Biol Invasions (2016) 18:1769–1780
DOI 10.1007/s10530-016-1119-0

ORIGINAL PAPER

Rapid range expansion of an invasive predatory snail, *Oxychilus alliarius* (Miller 1822), and its impact on endemic Hawaiian land snails

Patrick A. Curry · Norine W. Yeung · Kenneth A. Hayes · Wallace M. Meyer III · Andrew D. Taylor · Robert H. Cowie

Received: 9 November 2015 / Accepted: 10 March 2016 / Published online: 18 April 2016

Abstract The invasive predatory snail *Oxychilus alliarius* is established in many locations around the world including the Hawaiian Islands. Anecdotal evidence suggests that it negatively impacts indigenous snail species where it has been introduced, although such impacts have not been quantified. On the Hawaiian island of Oahu, we tested the hypothesis that indigenous snails, especially small ones (<3 mm in maximum dimension), would be less abundant where *O. alliarius* had established populations. Fifty-six sites at four locations were repeatedly surveyed for snails between July 2010 and April 2011. The composition of the snail fauna differed in relation to *O. alliarius* abundance, as well as location. Notably, the abundance of the native Succineidae was negatively related with that of *O. alliarius*. The abundance of the native Tornatellidinae was significantly related to *O. alliarius* abundance but this relationship differed among locations, negative at one site and positive at the other three; these snails do not appear to be negatively impacted by *O. alliarius*. We also monitored the rate of expansion of a newly introduced *O. alliarius* population along a transect through a bog on the summit of Oahu's highest mountain, Mt. Kaala. The population's range expanded linearly between 2008 and 2011 by approximately 300 m (mean c. 113 m/year). This is the first attempt to quantify the impacts of *O. alliarius* on threatened native island snail faunas. While the results are complex, its high abundance, rapid rate of population expansion and probable negative impacts on certain species caution vigilance in preventing its introduction and spread to as yet uninvaded islands and locations.

Keywords *Oxychilus alliarius* · Hawaiian Islands · Invasive · Succineidae · Predation · Snails

P. A. Curry (✉) · N. W. Yeung · K. A. Hayes · R. H. Cowie
Pacific Biosciences Research Center, University of Hawaii, 3050 Maile Way, Gilmore 408, Honolulu, HI 96822, USA
e-mail: currypat1985@gmail.com

P. A. Curry · A. D. Taylor
Department of Biology, University of Hawaii, 2538 McCarthy Mall, Honolulu, HI 96822, USA

N. W. Yeung
Bishop Museum, 1525 Bernice Street, Honolulu, HI 96817, USA

K. A. Hayes
Department of Biology, Howard University, 415 College Street NW, Washington, DC 20059, USA

W. M. Meyer III
Bernard Field Station, Department of Biology, Pomona College, 175 W. 6th Street, Claremont, CA 91711, USA

Introduction

The world is moving towards a state of biotic homogenization with often narrowly endemic species being replaced by species introduced widely by human activities (Olden et al. 2004; Rooney et al. 2007). These non-native species are becoming established over increasingly wider ranges, which has led to an increasing need to understand many aspects of their biology including their impacts on the indigenous species they encounter (McKinney and Lockwood 1999; Andersen et al. 2004). Oceanic island species are particularly susceptible to extinction, which is exacerbated by invading species, particularly those that are predatory (Fritts and Rodda 1998; Simberloff 2000; Reaser et al. 2007; Donlan and Wilcox 2008). The Hawaiian Islands in particular have seen major increases in species introductions over the last two centuries (Cox 1999), and although much conservation effort in Hawaii focuses on species listed as endangered or threatened, the numerous unlisted species receive much less attention but are affected by the same pressures. Conservation and restoration tend to focus on charismatic vertebrate species even though invertebrate biodiversity may be even more in need, as it probably experiences much greater losses (McKinney 1999; Régnier et al. 2009, 2015a, b; Zamin et al. 2010).

More land snails than any other invertebrate group are listed by IUCN (2015), notable among these being the achatinelline tree snails of the Hawaiian Islands and the partulid tree snails of other Pacific islands. Unfortunately these tree snails have suffered major extinctions, resulting from habitat destruction and predation by introduced species, including rats and the rosy wolf snail, *Euglandina rosea*. The rosy wolf snail was introduced in ill-conceived biological control programs directed at the previously introduced giant African snail, *Achatina fulica* (Cowie 1992, 2001a; Hadfield et al. 1993; Lydeard et al. 2004; Lee et al. 2009; Meyer and Cowie 2011; Sugiura et al. 2011), which itself will also prey on other land snails (Meyer et al. 2008). However, achatinellids and partulids represent only a small portion of the native terrestrial snail diversity of Pacific Islands (Lydeard et al. 2004). Many Pacific land snail species in diverse families are already extinct (Bouchet and Abdou 2001, 2003; Richling and Bouchet 2013; Sartori et al. 2013; Régnier et al. 2015b). In the Hawaiian Islands there were more than 750 native terrestrial snail species, over 99 % of them endemic (Cowie et al. 1995), yet it has been estimated that 65–90 % of them may already be extinct (Solem 1990; Cowie 2001b). In addition, 41 non-native land snail species have been considered established in the Hawaiian Islands (Cowie 1998; Cowie et al. 2008; Hayes et al. 2012; Christensen et al. 2012) but little is known of the ecology of most of these non-native snails.

Among these introduced species in the Hawaiian Islands, *Oxychilus alliarius* is a predatory snail that was accidentally introduced by at least 1937 (Cowie 1997, 1998) but that has received little attention. *Oxychilus alliarius* preys on native Hawaiian snails (Curry and Yeung 2013) and also feeds on other invertebrates and on non-animal foods (Barker and Efford 2004). It is now established in many parts of the world (Barker 1999; Giusti and Manganelli 2002; Herbert 2010) and is one of the most widespread species in the Hawaiian Islands (Hayes et al. 2012) extending over a wide elevational range (Meyer and Cowie 2010a). Anecdotal evidence suggests that where introduced it negatively affects indigenous snail populations (Severns 1984; Barker 1999), although no studies have quantified such impacts.

