

Original Article

# Positive effects of an invasive shrub on aggregation and abundance of a native small rodent

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Invasive plants can have dramatic effects on natural ecosystems. It is unclear, though, whether these will have a positive or negative effect on animal species' behavior and population parameters within ecosystems where invasive plants occur. Here, we use a 2-year time series of mouse trapping data to test the effects of an evergreen invasive shrub, *Rhododendron ponticum*, on population distribution and abundance in a population of wood mice (*Apodemus sylvaticus*) in southern England. Given the importance of aerial predators on rodent survival and the shield that the thick cover of *Rhododendron* branches and leaves provides, we predicted that *Rhododendron* would have a positive effect on mouse aggregation and abundance. The results confirmed both predictions: proximity to *Rhododendron* positively influenced mouse abundance, whereas a significant interaction between protective microhabitat features (logs) and *Rhododendron* suggest that reductions in predation risk drive the proximity results. In addition, as mouse densities increased, competition increased. During spring, when mouse territoriality was greatest, we found primarily large adults in the *Rhododendron* habitat, with subadult and juvenile mice more likely to be found away from *Rhododendron* patches. The effects of *Rhododendron*-driven increases in mouse density on lower (seed predation and dispersal) and upper trophic level (weasel populations) are also discussed. Questing tick's density and invertebrate biomass were also lower under *Rhododendron*. Our research shows that an invasive plant species can increase the abundance of a native mammal and that this could potentially lead to increases/decreases in other species populations within the community. *Key words:* *Apodemus sylvaticus*, edible invertebrate biomass, intraspecific competition, invasive shrub, predation risk, spatial variation, ticks, wood mouse. [*Behav Ecol*]

## INTRODUCTION

Invasive plant species can cause dramatic and long-lasting changes to native ecosystems (Ehrenfeld and Scott 2001) from the biochemical to the landscape level (Levine et al. 2003) and from species community effects to changes in food web architecture (Vitousek 1990; Gratton and Denno 2006; Bergstrom et al. 2009). *Rhododendron ponticum* (hereafter *Rhododendron*) is an invasive fast-growing Ericaceae shrub introduced from Spain into the UK in 1763, causing substantial changes to woodland ecosystems (Cross 1975; Milne and Abbott 2000; Dehnen-Schmutz et al. 2004; Tyler et al. 2006). Its competitive success comes partly from its evergreen leaves blocking sunlight, preventing the germination of native tree seedlings under its canopy (Rotherham and Read 1988), and from its leaves' unpalatability to native consumers (Cross 1981), which reduces predation pressure by herbivores (Keane and Crawley 2002). *Rhododendron* disrupts natural woodland regeneration (Thomson et al. 1993), modifies succession (Mitchell et al. 1997), and leads to declines in community plant diversity (Becker 1988). However, the effect of *Rhododendron* on native vertebrate fauna has not been yet explored. Here, we test the effect of *Rhododendron* canopy

cover presence on mouse abundance and indirectly related species.

Rodents have negative economic impacts on agriculture (Stenseth et al. 2003) and pose a health threat to humans, globally spreading (directly or indirectly) over 35 diseases, including plague, Lyme disease, and hemorrhagic fever (Lund 1988; Padovan 2006). They are also a key group in many terrestrial ecosystems dispersing seeds and being a staple prey for numerous predator species (Hulme 1994; Santos and Telleria 1997; Jensen and Nielsen 1986). Thus, the potential effects of rodent populations on human societies due to their impact on agriculture, human health, and biodiversity, together with the predicted increase of invasions due to climate change and globalization (Dukes and Mooney 1999; Lee and Chown 2009) that can enhance their effects, stresses the need to understand interactions between invasive plants and native rodents (Allan et al. 2010).

In contrast to their potential negative effects on humans, they often play important roles in many terrestrial ecosystems, dispersing seeds and being a staple prey for numerous predators (Jensen and Nielsen 1986; Hulme 1994; Santos and Telleria 1997). In the UK, small rodents make up more than half of the diets of tawny owls (*Strix aluco*) and weasels (*Mustela nivalis*) (King 1980; Southern and Lowe 1982), and the breeding success of these 2 rodent specialist predators (an aerial and a ground hunter, respectively) is affected by changes in rodent density (King 1985). This numerical response has proved general for other rodent-based predator-prey systems (O'Mahony et al. 1999; Gilg et al. 2003; Coulson

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and Malo 2008; Ims et al. 2008; Kausrud et al. 2008). Reduced abundance of the preferred prey can also lead to changes in a predator's main prey (Malo et al. 2004), sometimes shifting to more vulnerable prey species and having deleterious effects on the ecosystem (Kausrud et al. 2008).

