

Native seed dispersal by rodents is negatively influenced by an invasive shrub

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Abstract

Native seed dispersal by rodents is negatively influenced by an invasive shrub. Refuge-mediated apparent competition is the mechanism by which invasive plants increase pressure on native plants by providing refuge for generalist consumers. In the UK, the invasive *Rhododendron ponticum* does not provide food for generalist seed consumers like rodents, but evergreen canopy provides refuge from rodent predators, and predation and pilferage risk are key factors affecting rodent foraging and caching behaviour. Here we used a seed removal/seed fate experiment to understand how invasion by an evergreen shrub can alter seed dispersal, seed fate and early recruitment of native trees. We used seeds of four species, small and wind-dispersed (sycamore maple *Acer pseudoplatanus* and European ash *Fraxinus excelsior*) and large and animal-dispersed (pedunculate oak *Quercus robur* and common hazel *Corylus avellana*), and monitored seed predation and caching in open woodland, edge habitats, and under *Rhododendron*. In the open woodland, wind-dispersed seeds had a higher probability of being eaten in situ than cached seeds, while the opposite occurred with animal-dispersed seeds. The latter were removed from the open woodland and edge habitats and cached under *Rhododendron*. This pattern was expected if predation risk was the main factor influencing the decision to eat or to cach a seed. Enhanced dispersal towards *Rhododendron* cover did not increase the prospects for seed survival, as density of hazel and oak saplings under its cover was close to zero as compared to open woodland, possibly due to increased cache pilferage or low seedling survival under dense shade, or both. Enhanced seed predation of ash and sycamore seeds close to *Rhododendron* cover also decreased recruitment of these trees. *Rhododendron* patches biased rodent foraging behaviour towards the negative (net predation) side of the conditional rodent/tree interaction. This effect will potentially impact native woodland regeneration and further facilitate *Rhododendron* spread due to refuge-mediated apparent competition.

Key words: Seed dispersal, Seed caching, *Apodemus sylvaticus*, *Rhododendron ponticum*, Refuge-mediated apparent competition, Plant–animal conditional mutualism

Resumen

Un arbusto invasor influye negativamente en la dispersión de semillas autóctonas por roedores. La competencia aparente mediada por refugio es el mecanismo por el que las plantas invasivas aumentan la presión sobre las autóctonas proporcionando un refugio para los consumidores generalistas. En el Reino Unido, la especie invasora *Rhododendron ponticum* no proporciona alimento a los consumidores generalistas de semillas, pero el dosel perenne ofrece refugio frente a roedores depredadores, y la depredación y el robo son los principales riesgos que afectan al comportamiento de alimentación y almacenamiento de los roedores. En el presente estudio, llevamos a cabo un experimento sobre la retirada y el destino de las semillas con objeto de entender cómo puede afectar la invasión de un arbusto perenne a la dispersión y el destino de las semillas y al reclutamiento temprano de árboles autóctonos. Utilizamos semillas de cuatro especies: semillas pequeñas y anemócoras (arce blanco *Acer pseudoplatanus* y fresno común *Fraxinus excelsior*) y semillas grandes y zoócoras (roble común *Quercus robur* y avellano común *Corylus avellana*) e hicimos el seguimiento de la predación y el almacenamiento de semillas en bosques abiertos, en hábitats de transición y debajo de *Rhododendron*. En los bosques abiertos, las semillas anemócoras tuvieron una mayor probabilidad de ser consumidas in situ que almacenadas, mientras que en las semillas zoócoras ocurrió lo contrario. Estas últimas



se retiraron del bosque abierto y los hábitats de transición y se almacenaron debajo de *Rhododendron*. Esta pauta era la única esperable si el riesgo de predación era el factor más influyente en la decisión de consumir o almacenar las semillas. El aumento de la dispersión de las semillas hacia la cubierta de *Rhododendron* no hizo aumentar las perspectivas de supervivencia de las mismas, puesto que la densidad de las plántulas de avellano y roble debajo de la cubierta era prácticamente nula, a diferencia de lo que ocurre en el bosque abierto; un hecho se puede deberse al aumento del robo de las semillas almacenadas, a la baja supervivencia de las plántulas en condiciones de sombra densa o a ambas cosas. El aumento de la predación de semillas de fresno y arce cerca de la cubierta de *Rhododendron* también hizo disminuir el reclutamiento de estos árboles. Los parches de *Rhododendron* sesgaron el comportamiento de alimentación de los roedores hacia el lado negativo (predación neta) de la interacción condicional entre roedores y árboles. Es posible que este efecto influya en la regeneración de bosques autóctonos y facilite aún más la propagación de *Rhododendron* debido a la competencia aparente mediada por refugio.

Palabras clave: Dispersión de semillas, Almacenamiento de semillas, *Apodemus sylvaticus*, *Rhododendron ponticum*, Competición aparente mediada por refugio, Mutualismo condicional planta–animal

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Introduction

Invasive plants can cause dramatic and long-lasting changes in communities and ecosystems (Ehrenfeld and Scott, 2001; Callaway and Maron, 2006; Strayer et al., 2006). Understanding how invasive species interact with natives is crucial to detect and mitigate detrimental consequences to the native community. Invasive species and natives can interact directly or indirectly. Indirect competition can occur because invasive plants can affect animal behaviour (Mattos and Orrock, 2010) and population abundance (Pearson, 2009). Apparent competition is a general type of indirect interaction between victims that operates through changes in density or foraging preferences of shared consumers (Holt and Bonsall, 2017; Noonburg and Byers, 2005; Orrock et al., 2008). In the context of interactions between plants and consumers, refuge-mediated apparent competition occurs when a plant provides refuge for a shared consumer and increases its local abundance or foraging efficiency (Berryman and Hawkins, 2006; Orrock et al., 2010), which impacts another non-refuge-providing plant. This process has been documented in terrestrial (Caccia et al., 2006; Orrock et al., 2008; Orrock and Witter, 2010) and aquatic systems (Menge, 1995), and has been argued to play a role in determining the structure and invasibility of plant communities (for a review see Orrock et al., 2010). However, precise mechanisms of refuge-mediated apparent competition have not yet been thoroughly explored. Here we test whether refuge-mediated dynamics involving rodents could be altering seed predation and dispersal patterns of native trees in *Rhododendron ponticum*-invaded woodland, influencing native tree spatial distribution and altering competition outcome between native tree species and the invasive plant.

Rodents have a significant role in seed predation and dispersal in woodlands (Jensen and Nielsen, 1986; Crawley, 1992; Hulme and Borelli, 1999). The rodent-tree interactions is a classical plant-animal conditional mutualism as the outcome of the interaction may be either mutualistic (dispersal) or antagonistic (predation). The balance between mutualism and antagonism is contingent on both intrinsic properties partners (seed size and nutritive value, rodent abundance) and on the ecological setting in which the interaction occurs (competition and predation risk; see Gómez et al., 2019; Morán-López et al., 2021 for recent reviews). Three main hypotheses have been posed to explain what seeds to cache. First, the seed size/handling time hypothesis (Jacobs, 1992) poses that animals should decide to cache when food takes less time to cache than to eat. Second, the high-tannin hypothesis (Smallwood and Peters, 1986; Xiao et al., 2009) poses that animals should cache high-tannin seeds for later consumption, as seeds with higher tannins are less palatable and germinate later –less-perishable food and hence suitable to storage– than those with lower tannin levels (Smallwood and Peters, 1986; Smallwood et al., 2001). Third, the germination schedule hypothesis (Hadj-Chikh et al., 1996; Marti and Armario, 1998) poses that seed germination and perishability

influence the decision of whether to eat or cache a seed. However, in the context of foraging decisions, the relative importance of these three hypotheses remains debated, as competition, both intra- and interspecific, and predation risk strongly modifies rodent foraging decisions (Morán-López et al., 2021). Mice select areas of high shrub/dense cover to reduce predation risk (Southern and Lowe, 1982; Brown, 1988; Kotler et al., 1991), which leads to higher foraging and seed dispersal rates under shrubs (Herrera, 1984; Hulme, 1996; Perea et al., 2011). In some situations, such as in high-insolation Mediterranean scrublands, this can facilitate seedling survival through the provision of beneficial shade and the reduction of herbivory (Hulme, 1997). In contrast, in other environments the presence of a dense cover-providing plant can reduce germination and recruitment (Wada, 1993), potentially leading to a change in the spatial distribution of native trees. Furthermore, concentration of rodents under safer shrub cover can lead to increased cache pilferage, thus reducing cache survival and recruitment under shrubs that may become ecological traps (Jordano and Herrera, 1995; Smit et al., 2009).

Rhododendron ponticum (hereafter *Rhododendron*) is probably the introduced plant with the greatest negative impact in the British Isles (Williamson, 2002). During the eighteenth century it was introduced from Spain into Victorian country estates for its ornamental value. Its subsequent spread (Cross, 1975; Milne and Abbott, 2000) became a threat to native plants and biodiversity in the British isles (Dehnen-Schmutz et al., 2004; Tyler et al., 2006). The most serious effect on woodlands results from the lateral vegetative spread (Mejias et al., 2002) of large plants (> 12 years old) and the dense shade they cast, which excludes ground vegetation and prevents germination of native tree seedlings (Cross, 1981; Rotherham and Read, 1988). Its competitive success also comes from its ability to escape natural predators, i.e. the seeds and vegetation are not a significant food source for herbivores in their invaded range (Keane and Crawley, 2002). Its invasion results in the disruption of woodland regeneration (Thomson et al., 1993) and in successional changes (Mitchell et al., 1997) that lead to declines in plant community diversity (Becker, 1988).