In this study we assessed the possible impacts of *O. alliarius* on indigenous snails at four locations on the island of Oahu, and monitored the spread of a population of *O. alliarius* on Oahu's highest mountain. We tested the hypothesis that indigenous snails would be less abundant where *O. alliarius* had established populations. Also, because *O. alliarius* preferentially consumed small snails in controlled experiments when given a choice (Meyer and Cowie 2010b), although it can feed on larger snails (Curry and Yeung 2013), we hypothesized that small snails (adults <3 mm in maximum dimension) in particular would be less abundant where *O. alliarius* was established and would decline as *O. alliarius* expanded its range.

Methods

Study locations

Oxychilus alliarius was first recorded on the island of Oahu, in the Waianae mountain range near Mokuleia, on August 4, 2008 (21°32′41″N, 158°11′41″W, Hayes et al. 2012). On September 3, 2008 it was recorded 6.5 km away in the bog at the summit of Mt. Kaala, the highest point on the island (21°30′30″N, 158°8′45″W). It was subsequently recorded at Palikea, in the same mountain range (21°24′49″N, 158°5′59″W) and in the

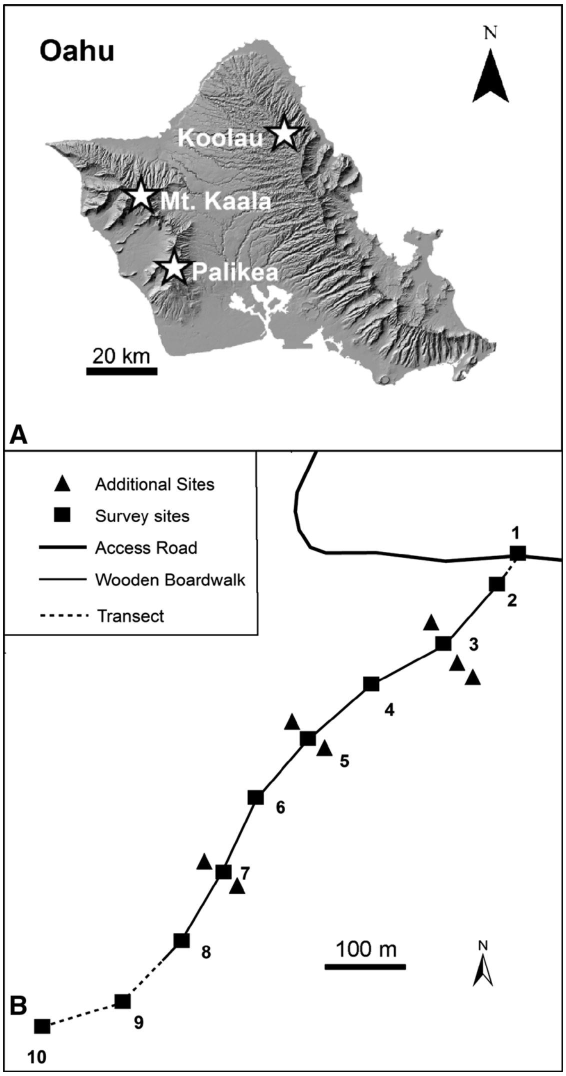

Fig. 1 **A** Locations of the four study locations on Oahu. The Mt. Kaala summit bog and Mt. Kaala northeast ridges locations are shown as a single star. **B** Map of the transect along the boardwalk at the summit of Mt. Kaala

northern Koolau mountain range (21°33′6″N, 157°55′6″W; Fig. 1A). We established four study locations: the Mt. Kaala summit bog, the ridges on the northeastern side of the Mt. Kaala summit, Palikea and the Koolau mountain location. These locations are dominated primarily by native Hawaiian vegetation, although Palikea has a larger proportion of non-native tree species than the other locations, for example it is the only location with Cook or Norfolk Island pines (*Araucaria* sp.), and is dominated by strawberry guava (*Psidium cattleyanum*). The understory of the Mt. Kaala bog and ridges locations and the Koolau location are dominated by non-native *Sphagnum* moss, while the understory at Palikea is dominated by a native fern species (*Dicranopteris linearis*).

Survey method

Replicated snail surveys were conducted at multiple sites at each location at different times of year from July 2010 to August 2011, as follows: Mt. Kaala bog, 10 sites each surveyed 9 times; Mt. Kaala ridges, 15 sites, 3 surveys each; Palikea, 14 sites, 5 surveys each; Koolau mountains 15 sites, 2 surveys each. At each site, all habitat types (under leaves, in ground level vegetation, in trees, under rocks, under bark, in leaf litter, etc.) available within an area of approximately 100 m^2 were searched for one person hour by two or more experienced snail biologists. Snail abundance data serve as an estimate of overall snail diversity at a site, and the standardized time and area searched allows us to compare site results without extrapolation.

We could not identify every specimen to a named species or morphospecies. The taxonomy of many groups of Hawaiian land snails is in serious need of revision and extensive field work and preliminary molecular analysis (Hayes and Yeung unpublished) has identified many cryptic species, as well as other undescribed species that exhibit significant morphological variation. Therefore, and as most identifications were done in the field to minimize the impacts on Hawaii's already severely threatened snail fauna, we identified snails to the lowest taxonomic level possible, based on shell morphology, and collected only vouchers of each taxon for preservation. The habits of species within many major Hawaiian land snail groups (genera, subfamilies, families) are often quite similar, such that Hawaiian land snail radiations are often suggested to be examples of non-adaptive radiation (e.g. Rundell and Price 2009). Thus, lumping taxa if we could not definitively distinguish them was appropriate, given the taxonomic and conservation status of the fauna.