The wood mouse (*Apodemus sylvaticus*) is a common nocturnal rodent in Britain (Wolton 1983), inhabiting both woodland and arable landscapes (Tew and Macdonald 1993; Mallorie and Flowerdew 1994). Seeds represent over 70% of wood mouse food resources (Watts 1968). Population size fluctuates seasonally (Flowerdew 1985). *Rhododendron* can potentially impact mice in several ways. The dense evergreen shrub cover and its intertwined branches can provide shelter from weather (Vickery and Rivest 1992) and aerial predators (Brown 1988) like the tawny owl, including in winter when the rest of the wood provides little protection from aerial predation. *Rhododendron* consequently potentially allows mice to forage longer compared with more open woodland where there is less cover and potentially constrained foraging time. Edible invertebrate biomass as well as parasitic tick densities may also be affected by *Rhododendron*.

In this paper, we use 2 years of weekly trapping data to address the role of the invasive *Rhododendron* on wood mice aggregation and abundance. Given the importance of aerial predators on rodent survival and the shield that the thick cover of *Rhododendron* branches and leaves provides, we predicted that *Rhododendron* would increase mouse aggregation and abundance. To ascertain whether *Rhododendron* benefits mice by reducing predation risk, we capitalized on the presence of other protective structures present in both habitat types. We predicted that protective microhabitat structures, such as logs, would influence mouse space use in the open-woodland habitat, but not under *Rhododendron*, where the invasive shrub already provides cover against predation. We also predicted that in spring, when intraspecific competition and aggression is highest, there would be habitat segregation by age class; larger mice outcompeting smaller mice for safe *Rhododendron* areas. We then use these findings to extrapolate how *Rhododendron* effects on the wood mouse population can impact native tree seed predation and dispersal. Lastly, we report *Rhododendron*'s influence on rodent parasitic tick abundance and edible invertebrate biomass and discuss their potential impact on mice.

## METHODS

### Study site

The study area, located in a 4-ha mixed deciduous woodland located at Nash's copse, Silwood Park, Ascot, UK ( $51^{\circ}24'52.47''N$ ,  $0^{\circ}38'41.73''W$ ), was divided into a trapping grid of  $10 \times 10$  m quadrats delimited by flags (100 m $^2$ ; Figure 1). Eight patches of the invasive *Rhododendron* (size: 2600, 270, 120, 80, 75, 60, 50, and 35 m $^2$ ; in all cases height between 3 and 5 m) were present in the study site (Figure 1).

### Trapping protocol

Trapping sessions were conducted weekly from October 2008 to July 2010. The trapping grid initially covered 1 ha (October 2008–April 2009) before being extended to 1.7 ha (May 2009). The *Rhododendron* represents 29% (0.29 ha) of the total study site before May 2009 and 19% (0.32 ha) after May 2009. The remaining percentage corresponds to open-woodland habitat. Total traps set up per trapping session varied due to variation in man power and weather constraints. Typically, each week 70–80% of the quadrats were trapped covering both *Rhododendron* and open-woodland areas. Traps

were first set up in the quadrats that had not been trapped the previous week and then ensuing a balanced design. A total of 6734 traps were set up during the study period (traps per session = 83.14, SD = 33.94,  $N_{\text{sessions}} = 100$ ).

Modified small Sherman traps were baited and set up before sunset and collected the next morning, before sunrise, and checked for mice (for more details on trap modification and trapping protocol, see Supplementary material). At first capture, mice were classified as adults, subadults, and juveniles according to weight (adults: 18 g or over; subadults: 14–17.99 g; and juveniles: 7–13.99 g). Mice heavier than 15 g were pit-tagged and juvenile mice uniquely fur clipped to allow individual identification. After handling and identification, mice were released back at their trapping location. Successful traps were thoroughly cleaned to avoid trapping bias (Wolf and Batzli 2002) and the potential risk of disease transmission between mice. We provide a few definitions associated with each trapping event—*Trapping session*: Data were collected in 100 trapping sessions. *Quadrat ID*: The  $10 \times 10$  m grid where the trap was set ( $n = 168$ ). *Habitat type*: *Rhododendron* presence and absence (open woodland). *Year*: Categorical variable coded as first or second. *Season*: Categorical variable with 4 levels depending on trapping date (autumn: 21 September–20 December; winter: 21 December–20 March; spring: 21 March–20 June; and summer: 21 June–20 September).