Rhododendron provides no food for generalist consumers such as rodents as neither its tiny seeds (average weight 0.063 g; Cross, 1975) nor its leaves are edible (Cross, 1981). However, its intertwined branches and dense evergreen cover provide refuge for them. Its structure is different from any native plant and it offers rodents protection from their main aerial predators. In fact, in our study site, mouse densities are two to five times higher under *Rhododendron* than on open woodland (Malo et al., 2013), leading to smaller home ranges under *Rhododendron* (Godsall et al., 2014). Such a response is not unusual; refuge-seeking behaviour of mammalian seed consumers is common (Clarke, 1983; Wolton, 1983; Spencer et al., 2005), including near exotic plants (Orrock et al., 2008). Thus, in *Rhododendron*-invaded woodlands, refuge-mediated apparent competition could lead to an increased negative impact of seed consumers

on nearby native plants through seed caching and predation, indirectly benefiting the refuge-providing invasive plant, and potentially altering the outcome of direct competition. Understanding whether rodents can impact *Rhododendron* spread through refuge-mediated apparent competition, has implications for the conservation and regeneration of UK native woodlands.

Here we report on a spatially-explicit seed-fate experiment conducted in a well-studied rodent population in England to gain insight into the effects of an invasive shrub on native rodent-seed interactions and explore the behavioural mechanisms whereby granivore-mediated apparent competition may influence regeneration patterns in a multi-species context. We monitored two foraging decisions of rodents: seed selection and fate. First, rodents could choose between small, wind-dispersed seeds, and large and nutritive animal-dispersed seeds. Second, we recorded two foraging behaviours (eating and caching). We thus tested for variation in rodent foraging behaviour when encountering seeds of a different size that require different handling times and offer different energy rewards, and when encountering them in habitat types with different predation risk and competition levels. Second, our approach allows testing how recruitment patterns of native trees with different seed dispersal modes can be influenced by *Rhododendron* presence. We hypothesized that (1) seed contact probability would increase with *Rhododendron* presence due to its positive influence on mouse abundance (Malo et al., 2013); and (2) that the decision to cache or eat depends on relative handling cost, which covaries with seed size and habitat-specific predation and pilferage risk. More specifically, we predicted that lighter seeds (wind-dispersed) would be preferentially predated in the open and that larger nuts and acorns (animal-dispersed seeds) would be preferentially picked from the open and then cached under *Rhododendron*. (3) *Rhododendron* areas, being safer foraging sites, would alter foraging behaviour, leading to asymmetric seed dispersal patterns, whereby dispersal from the open to the invasive-covered areas would be higher than the opposite possibility; (4) given that the shrub is known to impede seed germination of competitor native species and growth (Cross, 1981, 1982), we also predicted a deleterious impact on distribution and regeneration of saplings of native trees and a reduced density of samplings of native trees growing under *Rhododendron* cover.

Material and methods

Study site and rodents

The study site is located in a mixed deciduous woodland at Silwood Park, Ascot, England, UK (51° 24' 52.47" N, 0° 38' 41.73" W). This land is owned by Imperial College London. The study area is 1.7 ha and is divided in 10 m x 10 m grids (100 m² each, n = 170, fig. 1) and contains patches of the invasive *Rhododendron* (n = 6). We consider the different pat-

ches, to a large degree, independent spatial replicates because they are exposed mostly to different mice (71% as inferred by the trapping data). However, as we could not determine how many rodents really interact with seeds at each patch, spatial independence is only expected. The total number of different individual rodents, wood mice (m, *Apodemus sylvaticus*) and bank voles (v, *Myodes glareolus*), trapped during July and August 2009 in each *Rhododendron* patch and in the open area was recorded. We consider the results of this study reflect seed foraging behaviour mostly of mice, first because voles are not seed dispersers and second, because diet studies have shown that during the summer seeds constitute 73% of wood mice diet but only 19% of bank voles diets (Watts, 1968). Each rodent had a unique fur clip mark for individual recognition.

Seed removal/fate experiments

Dispersal by rodents of seeds and nuts is known to be influenced by seed type (Takahashi et al., 2007). We focused on caching and predation of two animal-dispersed (AD) seeds, pedunculate oak (*Quercus robur*), common hazel (*Corylus avellana*), and two wind-dispersed seed species (WD), sycamore maple (here forth sycamore, *Acer pseudoplatanus*) and European ash (*Fraxinus excelsior*). A total of 2,040 seeds (510 seeds per species; for more details see supplementary material) were individually tagged by piercing with a thin needle through the exocarp a 0.06 mm thick fluorocarbon coated string (80 mm) attached with a fluorescent orange tag (5 mm x 15 mm) labelled with a unique number. The fluorocarbon coating ensured there was no water absorption that could increase weight. The string length was minimised (80 mm) to reduce the chances of it getting entangled in the vegetation. Seed tagging has been shown to have a negligible effect on whether seeds were eaten or dispersed (Xiao et al., 2006; Morán-López et al., 2015, 2021). A group of 4 seeds was then placed in the centre of each 10 m x 10 m grid (N = 170 grids x 3 temporal replicates = 510 seed stations in total). Each grid was classified as under *Rhododendron* cover (R), edge habitat (E) or open woodland (O) (fig. 1), which for rodents would represent low, intermediate and high predation risk, respectively. Seed fall for the four tree species occurs between mid-July and September (Malo, unpublished data; Gurnell, 1993). To ensure that the experiment reflected natural rodent behaviour, the timing for experimental seed placement was selected to match start of the seed fall. Three seed trials were conducted: two in July (22nd and 29th) and one in August (5th) 2009. A 10-day pilot experiment was conducted in the field before the start of the experiment. The extent of seed removal conducted by species different to rodents was ascertained using 3 types of seed trays (accessible to invertebrates only, to invertebrates and rodents, and open to all). Removal rates by species different to rodents were negligible (see fig. 1s in supplementary material). Thus, open to all seed trays were used. In fact, further research on the study site testing habitat

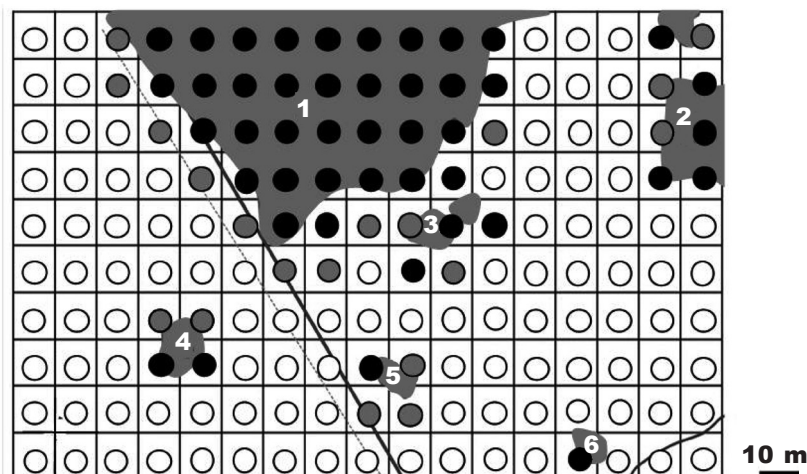


Fig. 1. Study site located at Silwood Park. Irregular grey patches represent *Rhododendron ponticum* cover areas. Black, grey and white circles represent grids where seed stations were located under *Rhododendron* ($n = 45$), at the *Rhododendron* edge ($n = 19$) and in open woodland ($n = 106$), respectively. Seeds were located under the *Rhododendron* in areas where the *Rhododendron* does not cover the central area of a quadrant. Lines depict a seasonal 0.5–1.5 m wide water ditch. White numbers indicate patch identity.

Fig. 1. Zona del estudio situada en el parque Silwood. Las manchas irregulares de color gris representan las zonas cubiertas por *Rhododendron ponticum*. Los círculos negros, grises y blancos representan los cuadrantes en los que se colocaron estaciones de semillas debajo de *Rhododendron* ($n = 45$), en el margen de *Rhododendron* ($n = 19$) y en el bosque abierto ($n = 106$), respectivamente. En las zonas en que *Rhododendron* no cubría el centro de ningún cuadrante, las semillas se colocaron debajo de este arbusto. Las líneas representan un canal de agua estacional de 0,5 m–1,5 m de ancho. Los números de color blanco indican la identidad de los parches de *Rhododendron*.

differences in seed survival using motion-activated infrared cameras (Brouard and Malo, unpublished data) has shown that in a total of 1,215 hours of seed station footage recorded, not a single instance of seed predation by species other than rodents was recorded.