We minimized the possible impact of disturbance associated with sampling on both habitat and snails by (1) limiting the number of specimens taken to just those needed for identification, (2) staying on the trails during the regular surveys, (3) taking care when we did go off the trails for supplemental surveys not to break the branches of trees and shrubs and to minimize trampling, and (4) being conscious of the possibility of inadvertently transporting snails between survey areas and taking measures to minimize this.

Statistical analysis

Sites were sampled on more than one occasion but the number of occasions differed among locations (see "Survey method"). However, preliminary analyses did not detect any seasonal trends in the abundance data. Therefore, all statistical tests were based on average abundances of each species at each site over the differing numbers of sampling occasions at each site. To investigate the hypothesis that land snail communities would be significantly different in areas with high ($\geq$10 *O. alliarius* recorded per person hour) and low (<1) average abundances of *O. alliarius* (referred to as the low and high groups), we used permutation-based hypothesis testing (ANOSIM) in the program PRIMER 6.1.15 (Clarke and Gorley 2006). Sites with intermediate average abundances were excluded from this analysis, allowing us to specifically test for differences in snail assemblages among sites with high and low *O. alliarius* densities. Prior to running the ANOSIM analysis, an abundance matrix of the snail species other than *O. alliarius* by sample was assembled for the four locations and the abundances (number recorded per person hour) were square root transformed to meet the variance assumptions of the analysis. Because native snail interaction with *O. alliarius* was the focus of this study, we did not include analysis of the low numbers of other non-native species recorded. Also, because they were not recorded at every location and were not found frequently we did not include the native *Achatinella* spp., Pupillidae and Helicinidae. Similarity matrices for each sampling location were created using the Bray-Curtis similarity coefficient. This method is preferable to using Euclidean distances for analyses with multiple variables using different scales of measurement or with large inter-sample differences (Legendre and Legendre 2012). Because we expected differences in land snail communities among the four sampling locations, we used a two-way crossed ANOSIM (999 permutations) with sampling location (blocks) and *O. alliarus* abundance (high and low) as a factor. The ANOSIM is a multivariate permutation analogue to a complete randomized block ANOVA. We report both the ANOSIM test statistic (R values) and the permutation based *P* values for the *O. alliarius* abundance factor. The R statistics are the average rank dissimilarities among and within groups, scaled so that R values vary between roughly 0 and 1 (there may be some negative values). A global R-statistic of 0 indicates that there are no differences among treatments, and a value of 1 indicates that all dissimilarities between samples in different treatments are larger than the average dissimilarity among samples within each treatment (Clarke 1993). The *P* values indicate whether R statistics differ significantly from zero (i.e. that there are significant differences among treatments).

We also used PRIMER to run a similarity percentage analysis (SIMPER) to determine the relative contributions of the various species to the dissimilarity between the high and low groups. The SIMPER analysis had a two-way crossed design using both *O. alliarius* average abundance and sampling location as factors. We report the species that had the largest influence on the dissimilarity between the high and low groups averaged across all locations. The average abundance values reported for the SIMPER analysis are back transformed from the square root abundances used in the ANOSIM.

We ran linear regressions to further investigate relationships between *O. alliarius* and specific native snail taxa. The regressions used native snail average abundances at each site as the dependent variable, and *O. alliarius* average abundance at each site and site location as the independent variables. We also tested for interactions between *O. alliarius* abundance and site location in the regressions. We used the Breusch-Pagan test in the R lmtest package (Zeileis and Hothorn 2002) to look for unequal variances in abundance of each native snail taxon at sites with different *O. alliarius* abundances. Finally we looked at snail taxon proportions, which were calculated as the sum of the average abundances of each specific taxon divided by the sum of the average abundances of all taxa, and displayed as pie charts. We did this for each of the four locations. These tests and calculations were all run using R (R Core Team 2014).

Oxychilus alliarius range expansion

At the Mt. Kaala summit bog, additional monthly surveys were conducted from May 2010 to May 2011 to record any changes in the extent of the *O. alliarius* population. The population was first discovered close to the summit access road and the surveys were conducted along the trail that runs through the bog from the access road, mostly along a boardwalk (Fig. 1B). These surveys focused solely on *O. alliarius*, aiming to determine the snail's contiguous range, which began at the access road and extended to the point along the boardwalk at which *O. alliarius* could no longer be found at consecutive sites 20 m (or 10 m, see below) apart. Surveys focused on the litter and on vegetation less than 1 m above the ground, and each covered approximately 100 m^2. Each one lasted 30 person minutes or until an *O. alliarius* specimen, live or shell, was found. On each occasion a new survey was carried out 20 m farther along the trail from the furthest point of the previously established extent of *O. alliarius*. If *O. alliarius* shells or live individuals were present 20 m past the previous established extent, an additional survey was carried out another 20 m along the trail, the process repeated until no *O. alliarius* specimens could be found. The surveyors then returned to the last point at which live snails had been found and performed a survey only 10 m farther along the transect. If shells but no live snails were found at this location, then the previous point was taken to represent the extent of the contiguous range of *O. alliarius*. This way the extent of the *O. alliarius* population's contiguous range was known to within 10 m. If an *O. alliarius* range extension survey coincided with one of the main faunal surveys (described above), the faunal survey served as the range extension survey. The combined experience of the field team, the back-tracking survey methodology, and the fact that *O. alliarius* is larger than many of the native snails that we can readily find in the kinds of habitats surveyed minimized the likelihood of false negatives (no *O. alliarius* found when in fact they were present). Thus, we do not think that false negatives impacted the essential story of range expansion. On occasion a live *O. alliarius* or empty shell was found hundreds of meters farther than had been previously recorded, and not as part of the contiguous range. These instances are presented and discussed below but were not considered as indicating the extent of the main population.