### Microhabitat data collection

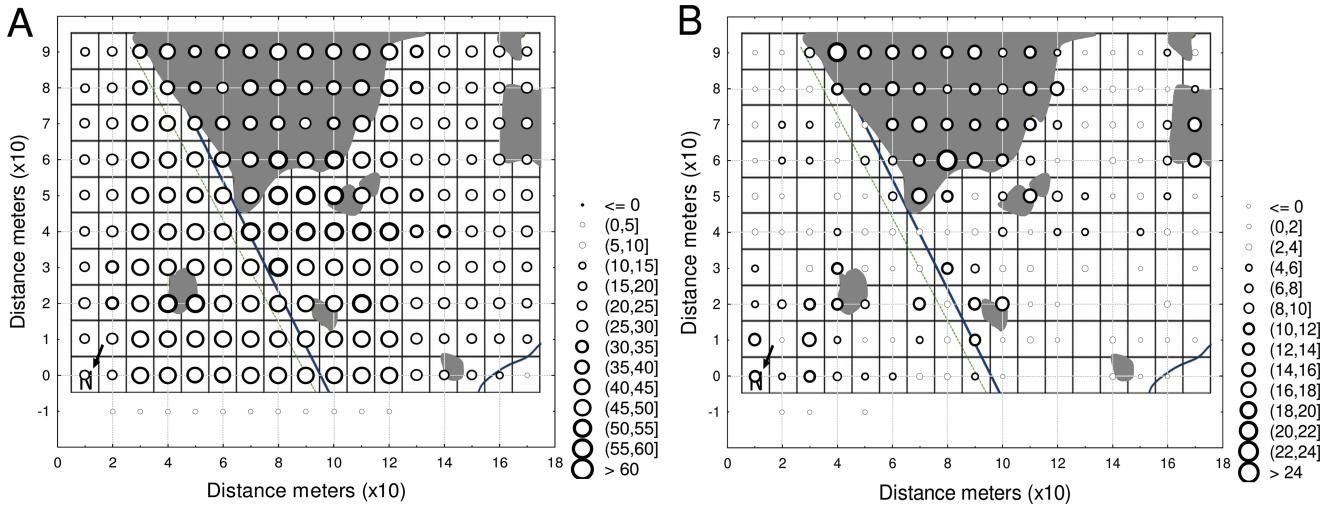
We collected data on microhabitat features. We define the following variables—*Log volume (m $^3$ )*: In each  $10 \times 10$  m quadrat, the diameter ( $2r$ ) and length ( $l$ ) of each log was recorded. The cylinder formula ( $\pi r^2 l$ ) was used to calculate the volume of each log, and these were summed within each quadrat (mean  $\pm$  SD =  $0.23 \pm 0.28$ ). *Stump volume (m $^3$ )*: The mean diameter of the stump was classified into small (0.3 m), medium (0.8 m), and large (1.3 m), and the volume calculated using  $\pi r^2 h$  where the average value  $h = 0.25$  m was used (mean  $\pm$  SD =  $0.12 \pm 0.29$ ). *Total microhabitat volume (m $^3$ )*: Total volume of log and stumps per quadrat was calculated. *Tree section area (TSA, cm $^2$ )*: The circumference for each tree was measured, the radius was calculated ( $C = 2\pi r^2$ ) and then used to obtain the TSA ( $A = \pi r^2$ ). The sum TSA per quadrat was then calculated (mean  $\pm$  SD =  $39.177 \pm 15.972$ ). *Tree Diversity*: The number of trees from different species was recorded per grid. Tree diversity per quadrat was then calculated using Simpson's reciprocal index ( $SRI = 1/D$ ). This index ranges from the minimum (1) to the maximum number of species:

$$D = \frac{\sum n(n-1)}{N(N-1)}$$

where  $n$  = number of trees per tree species ( $n = 9$  species: alder, beech, birch, hazel, oak, rowan, salix, sweet chestnut, and sycamore. See scientific names in Supplementary material) and  $N$  = number of trees per quadrat.

### Comparison of mouse abundance and aggregation between *Rhododendron* and open woodland

Our study site is a matrix of open woodland and *Rhododendron* patches between which mice can move. Thus, because mice are not necessarily restricted to a single habitat type, 2 response variables were used to assess how *Rhododendron* influences mice. *Aggregation*, a measure of intensity of habitat use (or concentration of mice in response to the matrix components), calculated as capture probability/quadrat.

**Figure 1**

Number of traps set up (A) and total mice caught (B) per quadrat during the whole study period in our study site in Ascot (UK). Circle sizes are proportional to the number of traps set up (A) and number of successful catches (B). Gray areas represent *Rhododendron* patches and the line depicts a dry ditch (0.5–1.5 m wide).

**Abundance**, the total number of different mice recorded per quadrat for each season  $\times$  year combination. Seasonal estimates of mouse density per hectare per habitat type were also calculated. Mark-recapture abundance estimators for open populations (POPAN, Link-Barker formulations of the Jolly-Seber model) were not used as they are explicitly discouraged to obtain population size estimates for distinct areas within a study site and because they are meant for sampling schemes with large spacing over time (Jolly 1965; Seber 1965).

#### Generality of *Rhododendron* effects on mouse abundance

To ensure that the effects of the *Rhododendron* on mice were not just site specific, independent trappings were conducted in a further 20 locations (*Rhododendron* patches surrounded by open woodland) up to 1 km away from the study site. Trap transects were laid out at 10-m intervals, starting 10 m inside the *Rhododendron*, and extending a further 50 m outside.

#### Mouse preference for *Rhododendron* areas

To ascertain whether the *Rhododendron* is a resource that mice compete for, we tested for an interaction between habitat type and age class on capture success during spring, known to be the season when intraspecific competition peaks in rodents (Flowerdew 1985; Eccard et al. 2011). We predicted that larger individuals should be able to successfully compete for *Rhododendron* displacing smaller individuals. More specifically, we predicted that adults would competitively exclude subadults more than juveniles, as these do not compete for mates and are more likely to be their own recently weaned offspring.

