Does enemy loss cause release? A biogeographical comparison of parasitoid effects on an introduced insect

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Abstract. The loss of natural enemies is a key feature of species introductions and is assumed to facilitate the increased success of species in new locales (enemy release hypothesis; ERH). The ERH is rarely tested experimentally, however, and is often assumed from observations of enemy loss. We provide a rigorous test of the link between enemy loss and enemy release by conducting observational surveys and an in situ parasitoid exclusion experiment in multiple locations in the native and introduced ranges of a gall-forming insect, *Neuroterus saltatorius*, which was introduced poleward, within North America. Observational surveys revealed that the gall-former experienced increased demographic success and lower parasitoid attack in the introduced range. Also, a different composition of parasitoids attacked the gall-former in the introduced range. These observational results show that enemies were lost and provide support for the ERH. Experimental results, however, revealed that, while some enemy release occurred, it was not the sole driver of demographic success. This was because background mortality in the absence of enemies was higher in the native range than in the introduced range, suggesting that factors other than parasitoids limit the species in its native range and contribute to its success in its introduced range. Our study demonstrates the importance of measuring the effect of enemies in the context of other community interactions in both ranges to understand what factors cause the increased demographic success of introduced species. This case also highlights that species can experience very different dynamics when introduced into ecologically similar communities.

Key words: cynipid; enemy release hypothesis; exclusion experiment; gall-former; intra-continental introduction; invasion success; native and introduced range; Neuroterus saltatorius; *parasitoids.*

INTRODUCTION

Species' distributions are changing as they are transported around the globe and shift in response to climate change (Vitousek et al. 1997, Parmesan and Yohe 2003). Interacting species are not likely to move in concert; consequently, they are creating novel and altered community associations (Parmesan and Yohe 2003, Pelini et al. 2009, Hellmann et al. 2012). The loss of natural enemies, for example, has been demonstrated for introduced species and species moving in response to climate change (e.g., Cornell and Hawkins 1993, Mitchell and Power 2003, Torchin et al. 2003, Menéndez et al. 2008, Phillips et al. 2010). Enemy loss and release from enemy control is a key hypothesis to explain the increased demographic success or fitness of species in new locales: enemy release hypothesis (ERH; Elton 1958, Keane and Crawley 2002, Shea and Chesson 2002, Colautti et al. 2004).

Most evidence for the ERH comes from observational studies that compare enemy richness, abundance, or attack rates between species' native and introduced ranges (Colautti et al. 2004, Prior and Hellmann, *in press*). Most cases document a reduction in enemy species or abundance, suggesting that losing enemies may be a common phenomenon for introduced species (Mitchell and Power 2003, Torchin et al. 2003). These observational surveys only address one aspect of the ERH: "enemy loss." Enemy loss will, however, not always translate into increased demographic success ("enemy release"); for example, if enemies do not limit species in their native range (an important assumption of the ERH; Maron and Vilá 2001, Keane and Crawley 2002, Colautti et al. 2004; e.g., MacDonald and Kotanen 2010, Williams et al. 2010). A more correct and complete way to test the ERH is to conduct in situ manipulative enemy exclusion experiments in both ranges to compare the effect of enemy communities on species' demographics in the context of other important interactions (i.e., "biogeographical experiments"; Colautti et al. 2004, Hierro et al. 2005; e.g., Callaway et al. 2004, DeWalt et al. 2004, Williams et al. 2010). The ERH predicts that the native enemy community has stronger effects on species performance in their native range compared to the enemy community in the

introduced range, suggesting that differences in enemy pressure are causing release (Appendix A).

Biogeographical experiments that test the ERH have largely been conducted in invasive plant systems (Colautti et al. 2004, Pyšek et al. 2008; Prior and Hellmann, *in press*). The ERH, however, is often cited as an explanation for the increased success of species in higher trophic levels (Colautti et al. 2004, Torchin and Mitchell 2004, Roy et al. 2011). Parasitoids, for example, are major mortality agents of phytophagous insects (e.g., Hassell 1980, Washburn and Cornell 1981) and release from parasitoid control is a common explanation for the increased success of insects in new locales (McClure 1986, Hicks et al. 2008, Menéndez et al. 2008, Roy et al. 2011). Many studies have found reduced parasitoid attack rates or changes in parasitoid community composition for insect species that have been introduced or have expanded into a new range (McClure 1986, Cornell and Hawkins 1993, Schönrogge et al. 1998, Gröbler and Lewis 2008, Menéndez et al. 2008). None of these studies, however, examined if enemy loss caused demographic release using experimental manipulations in both ranges. Given the lack of experimental studies in non-plant systems, citing the enemy release as a general explanation of increased demographic success for introduced species is premature.

