Biol Invasions
https://doi.org/10.1007/s10530-019-01916-y

ORIGINAL PAPER

Non-native gastropods in high elevation horticultural facilities in Hawaii: a threat to native biodiversity

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Received: 29 August 2018 / Accepted: 7 January 2019

Abstract To preserve native floras and faunas of tropical oceanic islands, it is critical to limit the establishment of terrestrial non-native gastropods (i.e. snails, including slugs), particularly those from temperate regions, as they can become abundant in high elevation areas, often the last refuges of native species. In Hawaii, the horticultural trade has been associated with many introductions, but threats posed by nurseries at high elevations have not been assessed. To examine these potential threats, we surveyed gastropods in 21 high elevation (> 500 m) horticultural/agricultural facilities on three Hawaiian Islands (Oahu, Maui and Hawaii) and compared these surveys to 31 previous low elevation nursery surveys (< 500 m) on the same islands. High elevation nurseries harbored distinct non-native gastropod assemblages, which were composed primarily of species from temperate regions. Gastropods from temperate regions had larger elevation ranges in nurseries than those from tropical areas. Our results highlight that nurseries, particularly those at higher elevations, represent key sources for establishment of temperate gastropods, a critical threat to the remaining Hawaiian biodiversity. We also found that high elevation nurseries on Maui and Hawaii supported non-native species not found in Oahu nurseries, indicating that Oahu may not be the only source of introductions into high elevation nurseries. We hope these results will spur active control of non-native gastropods in nurseries, particularly those at higher elevations, to potentially prevent further ecological damage to the already imperiled Hawaiian flora and fauna.

Keywords Gastropoda · Snails · Conservation · Endangered species · Invasive species · Pacific islands

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Introduction

Limiting the establishment and spread of terrestrial non-native gastropod (i.e. snail and slug) species is of critical importance if we are to preserve the remaining floras and faunas of tropical oceanic islands (Joe and Daehler 2008; Meyer and Cowie 2010a). Terrestrial

Published online: 17 January 2019

gastropods, particularly those of oceanic islands, have suffered the highest number of recorded extinctions among major animal groups, driven primarily by anthropogenic impacts, including those of non-native species (Régnier et al. 2009, 2015; Chiba and Cowie 2016). Estimates of extinction rates in Hawaii range from 50 to 90% (Solem 1990; Lydeard et al. 2004; Yeung and Hayes 2018) and are probably similar across other Pacific islands. Invasive predatory snails, introduced accidently (i.e. *Oxychilus alliarius*) or intentionally (i.e. *Euglandina* spp.), have been implicated in the decline, extirpation and extinction of native terrestrial gastropod species throughout the Pacific (e.g. Hadfield 1986; Gerlach 2001; Coote and Loève 2003; Meyer and Cowie 2010a; Gargominy et al. 2011; Curry et al. 2016). Non-native terrestrial gastropods (e.g., *Limax maximus*, *Limacus flavus*, *Deroceras laeve*, *Veronicella cubensis*) have also been highlighted as an important factor contributing to plant endangerment (Joe and Daehler 2008; Shiels et al. 2014).

Not all non-native terrestrial gastropod species pose similar threats to tropical island biodiversity. Meyer and Cowie (2010b) suggested that gastropod species from temperate regions represent a greater threat to tropical island biodiversity than non-native species from tropical regions because: (1) non-native species from temperate regions occupy wide elevation ranges (in some cases sea level to high elevation forests) in Hawaii and are the most abundant species at higher elevations (> 500 m), and (2) higher elevation areas in Hawaii and most other tropical islands harbor a major proportion of the remaining native biodiversity (Loope and Giambelluca 1998; Benning et al. 2002; Rolett and Diamond 2004; Yeung and Hayes 2018). As these high elevation areas are often the last refuges for native species, preventing establishment of non-natives from temperate locales is of critical conservation importance.