#### *Rhododendron*-mediated mouse density effects on seed predation and dispersal

A simple theoretical model was constructed to gain insight into the effects of *Rhododendron*-mediated increases of mouse density on the trophic level immediately below: on seed predation and dispersal. Seeds represent over 70% of wood mouse food resources (Watts 1968). The daily energy expenditure (DEE) of a mouse (67.9 kJ/day) (Corp et al. 1999) and the average weight and energy contained per seed (ECS) of

oak, beech, sweet chestnut, and hazel (Gurnell 1993; Table S3) were retrieved from the literature. The expected seed predation of the main tree species in the plot was then estimated as DEE/ECS  $\times$   $N_{\text{mice}}$ .

#### Tick density and edible invertebrate biomass estimation

For the tick and edible invertebrate data collections, the open habitat was classified into 4 finer habitat levels (bluebells, mixed habitat, sorrel, leaf litter or bare ground). To estimate the difference in questing tick (*Ixodes ricinus*) abundance between *Rhododendron* and open-woodland habitat types during spring and early summer—when tick populations peak (Randolph et al. 2002)—3 tick surveys were carried out during May, June, and July 2009. To estimate the difference in edible invertebrate biomass between *Rhododendron* and open-woodland habitat types during the summer—when protein demands are highest—pitfall trappings were conducted. Each quadrat ( $N = 60$ ) was sampled for 3 consecutive days in the first week of July 2010 (for more details, see *Supplementary material*).

#### Statistical analyses

To test whether *Rhododendron* increases mouse aggregation and abundance, we used generalized linear mixed effects models and generalized linear models in R (v2.8.1; R Core Development Team 2010). To test for the effect of *Rhododendron* presence on mouse aggregation (capture success), binomial error structures fitted by Laplace approximation were used (lmer function in R). To test for *Rhododendron* effects on mouse abundance (count data), we conducted glm using quasi-likelihood (glm, with quasifamily in R), avoiding the biasing effects of overdispersion on parameter estimates (Crawley 2007). For the aggregation and abundance models, *Rhododendron* presence, year, and season were fitted as fixed categorical effects and log volume, total volume, TSA, and tree diversity (SRI) per quadrat as fixed continuous effects. The 2-way interactions between structure types and *Rhododendron* presence were also included. Two random factors were included in the aggregation model: *Trapping session*, to statistically account for the repeated trappings conducted in the aggregation model and *quadrat ID*, to account for spatial variation. In order to test for the antipredatory role of *Rhododendron*, the significance

of the interaction between structures and habitat type, such as log volume  $\times$  *Rhododendron*, were assessed. Maximal models for aggregation and abundance were constructed, and stepwise simplified to the minimal adequate models (MAMs) by only retaining those terms that, after removal, significantly increased deviance as assessed by the chi-square test (Crawley 2007). MAMs presented the lowest Akaike information criterion (AIC) values. Coefficient estimates and standard errors for the terms in the MAMs are reported, as well as Z- and t-statistics for the aggregation and abundance models, respectively.

Whether antipredatory benefits provided by the *Rhododendron* generated intraspecific competition for this habitat type was tested for by looking at habitat segregation by age class during spring. Lastly, the differences in rodent parasitic tick abundance and edible invertebrate biomass between habitat types was tested using 1-way Anova.

## RESULTS

A total of 6523 traps were set up over 100 trapping sessions, spanning 22 months, which generated 860 wood mouse trapping events. Recapture rates varied between 58% and 79% per session and did not differ significantly between years or seasons (Table S1). The population size fluctuated both yearly and seasonally (Tables 1 and 2; Figure S1A), showing a minimum abundance in spring, followed by a small rise and summer plateau, a steep increase during autumn, before finally declining in winter (Figure S1A; Table 2). Yearly differences in population size were largest for the autumn. Sex ratio, age structure, and average weight also fluctuated seasonally (Figure S1B–D). Inspection of these figures suggests that increases in mouse abundance are associated with new juveniles being recruited to the population, which leads to a decrease in population mean age and body weight.

### Effect of *Rhododendron* on mouse aggregation and abundance

There are no major differences between the aggregation model (mouse capture probability) and abundance model (total number of mice), suggesting that the higher aggregation of mice under *Rhododendron* areas (higher intensity of use) is triggered by a higher number of different mice using this area. Mice had higher capture probability ( $1.90 \pm 0.21$ ,  $Z = 9.16$ ,  $P < 0.001$ , Figure 1B) and were also more abundant (total number of unique mice per quadrat:  $1.28 \pm 0.10$ ,  $t_{1248} = 12.3$ ,  $P < 0.001$ ) under the *Rhododendron* than in the open woodland. *Rhododendron* had a strong positive effect on mouse capture success year-round (Figure 2A). Overall, there was up to a 5-fold difference in capture success between the *Rhododendron* and open-woodland areas (36 vs. 8 mice/ha trapped, respectively). *Rhododendron* influenced mouse aggregation and abundance to a similar extent across seasons, as there was no interaction between habitat and season (results not shown). *Rhododendron* areas had higher mouse capture probability per hectare than the open woodland (Table 2 and Figure 2A). Mouse abundance was also higher in *Rhododendron* than in open-woodland areas (Table 1B and Table S2). The random factors in the aggregation model, grid and session, presented a variance of 0.68 and 0.21, respectively.