In each trial, 170 seed stations ($R = 45$, $E = 19$, $O = 106$) were set up, each one containing 4 seeds from each species ($4 \text{ seeds} \times 170 \text{ grids} = 680 \text{ seeds/trial}$). These were arranged in a 10 cm x 10 cm square to ensure that all seeds were detected if the seed station was visited. One seed station was placed in each 100 m² square. The plot was then left unvisited for three days (days 1, 2, and 3 after set up) to minimise disturbance. On day 4 each seed station was checked and the 100 m² area per grid was checked for seeds. Grids where seeds had been removed had all microhabitat structures inspected. Grids with larger number of microhabitat features that hindered detection were searched for longer. This procedure was repeated on day 5. Seed stations were recorded as visited if they had at least one seed disturbed. Each disturbed seed was then classified as either eaten *in situ* (E, if the remains of the seed were found at the seed station), cached (C, if not found at the corresponding seed station but the tag and seed later retrieved) and two binomial variables, seed eaten (0–1) and seed cached (0–1), recorded. Regarding the

cached seeds after dispersal, we also recorded the new habitat type the seed was found in (R, E, O). All seeds retrieved were assessed for teeth marks to ensure rodents were the consumers.

Data collection

The following variables were recorded: (1) grid ($n = 170$): categorical variable naming each 100 m² area where the seed-station was placed. (2) *Rhododendron* patch identity: a categorical fixed factor including six different patches to allow for spatial replication of *Rhododendron* effects (fig. 1). (3) *Rhododendron* patch size: a continuous variable to test for the effects of patch size (see supplementary material for patch size details). (4) volume of logs: defined as the sum of individual volume of logs (fallen trees) per grid using the cylinder formula ($\pi \cdot r \cdot 2 \cdot l$; diameter = $2r$ and length = l); logs help protect rodents against aerial predation and aid silent travelling in the woodland, and this continuous variable (mean = 2.22, SD = 2.71 m³/grid) was included as a surrogate of habitat accessibility influencing seed encounter probability. (5) distance to *Rhododendron*: to characterize predation risk we calculated two variables: (i) the sum of the distances from each seed station to every other grid with *Rhododendron* presence (Rhodo dist) within a 20 m distance from the seed stations, and (ii) the total

number of grids with *Rhododendron* presence within a 20 m distance from the seed stations (Rhodo num). (6) seed species: categorical variable (four levels: AP, FE, QR, CA). For some analyses, seeds were also ranked according to the total energy content of the endosperm (1, sycamore [lowest]; 2, ash; 3, oak; 4, hazel [highest]; table 3 from [Grodzinski and Sawicka-Kapusta, 1970]). And (7) seed encounter: a seed station was scored as visited (or encountered by mice) when at least one of the 4 seeds had been disturbed.

All the seedlings, saplings and adult trees of the four species present on the study area, were identified, measured and mapped. The number of ash ($n = 7$, WD) and oak individuals ($n = 29$, AD) was one order of magnitude smaller than that of sycamore ($n = 370$, WD) and hazel ($n = 265$, AD). Given that the sparse distribution and small number of ash and oak trees could influence the absence of these species under *Rhododendron*, we discarded these two and focused on the more abundant and widespread sycamore and hazel. The number of saplings (diameter at breast height, dbh < 15 cm) of hazel and sycamore per grid (10 x 10 m) was recorded, and their frequency of occurrence and density per grid by habitat type were calculated and compared. In this analysis, grids were only considered as *Rhododendron* habitat if 100% of their area was under the evergreen invasive canopy. Thus, some of the grids previously classified as R (because seeds were deployed well under *Rhododendron* cover), were coded as E ($R = 23$, $E = 37$, $O = 110$). Otherwise, individual trees located a couple of meters outside *Rhododendron* habitat, but falling within a grid classified as R (seed station placed under *Rhododendron*), would be analysed as if they were under cover.

Data analyses

In all cases, generalized linear mixed effects models with binomial families were conducted and fitted by Laplace approximation in R (R Development Core Team, 2008). Stepwise model simplification was used to select the minimal adequate model (MAM) (Crawley, 2007). The MAM retained those terms that significantly increased deviance after removal. To account for spatial autocorrelation, grid was included as a random effect. However, because grid (random factor) and distance to *Rhododendron* (fixed covariate) were not expected to fully account for the spatial covariance inherent in all of the sampling points, the residuals of each final model were saved and used to test for spatial autocorrelation using variograms. For all models conducted, variogram methods confirmed the absence of spatial autocorrelation effects. Sample semivariogram, as derived from the residual variance in the model (Pinheiro and Bates, 2000), did not increase with increasing distance between sampled grids (fig. 3s in supplementary material). Initially, either patch identity or patch size were included in the same set of models to compare their effects. As there were no significant differences between models run with patch identity or size, we used patch identity in all subsequent models.

Habitat effects on seed encounter probability

A logistic regression model was constructed using the seed station as the sampling unit (lmer, binomial link function in R, $N = 510$):

$$\text{Seed-station visited (Y/N)} \sim \text{grid (random)} + \text{volume of logs} + \text{Rhodo num} + \text{Rhodo dist} + \text{habitat} + \text{trial} + \text{patch} + \text{log} * \text{habitat} + \text{patch} * \text{habitat} + \text{trial} * \text{habitat}$$

The non-significant effect of trial number in all of the models ($P > 0.5$) showed absence of temporal covariation effects (see fig. 4s in supplementary material).

Habitat and seed type effects on seed collection

Once a seed station has been detected, seeds are either collected or not. Hence, to test for the determinants of seeds being collected, we used the following logistic regression models ($N = 1,008$):

$$\text{Collected (0-1)} \sim \text{grid (random)} + \text{volume of logs} + \text{Rhodo num} + \text{Rhodo dist} + \text{patch} + \text{trial} + \text{seed type} + \text{habitat} + \text{log} * \text{habitat} + \text{seed type} * \text{habitat} + \text{seed type} * \text{trial} + \text{seed type} * \text{patch}$$

Note that in these two models the binomial response captures two events per model: in the seed predation model a seed being eaten (1) vs. a seed not being eaten (0, cached or left untouched). In the seed caching model a seed being cached (1) vs. a seed not being cached (0, eaten or left untouched).

We also conducted a third model with a binomial response capturing the two actions conducted by mice at seed encounter (eating vs. caching). Thus, we included only seeds that were either eaten or cached and excluded those cases in which a rodent did not interact with the seed. Dispersal mode was included as a predictor at this stage of the analysis:

$$\text{Action (eaten/cached)} \sim \text{volume of logs} + \text{Rhodo num} + \text{Rhodo dist} + \text{patch} + \text{trial} + \text{habitat} + \text{dispersal type (AD/WD)} + \text{log} * \text{habitat} + \text{dispersal} * \text{trial} + \text{dispersal} * \text{patch} + \text{dispersal} * \text{habitat} + \text{grid (random)}$$

Native seed dispersal asymmetry between habitats

To test for the effect of habitat type at seed encounter on the habitat type where the seed was finally cached, we calculated the number and proportion of seeds that were cached in the same or different habitat type from where the seed was originally collected by rodents. In the cases in which caching or eating could not be determined in a contacted seed station (individual seeds = 758; seed stations = 213) these were excluded from the analysis. The expected and observed frequencies of seeds dispersed and cached between habitat types are reported. By expected we refer to the null hypothesis of no differences between dispersed and cached seeds by habitat type.

To address the effect of predation risk on caching behaviour (high in Open woodland, medium in Edge and low in *Rhododendron*) we used χ^2 -tests (prop.trend.test function in R) to test for a significant trend in the proportion of seeds cached in O, E and R (by seed type).

Results

During July and August 2009 we trapped 31 rodents, 23 wood mice and 8 bank voles in 5 *Rhododendron* patches (mean \pm SD mouse number per patch = 7.33 ± 7.23 ; mean \pm SD vole number per patch = 3 ± 2.89). Regarding mice, 23 appeared only in one patch, 6 appeared in two and 3 appeared in three patches. This suggests that the minimum spatial independence (between patches) achieved is at least of a 71%, as 23 of the 32 mice only use seed stations from a single patch.

Habitat effects on seed encounter probability

Overall, 49% of the seed stations were visited by rodents (252/510). Habitat type strongly influenced seed encounter by rodents (table 1A). Rodents encountered 29% of seed stations in the open habitat, 89% on the edge and 77% under *Rhododendron* (logistic regression model parameter estimates \pm SE for Open = -1.24 ± 0.67 ; Edge = 2.87 ± 0.63 ; *Rhododendron* = 1.71 ± 0.71). Significantly fewer stations were detected in the Open than in the other two habitats (Open vs Edge, $\chi^2 = 86.95$, $df = 1$, $p < 0.0001$ and Open vs *Rhododendron* $\chi^2 = 71.28$, $df = 1$, $p < 0.0001$). There was a close-to-significant difference in seed encounter probability between the *Rhododendron* and the edge habitat ($\chi^2 = 3.59$, $df = 1$, $p = 0.06$). There was also a marginally non-significant interaction between volume of logs and habitat (table 1A, fig. 5s in supplementary material). Further exploration of this interaction using habitat-specific linear regressions showed that the volume of logs had a strong negative effect on encounter probability under *Rhododendron* (linear model: param. estim. = -0.29 ± 0.13 , $p = 0.027$), but not in the open and edge habitats. Neither trial nor patch identity had an effect on seed encounter probability (table 1A).