Here, we examined the ERH for a phytophagous, gall-forming insect. *Neuroterus saltatorius* (Edwards) is an oak gall wasp (Hymenoptera: Cynipidae) that was introduced to southern Vancouver Island, British Columbia, Canada, ca. 1986 ("introduced range"; see Appendix B; Smith 1995, Duncan 1997). It naturally occurs from north Texas to mainland Washington, USA ("native range"). *Neuroterus saltatorius* occurs on a variety of white oak species in the southern portion of its range, but exclusively on *Quercus garryana* Dougl. *ex* Hook (Fagaceae) in the northern portion of its range, from Oregon, USA, to its introduced range on Vancouver Island. This species is "outbreaking" in its introduced range, in that it occurs in high densities on its host plant (Duncan 1997; see Plate 1). When densities are high, *N. saltatorius* causes foliar necrosis and affects native herbivores (Duncan 1997, MacDougall et al. 2010, Prior and Hellmann 2010). A community of parasitoid wasps (Hymenoptera: Chalcidoidea) attacks *N. saltatorius*, and are a major source of mortality for this species (Smith 1995, Duncan 1997). We examined if differences in parasitoid communities between the two ranges facilitates the demographic success of *N. saltatorius*.

The aim of this study was to provide a rigorous test of a key hypothesis for an introduced insect that is outbreaking in its introduced range. We took multiple approaches to examine the ERH. First, we conducted observational surveys in the native and introduced ranges to quantify the increased demographic success of the gall-former. Second, we conducted surveys of the parasitoid community to assess changes in parasitoid attack rates and parasitoid community composition. Finally, we conducted a parasitoid exclusion experiment at multiple sites in both ranges to compare the effects of the parasitoid community on gall-former demographics in the context of other interactions. As far as we know, this is the first examination of the ERH using a "biogeographical experimental" approach for an introduced animal species (Roy et al. 2011; Prior and Hellmann, *in press*).

MATERIALS AND METHODS

Study system

Neuroterus saltatorius has two generations: a sexual (gamic) generation that forms foliar cluster galls in the spring, and an asexual (agamic) generation that forms single spherical galls (1 mm) on the underside of leaves in mid-June (Smith 1995). The agamic generation can occur in high abundance and causes foliar necrosis (Duncan 1997, Prior and Hellmann 2010). Agamic galls drop from leaves from July through September with over 50% of galls dropping by mid-July. Adults overwinter in the leaf litter and emerge the following spring (Smith 1995). Parasitoid-caused mortality is low in the gamic generation and high in the agamic generation (Smith 1995). Thus, we focused on the agamic generation as this is where enemy release is most likely to occur. Mortality from other enemies such as other insects, vertebrates, and fungal endophytes are thought to be low relative to mortality caused by parasitoids (Liu 1991, Smith 1995, Duncan 1997).

Studies were conducted in one portion of the native range of *N. saltatorius*, in Southern Puget Sound, Washington, and in the introduced range on Vancouver Island, British Columbia (Appendix B). The Southern Puget Sound region contains the largest populations of *Q. garryana* and *N. saltatorius* in the closest proximity to the introduced range (K. M. Prior, *personal observation*). It is suspected that *N. saltatorius* was introduced via ferry traffic between the Puget Sound and Vancouver Island (Duncan 1997); thus, the sound likely contains populations that provided colonists for this introduction. A comparison of likely source populations and introduced populations, rather than over the entire range of a species, is appropriate for examining the ERH, as enemy control often happens at a more local level and not over the entire range of a species (Colautti et al. 2004). Studies were conducted at multiple study sites in both ranges. *Quercus garryana* is patchily distributed in Washington and British Columbia, and each study site consisted of a patch of *Q. garryana* that was isolated from other patches by natural forest, or anthropogenic barriers. Our nearest sites were 1.5 km apart, and sites were 12.9 km apart on average (Appendix B).

Observational surveys: gall-former and parasitoid surveys

Surveys were conducted over two years at four sites in the native range and at 8 (2007) and ten (2008) sites in

the introduced range. To see if *N. saltatorius* was experiencing increased demographic success, gall-former damage was assessed at each site by randomly surveying 150 (2007) and 90 (2008) trees and placing them into low-, moderate-, or high-damage categories (see Appendix B for details; Prior and Hellmann 2010).

To estimate enemy loss, we randomly collected 1200 (2007) and 1300 (2008) galls at each study site multiple times between late June and early September. Each gall was placed into a gelatin capsule and allowed to overwinter in a greenhouse set to southern Vancouver Island conditions. Parasitoid attack rates were calculated from the proportion of emerged parasitoids at each site. Half of the emerged parasitoids were identified to genus or species with the help of experts from Agriculture Canada (Ottawa, Ontario, Canada) to assess changes in parasitoid community composition (see Appendix B for details).