### Generality of *Rhododendron* and distance to *Rhododendron* effects on aggregation

Our results are also general and not site specific, as shown by the results obtained from independent trappings conducted in a further 20 locations (*Rhododendron* patches surrounded

**Table 1**

(A) Generalized linear mixed effects model (lmer, link function = binomial) for the effects of *Rhododendron*, season, and microhabitat on mouse capture success (mouse aggregation) and (B) generalized linear model (glm, link function quasi-Poisson) for the effects of the variables above on total number of different mice caught per quadrat (mouse abundance)

Terms		$\chi^2$	df	<i>P</i>
(A) MAM for mouse aggregation				
<i>Rhododendron</i>		77.19	2	<0.0001
Season		35.76	3	<0.0001
Log volume		12.22	1	0.002
<i>Rhododendron</i> $\times$ log volume		8.422	1	0.0037
Terms	Deviance	df		<i>P</i>
(B) MAM for mouse abundance				
<i>Rhododendron</i>		42.87	2	<0.0001
Season		26.8	3	<0.0001
Log volume		1.1	1	0.23
Tree diversity		5.03	1	0.007
<i>Rhododendron</i> $\times$ tree diversity		13.7	1	<0.0001
<i>Rhododendron</i> $\times$ log volume		12.40	1	<0.0001

(A) Quadrat ID and trapping session were included as random factors. Number of observations: 6400; groups: quadrat, 168; session, 98; AIC = 4396. (B) Number of observations: 1248. (A, B) Only the final model is shown. Other terms [stump, tree, total volume, TSA, tree diversity (SRI), and the 2-way interactions between these and *Rhododendron*] remained nonsignificant.

**Table 2**

Wood mouse density per hectare/night in *Rhododendron* and open-woodland areas

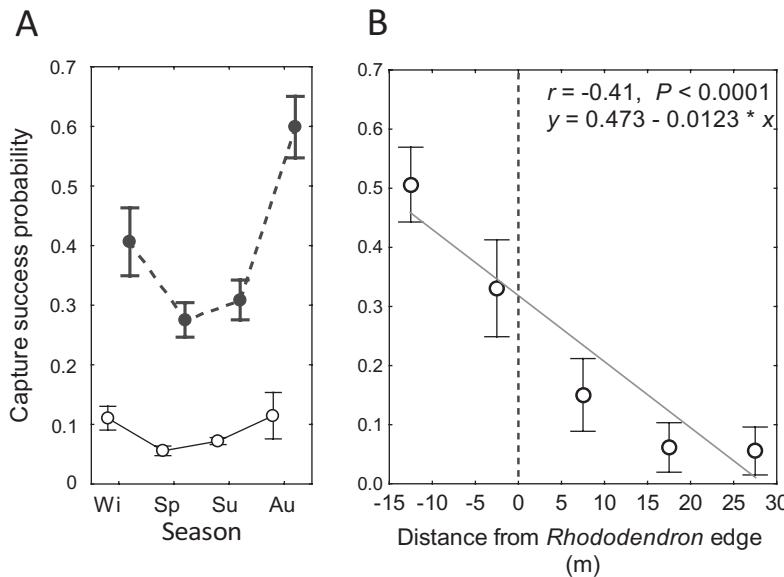
Season	Average wood mouse density and biomass per hectare			
	<i>Rhododendron</i>		Open woodland	
	Mouse density/ha	Mouse biomass (g)	Mouse density/ha	Mouse biomass (g)
Autumn (9)	59.87 (5.43)	1035 (94)	11.46 (5.28)	198 (91)
Winter (10)	40.63 (6.00)	707 (104)	11.04 (2.71)	192 (47)
Spring (22)	27.53 (3.05)	605 (67)	5.57 (2.28)	122 (50)
Summer (18)	30.87 (3.51)	642 (73)	7.20 (1.39)	150 (29)
Total (59)	35.70 (2.47)	691 (48)	7.89 (4.09)	153 (79)

Data are derived from those trapping sessions for which a minimum of 46 traps were set up (max = 146) and a minimum of 10 in each habitat type (max<sub>open</sub> = 118 and max<sub>rhodo</sub> = 67). Numbers inside brackets for the season column indicate the total number of trapping sessions included and for the density and biomass columns, these indicate number of individual standard errors. Average mouse weight used for biomass estimates was calculated seasonally (autumn 17.28 g, spring 21.96 g, summer 20.70 g, and winter 17.41 g).

by open woodland) up to 1 km away from the study site (Figure 2B). Distance from *Rhododendron* shows a negative association with mouse capture probability throughout the year, varying from 40% under *Rhododendron* cover to 5% at a 20-m distance from *Rhododendron*.