Habitat, seed type and seed dispersal type effects on seed predation and caching

Overall, 1,032 seeds remained untouched (including those that had not been detected in the seed stations), 368 seeds were eaten, and 256 were cached (140 seeds were moved but not found, hence they were not scored as cached). Once a seed station was located, the probability that rodents would manipulate the seeds (eat or cache) was: ash (0.4) > hazel (0.39) > sycamore (0.23) > oak (0.19). Also, larger seeds (animal-dispersed) tended to be cached whereas the smaller, easier to handle seeds (wind-dispersed) tended to be eaten *in situ* (fig. 2). The first logistic regression model showed that the probability

of a seed being eaten was affected by habitat, seed type and their interaction (table 1B). A second model showed that the probability of being cached was influenced by the same factors (habitat, seed type and their interaction). Patch identity did not influence seed predation or seed caching (table 1B). The third model (binomial response: eaten or cached) showed that dispersal type and habitat had a significant effect on the probability of being eaten or cached (table 2). There was also a significant interaction between habitat type and seed dispersal type on the probability of a seed being eaten or cached (table 2; fig. 3). Large seeds (hazel and oak) were cached more often than eaten in open and edge habitats and eaten more often than cached in *Rhododendron* habitat (for detailed results see fig. 6s in supplementary material). For small seeds there was also a significant interaction ($\chi^2 = 49.6$, $df = 2$, $p < 0.00001$) driven by the higher caching in open as compared to edge habitat, and higher eating in edge as compared to open habitat ($\chi^2 = 16.6$, $df = 1$, $p < 0.0001$). Only the ash seeds were more frequently eaten than cached seeds in the open woodland habitat (fig. 6s in supplementary material).

Is native seed dispersal by rodents symmetrical between habitats?

Overall, the total number of seeds that were collected and cached in the same habitat type differed between habitats (Open = 66%: 115 collected vs. 76 cached; Edge = 61%: 54 collected vs. 33 cached; *Rhododendron* = 168%: 87 collected vs. 147 cached; $\chi^2 = 28.42$, $df = 2$, $p < 0.0001$). Significantly more seeds were cached in the *Rhododendron* than in the edge ($\chi^2 = 14.95$, $df = 1$, $p < 0.001$) and in the open woodland habitats ($\chi^2 = 22.36$, $df = 1$, $p < 0.0001$). No differences were observed between the edge and open habitat ($p < 0.87$). In the open woodland and edge, 33% and 39% of the collected seeds were cached elsewhere, respectively. The reverse pattern occurred in the *Rhododendron*, where all collected seeds appeared in the same habitat type, plus an extra 60 seeds not collected from *Rhododendron* habitat, representing a 69% increase over the seeds originally deployed and cached in this habitat type. All seeds showed a higher caching probability than expected under *Rhododendron*, and lower than expected in the edge and open habitats (fig. 4A). There was a significant association between habitat type and caching probability for the four seed types (sycamore, $\chi^2 = 40.3$; ash, $\chi^2 = 70.7$; oak, $\chi^2 = 48.5$; hazel, $\chi^2 = 61.6$; in all cases $df = 1$, $p < 0.0001$). This shows that caching behaviour was asymmetrical across habitat types: the probability of a seed from open or edge being cached in *Rhododendron* was much higher than the probability of a seed from *Rhododendron* or edge being cached in open woodland.

Native tree sapling density differences between habitats

We have shown above that hazel and sycamore seeds were consistently cached by rodents under

Table 1. Results for three sets of generalized linear mixed effects models (binomial distribution) testing for the determinants of: A, seed station encounter (N = 510 observations); B, seed predation and seed caching (N = 1,138 observations [2040–902]); V.logs, volume of logs.

Tabla 1. Resultados de tres conjuntos de modelos mixtos lineales generalizados de los efectos (distribución binomial) en los que se analizan los factores determinantes de: A, modelo sobre el encuentro de las estaciones de semillas (N = 510 observaciones); B, modelos sobre la predación y el almacenamiento de semillas (N = 1.138 observaciones [2040-902]); V.logs, volumen de troncos.

A Seed station encounter model

Terms	χ^2	df	P
Volume of logs	1.13	1	0.28
Rhodo number	0.35	1	0.56
Rhodo distance	0.22	1	0.64
Habitat	84.96	2	< 0.0001
Patch	8.80	6	0.19
Trial	0.50	2	0.78
V.logs * habitat	5.79	2	0.055
Trial * habitat	< 0.5	4	0.9

B Seed predation and seed caching models

Terms	Seed predation model			Seed caching model		
	χ^2	df	P	χ^2	df	P
Volume of logs	0.39	1	0.53	1.25	1	0.26
Rhodo distance	0.71	1	0.40	0.001	1	0.97
Rhodo number	0.33	1	0.57	0.15	1	0.70
Seed	132.24	3	< 0.001	128.16	3	< 0.001
Patch	4.43	6	0.62	8.66	6	0.19
Habitat	129.64	2	< 0.001	29.11	2	< 0.001
Trial	0.28	2	0.87	0.75	2	0.69
V.logs * habitat	3.89	3	0.27	1.65	2	0.44
Seed * patch	22.26	18	0.22	24.72	18	0.13
Seed * trial	3.49	6	0.75	2.47	6	0.87
Habitat * seed	42.97	6	< 0.001	51.75	6	< 0.001

the evergreen *Rhododendron* cover. This leads to the expectation –which we test below– that hazel and sycamore seeds would have lower survival rates due to the dense shade of the invasive, and that there will be a lower density of saplings under *Rhododendron*. Across the whole study site, a total of 643 hazel and 396 sycamore saplings were recorded. For both species, we found that the probability of sapling (< 15 cm) occurrence per grid was negatively related to

Rhododendron cover (test for a non-zero slope: hazel, Open = 64 %, Edge = 47 %, *Rhododendron* = 4 %, $\chi^2 = 7.78$, df = 1, $p = 0.005$; sycamore, Open = 67 %, Edge = 55 %, *Rhododendron* = 4 %, $\chi^2 = 5.46$, df = 1, $p = 0.019$). In the grids where saplings were present, their density by grid was also significantly lower in *Rhododendron* habitat than in the Edge and Open habitat (ANOVA test: hazel, $F_{3,87} = 52.6$, $P < 0.0001$; sycamore, $F_{3,93} = 30.02$, $P < 0.0001$; fig. 4B).