Seven supplementary sites 25 m away from the transect in a direction approximately perpendicular to it and on both sides of it adjacent to transect sites 3, 5 and 7 (Fig. 1B) were searched for *O. alliarius* in February and April 2011 to assess its possible range extension beyond the immediate proximity of the trail transect. An additional site 50 m south-east of transect site 3, in a direction perpendicular to the transect (Fig. 1B), was also surveyed, in February 2011. Surveys at these sites lasted 30 person minutes and covered the same area as the transect surveys.

Results

Impacts on native snails

The ANOSIM revealed a significant difference in community structure between high and low *O. alliarius* abundance groups ($P = 0.006$, global $R = 0.442$). There was also a significant difference in community structure among locations ($P = 0.001$, global $R = 0.53$).

The SIMPER analysis showed that relative abundances of most taxa were greater in the sites with low *O. alliarius* abundance. The dissimilarity between the low and high groups is ascribed primarily to just a few of the native snail species, with the Succineidae explaining the greatest amount of dissimilarity (21.1 %; Table 1). The overall average abundances for the high group and the low group, calculated from the abundances of each of the snail species, were 30.41 snails recorded per person hour and 109.71 snails recorded per person hour respectively, indicating that native snails were much less abundant in high *O. alliarius* abundance sites.

Oxychilus alliarius was the most common snail overall, accounting for approximately 28 % of all snails recorded. Although it was not the most common species at either the Mt. Kaala bog location (17 %) or the Koolau location (7 %), it made up 36 % of the snails at the Mt. Kaala ridge locations, and 56 % at Palikea (Fig. 2). Its highest mean abundance was at Palikea (284.60 snails recorded per person hour), followed by the Mt. Kaala ridges (108.58), Mt. Kaala bog (43.16) and Koolau (5.24) locations. The proportions of native species also varied widely by location. For example, Succineidae ranged from 3 to 31 % of the total at the Palikea and Koolau sites respectively, and Tornatellininae generally made up a substantial but variable proportion of the snails recorded (11–29 %; Fig. 2). The Mt. Kaala endemic, *Kaala subrutila*, made up approximately 5 % of the snails at the Mt. Kaala bog.

Table 1 Results of the SIMPER analysis showing the average square root abundances of each native snail species at the high and low *Oxychilus alliarius* abundance sites as well as the average dissimilarity, the average dissimilarity divided by the standard deviation, the percent contribution to the explanation of the dissimilarity between high and low *O. alliarius* abundance sites, and the cumulative percent contribution, beginning with the taxon that explained the most

Snail taxa	Average abundance (high)	Average abundance (low)	Average dissimilarity	Dissimilarity/ standard deviation	Contribution %
Succineidae	2.25	57.30	11.64	1.40	21.09
Tornatellininae	13.84	17.72	8.82	1.56	15.98
Tornatellidinae	8.58	7.13	5.95	1.63	10.78
Philonesia	2.13	14.90	5.05	1.40	9.16
Auriculellinae	1.59	8.76	4.06	1.07	7.35
Pacificellinae	1.19	2.02	2.46	1.17	4.46
Kaala subrutila	0.00	1.69	1.03	0.47	1.87
Total	29.58	109.52			

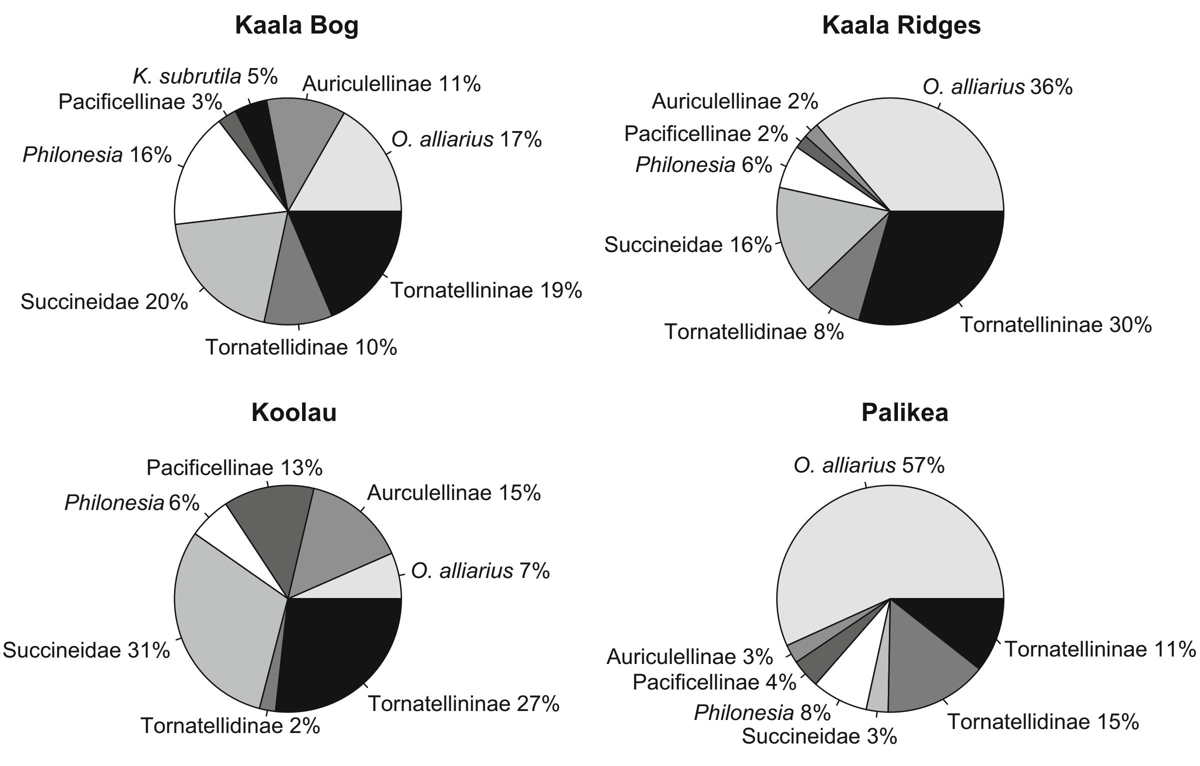

Fig. 2 Pie charts showing the proportions of each taxon recorded at each site. *Achatinella* spp., Pupillidae and Helicinidae are omitted because these taxa were not recorded at every location and were found extremely infrequently