### Interaction between log volume and habitat type on aggregation and abundance

The MAMs for both capture probability and total number of mice included the interaction of *Rhododendron* presence and log volume (Table 1). Thus, the effects of log volume on mouse capture success and abundance differed between

**Figure 2**

(A) Mouse capture probability in *Rhododendron* (gray dots) and open-woodland areas (open circles) by season. Bars represent standard errors. There were also seasonal differences within habitats (*Rhododendron*,  $F_{3,55} = 10.08$ ,  $P < 0.0001$ ; open woodland,  $F_{3,55} = 3.05$ ,  $P = 0.036$ ). Number of trapping session per season: winter = 10, spring = 22, summer = 18, and autumn = 9. (B) Effect of distance to *Rhododendron* areas on mouse capture probability. The dotted gray line represents the *Rhododendron* edge. Data derived from 20 trapping sessions conducted in different *Rhododendron* patches located up to 1 km away from the study site (total trapping effort = 762).

habitats (aggregation model,  $Z = 3.00$ ,  $P = 0.002$ ; abundance model,  $t_{1248} = -4.27$ ,  $P < 0.001$ ). In the open woodland, mice were captured more frequently in quadrats with higher log volume ( $r = 0.26$ ,  $P < 0.01$ ) whilst an opposite and nonsignificant trend ( $r = -0.23$ ,  $P = 0.06$ ) was found in *Rhododendron* areas (Figure S2). Correlation coefficients for the linear association between log volume and mouse capture success for autumn, winter, spring, and summer were all positive in open woodland (0.26, 0.05, 0.22, and 0.14) and all negative under *Rhododendron* cover (-0.23, -0.04, -0.19, and -0.06; see autumn example in Figure S2). There was also a significant interaction between *Rhododendron* presence and tree diversity on abundance (Table 1B). Under *Rhododendron*, mouse abundance decreased with increasing tree diversity ( $-0.024 \pm 0.005$ ,  $P < 0.0001$ ) but no effect of tree diversity on abundance was observed in the open woodland ( $P = 0.85$ ). No significant effects of total microhabitat structure volume or tree diversity on mouse capture success were found (Table 1).

### Mouse preference for *Rhododendron* areas

The interaction between habitat type and age class on spring capture success was significant; adults were much more likely to be found under the *Rhododendron* than elsewhere and subadults and juveniles more likely to be found in the open areas ( $F_{1,234} = 13.86$ ,  $P = 0.0002$ ). There were nonsignificant differences for the 6 pairwise comparisons corresponding to the 3 other seasons ( $0.33 > P > 0.26$ ;  $N_{\text{autumn}} = 241$ ;  $N_{\text{winter}} = 216$ ;  $N_{\text{summer}} = 140$ ). Also, during spring, habitat segregation was stronger between adults and subadults than between adults and juveniles (Figure 3).

### *Rhododendron*-mediated mouse density effects on seed predation and dispersal

The average daily energetic requirement of a mouse weighing 20.5 g is 67.9 kJ/day (Corp et al. 1997), and the average amount of ECS varies between 19.4 and 34.5 kJ/g for sweet

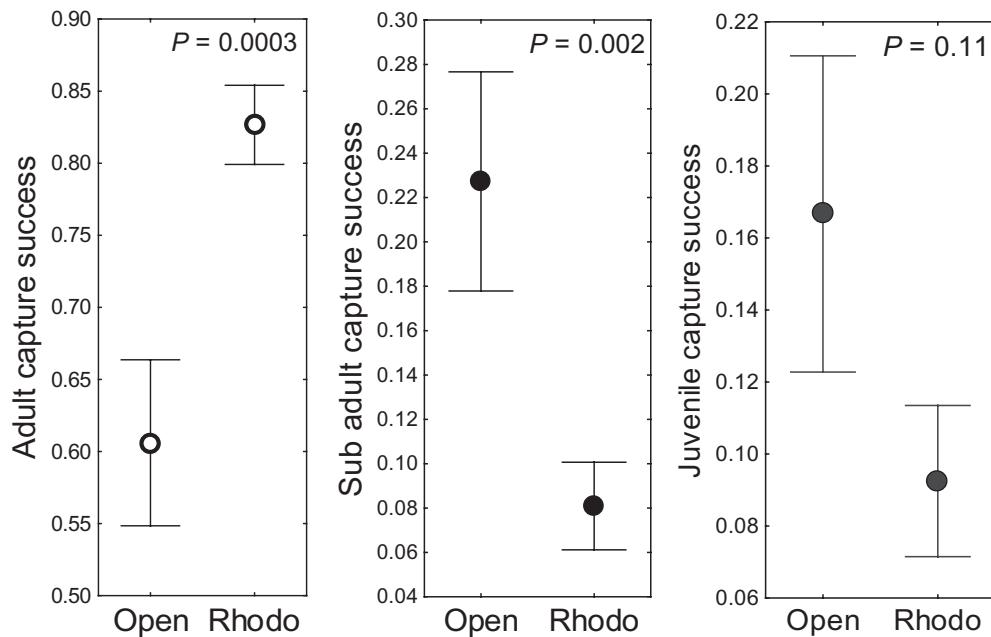
chestnut and hazel, respectively, with oak and beech seeds' energetic content lying between these two. Using these values, we estimated the number of seeds required from each species per mouse per day (Table S3). Given the mean densities of mice per hectare in open woodland ( $n = 8$ ) and *Rhododendron* ( $n = 36$ ) areas (Table 2), the total daily seed consumption was calculated for the aforementioned tree species (Table S3). For example, the daily seed consumption estimate of hazel was 49 seeds/ha in open woodland and 220 seeds/ha in the *Rhododendron*.

