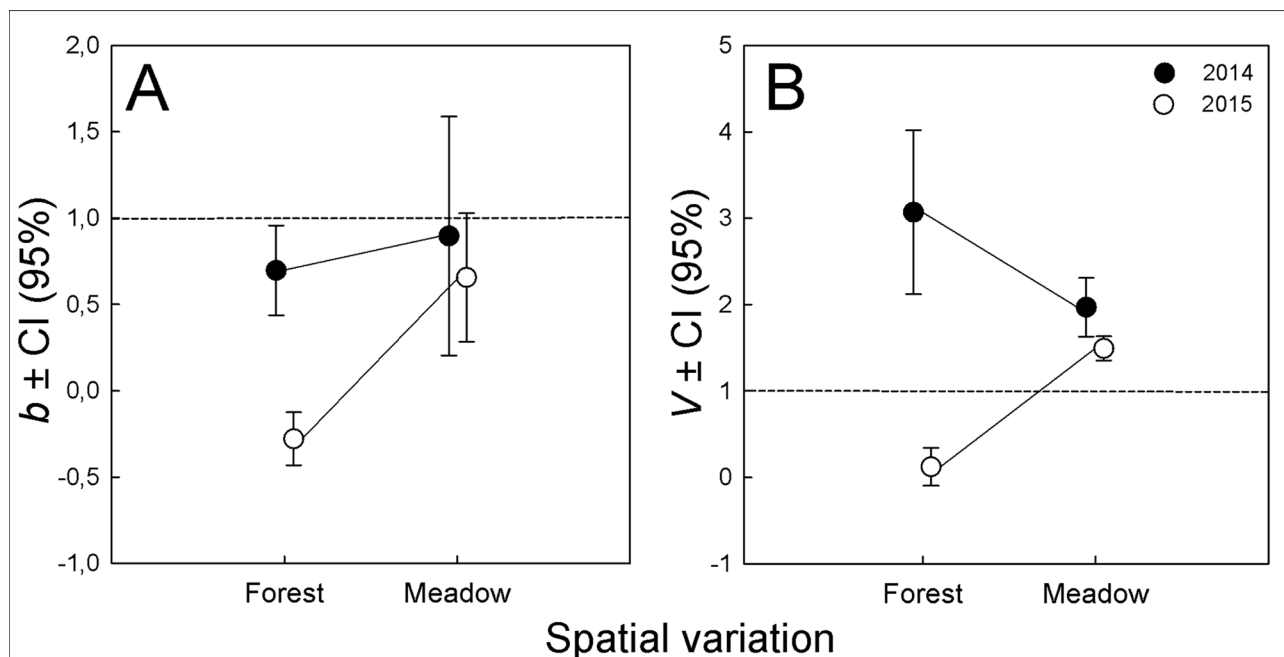


Figure 3. Selection ($b \pm 95\%$ of CI) (A) and bias ($V \pm 95\%$ of CI) (B) in the consumption of fruits and galls in forest and meadow, during 2014 and 2015. Both parameters were obtained from simple regression analyses that were significant under all experimental conditions. It was considered that there are significant differences from one (frequency-independent selection for b and non-biased preference for V) if confidence intervals (CI) exclude the value of 1.

Phenotypic similarity between fruits of *Gevuina avellana* (Proteaceae) and wasp-induced galls of *Nothofagus dombeyi* (Nothofagaceae) does not protect fruits from predation by rodents

The removal of galls during the first year was almost two times lower in the meadow than in the forest (13.5 % and 15.8% respectively), while during the second year, removal was three times lower in the meadow with respect to the forest (8.8 % and 24.6 % respectively). Consequently, the proportion of fruits and galls removed by rodents differed significantly between sites, and with the frequency of both taxa present in the environment, only exhibiting a tendency to change during two consecutive years (ANCOVA: $F_{\text{frequency}} = 13.857$, $P < 0.001$; $F_{\text{sites}} = 5.632$; $P = 0.021$; $F_{\text{year}} = 2.979$; $P = 0.090$; $F_{\text{sites} \times \text{year}} = 0.016$, $P = 0.897$).

The proportion of fruits and galls removed was not only significantly affected by the frequency of both taxa in the environment as a whole, but also individually (Analysis of simple linear regression: Forest in 2014, $F_{(1, 17)} = 32.498$, $P < 0.001$; Forest in 2015, $F_{(1, 18)} = 13.884$, $P = 0.002$; Meadow in 2014, $F_{(1, 11)} = 8.256$, $P = 0.015$; Meadow in 2015, $F_{(1, 7)} = 17.039$, $P = 0.004$) (Fig. 3). In fact, while in the forest there was an anti-apostatic selection in the removal of fruits during both years, selection of fruits and galls was independent of the frequency of the other taxa in the meadow (Fig. 3). In addition, there was a bias towards fruit removal in the forest during 2014, which was reversed towards galls during 2015 (Fig. 3). By contrast, there was always a bias towards the removal of fruits in the meadow (Fig. 3).