Abundances of only two native snail taxa were significantly related to *O. alliarius* abundance. The abundance of the Succineidae (adults of which have a maximum dimension >3 mm) was significantly negatively related to *O. alliarius* abundance ($P = 0.000026$, $F = 21.37$; Fig. 3). For the Tornatellidinae (adult snails with maximum dimension <3 mm) there was a significant interaction between location and *O. alliarius* abundance ($P = 0.0046$, $F = 4.92$), with the slope of the relationship at the Mt. Kaala ridge site being negative and the slopes of the relationships at all other sites being positive (Fig. 4).

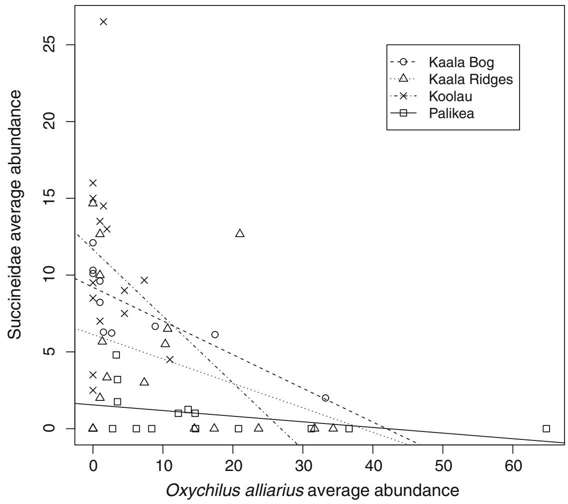

Fig. 3 Scatterplot showing the average abundance values for the Succineidae plotted against the square root average abundance values for *O. alliarius* at each of the sites. The lines are the calculated regressions at each of the four locations

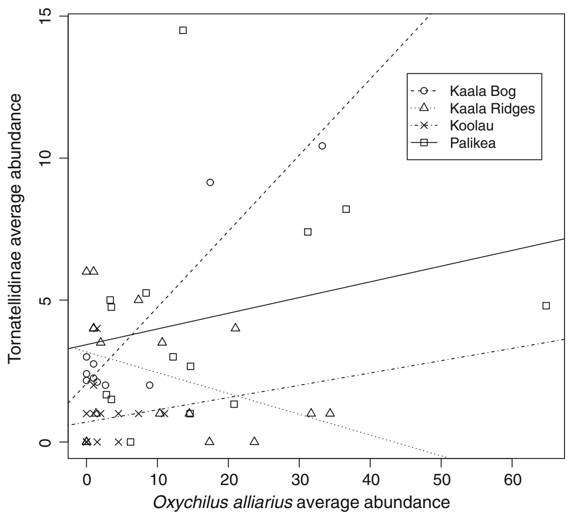

Fig. 4 Scatterplot showing the average abundance values for the Tornatellidinae plotted against the square root average abundance values for *O. alliarius* at each of the sites. The lines are the calculated regressions at each of the four locations

The proportion of the fauna composed of Tornatellidinae varied from 2 % at the Koolau location to 15 % at Palikea (Fig. 2), respectively the locations at which *O. alliarius* comprised the smallest and largest proportion of snails recorded. There are clear differences among the four locations in the proportions of the snails that make up the community (Fig. 2). At the Palikea and the Kaala ridges locations, where *O. alliarius* made up 56 and 36 % of the snails recorded, Succineidae, Auriculellinae and *Philonesia* (adult snails with maximum dimensions >3 mm) constituted smaller proportions of the fauna than at the Kaala bog and Koolau locations, where *O. alliarius* makes up just 17 and 7 % of the snails recorded. The Tornatellininae, another group of snails with adult sizes of less than 3 mm, were recorded in relatively high numbers at all sites (11–29 %), and were the most abundant native snail group overall. However, there were no significant relationships between Tornatellininae and *O. alliarius* abundances.

Range expansion

Oxychilus alliarius was first recorded on Oahu in September 2008 on the north-east side of the Mt. Kaala summit bog. Its population extended from the access road to approximately 70 m from the access road. Between the date of this first record and the end of the study in May 2011 (32 months) its population expanded approximately 300 m further from the access road (Table 2). The rate of expansion (average approximately 113 m/year) was not constant. Specifically, between September 2008 and December 2009 *O. alliarius* moved at approximately 12.7 m/month (152 m/year). Then between December 2009 and May 2010 there was no discernible range expansion. Subsequently, between November 2010 and February 2011 it expanded its range in jumps. At times the extent even seemed to contract, although these instances may have been sampling artifacts. On a few occasions shells and/or live *O. alliarius* were found in small numbers at locations far beyond the extent of the contiguous range, and up to 450 m beyond the access road (Table 2). Because these propagules were not part of the contiguous population they were excluded from assessments of population expansion.

Throughout the study, *O. alliarius* abundances were highest at sites 1 and 2, where the population was first recorded. Average abundance decreased sharply within the next 100 m, and nowhere during the year-long monitoring study did abundance reach the same level as close to the road. In February and April 2011 low levels of *O. alliarius* were recorded at the supplementary sites 25 m north-west and 25 and 50 m south-east of the transect at approximately

Table 2 Dates and distances of the *Oxychilus alliarius* range expansion along the transect running through the Mt. Kaala bog location

Date	Months since first record	Extent of contiguous range from access road (m)	Expansion of contiguous range since previous survey (m)	Distance of unconnected propagules from access road (m)
Sep 2008	0	70	–	–
Jun 2009	9	150	80	–
Dec 2009	15	200	50	–
May 2010	20	180	-20	450
Jun 2010	21	205	25	–
Jul 2010	22	195	-10	–
Aug 2010	23	200	5	270
Sep 2010	24	210	10	450
Oct 2010	25	210	0	–
Nov 2010	26	250	40	330, 350
Dec 2010	27	240	-10	350
Jan 2011	28	250	10	330
Feb 2011	29	330	80	–
Mar 2011	30	330	0	–
Apr 2011	31	360	30	–
May 2011	32	370	10	–

160 m from the access road. Similar surveys (25 m north-west and south-east of the transect) were conducted at approximately 360 and 560 m from the access road, but no *O. alliarius* were found.