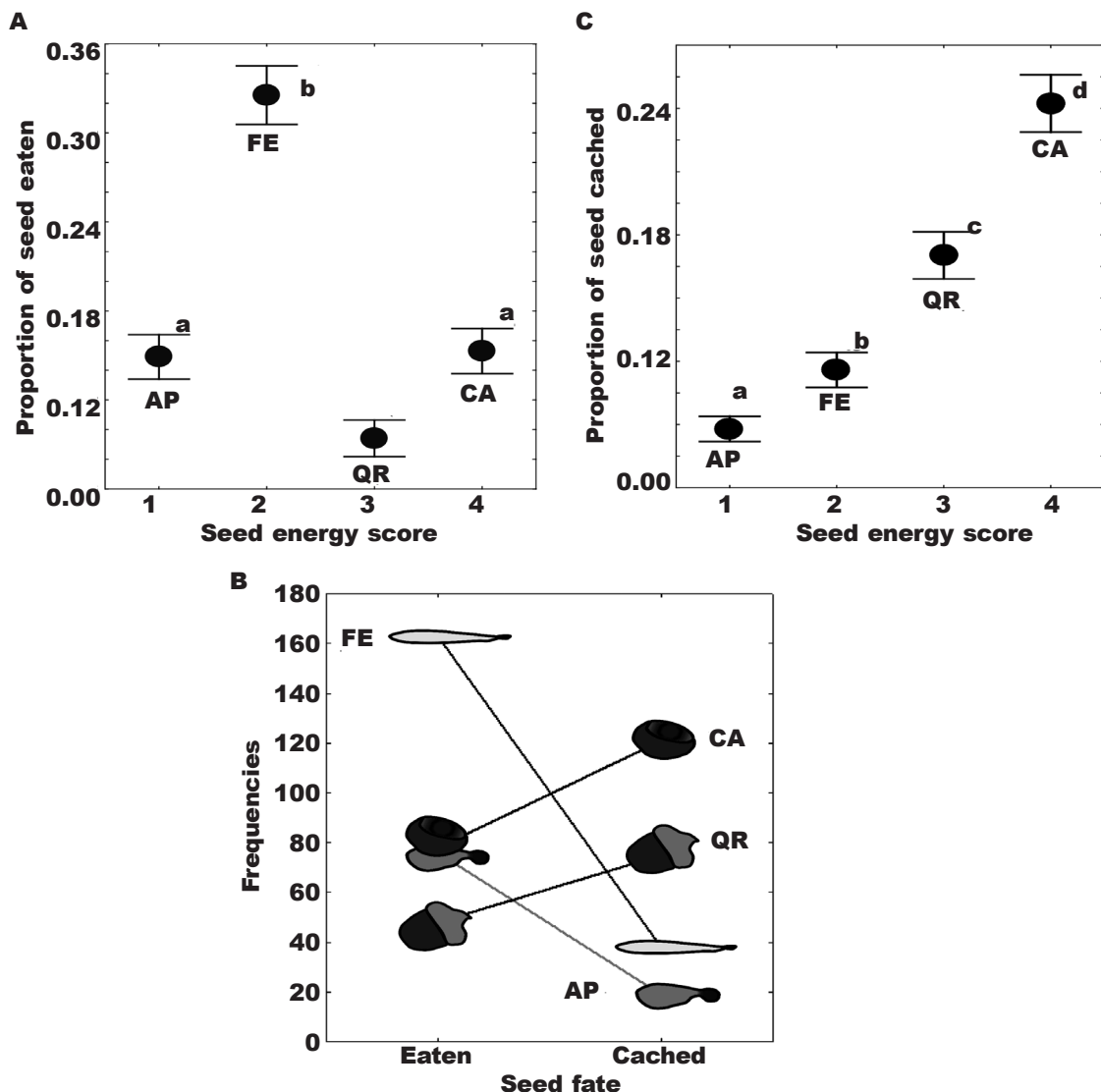


Fig. 2. Mice preference to eat less energy-rich wind-dispersed seeds on site, instead of caching them (A, B), and do the opposite with the more energy-rich animal-dispersed seeds (B, C): ash, highest eaten; sycamore, lowest cached; hazel, highest cached; Oak, lowest eaten). B, seed fate interaction between wind-dispersed (FE, ash, *Fraxinus excelsior*; AP, sycamore, *Acer pseudoplatanus*; light grey) and rodent-dispersed seeds (CA, hazel, *Coryllus avellana*; QR, oak, *Quercus robur*; dark grey). (Bars represent standard errors, N = 618, different lowercase letters indicate significant differences between factors).

Fig. 2. Preferencia de los ratones por consumir in situ las semillas anemócoras de menor contenido energético en lugar de almacenarlas (A, B) y hacer lo contrario con las semillas zoócoras de mayor contenido energético (B, C): fresno, la más consumida; arce, la menos almacenada; avellano, la más almacenada; roble: la menos consumida). B, destino de las semillas según su tipo de dispersión: anemócoras (FE, fresno, *Fraxinus excelsior*; AP, arce, *Acer pseudoplatanus*; en gris claro) y dispersadas por roedores (CA, avellano, *Coryllus avellana*; QR, roble, *Quercus robur*; en gris oscuro). (Las barras representan el error estándar, N = 618, las letras en minúscula indican las diferencias significativas entre factores.)

Discussion

Patches of invasive *Rhododendron* strongly influenced rodent foraging behaviour, as expected from refuge-mediated dynamics model. Habitat type influenced

the probability of rodents detecting seeds, with more seed stations being encountered under *Rhododendron*, probably due to its higher rodent density and lower risk of predation. Second, habitat type influenced whether different types of seeds were eaten or cached. Small,

Table 2. Results from a set of generalized linear mixed effects models showing the effect of habitat, dispersal type and their interaction on the probability of seed eating and caching behaviour (binomial response): AD, animal-dispersed; WD, wind-dispersed.

Tabla 2. Resultados de un conjunto de modelos mixtos lineales generalizados de los efectos en los que se observa el efecto del hábitat, el tipo de dispersión y su interacción en la probabilidad de que se produzca el comportamiento de alimentación y de almacenamiento (respuesta binomial): AD, zoócora; WD, anemócora.

Terms	χ^2	df	P
Volume of logs	0.11	1	0.74
Rhodo distance	0.83	1	0.36
Rhodo number	0.74	1	0.39
Dispersal (AD/WD)	136.34	1	< 0.001
Patch	4.59	6	0.59
Habitat	40.77	2	< 0.001
Trial	0.45	2	0.80
V.logs * habitat	2.93	2	0.23
Dispersal * patch	6.72	6	0.35
Dispersal * trial	0.10	2	0.95
Habitat * dispersal	8.34	2	0.015

wind-dispersed seeds were mostly eaten in the open woodland, and proximity to *Rhododendron* patches increased predation rates, whereas large, animal-dispersed seeds were mainly cached. Large seeds were however 3-fold more likely to be eaten under *Rhododendron*, again probably due to higher rodent abundance (and hence cache pilferage) and lower perceived risk of predation (Morán-López et al., 2021). Low predation risk under *Rhododendron* thus relaxed the potential effect of seed nutritive value, size or secondary compounds on seed preferences by allowing rodents enough safe time to circumvent potential seed defences by granivores (see Díaz 1996 for equivalent examples with other seed-eating animals). Third, large and small seeds were preferentially cached under the invasive *Rhododendron*. This generates anisotropic seed dispersal kernels, with potential implications for the spatial structure and dynamics of native trees. Lower survival of seeds (this work) and seedlings (Cross 1981, 1982) under *Rhododendron* produced, however, lower densities of native tree saplings under *Rhododendron* cover, so that negative influences of the invasive plant extended well over their canopies through the foraging behaviour of rodents.

Native rodents play an important role in seed dispersal and native woodland regeneration (Jensen and

Nielsen, 1986), but this role can be modified by the biological integrity of the system where the interaction occurs (Morán-López et al., 2021). The prediction that consumer density increases with proximity to alien plants (Orrock et al., 2008) is supported by our results showing that mice present a 2–5 fold increased density under *Rhododendron* (Malo et al., 2013). In our study, this should be related to a decreased risk of predation since food resources are not higher under the invasive plant (Holt, 1977). Rodents found seeds more frequently under *Rhododendron* and edge habitats than in the open woodland. The lack of an effect of *Rhododendron* patch identity suggests that different rodents behaved similarly in different *Rhododendron* patches, as of the 32 mice present at the time, 23 used only a single habitat patch.

The volume of logs per grid negatively affected seed encounter probability under *Rhododendron*, although not in the open woodland and edge habitats. This result is consistent with previous results showing that under the invasive *Rhododendron* (which already provides cover from aerial predation) mice tend to avoid areas with a high abundance of fallen trees (Malo et al., 2013). We speculate that this avoidance behaviour of areas with high volume of logs under *Rhododendron* might be a strategy of rodents to minimize predation from terrestrial predators such as the least weasel (*Mustela nivalis*), their second most important predator after tawny owls (*Strix aluco*) (Korpimäki and Krebs, 1996; Godsall et al., 2014).

Under stressful conditions, seed size, germination schedule and tannins are the three main factors expected to influence rodent caching decisions (Marti and Armario, 1998). Although we did not collect data on handling times, our results support the seed size/handling cost hypothesis (Jacobs, 1992). Overall, the trade-off between eating and caching was resolved towards eating the lighter, easier-to-open seeds of ash and sycamore, and towards caching the heavier and more nutritious animal-dispersed hazel and oak seeds in safer places. Preference for eating smaller seeds *in situ* and scatter-hoarding larger seed has also been shown in other rodents (Chang et al., 2009; Vander Wall, 2010), but these preferences vary under manipulated levels of competition and predation risk (Morán-López et al., 2021). Here we document how safer *Rhododendron* canopies interacted with seed choices and foraging decisions: preference for caching larger seed species in open habitat was reversed under *Rhododendron* cover, where predation risk by specialist aerial predators is minimized (Southern and Lowe, 1982), suggesting that predation risk influences the decision of eating or caching a seed: the cost of eating large seeds in the open was lower under safer *Rhododendron* cover. Under the invasive shrub, large seeds were more frequently eaten than cached, the opposite of what happens in the edge and open habitats.

Our study considered spatial replication at the *Rhododendron* patch level and temporal replication at the weekly level. However, two limitations of our experimental design are that it lacked between-site replication and between-year replication. Regarding

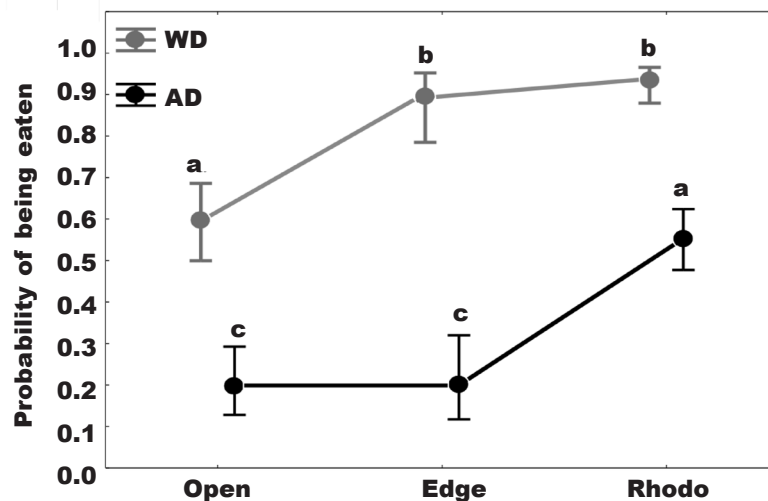


Fig. 3. Interaction between habitat and dispersal type on seed action (eaten vs. dispersal) ($\chi^2 = 8.34$, $df = 2$, $P = 0.01$). Lines are left in the graph to highlight the change in slopes between habitats and seed types. Bars represent standard errors. Data includes only seed stations that were encountered by mice ($N_{\text{seed station}} = 252$). Different lower case letters indicate significant differences between factors: AD, animal-dispersed; WD, wind-dispersed.