Parasitoid exclusion experiment

To experimentally examine the ERH, a parasitoid exclusion experiment was performed in 2008 at four sites in the native range and five sites in the introduced range (Appendix B). Variation in host plant and micro-environmental conditions were controlled for by deploying paired exclosure and control treatments on individual trees at sites ($n = 7$). This paired approach enabled us to examine the effect of parasitoids on gall-formers in the context of other potentially important interactions. Exclosure treatments consisted of fine mesh to prevent parasitoids access to developing galls, and controls consisted of coarse mesh that allowed parasitoids access (see Appendix B for details). Galls drop from leaves at the end of development and the ground may act as a refuge from tree-searching parasitoids (Askew and Shaw 1986, Smith 1995). We collected galls from catchments in cages after they dropped from leaves (end of August) so that the galls were exposed to parasitoids during the window of time when they were most likely to be attacked by parasitoids.

The fates of 100 galls from each treatment in each replicate were determined by opening up galls. Survivorship occurred if we found an adult female wasp in the gall. Wasps overwinter as adults (Smith 1995), so we assumed that individuals that failed to develop into adults by the spring may fail to successfully emerge. Gall-former mortality occurred if we found: an intact gall wasp larva (i.e., not desiccated), an intact gall wasp pupa, a parasitoid emergence hole, a parasitoid adult, an intact parasitoid larva, an intact parasitoid pupa, an empty gall, or a desiccated larva/pupa (could be a parasitoid or a gall wasp) (see Appendix B for details).

The ERH predicts that the effect of enemies on prey performance (i.e., gall-former survivorship) is higher in the native range and lower in the introduced range (Appendix A; Torchin and Mitchell 2004). Thus, a change in the effect of the parasitoid community is *causing* increased success. Enemy effects are defined as the effect of the parasitoid community on gall-former survivorship (ΔS) and were calculated as the difference in survivorship between paired exclosures and controls on each tree. The ERH predicts that $\Delta S_n > \Delta S_i$, where n represents the native range and i represents the introduced range. Any other pattern in enemy effects provides evidence against the ERH. Enemy effects were calculated in two ways: (1) absolute differences between paired exclosures and controls on trees, and (2) and differences between paired exclosures and controls relative to background survivorship (i.e., divided by survivorship in exclosure). The first metric (i.e., absolute difference) measures enemy effects in the context of alternative factors (e.g., host plant, environmental conditions); the second metric (i.e., relative difference) controls for alternative factors (see Appendix A for details).

Statistical analyses

A generalized linear model (GLM) with a quasi-binomial error distribution and a logit link function was conducted to see if the proportion of trees in the medium- and high-damage categories was different between ranges and years (see Appendix B for statistical details). A GLM was also conducted to test for differences in the proportion of galls attacked by parasitoids from parasitoid surveys between ranges and years (Crawley 2007). We ran a Mantel test to examine if parasitoid community composition was more similar in sites that were closer together (i.e., within ranges) than those that were further apart (i.e., between ranges; Smouse et al. 1986). We also conducted a principal-components analysis (PCA) on parasitoid abundance data to examine patterns in species composition among sites (see Appendix B for statistical details; Legendre and Gallagher 2001).

Linear mixed-effects models (LMMs) were conducted on ΔS with range as a fixed factor and site as a random factor nested within range (Zuur et al. 2009). Analyses were conducted using ΔS calculated both as absolute and relative differences in survivorship (Appendix A). Similar tests were conducted where we assumed that immature gall wasp stages had the potential to develop into adults and counted survivorship as adults and intact immature larvae and pupae. LMMs were also conducted on the absolute change in mortality due to parasitoids (ΔP; emergence holes and adults), parasitism including immature stages, and the change in mortality due to unknown factors (ΔU) including empty galls and desiccated larvae/pupae. Arcsine square-root transformations were conducted to normalize model residuals and equalize variances. Statistical tests were conducted in R version 2.12.0 (Appendix B; R Development Core Team 2010).

RESULTS

Observational surveys: gall-former and parasitoid surveys

A higher proportion of trees had moderate to high *N. saltatorius* damage at sites in the introduced range
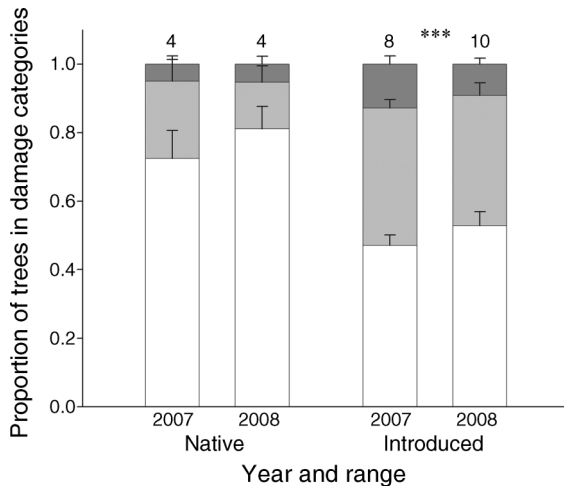
FIG. 1. Observational surveys of foliar damage caused by the gall-forming insect *Neuroterus saltatorius* in the native and introduced range in 2007 and 2008. Shown are the proportions of trees at sites in low (white), moderate (light gray), and high (dark gray) damage categories (mean + SE). Significant differences between groups (proportion of trees in moderate and high damage categories) are shown with asterisks. Sites are replicates, as presented above the bars.