Discussion

This study demonstrated differences in native snail communities among the four locations. Although these differences could be related to differences in *O. alliarius* abundances among the locations, it is also possible that they are related to the different ecological needs of the various snail taxa and reflect differences in, for example, vegetational composition and/or local climatological factors. Within locations, the abundances of the various native snail taxa were not related to that of *O. alliarius* in the same way. In particular, there were specific and different relationships between *O. alliarius* abundance and abundances of native Succineidae and Tornatellidinae. The study also demonstrated that a newly established *O. alliarius* population can expand at a rate of over 100 m/year, and that this expansion may happen intermittently.

We had hypothesized that succineid abundance would not be negatively related to *O. alliarius* abundance because of the relatively large size of adult succineids and the fact that in preference tests *O. alliarius* preferred prey <3 mm in maximum dimension (Meyer and Cowie 2010b). However, Succineidae abundance was negatively related to that of *O. alliarius*. Succineids were relatively common and lived not only in the trees and shrubs, but were also found in the leaf litter more frequently than most other taxa, such as the *Auriculella*, Tornatellidinae, and Tornatellininae. *Oxychilus alliarius*, which is primarily a ground dwelling species, would have encountered Succineidae more frequently than these groups, presumably increasing predation. We now know that *O. alliarius* will indeed prey on larger snails (Curry and Yeung 2013) and may have negative effects on these larger species. Many Hawaiian Succineidae are unable to fully retract their bodies into their shells, which may make them more susceptible to predation regardless of their size. *Oxychilus alliarius* also could have been preying on juvenile Succineidae. Meyer and Cowie (2010b) found that *O. alliarius* consumed juvenile Succineidae, which are less than 3 mm in maximum dimension during the first few months of their lives. It is possible that *O. alliarius* consumes these juveniles at high enough levels to influence the Succineidae population. Another possibility is that *O. alliarius* was consuming Succineidae egg masses. Multiple *Oxychilus* species, including *O. alliarius*, are snail egg predators (Baur 1988; Barker and Efford 2004), and Hawaiian Succineidae lay large egg masses both in the leaf litter and on the shrubs. However, in experiments, *O. alliarius* did not feed on succineid eggs (WMM, unpublished).

The relationships of Tornatellidinae abundance to that of *O. alliarius* (Fig. 4) differed among locations, being positive at the Palikea, Koolau mountains and Mt. Kaala bog locations, but negative at the Mt. Kaala ridges location. Tornatellidinae also had a higher overall average abundance at sites with high numbers of *O. alliarius* (Table 1). The relationship between *O. alliarius* and the Tornatellidinae did not conform to the hypothesis that abundances of smaller snails would be negatively related to *O. alliarius* abundance. However, the differences in the slopes of the relationships at the different sites make it difficult to draw any specific conclusions about potential impacts of *O. alliarius* on the Tornatellidinae. These Tornatellidinae are primarily found on plants and the lack of a clear pattern may be related to the generally different microhabitat/plant preferences of *O. alliarius* and Tornatellidinae such that they rarely encounter each other; or it could be that conditions are especially suitable for both taxa at some locations, but for only one or other at other locations. It is also possible that Tornatellidinae fecundity is high enough to withstand *O. alliarius* predation pressure. Such relationships may also explain the lack of correlations with other taxa, for example, the Tornatellininae whose high overall abundance showed no apparent relation to *O. alliarius* abundance.

Based on our intensive surveying within the Mt. Kaala Bog, we found that *Oxychilus alliarius* is rapidly colonizing new habitat on Mt. Kaala, the highest mountain on Oahu. The *O. alliarius* population is expanding out from the Kaala access road, at the northeast end of the study area, to the trail leading down the mountain on the southwest end of the study area. This indicates that the original colonizers probably came up the road on vehicles rather than being accidentally brought up to the bog by hikers accessing Mt. Kaala from the trail.

Overall, from September 2008 to May 2011, *O. alliarius* moved approximately 300 m, expanding its range along the transect at a rate of approximately 113 m/year. However, this rate was not constant (Table 2). In several instances one or a few snails were found distant from the main population. In May and September 2010 a single live *O. alliarius* individual was found far ahead of the main population (270 m from the main population in May), and shells were recorded at the same location in December 2010, which suggests that there was a small population at this location during 2010. One or a few snails probably established the population, but the snails did not survive long enough for the main population to extend contiguously to this point during the study. Additionally, from November 2010 through January 2011 we observed a small population of *O. alliarius* separated from the main contiguous population by approximately 100 m. By February 2011, expansion of both the contiguous range and the isolated population had closed the gap, resulting in a much-extended contiguous range. These instances suggest the possibility that propagules were accidentally transported along the boardwalk by either natural or unnatural events, rather than only by the snails' own active dispersal. However, it is possible that these individuals were actually part of the contiguous population. Nonetheless, given that no other individual, live or shell, was detected between these individuals and the contiguous population over the course of the entire study, we consider it reasonable not to consider these individuals to be part of the contiguous population. An alternative explanation of the patterns we observed is that *O. alliarius* was already well distributed in the bog at the start of the study and what we were detecting was foci of higher densities. However, in the supplementary surveys either side of the boardwalk we found *O. alliarius* only at sites close to the trail, and the fact that the presence of *O. alliarius* increased farther along the boardwalk trail through time, suggests that range expansion is the more parsimonious explanation.