Fig. 3. Destino de las semillas (consumidas o dispersadas) según la interacción entre el hábitat y el tipo de dispersión de las semillas ($\chi^2 = 8,34$, $df = 2$, $P = 0,01$). Se dejan las líneas en el gráfico para destacar el cambio de las curvas entre hábitats de tipos de semillas. Las barras representan el error estándar. Los datos solo se refieren a las estaciones de semillas que fueron encontradas por ratones ($N_{\text{estación de semillas}} = 252$). Las letras en minúscula indican las diferencias significativas entre factores: AD, zoócora; WD, anemócora.

the lack of site replication, the lack of a patch effect albeit large variation in patch sizes, and the strength of all patterns observed makes us believe that these results are generalizable to other woodlands invaded by *Rhododendron*. Regarding the between-year replicates, the strength of the observed patterns –seed detection probability and seed predation and caching drivers– and the lack of differences between within-year trials makes it unlikely for the results obtained to have substantially changed had the experiment been replicated between years. Background seed availability should not drastically alter our results. We have data showing that even after seed fall, rodents are absent from areas of the study site without shrub cover and fallen trees but completely loaded with beech seeds (under a >1 m diameter beech in the corner of my study site). This suggests that predation risk factors are more important drivers of foraging behaviour than seed abundance changes.

The preference for dispersing seeds under *Rhododendron* cover predictably has ecological consequences. Previous research suggests that the caching of seeds under the dense shade of *Rhododendron* would prevent them from germinating (Cross, 1981; Phillips and Murdy, 1985; Rotherham and Read, 1988). To test this possibility, we identified and measured every single tree sapling on the study site, comparing the differences in mean density/grid

of sycamore and hazel (the most abundant trees for each seed dispersal type). The results are striking; both native tree occurrence and density decreased from the open woodland to the *Rhododendron*, where the majority of the seeds were cached. Bamboo also provides refuge to small-mammal seed consumers, and has been shown elsewhere to reduce tree seed and seedling survival within bamboo dominated habitats (Wada, 1993; Caccia et al., 2006, 2009). This consistent asymmetric seed dispersal from open and edge habitats to *Rhododendron*, together with the absence of hazel and sycamore tree saplings under *Rhododendron*, suggests that seed survival is greatly reduced. This modifies the spatial structure of the native tree community and has potential implications for the dynamics and composition of communities (Tilman, 1994). Regarding the edge habitat, where competition for light between native and the invasive is more intense, we have shown, first that seeds were removed from the edge, transported and consistently cached under the invasive; second, that the edge also presents a significantly lower number of saplings than in the open woodland. This can have important implications; given that *Rhododendron* spreads vegetatively by lateral horizontal growth of the branches (Pierik and Steegmans, 1975; Cross, 1981; Mejias et al., 2002), native seed removal in the edge habitat could prevent future native seedlings from growing,

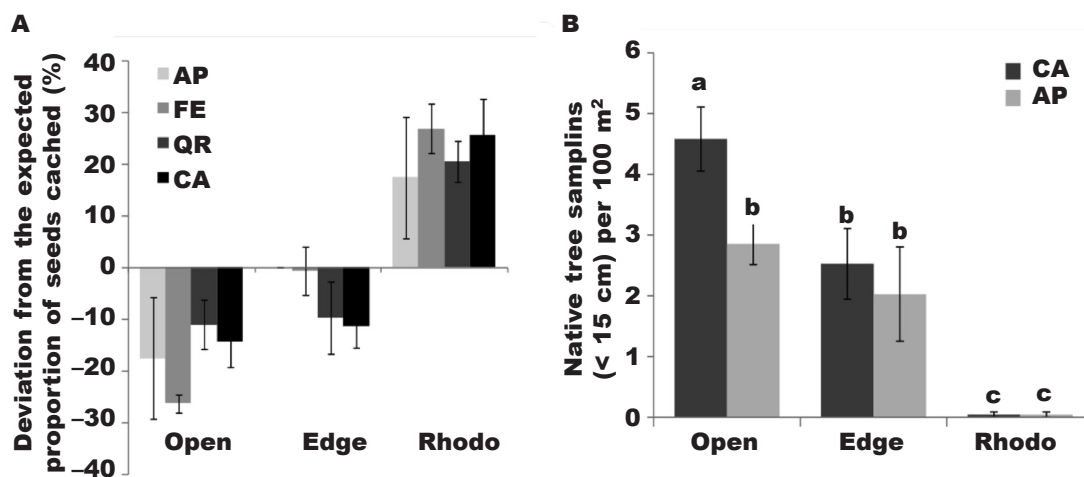


Fig. 4. A, deviation from the expected proportion of seeds cached (%) (by species) in each habitat type. Zero indicates the null expectation of no habitat effect on caching behaviour: seeds collected from a certain habitat type are expected to be cached in that same habitat. Mean percentage and standard error bars calculated from the three independent seed release trials conducted: AP, sycamore, *Acer pseudoplatanus*; FE, ash, *Fraxinus excelsior*; QR, oak, *Quercus robur*; CA, hazel, *Corylus avellana*. B, mean density per 100 m² of hazel and sycamore saplings (< 15 cm) recorded in each habitat type (open woodland, edge habitat and *Rhododendron*).

Fig. 4. A, desviación de la proporción esperada de semillas almacenadas (%) (por especie) en cada tipo de hábitat. Cero significa que no se espera ningún efecto del hábitat en el comportamiento de almacenamiento: se prevé que las semillas recogidas en un determinado tipo de hábitat se almacenen en ese mismo hábitat. Barras de porcentaje medio y error estándar calculadas a partir de los tres estudios independientes realizados de introducción de semillas en el medio: AP, arce, *Acer pseudoplatanus*; FE, fresno, *Fraxinus excelsior*; QR, roble, *Quercus robur*; CA, avellano, *Corylus avellana*. B, densidad media por 100 m² de plántulas de avellano y arce (< 15 cm) registrada en cada tipo de hábitat (bosque abierto, hábitat de transición y *Rhododendron*).

helping the invasive shrub by reducing competition for light and potentially increasing the rate of spread of the invasive shrub throughout the woodland understory. However, this possibility remains to be tested in the field.

By demonstrating *Rhododendron*'s effect on mouse caching behaviour, our results suggest that the presence of native rodent communities in *Rhododendron* invaded areas might increase the invasibility of these habitats by (1) reducing the survival of native trees and (2) eliminating competition for light at the edge of *Rhododendron* patches, where more native seeds were removed thus preventing native tree recruitment. A second factor decreasing seed survival is their higher consumption under the invasive plant compared to the open woodland, which may be partly explained by conspecific pilferage (Leaver and Daly, 2001; Morán-López et al., 2021). However, our results cannot be extrapolated to very old or large *Rhododendron* patches. First, old patches that have precluded native seed regeneration should have lower seed densities as a result of having had no native tree regeneration for decades, and provide less food for mice. Likewise, very large patches over

the home range size of mice should make it difficult for them to forage in the edge and open habitat. It is likely that *Rhododendron* monocultures would result in declines in mouse population density due to the reduction in native tree seed supply. Previously we have shown that another important food resource during the spring and summer period, edible invertebrate biomass, is also reduced under *Rhododendron* (Malo et al., 2013). Hence, refuge-mediated interactions described here might be influential during initial and intermediate stages of *Rhododendron* vegetative spread under the woodland understory, and strictly to spread due to lateral growth, and not due to new invasions through colonisation of *Rhododendron* seeds (Stephenson et al., 2006).

Previous studies have shown how native species behaviour can mitigate the impact of invasive seaweeds (Wright et al., 2010). The present study is one of the few (Chaneton and Bonsall, 2000; Orrock et al., 2010) reporting the opposite; an ecological mechanism –unbalance of conditional mutualism towards its antagonistic side– through which native fauna could increase the deleterious impact of an invasive species by disrupting native woodland regeneration.

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Supplementary material

Malo, A. F., Taylor, A., Díaz, M., 2022. Native seed dispersal by rodents is negatively influenced by an invasive shrub. *Animal Biodiversity and Conservation*, 45.1: 53–67, Doi: <https://doi.org/10.32800/abc.2022.45.0053>

Rhododendron patch size information

Rhododendron seedlings started growing in the study area in 1953 (Mick Crawley, pers. comm.).

Although there were 8 discrete patches in the study site only 6 patches were considered, given that two of them were very close to two other patches: first, a small one (50 m²) very closely located to a much larger one (300 m²) (top right corner fig. 1) and second, another 2 that were too close together (1 m distance) to be considered different. The sizes of the 6 final patches considered were 2,600 m², 350 m², 120 m², 110 m², 75 m², 35 m².

Seeds released

The seeds released were purchased from Nicky's Nursery Ltd., Fairfield Road, Broadstairs, Kent, UK.

Seed removal rates

Before the onset of the field trials, a control experiment was conducted to determine the rates of removal by other animal species within the woodland. Post-dispersal predators are typically larger generalist mammals and birds, but insects such as ants can also be important (Crawley, 2000). Three separate feeding stations were established, one accessible to all creatures (open), one accessible to rodents and insects (5 cm high roof), and one only accessible to insects (2 cm mesh). The mass of seeds removed over a one night period were collected on ten occasions.