*** $P < 0.001$.

compared to the native range (generalized linear model [GLM], $F_{1,26} = 28.77$, $P < 0.0001$; Fig. 1). There was no difference in damage between years ($F_{1,25} = 1.85$, $P = 0.1864$) and no interaction between range and year ($F_{1,24} = 0.05$, $P = 0.8323$). The proportion of galls parasitized was higher in the native range than in the introduced range ($F_{1,25} = 7.56$, $P = 0.0114$), and higher in 2007 than in 2008 ($F_{1,24} = 8.28$, $P = 0.0085$; Fig. 2), but there was no interaction between range and year ($F_{1,23} = 0.02$, $P = 0.8725$).

Seven species of parasitoids and one inquiline emerged from the collection of galls (Appendix C). All species were found in both ranges, except for the inquiline, *Synergus* sp., that was only found at site NA4 (NA represents native site) and *Mesopolobus* sp. that was only found at site IN10 (IN represents introduced site). *Aprostocetus pattersonae* (Fullaway) was the most abundant species in both ranges, accounting for 57% of overall parasitism. *Amphidocius schickae* (Heydon and Boucek), *Aprostocetus* n. sp., *Aprostocetus* sp., *Aprostocetus verrucarii* (Balduf), *Brasema* sp., and *Aprostocetus verrucarii* (Balduf) were reared from galls from both ranges and accounted for 2–13% of total parasitism.

There was a relationship between community composition and distance between sites (Mantel test, $r = 0.3269$, $P = 0.0195$), suggesting that parasitoid communities are more similar at sites that are closer together. A principal-components analysis (PCA) revealed patterns in the parasitoid community among sites. PC1 accounted for 52% of the variance of all the components and was driven by changes in *Brasema* sp. (-0.75) and

Aprostocetus sp. (0.59; Fig. 3). PC2 accounted for 28% of the variance in the components and was driven by changes in *A. pattersonae* (0.56), *Brasema* sp. (-0.51), *Aprostocetus* n. sp. (-0.45), and *Aprotocetus* sp. (-0.41). Sites in the native and introduced range did not overlap with respect to PC1 (Fig. 3).

Parasitoid exclusion experiment

The ERH predicts higher enemy effects on gall-former survivorship in the native range compared to the introduced range ($\Delta S_n > \Delta S_i$; Appendix A). We found that enemy effects calculated as absolute differences in survivorship were higher in the introduced range compared to the native range ($\Delta S_n < \Delta S_i$; linear mixed model [LMM], $t_6 = -15.35$, $P < 0.0001$; Fig. 4). This was a regional phenomenon as site explained a small amount of variation (standard deviation $[\hat{d}] = 0.04$) and was not retained in the final model (likelihood ratio [LR] = 0.92, $P = 0.1681$). Although survivorship was low in the controls in both ranges, survivorship increased by a factor of 5.9 between controls in the native range and the introduced range (Fig. 5). Survivorship also increased by a factor of 4.4 between exclosures in the native range and in the introduced range. This difference in survivorship between the exclosures contributed to higher enemy effects (ΔS) in the introduced range. Enemy effects calculated as relative differences in survivorship were higher in the native range compared to the introduced range ($t_6 = 2.23$, $P = 0.0322$; Appendix A).

One reason for gall-former mortality was that many individuals failed to mature into adults (i.e., intact gall-former larvae were found in galls). Taking a more conservative approach, if we assume that these individ-
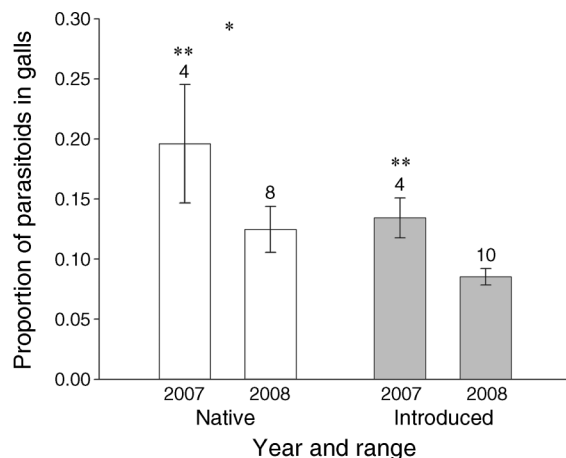