Discussion

Variation between sites, more than interannual variation, had a significant effect on the consumption of fruits and galls. While in the forest there was a strong consumption pressure on fruits, in the meadow this pressure was reduced. Although we did not evaluate the richness and abundance of rodents during the field work, the most probable cause of this reduction seems to be a lower abundance of these animals, which has already been observed in the study site (data not shown). Similarly, while in the forest the galls seem to trigger an increased consumption of fruits by rodents, in the meadow fruit consumption was independent of the frequency of galls. Therefore, despite the significant phenotypic similarities between galls and fruits, from the human perception, the Batesian mimicry between both is discarded. This is because the higher frequencies of galls do not switch consumption from fruits to galls, which decreases the survival of fruits, even at low frequencies.

Species may respond to spatial and temporal variations in the quality of habitats by emigrating or remaining in them (Boyle *et al.* 2010; Ropert-Coudert *et al.* 2014; Alarcón *et al.* 2015). The decision will ultimately depend on the balance between the costs and benefits perceived by animals (Alarcón *et al.* 2015). In fact, the higher cost between staying in affected areas or migrating, is the loss of familiar areas, so, eventually, the decision to migrate is only taken when the health and survival of individuals are at risk (Streby

et al. 2015). For this reason, during 2015 (i.e. during the eruption of the Calbuco volcano) in the meadow (i.e. a deforested areas), local populations of rodents could be modified by mortality and migration associated with both types of disturbances. Unfortunately, there is no record available to evaluate the separate effects of mortality and migration on the rodent populations.

Because of the putative changes in the abundances of rodents, the pattern of consumption of fruits and galls seems to be altered by deforestation at the meadow and, to a lesser extent, in 2015. In fact, in the meadow changed the fruit removal pattern, in relation to the frequency of galls in the environment, from an anti-apostatic pattern to one in which the frequency of galls is irrelevant to fruits. This pattern is similar to that observed by Celis-Diez *et al.* (2004), who also found an anti-apostatic selection of differently sized seeds exerted by the same species of native rodents, *A. longipilis*, *A. olivaceus* and *O. longicaudatus*, on fruits of *Cryptocarya alba*. From both situations it is possible to observe a common pattern, larger fruits of *C. alba* are richer in energy than smaller ones, and the fruits of *G. avellana* are also more energetic than the galls of *N. dombeyi*. In fact, the fruits of *G. avellana* present 2800 times more energy than galls, with a mean of 5.6 kcal/g dry weight for fruits (Rau *et al.* 1981) and 0.002 kcal/g for galls, since the latter are composed only of fiber. Therefore, the rodents studied seem to maximize the energy intake focusing consumption on larger and/or energy-richer preys, in spite of their low frequencies in the environment. A putative handicap of this foraging strategy is the investment of a longer time in the search and selection of these preys which, nonetheless, seem to compensate the effort (Celis-Diez *et al.* 2004). This situation, however, may change in deforested areas, where the selection is independent of the frequency of galls as an alternative prey.

The fruits of *G. avellana* and galls of *N. dombeyi* induced by *A. coihuensis* have important similarities in their external appearance and phenology, but only from the perspective of human perception. In fact, these similarities are unlikely to have arisen by Batesian mimicry because fruits are disproportionately more consumed than galls, even at low frequencies; that is, they are selected in an anti-apostatic manner. Therefore, galls seem to confer no protection to fruits under any ecological context, such as contrasting habitats (i.e. at the forest or meadow) or throughout the time (Ruxton *et al.* 2004). In this sense, the similarities between fruits and galls seem more the result of phylogenetic and/or developmental constraints, rather than the result of a Darwinian coevolutionary pathway mediated by rodents.

In the meadow, there was a reduction in granivory and changed the patterns of consumption of fruits. In fact, plants that have large seeds and nuts, such as *G. avellana*, could be favored by deforestation of the temperate forests of South America. Nevertheless, this putative positive effect may be reversed at the seedling stage, in which individuals



are usually more vulnerable than at the seed stage. Therefore, it is important to expand the studies about the effects of habitat and temporal variations to other stages of the lifecycle of *G. avellana* and other dry-fruited species due to its importance to accurately understand the regeneration of the forest under multiple interspecific direct and indirect interactions.

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