There were significantly more seeds removed in the available to rodent and all open seed trays as compared to the available to insects ($t = 7.93$, $df = 27$, $p = 1.60 \times 10^{-8}$; $t = 8.10$, $df = 27$, $p = 1.08 \times 10^{-8}$ respectively). The difference between the rodent and all open available seed trays was not significant ($t = 0.17$, $df = 27$, $p = 0.87$, see fig. 2s in supplementary material).

Crawley, M. J., 2000. Seed Predators and Plant Population Dynamics. In: *Seeds: The Ecology of Regeneration in Plant Communities*, 2nd edition: 167–182 (M. Fenner, Ed.). CAB International, Wallingford, UK, Doi: [10.1079/9780851994321.0167](https://doi.org/10.1079/9780851994321.0167)

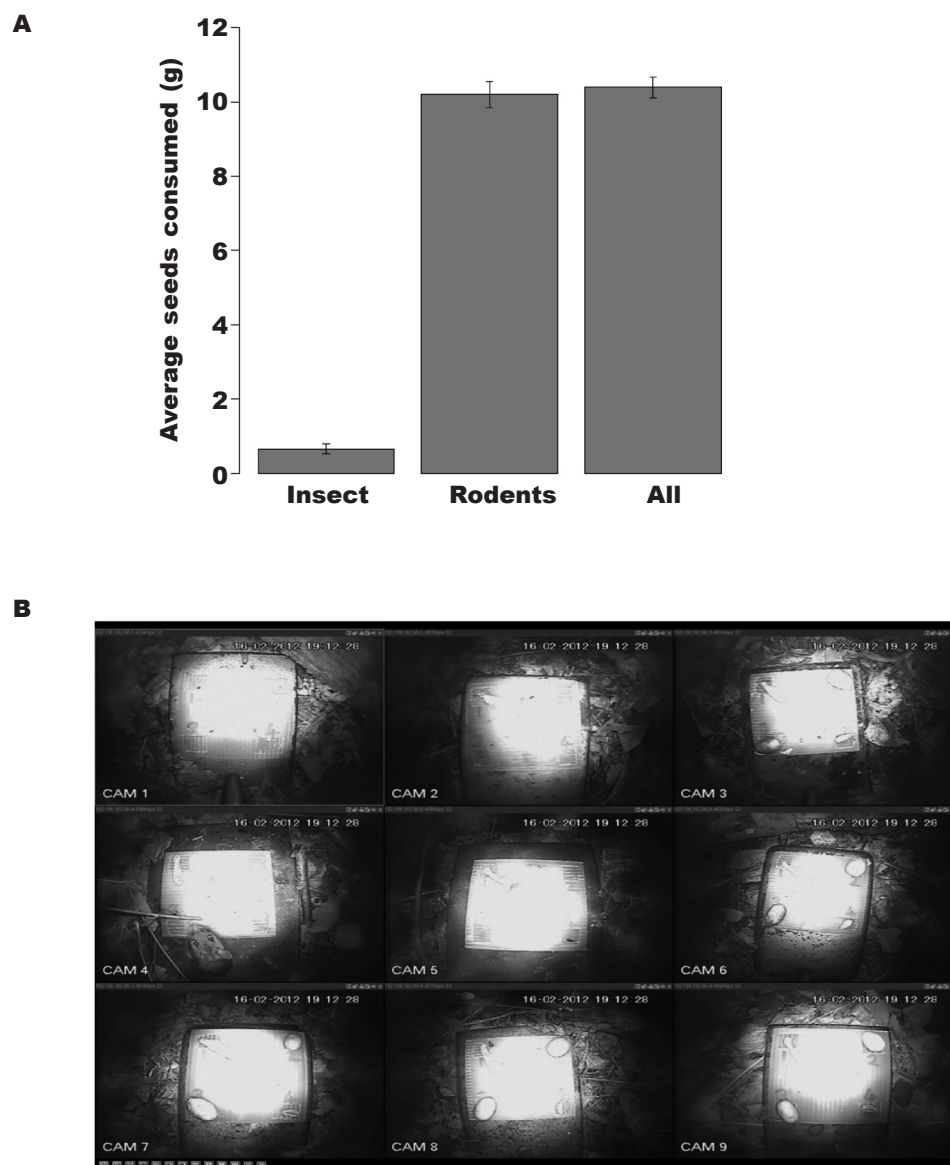


Fig. 1s. A, average seed consumption for the 3 different seed station types; B, picture of the motion-activated infrared camera array used to measure habitat effects on seed survival (Brouard and Malo, unpublished data). From a total of 1,215 hours of footage only rodents were observed to remove the seeds.

Fig. 1s. A, consumo medio de semillas en tres tipos diferentes de estación de semillas; B, imagen de la cámara de infrarrojos activada por el movimiento que se empleó para medir los efectos del hábitat en la supervivencia de las semillas (Brouard y Malo, datos sin publicar). En un total de 1.215 horas de grabación, solo se observó a roedores retirando las semillas.

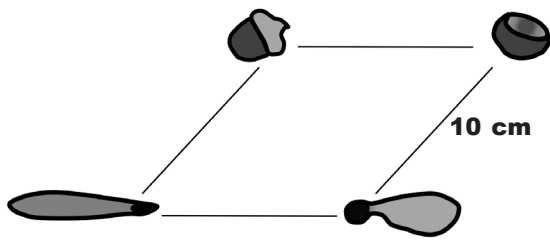


Fig. 2s. Schematic representation of a seed station. Small distance between seeds (represented by lines) allows the assumption to be met that all seeds are detected once the seed station is encountered. Dark areas reflect relative energetic content of the 4 seeds represented (top left, oak; top right, hazel; bottom left, ash; bottom right, sycamore). (Total number of seed stations = 510, total number of individually tagged seeds released = 2,040). Dominant feature within the 10 x 10 m² where the seed station was located was also recorded.

Fig. 2s. Representación esquemática de una estación de semillas. La escasa distancia entre semillas (representada por líneas) permite suponer que se detectan todas las semillas una vez se encuentra la estación de semillas. Las zonas oscuras reflejan el contenido energético relativo de las 4 semillas presentadas (arriba a la izquierda, roble; arriba a la derecha, avellano; abajo a la izquierda, fresno; abajo a la derecha, arce). (Número total de estaciones de semillas = 510, número total de semillas etiquetadas individualmente introducidas en el medio = 2.040). También se registró la característica principal de la superficie de 10 x 10 m² donde se colocó la estación de semillas.

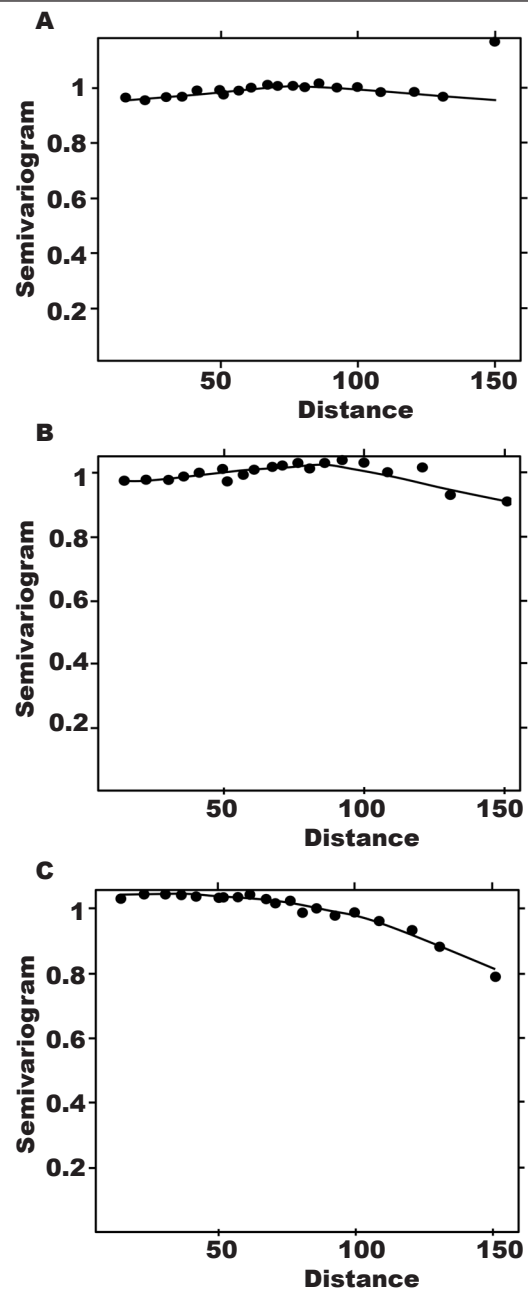


Fig. 3s. Variogram plot conducted to test for residual spatial autocorrelation in the models conducted for: A, seed station encounter; B, seed predation probability; and C, seed caching, remaining after already accounting for distance to *Rhododendron* patches and other spatial covariates.