FIG. 2. Observational surveys of parasitoid attack rates of *Neuroterus saltatorious* in the native and introduced range in 2007 and 2008. Shown is the proportion of parasitoids found in galls at sites in the native (white) and introduced (gray) ranges (mean ± SE). Significant difference between groups is shown with asterisks. Sites are replicates as presented above the bars.
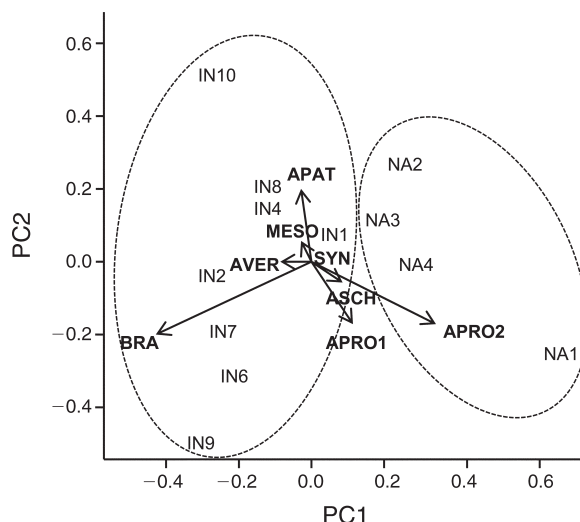
* $P < 0.05$; ** $P < 0.01$.

FIG. 3. Correlation bi-plot of the first and second axes of the principal-components analysis of parasitoid species abundance data. PC1 explains 52% of the variation, and PC2 explains 28%. Sites are represented by site names (IN, introduced; NA, native), and arrows represent parasitoid species: APAT, *Aprostocetus pattersonae*; APRO1, *Aprostocetus* n. sp.; APRO2, *Aprostocetus* sp.; ASCH, *Amphidocius schickae*; AVER, *Aprostocetus verrucarii*; BRA, *Brasema* sp.; MESO, *Mesopolobus* sp.; SYN, *Synergus* sp. Sites in the native and introduced range are circled and do not overlap with respect to PC1.

uals have the potential to eventually develop into adults, enemy effects were still stronger in the introduced range ($t_6 = -8.34$, $P < 0.0001$; Fig. 5). Site explained a small amount of variation ($\hat{d} = 2.36 \times 10^{-6}$) and was not included in the final model (LR = 2.44×10^{-9}, $P = 0.5$). Twenty percent more individuals failed to fully develop into adults in the exclosures in the native range, compared to the introduced range.

Gall-former mortality also resulted from parasitoid attack in controls. The difference in gall-former mortality due to adult parasitoids (ΔP) was higher in the native range compared to the introduced range ($\Delta P_n > \Delta P_i$; $t_6 = 2.87$, $P = 0.0067$). However, there were no differences between ranges when we included immature (undeveloped) parasitoids (larva and pupa) in the analysis ($t_6 = 1.67$, $P = 0.1033$; Fig. 5). Site explained little variation in both cases and was removed from the final models (parasitoid adults and emergence holes, $\hat{d} = 0.04$, LR = 0.38, $P = 0.2682$; including immature parasitoids, $\hat{d} = 4.5 \times 10^{-6}$, LR = 2.16×10^{-9}, $P = 0.5$). We found similar decreases in parasitoid attack rates from the native to introduced range in our surveys and experiment (survey 2007 = 29%, 2008 = 33%; experiment = 30%; Figs. 2 and 5); however, overall parasitoid attack rates were higher in the experiment because galls were exposed to parasitoids for a longer period of time (Appendix B).

Gall-former mortality also occurred due to unknown factors, i.e., empty galls or desiccated immature wasps (could be gall wasps or parasitoids). There was a larger

difference in unknown mortality ($\Delta U_n < \Delta U_i$) in the introduced range compared to the native range ($t_6 = -7.08$, $P < 0.0001$), with site explaining a small amount of variation ($\hat{d} = 1.60 \times 10^{-6}$, LR = 5.72×10^{-10}, $P = 0.5$; Fig. 5).