The horticultural trade has been identified as a principal vector for the introduction of many non-native terrestrial gastropod species (Robinson 1999; Cowie and Robinson 2003; Horsák et al. 2004; Cowie et al. 2008; Bergey et al. 2014; McCullough et al. 2006). However, previous surveys in 2004–2006 (Hayes et al. 2007; Cowie et al. 2008) of gastropods in horticultural and small-scale agricultural facilities generally supplying produce directly to stores and restaurants (herein referred to as nurseries) across the six largest Hawaiian Islands assessed facilities only at low elevations (below 500 m in elevation). Examining the diversity and community structure of introduced gastropods in high elevation nurseries is a key step in understanding if these nurseries and the non-native species they harbor pose a serious threat to Hawaiian island biodiversity by increasing the probability of establishment of non-native terrestrial gastropod species from temperate regions.

The objectives of this study were therefore to: (1) determine if gastropod communities differ significantly between low (< 500 m) and high (> 500 m) elevation nurseries, (2) assess if temperate species are more likely to be found in high elevation nurseries, (3) determine if native region (temperate or tropical) can be used to predict species elevation ranges in nurseries, and (4) evaluate if species richness of non-native species is higher on Oahu, the main port of entry into the Hawaiian Islands (as predicted by Cowie et al. 2008). The results combined with those of Cowie et al. (2008) should provide a more holistic evaluation of the threats nurseries pose.

Materials and methods

Between October 2008 and April 2010, surveys of 21 nurseries above 500 m elevation on the three main Hawaiian Islands with high elevation nursery facilities, Oahu (1), Maui (14) and Hawaii (6), were completed. There is only one high elevation nursery on Oahu and we made efforts to comprehensively survey all high elevation nurseries on the other islands. The 500 m elevation cutoff for high versus low elevation nurseries was made based on previous studies that suggest habitats above 500 m tend to be less dominated by human impacts and invasive plants, support more native vegetation, and have different assemblages of gastropod species (Juvik and Juvik 1998; Meyer and Cowie 2010b). Survey teams consisted of 2–4 experienced terrestrial gastropod researchers. Survey protocols followed Cowie et al. (2008) and were largely conducted by the same individuals as were involved in those low elevation surveys. Surveys were timed and considered complete when no additional species were found after a period of 20 min from recording the last new species. All available vegetation and microhabitats were surveyed in each facility. All shells and live specimens were collected and returned to the laboratory for identification and subsequently vouchered at the Bernice Pauahi Bishop Museum in Honolulu, Hawaii (Catalogue Numbers BPBM 270770, 270819–270822, 270825–270826, 270842, 274326–274390, 275066–275131).

Specimens were identified to the lowest taxonomic level possible and categorized as native or non-native and as either tropical, temperate, or both based on their native ranges. Identifications were made using diagnostic anatomical features as referenced in species identification guides (i.e. Kerney and Cameron 1979; Pfleger and Chatfield 1983; Cowie 1997) and through consultation with experts, and/or use of DNA barcodes (e.g. Hayes et al. 2012). Species were considered tropical if the majority of their native range is bounded by the tropics of Capricorn and Cancer and temperate if the majority of their native ranges are at higher latitudes in both northern and southern hemispheres, as indicated in the publications above. Species that have native ranges that extend broadly through tropical and temperate latitudes were classified as both tropical and temperate.

A presence/absence matrix of all species by nursery was assembled. The matrix consisted of the 21 high elevation nurseries (this study) combined with the 31 low elevation nurseries on Oahu (13), Maui (5), and Hawaii (13) from Cowie et al. (2008). A presence/absence matrix was used because the aim of the visual search method was to maximize the number of different microhabitats sampled to better inventory species richness and composition in each facility as opposed to determine relative abundances. The presence/absence data of species by nursery, island, and elevation are available on the KNB network (https://doi.org/10.5063/F1NV9GGF).

To investigate if non-native gastropod communities differed significantly between low (< 500 m) and high (> 500 m) elevation nurseries and if these communities differed among islands, we used a two-way crossed ANOSIM (9999 permutations) implemented in PRIMER 5.2.9 (Clarke and Gorley 2001) with island and nursery elevation (high or low: above or below 500 m) as factors. Similarity matrices for each sampling location were created using the Bray–Curtis similarity coefficient (Legendre and Legendre 1983). To determine the relative contribution of each species to the dissimilarity among nurseries at different elevations and nurseries on different islands, we also ran a two-way crossed similarity percentage analyses (SIMPER) using the presence/absence matrices and elevation and island as factors. We created a multi-dimensional scaling (MDS) plot to represent visually how sites at different elevations relate to one another based on the presence/absence of species.