Fig. 3s. Variograma realizado para analizar la autocorrelación espacial residual en los modelos elaborados para: A, el encuentro de la estación de semillas; B, la probabilidad de predación de las semillas; y C, el almacenamiento de las semillas, después de haber tenido en cuenta la distancia a parches de *Rhododendron* y otras covariables espaciales.

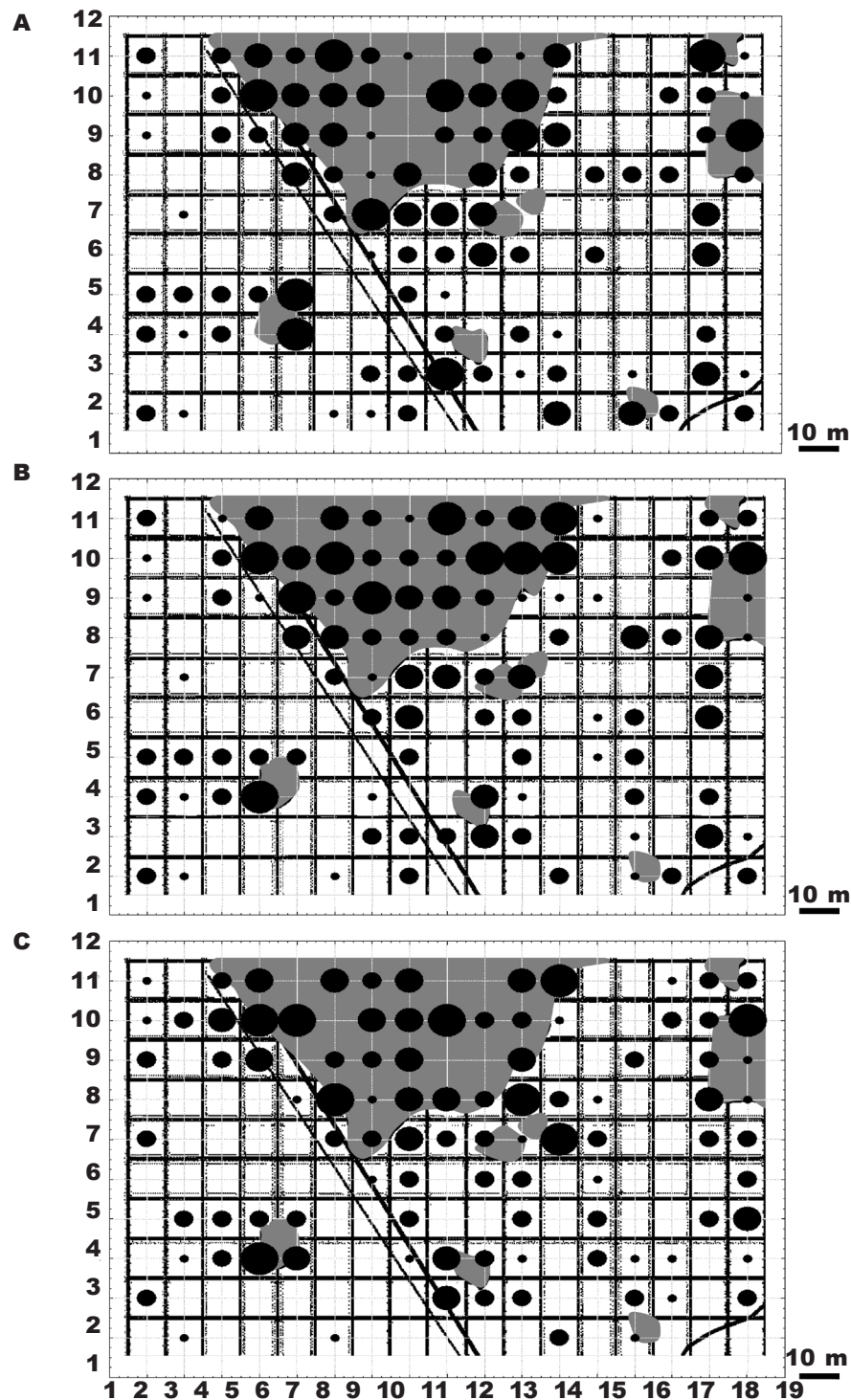


Fig. 4s. Total number of seeds disturbed in the first (A), the second (B), and the third (C) trial. Dot size proportional to the number of seeds disturbed (1–4). Zero seeds are represented by blank squares. Each grid represents an area of 100 m².

Fig. 4s. Número total de semillas consumidas o almacenadas en el primer (A), el segundo (B) y el tercer (C) estudio. Tamaño del punto proporcional al número de semillas consumidas o almacenadas (1–4). La ausencia de semillas se representa con un cuadrante vacío. Cada cuadrante de la cuadrícula representa una superficie de 100 m².

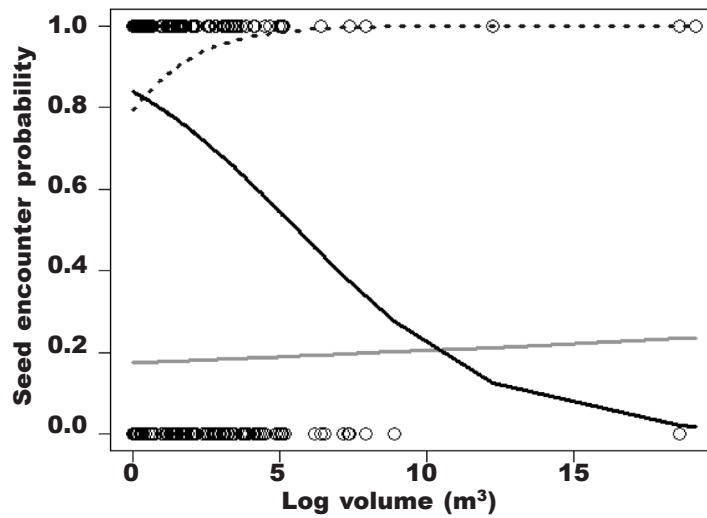


Fig. 5s. Interaction between log volume and habitat type on seed encounter probability. Solid black line, dotted line and light grey line stand for *Rhododendron*, edge and open habitat, respectively.

Fig. 5s. Influencia de la interacción entre el logaritmo del volumen y el tipo de hábitat en la probabilidad de encontrar las semillas. La línea continua negra, la línea punteada y la línea gris representan, respectivamente, *Rhododendron*, hábitat de transición y hábitat abierto.

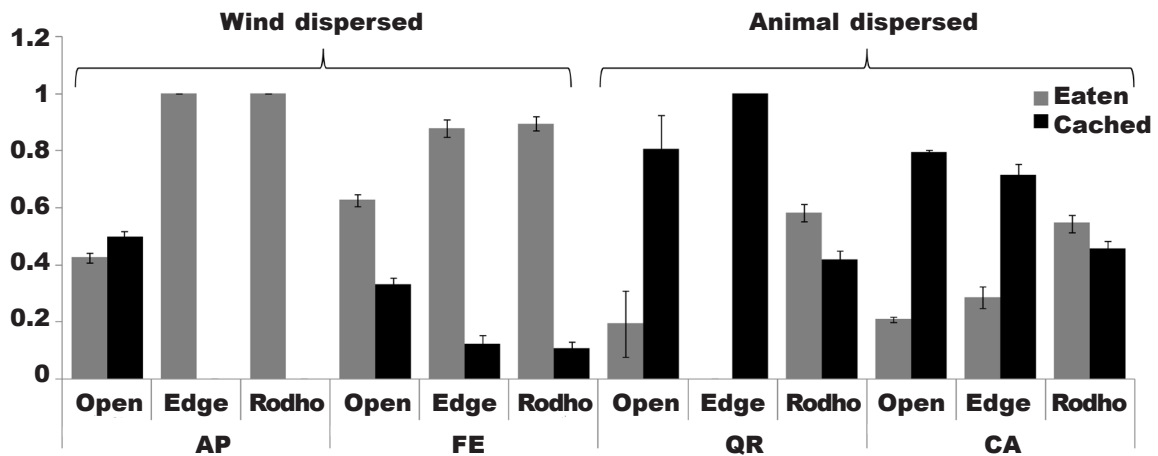


Fig. 6s. Proportion of seeds eaten and cached by mice (including only seed stations that were encountered by mice, $N_{\text{seed stations}} = 252$). Seeds from left to right represent lower to higher energetic content. For AD (O vs E: $\chi^2 = 4.84$, $df = 1$, $P = 0.02$; O vs I (NA inc): $\chi^2 = 270.9$, $df = 2$, $P < 0.00001$; E vs I (NA inc): $\chi^2 = 19.3$, $df = 2$, $P < 0.0001$).

Fig. 6s. Proporción de semillas consumidas y almacenadas por ratones (incluidas solo las estaciones de semillas que fueron encontradas por ratones, $N_{\text{estación de semillas}} = 252$). De izquierda a derecha, las semillas tienen mayor contenido energético. Para AD (O vs E: $\chi^2 = 4,84$, $df = 1$, $P = 0,02$; O vs I (NA inc): $\chi^2 = 270,9$, $df = 2$, $P < 0,00001$; E vs I (NA inc): $\chi^2 = 19,3$, $df = 2$, $P < 0,0001$).