DISCUSSION

Our observational results provide evidence for increased demographic success and enemy loss, but experimental results suggest that factors other than enemies also contribute to this species increased success. Contrary to predictions of the ERH, absolute differences in enemy effects were higher in the introduced range because there was higher background mortality (i.e., in the absence of enemies) in the native range (Fig. 5). *Neuroterus saltatorius* experienced demographic release in the introduced range as survivorship in the controls increased by a factor of 5.9. This release, however, was likely driven by factors other than enemies because we also detected an increase in survivorship by a factor of 4.4 in the absence of enemies. Our results were consistent among sites within ranges suggesting that some factor(s) other than parasitoids, operating at the range level, is limiting this species in its native range and contributing to its increased success in its introduced range. Greater absolute enemy effects on gall wasp survivorship in the introduced range could reflect a release from an alternative limiting factor in the native range and a switch to enemy limitation in the introduced range

How we calculated enemy effects provides alternative interpretations for our results. Enemy effects calculated as the relative difference in survivorship between
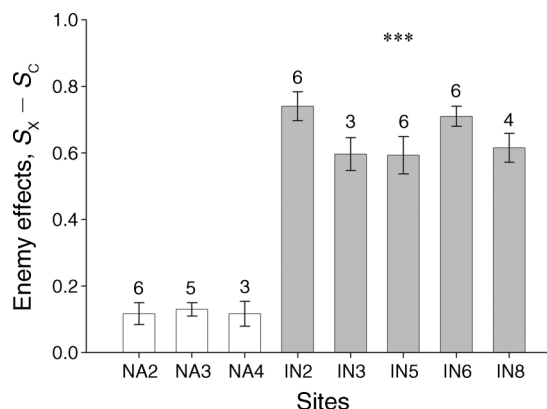

FIG. 4. Enemy effects (absolute differences) on the survivorship of *Neuroterus saltatorius* from the parasitoid-exclusion experiment in the native (NA) and introduced (IN) range. Shown are enemy effects on gall-former survivorship at sites in the native (white) and the introduced (gray) range (mean ± SEM). Enemy effects were measured as the mean difference in the number of gall-former adults found in galls between paired exclosures (X) and controls (C) on trees at a site (ΔS; Appendix A). Trees are replicates as presented above the bars. Significant difference between groups is shown with asterisks. Untransformed data are shown.
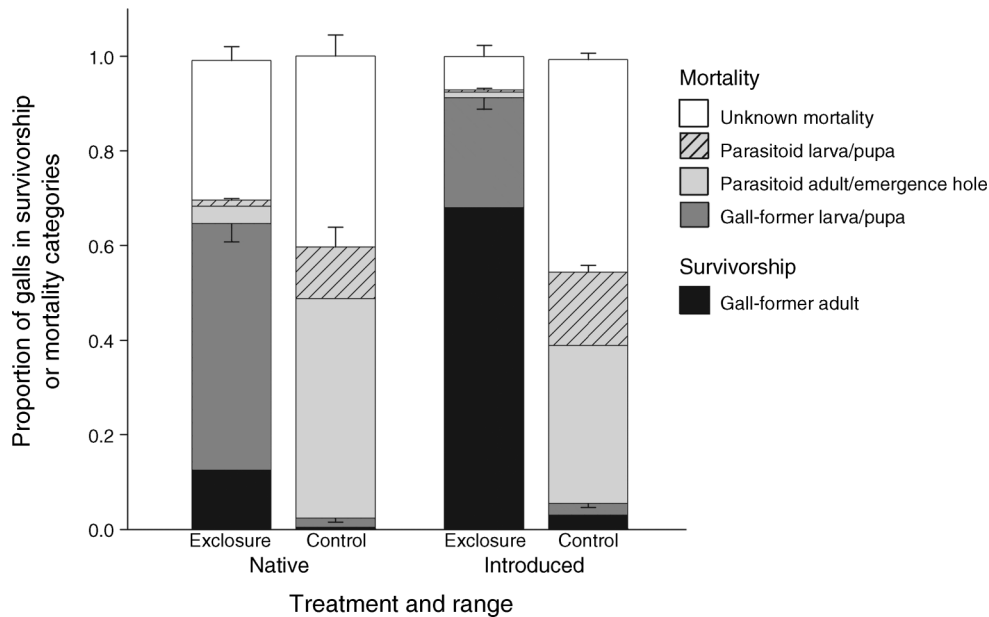*** $P < 0.001$.

FIG. 5. Proportion of *Neuroterus saltatorius* galls in survivorship and mortality categories from the parasitoid exclusion experiment. Shown are the mean proportions of galls in survivorship and mortality categories in controls and exclosures in both ranges. Survivorship occurred when adult gall-formers were found in galls. Survivorship was also analyzed including immature gall-formers. Mortality occurred when adult or immature parasitoids were found in galls or due to unknown mortality (i.e., unidentifiable tissue and empty galls). Error bars are standard error of the sum of all gall-formers (adults + immature stages), parasitoids (emergence holes + adults + immature stages), and unknown mortality. For clarity, only unidirectional error bars are shown. Sites are replicates (native, $n = 3$; introduced, $n = 5$).