Propagule transport could have happened accidentally by people, on clothes and footwear, perhaps as eggs in aggregate dirt clods, on construction materials used in maintenance of the boardwalk, or naturally during flooding. These mechanisms of spread may explain the occasional individuals found along the transect beyond the contiguous distribution at various times. While the boardwalk may have facilitated *O.*

alliarius expansion through the bog, it did allow surveys to be conducted with minimal damage to the native ecosystem, and it continues to allow hikers to move through the bog without trampling vegetation or causing erosion.

In February 2011 the contiguous range of *O. alliarius* extended approximately 330 m from the access road (Table 2), and by about April 2011 the contiguous range had reached site 5 (approximately 360 m from access road). *Oxychilus alliarius* was recorded at the sites to the northwest and southeast at approximately 160 m from the access road, but not at the supplemental sites to the northwest and southeast at 360 or 560 m from the access road. This indicates that the snail population had probably not expanded as far into the forest as it had along the trail, but that it was moving into the forest.

The Mt. Kaala endemic helicarionid, *Kaala subrutila*, was recorded almost exclusively in the leaf litter. At the Mt. Kaala bog, the only location where *K. subrutila* was recorded, live individuals were absent from sites where *O. alliarius* was already established at the beginning of the study. However, a *K. subrutila* shell was found within the range of the established *O. alliarius* population, indicating that previously its range probably extended at least this far. Generally the highest numbers of *K. subrutila* were found approximately 350 m from the access road. By the end of the study the *O. alliarius* population had extended to this site. At that time an *O. alliarius* was recorded consuming a *K. subrutila* in the field (Curry and Yeung 2013). While there was no significant relationship between overall abundance of Helicarionidae (probably because of low sample size) and that of *O. alliarius*, and we only observed range overlap of *K. subrutila* and *O. alliarius* at the end of the study, the status of this extremely narrow endemic snail in the face of expansion of *O. alliarius* into its extremely small remaining range should be carefully monitored.

Oxychilus alliarius may have impacted the native snails of other locations to which it has been introduced, including New Zealand (Barker 1999), South Africa (Herbert 2010), and various other places (Giusti and Manganelli 2002). Quarantine measures are important from regional to local scales (Cowie 2004). At local scales, specific preventative measures are the best ways to minimize its establishment and spread into other sensitive areas like Mt. Kaala, which is a designated nature reserve. Such measures include regularly brushing dirt and debris off boots and clothes, in designated areas, and cleaning equipment used for working in sensitive areas or transporting materials to and from them, especially out-plantings for ecological restoration. Effective management aimed at conserving the native land snail faunas, however, will require understanding of the ecology not only of *O. alliarius* but also of each of the native species potentially affected. In particular, ground dwelling snails seem to be at higher risk than arboreal snails. Knowing which species are most vulnerable will be important for the development of conservation plans.

Acknowledgments This study was funded in part by National Science Foundation Grant DEB-1120906 and a grant from the Oahu Army Natural Resources Program. We thank Jaynee Kim, Torsten Durkan, Dylan Ressler, Kelsey Coleman, David Sischo, Travis Skelton, Vincent Costello, and Stephanie Joe for help conducting field surveys, Chris Lepczyk for discussion, and the Division of Forestry and Wildlife and Natural Area Reserve System for permits.

References

Andersen MC, Adams H, Hope B, Powell M (2004) Risk analysis for invasive species: general framework and research needs. Risk Anal 24:893–900

Barker GM (1999) Fauna of New Zealand Ko te Aitanga Pepeke o Aotearoa Number 38. Naturalised terrestrial Stylommatophora (Mollusca: Gastropoda). Manaaki Whenua Press, Lincoln, Canterbury, New Zealand

Barker GM, Efford MG (2004) Predatory gastropods as natural enemies of terrestrial gastropods and other invertebrates. In: Barker GM (ed) Natural enemies of terrestrial molluscs. CABI Publishing, Wallingford, pp 279–403

Baur B (1988) Population regulation in the land snail *Arianta arbustorum*: density effects on adult size, clutch size and incidence of egg cannibalism. Oecologia 77:390–394

Bouchet P, Abdou A (2001) Recent extinct land snails (Euconulidae) from the Gambier Islands with remarkable apertural barriers. Pac Sci 55:121–127

Bouchet P, Abdou A (2003) Endemic land snails from the Pacific Islands and the museum record: documenting and dating the extinction of the terrestrial Assimineidae of the Gambier Islands. J Molluscan Stud 69:165–170

Christensen CC, Yeung NW, Hayes KA (2012) First records of *Paralaoma servilis* (Shuttleworth, 1852) (Gastropoda: Pulmonata: Punctidae) in the Hawaiian Islands. Bish Mus Occas Pap 112:3–7

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Clarke KR, Gorley RN (2006) Primer v6. User manual/tutorial. PRIMER-E, Plymouth

Cowie RH (1992) Evolution and extinction of Partulidae, endemic Pacific island land snails. Philos Trans R Soc B 335:167–197

Cowie RH (1997) Catalog and bibliography of the nonindigenous nonmarine snails and slugs of the Hawaiian Islands. Bish Mus Occas Pap 50:1–66

Cowie RH (1998) Patterns of introduction of non-indigenous non-marine snails and slugs in the Hawaiian Islands. Biodivers Conserv 7:349–368

Cowie RH (2001a) Can snails ever be effective and safe biocontrol agents? Int J Pest Manag 47:23–40

Cowie RH (2001b) Invertebrate invasions on Pacific Islands and the replacement of unique native faunas: a synthesis of the land and freshwater snails. Biol Invasions 3:119–136

Cowie RH (2004) Disappearing snails and alien invasions: the biodiversity/conservation interface in the Pacific. J Conchol Spec Publ 3:23–37