To test if species introduced from temperate areas had wider elevation ranges in nurseries than species introduced from tropical areas, a Mann–Whitney U-test was used, which does not require the assumption of equal variances (Sokal and Rohlf 1995). The number of years since the species became established could be a confounding factor affecting the ability to detect differences in elevation range among species from temperate and tropical regions, because species that have been established longer may have been able to colonize a larger elevation range. To visualize this pattern the elevation range of non-native species from both temperate and tropical areas were plotted against the number of years since the species was first recorded in the Hawaiian Islands, and regression lines were generated.

To determine if species richness is higher in nurseries on Oahu, the main port of entry into the Hawaiian Islands, we created three rarefaction curves, one for each island, using the program EcoSim 7.0 (Gotelli and Entsminger 2001). Each rarefaction curve was constrained to end after the collection of 15 sites, the total number of nurseries surveyed on Oahu. Statistical significance was based on non-overlap of the 95% confidence intervals.

Results

In total, 11 species were collected in high elevation nurseries that were not collected in low elevation nurseries, bringing the total number of gastropod species collected in all nurseries to 39 (Fig. 1). Of the 11 new species collected in high elevation nurseries, two species, *Euconulus* sp. and *Punctum horneri*, were classified as native, and the remainder as introduced. Eight of the nine introduced species were from temperate regions, and the native range of one species, *Succinea* sp., was unknown, but members of the family Succineidae are globally distributed and occur in temperate and tropical regions.

ANOSIM revealed significant differences in community composition between low (< 500 m) and high