treatments reflects how a change in the parasitoid community influences gall-former survivorship while controlling for background mortality due to alternative factors. This interpretation provides evidence in support of ERH as enemy effects were slightly higher in the native range than in the introduced range (Appendix A). These results, along with our observational results (Fig. 2), suggest that some enemy loss is occurring and contributing to increased survivorship. Enemy effects calculated as the absolute difference in survivorship between treatments is a measure of how a change in the effect of the parasitoid community influences gall-former survivorship in the context of other potentially important factors. This interpretation provides evidence against the ERH as enemy effects were higher in the introduced range than in the native range (Fig. 4). If alternative factors limit species in their native range, then enemy loss may contribute little to the success of an introduced species (Maron and Vilá 2001, Williams et al. 2010). Thus, estimating enemy effects in the context of other interactions is a more realistic and useful way to evaluate what factors cause a species increased success. Overall, we found lower parasitoid attack rates in the introduced range, yet parasitoids are not likely the primary driving factor causing demographic success. Other factors, such as host plant and environmental conditions, affect gall-former populations (e.g., Price and Hunter 2005), and our results suggest that changes in these or other factors between the two ranges

significantly contributes to the demographic success of *N. saltatorius*.

Mortality due to parasitoid attack accounted for 16% of the change in absolute enemy effects between the two ranges. Mortality due to larvae not developing into adults, and to unknown mortality accounted for 44% and 41% to the change in absolute enemy effects, respectively (Fig. 5). Unknown mortality could be a result of parasitoid-caused mortality or mortality due to other factors. In the absence of parasitoids, unknown mortality likely occurred due to alternative factors such as environmental or host plant conditions. Since patterns of unknown mortality were similar between treatments in the native range, we can assume that mortality in the controls could be caused by a similar factor causing unknown mortality in the exclosures. However, in the introduced range, unknown mortality occurred almost exclusively in the treatment exposed to parasitoids (Fig. 5). In this case, mortality could be caused by parasitoid attack that fails to produce viable offspring. Adult parasitoids can feed on hosts causing host mortality (Heimpel and Collier 1996). Also, failed parasitism attempts could cause mortality of both the host and the parasitoid. Failed parasitism attempts could occur more frequently in the introduced range if parasitoid populations are not adapted to attacking novel hosts due to morphological or physiological incompatibilities, host–parasitoid phenological mis-

PLATE 1. (Upper) Agamic galls of *Neuroterus saltatorius* on its host plant, *Quercus garryana*, in its introduced range on Vancouver Island, British Columbia, Canada. (Lower) *Aprostocetus pattersonae* is the most abundant parasitoid species that attacks *N. saltatorius* in both ranges. Gall diameter is 1 mm. Photo credits: K. M. Prior.

matches, or altered parasitoid–parasitoid interactions (McClure 1986, van Nouhuys and Tay 2001).

If unknown mortality is a result of parasitoid-caused mortality, than we are likely underestimating the total effects of parasitoids on gall-former survivorship. This is especially likely for controls in the introduced range where mortality cannot be explained by other factors. This supports our interpretation of rejecting the ERH as it provides an explanation for how enemy effects may be higher in the introduced range than in the native range. Estimating parasitoid attack by counting healthy parasitoids is not a precise way to estimate the actual effect of parasitoids on mortality given that parasitoids may induce host mortality without producing viable offspring (van Driesche et al. 1991, Heimpel and Collier 1996). We also found a higher proportion of immature parasitoids in the introduced range (Fig. 5). Perhaps a greater proportion of parasitoids in the introduced range failed to fully develop into adults because they were not well adapted to the novel host.

While parasitism rates were lower in the introduced range, this was not caused by a loss of parasitoid species, but rather lower attack rates of the most abundant parasitoid, *A. pattersonae*. The majority of parasitoids attacking *N. saltatorius* in the introduced range have been reared from alternative cynipid hosts (Smith 1995).

Host-switching is common in parasitoid communities (Menéndez et al. 2008, Nicholls et al. 2010), and many of the species attacking *N. saltatorius* on the island may have switched from these alternative hosts. Despite the large overlap in the number of parasitoid species between ranges, we found evidence for enemy loss because parasitoid attack rates were lower in the introduced range. Populations of enemies that have co-evolved with other species of gall-formers in the introduced range may be adapted to alternative hosts, precluding them from effectively attacking *N. saltatorius* (Vos and Vet 2004, Thompson 2005). Host-switching by populations of enemies that are not well adapted to attacking novel hosts could be a common feature for species undergoing short-distance introductions or range expansions where there may be large overlaps in enemy species (e.g., Menéndez et al. 2008).