### Tick density and edible arthropod biomass habitat comparisons

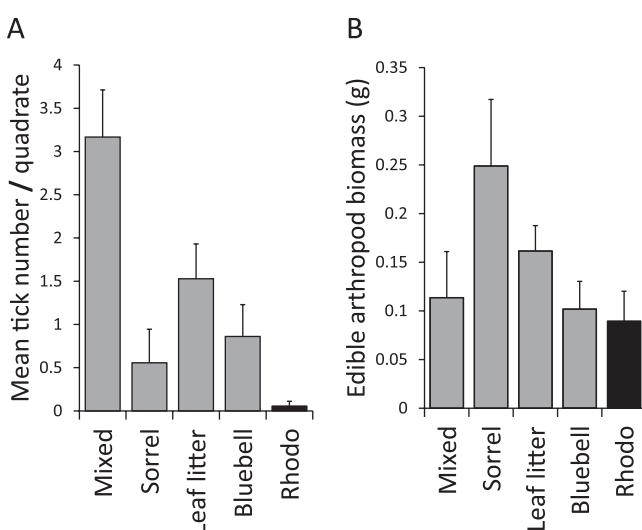
During spring, *Rhododendron* areas present lower tick densities (larvae, nymphs, and adults,  $F_{1,106} = 10.49$ ,  $P < 0.01$ , Figure 4A) than open areas. Edible arthropod biomass was also lowest in the *Rhododendron* as compared with any other habitat type in the open woodland (Figure 4B). The differences were not statistically significant though ( $F_{1,55} = 2.95$ ,  $P = 0.091$ ), due to similarly low invertebrate edible biomass in open-woodland areas covered with bluebells.

## DISCUSSION

Negative effects of invasive species on natives are frequently reported. However, fewer examples have been reported suggesting positive effects of an invasive plant species on the density of native fauna (Rodriguez 2006; White et al. 2006). In the present study, we show that areas under *Rhododendron* cover allow higher mouse aggregation and abundance than open-woodland areas. Mice habitat selection of *Rhododendron* and its disproportionate usage as compared with its availability in the study site suggest that mice show preference (Johnson 1980) for *Rhododendron* areas. The habitat segregation by age class, showing larger mice preferentially occupy *Rhododendron* areas suggest that mice compete for them. This is most likely due to the associated reduction in predation risk, with the invasive

**Figure 3**

Mice habitat segregation by age class in spring between open-woodland areas (open) and *Rhododendron* (Rhodo). *P* values for Kruskal–Wallis Anova test are reported in the graphs (adults: KW-H<sub>1,239</sub> = 12.89; subadults, KW-H<sub>1,239</sub> = 9.56; and juveniles KW-H<sub>1,239</sub> = 2.612).

**Figure 4**

Tick density (A) and edible arthropod biomass (B) in *Rhododendron* (black) and open-woodland habitats (gray) during spring. Error bars denote standard errors.

shrub providing cover from generalist aerial predators. This explanation is supported by the fact that in the open woodland, where no thick cover is available, areas with higher log volume are more used by mice, providing protective structures against predator attacks and effective, silent escape runways. This positive relationship between log volume and mouse abundance was lost under *Rhododendron* cover, where aerial predation risk is minimized. The mouse aggregation and abundance increase under the invasive species cover can have effects on the ecosystem via prey and predator trophic levels. Lastly, our results show negative effects of *Rhododendron* on mouse ectoparasite densities and edible invertebrate biomass. This agrees with *Rhododendron*-driven reductions in soil microorganisms (Sutton and Wilkinson 2007) and soil

invertebrates, such as earthworms (Cross 1975). This is probably due to the effects of polyphenols and cyanidin contained in *Rhododendron* leaf litter (Wurzburger and Hendrick 2007). Given that ticks are parasites and biomass is food, positive and negative effects on mice are expected, respectively. This highlights possible indirect pathways through which invasive species can also positively or negatively impact fitness of native species.