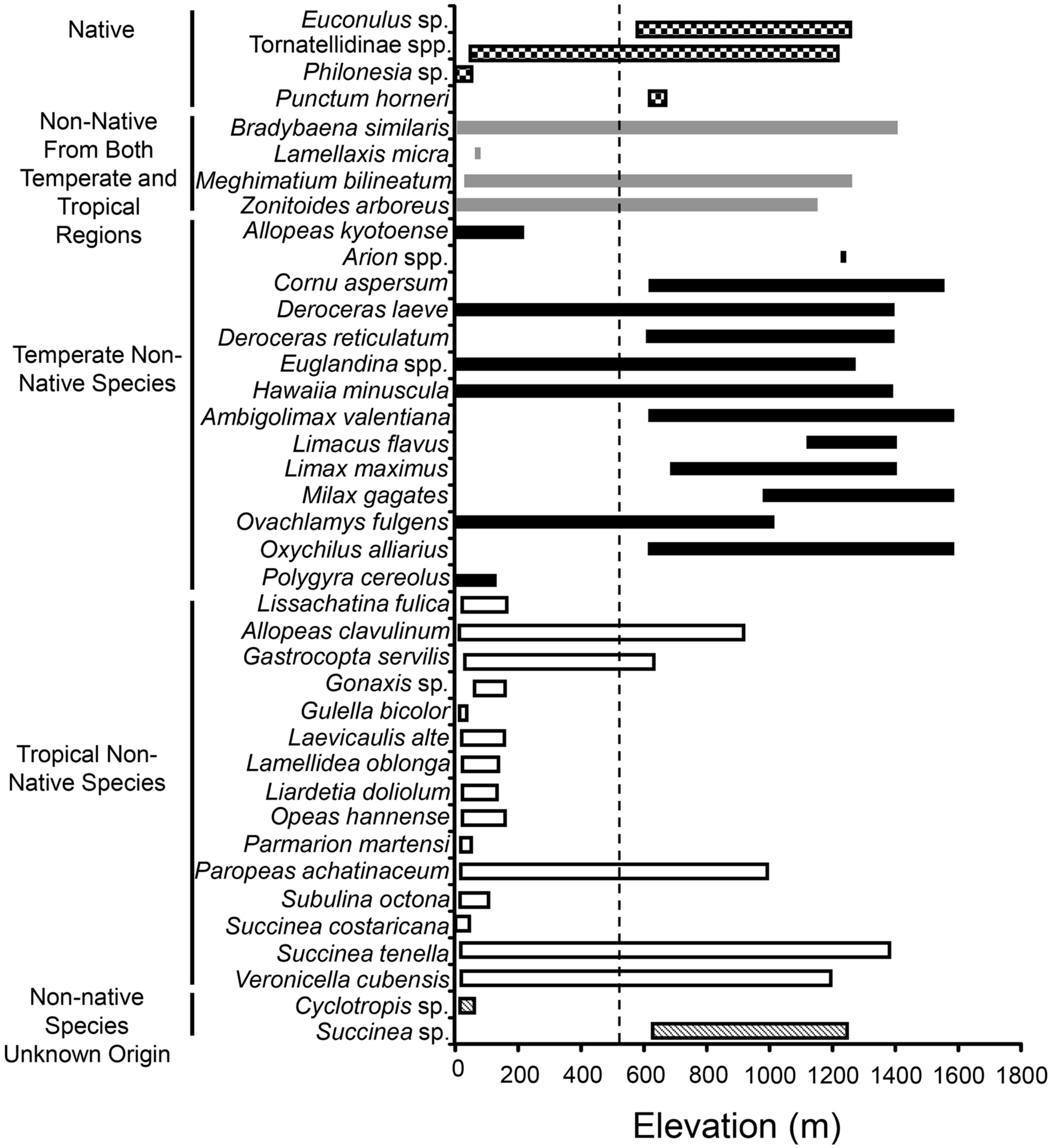

Fig. 1 Elevation ranges of native and non-native terrestrial gastropods collected in nurseries on three Hawaiian Islands, Oahu, Maui and Hawaii. Non-native species are categorized according to their native latitudinal range. Checkered—native species; grey—non-native species from both temperate and tropical regions; black—non-native temperate species; white with black outline—non-native tropical species; striped—non-native species of unknown origin

(> 500 m) elevation nurseries ($R = 0.839$, $P = 0.001$; Fig. 2) and among islands ($R = 0.39$, $P = 0.001$). Significant differences were found in all pair-wise comparisons of the three islands (Oahu vs. Maui, $R = 0.614$, $P = 0.002$; Oahu vs. Hawaii, $R = 0.359$, P = 0.001; Maui vs. Hawaii $R = 0.227$, $P = 0.020$).

The SIMPER analyses examining the species that contributed most to the dissimilarity between high and

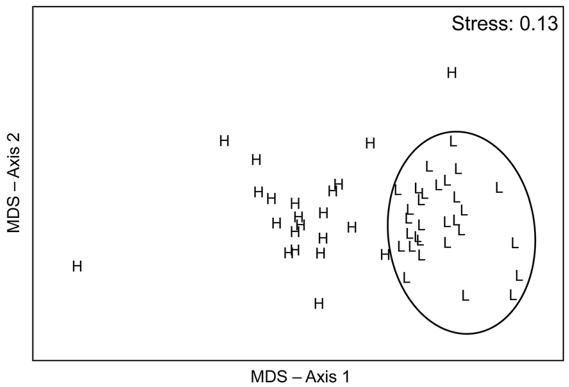

Fig. 2 nMDS ordination of sites according to the composition of terrestrial gastropod species at each site. H—high elevation (> 500 m) nurseries, L—low elevation (< 500 m) nurseries. Sites that are closer together are more similar in terms of terrestrial mollusc composition

low elevation nurseries showed that differences among assemblages in nurseries at high and low elevations were driven primarily by species introduced from different latitudinal regions. Temperate species were more common in high elevation nurseries, while tropical species were more common in low elevation nurseries (Fig. 1, Table 1). SIMPER analysis also showed that dissimilarities among nurseries on different islands are largely influenced by differences in the proportion of nurseries a species occurs in on each island, and to a lesser extent, on species unique to a particular island (Table 2). However, *Cornu aspersum* and *Ambigolimax valentianus* were not collected on Oahu and *Polygyra cereolus*, Tornatellidinae spp., and *Hawaiia minuscula* were not collect in high elevation nurseries on Hawaii.