Neuroterus saltatorius experienced demographic release in the introduced range, yet, despite some amount of enemy, loss we have evidence that alternative factors contributes to its demographic success. One question is how the contribution of these limiting factors and the release we detected translates into long-term population growth of this species. An increase in survivorship by a factor of 5.9 could have large implications for the trajectories of these populations. We know little about other vital rates in both populations of this species. We do know that survivorship is high in the second generation compared to the first generation (Smith 1995); thus, we could assume that the differences in survivorship that we detected could translate into large differences in population growth. Additionally, we know little about birth rates; however, if factors such as host plant conditions are more suitable in the introduced range, we may also expect these populations to have higher birth rates. This would support our interpretation that enemies alone may not drive demographic success. Ideally, long-term observations and experimental studies of both generations in both ranges could be conducted to parameterize full demographic models for each case. Comparisons between these models would be the most complete way to study the relationship between community interactions and demographic success in this species (e.g., Williams et al. 2010). However, arriving at such a comprehensive understanding of the forces affecting the dynamics of particular insect populations often may not be feasible (i.e., Murdoch 1994).

Many other factors could be causing higher background mortality in the native range compared to the introduced range. Abiotic factors, for example, could be driving this difference; however, we found that abiotic conditions were similar between ranges being slightly warmer in the native range (opposite of what we would expect, given that fitness was higher in the introduced range). Pathogens could also be important and cause differences between the two ranges. However, previous studies have found that endophytes likely do not cause mortality in *N. saltatorius* (Liu 1991, Wilson and Carroll 1997), and we found no evidence of hyphae inside intact galls. We cannot rule out the effect of entomopathogens, however. We do have multiple lines of evidence to suggest that differences in host plant conditions may play an important role. Gall-formers have intimate relationships with their host plants (Stone et al. 2002), and native populations of oaks may be more resistant to gall-formers. We observed higher levels of background mortality and slow or incomplete gall-former development in the native range (Fig. 5). Also, gall-formers were more patchily distributed among trees (i.e., fewer high-damage trees, surrounded by more low-damage trees), within sites in the native range (Fig. 1). Finally, we found high failed gall development on leaves in the native range (Appendix D). Higher host plant suitability in the introduced range could be a result of host plants having decreased defenses at higher latitudes (Rasmann and Agrawal 2011). Genotypic diversity of *Q. garryana* is also lower on the island compared to the mainland (Marsico et al. 2009). Thus, missing resistant genotypes or a more homogenous resource base could be facilitating this species increased success. Recent studies have found that host plant naiveté can facilitate invasion success in phytophagous insects (Desurmont et al. 2011, Woodward et al. 2012), and examining the role of host plants (and their interactions with parasitoids) in this system would be a promising avenue for future research.

Increased demographic success could also result from more complex processes such as interactions among multiple factors, including enemies. For example, phenology plays an important role in gall-former systems (Egan and Ott 2007), and we observed that gall-former phenology was different between the ranges. Galls drop from leaves earlier in the introduced range, with peak gall drop occurring in mid-July, compared to the native range where galls often stay on the trees for a longer period of time (Rosenthal and Koehler 1971, Smith 1995). This increased development time could be a result of higher host plant suitability or differences in abiotic conditions on the island. The ground could act as a refuge from tree-searching parasitoids (Askew and Shaw 1986). High background survivorship in the absence of enemies, faster gall development time, and the ground acting as a refuge from parasitoids could all be contributing to gall-former success and examining these multiple, interacting factors is a promising avenue for future research.

The relatively short-distance, poleward nature of this introduction is analogous in many ways to species' range change under climate change. Specifically, species that undergo short-distance or intra-continental introductions and climate-driven range expansions will likely move into more similar habitats and experience relatively large overlaps in interacting community members. This contrasts with intercontinental or long-distance introductions, where species are often introduced into very different communities (Engelkes et al. 2008, Mueller and Hellmann 2008). Our study suggests that species moved

over short distances have the potential to experience different dynamics in their new range, even when they are introduced into communities with similar species.

The ERH is a popular explanation for species' increased success in new locales (Keane and Crawley 2002). However, evidence in most cases remains observational. Our observational results suggest enemy loss, yet our experimental results reveal a more complicated explanation for the demographic success of *N. saltatorius* than simply enemy release. Future studies should strive to manipulate multiple important factors in both ranges to determine what causes the increased success of species in new locales (e.g., Williams et al. 2010). Importantly, our study illustrates that caution should be taken when interpreting cases of increased demographic success using observations of enemy loss.

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SUPPLEMENTAL MATERIAL

Appendix A

Calculating enemy effects and predictions of the enemy release hypothesis, ERH (*Ecological Archives* E094-090-A1).

Appendix B

Detailed methods of observational surveys, exclusion experiment, and statistical analyses (*Ecological Archives* E094-090-A2).

Appendix C

Parasitoid community details (*Ecological Archives* E094-090-A3)

Appendix D

Picture of failed galls of *Neuroterus saltatorius* (*Ecological Archives* E094-090-A4).