Invasive species tend to have negative impacts on natives, either by the substitution of natives by closely related invasives or by leading to negative interactions between invasive and native species that often suppress the population size of other natives (Keeler et al. 2006; Longland 2007; Phiri et al. 2009). Positive effects of invasive plants on exotic fauna have also been reported (Kourtev et al. 1999). However, positive effects of invasive plants on natives are rare. One example is the effect of the spotted knapweed and its gall fly control agents (*Urophora* spp.) on the deer mouse, *Peromyscus maniculatus* (Pearson et al. 2000; Pearson and Callaway 2003; Ortega et al. 2004). A dietary shift to *Urophora* resulted in higher densities of mice in knapweed covered areas: when no gall fly larvae were present in the seed heads, no differences in rodent density were found. Invertebrates, such as *Dictyna* spiders, have also shown a positive population response to the spotted knapweed (Pearson 2009). Another similar example is the effect of the invasive tamarisk (treated with another beetle control agent) on the endangered southwestern willow flycatcher (Pearson and Callaway 2003) although the extent to which the plant has a net positive effect on bird abundance remains unclear (Sogge et al. 2008; Paxton et al. 2011).

The 2–5-fold increase in mouse population abundance reported here shows a clear positive effect of an invasive shrub on a native rodent. This is most likely driven by the *Rhododendron*'s structure reducing predation risk. Contrary to the case of the *Peromyscus*-knapweed example, this habitat selection does not come through the increased availability of food resources under the presence of the invasive as there is both lower density of seed producing trees in the *Rhododendron* than in the open woodland (Malo et al.,

unpublished data) and lower invertebrate abundance. Several lines of evidence suggest that the benefits of a reduction in predation risk drive habitat selection leading to the higher densities we observed in *Rhododendron* areas. First, wood mouse populations can be strongly influenced by aerial predators including the tawny owl (Jedrzejewski and Jedrzejewska 1993), which rarely catch prey in covered habitats (Southern and Lowe 1968) and that are also present in our study site. Second, in our study, log volume, which provides protection from aerial predators (Montgomery 1980), is positively associated with mice capture success in the open woodland but not under *Rhododendron*. Third, experimental evidence shows that shrub cover is valued by foraging mice (Downes and Hoefer 2007; Mattos and Orrock 2010), probably because it also increases foraging efficiency (Fedriani and Manzanares 2005). Thus, the structural habitat changes triggered by the invasive species can negatively impact a generalist aerial predator and, hence, turn out to be a valuable resource for a native prey species. Indeed, our results show that in spring—when territoriality is strongest (Flowerdew 1985; Wolton 1985)—there is habitat segregation between adult and young age classes. This is most likely due to intraspecific interference competition for *Rhododendron*-covered areas, with older, heavier mice outcompeting smaller, lighter mice. The fact that the effect is stronger for subadults, which can compete with adults for mating opportunities, than for the nonreproductive juveniles supports the idea that interference competition for reproduction is taking place.

Invasives can have cascade effects throughout the ecosystem. For example, in Flathead Lake (Montana), an invasive shrimp shifted plankton community size structure, facilitating predation by lake trout. This indirectly endangered other native fish and redirected energy flow through the ecosystem away from top predators such as bald eagles (Ellis et al. 2011). Invasive predators introduced in islands can also lead to extinctions (Nogales et al. 2004). In our native deciduous woodland ecosystem, *Rhododendron*-driven increases in mouse abundance can also have effects on the upper trophic levels (affecting tawny owls or weasels) and lower trophic levels through increases in seed predation.

Regarding the lower trophic level, increased mouse density can enhance seed predation and removal (Zwolak et al. 2010), reducing seed availability and the number of caches leading to more efficient cache management and reducing overall seed germination (Jansen et al. 2004). Seed dispersal distance is also expected to be reduced (Vander Wall 2002; Li and Zhang 2007), potentially reducing forest recolonization and regeneration (Stapanian and Smith 1978).

The increase in mouse density potentially affects the upper trophic level by making more biomass available to predators under *Rhododendron*. The predators concerned are most likely specialists such as weasels that can easily reach the entire mouse population and whose populations' reproductive output is strongly tied to rodent abundance (King 1985; Buesching et al. 2010). However, the potential effect on weasel numbers calls for more research as it depends critically on the percentage of ground area occupied by *Rhododendron* estimated at a meaningful scale to a breeding weasel population, that is, hundreds of hectares. Thus, the increased spread of *Rhododendron* in the UK and its effects on other species can vary from minor to substantial, leading to changes in food web architecture (Gratton and Denno 2006), not just restructuring the flora (where the most work has been done) but also the fauna.

In conclusion, we have shown that by reducing aerial predation risk, an invasive can have direct positive effects on native rodent abundance. Competition for *Rhododendron*-covered areas leads to habitat segregation between age classes in

spring. *Rhododendron*-driven increase in rodents could lead to increases or decreases in other species within the community. These effects can be substantial, ranging from the alteration of competitive interactions between other species to the direction of succession and the spread of disease. However, with careful monitoring of the demography of potentially affected species, it is possible to both quantify the direction and magnitude of the effects of an invasive and then use these insights to link together published studies in order to make predictions about the indirect consequences of invasion on an ecosystem.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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