Cowie RH, Evenhuis NL, Christensen CC (1995) Catalog of the native land and freshwater molluscs of the Hawaiian Islands. Blackhuys Publishers, Leiden

Cowie RH, Hayes KA, Tran CT, Meyer WM III (2008) The horticultural industry as a vector of alien snails and slugs: widespread invasions in Hawaii. Int J Pest Manag 54:267–276

Cox GW (1999) Alien species in North America and Hawaii: impacts on natural ecosystems. Island Press, Washington

Curry PA, Yeung NW (2013) Predation on endemic Hawaiian land snails by the invasive snail *Oxychilus alliarius*. Biodivers Conserv 22:3165–3169

Donlan CJ, Wilcox C (2008) Diversity, invasive species and extinctions in insular ecosystems. J Appl Ecol 45:1114–1123

Fritts TH, Rodda GH (1998) The role of introduced species in the degredation of island ecosystems: a case history of Guam. Annu Rev Ecol Syst 29:113–140

Giusti F, Manganelli G (2002) Redescription of two west European *Oxychilus* species: *O. alliarius* (Miller, 1822) and *O. helveticus* (Blum, 1881), and notes on the systematics of *Oxychilus* Fitzinger, 1833 (Gastropoda: Pulmonata: Zonitidae*)*. J Conchol 37:455–476

Hadfield MG, Miller SE, Carwile AH (1993) The decimation of endemic Hawai'ian [sic] tree snails by alien predators. Am Zool 33:610–622

Hayes KA, Yeung NW, Kim JR, Cowie RH (2012) New records of alien Gastropoda in the Hawaiian Islands: 1996–2010. Bish Mus Occas Pap 112:21–28

Herbert DG (2010) The introduced terrestrial Mollusca of South Africa. South African National Biodiversity Institute, Pretoria

IUCN (International Union for the Conservation of Nature) (2015) The IUCN Red List of Threatened Species. Version 2015-3. www.iucnredlist.org. Downloaded on 25 September 2015

Lee T, Burch JB, Coote T, Pearce-Kelly P, Hickman C, Meyer JY, Ó Foighil D (2009) Moorean tree snail survival revisited: a multi-island genealogical perspective. BMC Evol Biol 9:204

Legendre P, Legendre LFJ (2012) Numerical ecology, 3rd English edn. Elsevier Science, Amsterdam

Lydeard C, Cowie RH, Ponder WF, Bogan AE, Bouchet P, Clark SA, Cummings KS, Frest TJ, Gargominy O, Herbert DG, Hershler R, Perez KE, Roth B, Seddon M, Strong EE, Thompson FG (2004) The global decline of non-marine mollusks. Bioscience 54:321–330

McKinney ML (1999) High rates of extinction and threat to poorly studied taxa. Conserv Biol 13:1273–1281

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

Meyer WM III, Cowie RH (2010a) Invasive temperate species are a threat to tropical island biodiversity. Biotropica 42:732–738

Meyer WM III, Cowie RH (2010b) Feeding preferences of two predatory snails introduced to Hawaii and their conservation implications. Malacologia 53:135–144

Meyer WM III, Cowie RH (2011) Distribution, movement, and microhabitat use of the introduced predatory snail *Euglandina rosea* in Hawaii: implications for management. Invertebr Biol 130:325–333

Meyer WM III, Hayes KA, Meyer AL (2008) Giant African snail, *Achatina fulica*, as a snail predator. Am Malacol Bull 24:117–119

Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. Trends Ecol Evol 19:18–24

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reaser JK, Meyerson LA, Cronk Q, De Poorter MJ, Eldrege LG, Green E, Kairo M, Latasi P, Mack RN, Mauremootoo J, O'Dowd D, Orapa W, Sastroutomo S, Saunders A, Shine C, Thrainsson S, Vaiutu L (2007) Ecological and socioeconomic impacts of invasive alien species in island ecosystems. Environ Conserv 34:98–111

Régnier C, Fontaine B, Bouchet P (2009) Not knowing, not recording, not listing: numerous unnoticed mollusk extinctions. Conserv Biol 23:1214–1221

Régnier C, Achaz G, Lambert A, Cowie RH, Bouchet P, Fontaine B (2015a) Mass extinction in poorly known taxa. Proc Natl Acad Sci 112:7761–7766

Régnier C, Bouchet P, Hayes KA, Yeung NW, Christensen CC, Chung DJD, Fontaine B, Cowie RH (2015b). Extinction in a hyperdiverse endemic Hawaiian land snail family and implications for the underestimation of invertebrate extinction. Conserv Biol 29:1715–1723

Richling I, Bouchet P (2013) A remarkable, mostly extinct radiation of minute snails (Gastropoda: Neritopsina: Helicinidae) on the Gambier Islands, French Polynesia. Biodivers Conserv 22:2433–2468

Rooney TP, Olden JD, Leach MK, Rogers DA (2007) Biotic homogenization and conservation prioritization. Biol Conserv 134:447–550

Rundell RJ, Price TD (2009) Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. Trends Ecol Evol 24:394–399

Sartori AF, Gargominy O, Fontaine B (2013) Anthropogenic extinction of Pacific land snails: a case study of Rurutu, French Polynesia, with description of eight new species of endodontids (Pulmonata). Zootaxa 3640:343–372

Severns M (1984) Another threat to Hawaii's endemics. Hawaii Shell News 32(1):9

Simberloff D (2000) Extinction-proneness of island species—causes and management implications. Raffles Bull Zool 48:1–9

Solem A (1990) How many Hawaiian land snail species are left? And what we can do for them. Bish Mus Occas Pap 30:27–40

Sugiura S, Holland BH, Cowie RH (2011) Predatory behavior of newly hatched *Euglandina rosea*. J Molluscan Stud 77:101–102

Zamin TJ, Baillie JEM, Miller RM, Rodríguez JP, Ardid A, Collen B (2010) National red listing beyond the 2010 target. Conserv Biol 24:1012–1020

Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. R News 2:7–10