Species from temperate and tropical regions have different distributional patterns. Of those introduced from temperate regions, 8 of 14 (57%) were only found in high elevation nurseries, while only 2 of 14 (14%) were only found in low elevation nurseries. Conversely, 9 of the 15 (60%) species introduced from tropical regions were only found in low elevation nurseries, and none was found solely in high elevation nurseries (Fig. 1). Species from temperate areas had greater elevation ranges than those from tropical regions (U = 189.5, $P = 0.014$), regardless of when they were first detected in Hawaii and therefore the amount of time they have had to expand their ranges (Fig. 3). Lastly, islands did not differ in species richness when data from low and high elevation nurseries were combined (Fig. 4).

Discussion

Our results show that high elevation nurseries harbor non-native gastropods that may pose a threat to Hawaiian Island biodiversity (Joe and Daehler 2008;

Table 1 Results from SIMPER analyses listing the 15 most important species according to their contribution to the dissimilarity between nurseries at high and low elevations

Species	Proportion of sites present		Avg. dissimilarity ± 1 SD
	Low	High	
Veronicella cubensis[TROP]	0.87	0.09	9.28 ± 1.12
Oxychilus alliarius[TEMP]	0.00	0.82	6.74 ± 1.03
Succinea tenella[TROP]	0.60	0.14	5.37 ± 0.86
Deroceras laeve[TEMP]	0.47	0.64	5.35 ± 0.84
Paropeas achatinaceum[TROP]	0.77	0.23	5.21 ± 0.98
Euglandina spp.[TEMP]	0.47	0.14	4.65 ± 0.92
Deroceras reticulatum[TEMP]	0.00	0.33	4.38 ± 0.78
Allopeas clavulinum[TROP]	0.30	0.23	4.16 ± 0.85
Lissachatina fulica[TROP]	0.60	0.00	3.96 ± 0.82
Subulina octona[TROP]	0.43	0.00	3.83 ± 0.86
Bradybaena similaris[BOTH]	0.47	0.32	3.39 ± 0.79
Cyclotropis sp.[UNKN]	0.47	0.00	3.10 ± 0.71
Ambigolimax valentianus[TEMP]	0.00	0.55	3.05 ± 0.77
Laevicaulis alte[TROP]	0.23	0.00	2.50 ± 0.44
Cornu aspersum[TEMP]	0.00	0.55	2.42 ± 0.72

Each species is followed by a superscript identifying that species' native range (TEMP = temperate, TROP = tropical, BOTH = both temperate and tropical native distribution, UNKN = unknown native distribution)

Table 2 Results from pairwise SIMPER analyses listing the ten most important species according to their contribution to the dissimilarity between islands (Oahu, Maui and Hawaii)

Pairwise comparison	Proportion of sites present		Avg. dissimilarity ± 1 SD
Species	Islands		
Oahu versus Maui	Oahu	Maui	
Euglandina spp.	0.53	0.22	5.78 ± 1.12
Deroceras laeve	0.40	0.61	4.41 ± 1.00
Allopeas clavulinum	0.20	0.33	4.27 ± 1.10
Bradybaena similaris	0.73	0.44	3.41 ± 0.89
Cornu aspersum	0.00	0.61	2.99 ± 0.56
Tornatellidinae spp.	0.07	0.44	2.93 ± 0.61
Paropeas achatinaceum	0.93	0.33	2.69 ± 0.69
Ambigolimax valentianus	0.00	0.56	2.51 ± 0.54
Hawaiia minuscula	0.13	0.39	2.50 ± 0.67
Succinea tenella	0.60	0.33	2.47 ± 0.65
Oahu versus Hawaii	Oahu	Hawaii	
Bradybaena similaris	0.73	0.11	5.93 ± 1.50
Lissachatina fulica	0.80	0.21	4.82 ± 1.16
Cyclotropis sp.	0.67	0.11	4.72 ± 1.19
Euglandina spp.	0.53	0.26	4.59 ± 0.67
Paropeas achatinaceum	0.93	0.42	4.21 ± 0.86
Deroceras laeve	0.40	0.58	4.15 ± 0.85
Polygyra cereolus	0.53	0.00	3.91 ± 1.07
Succinea tenella	0.60	0.32	3.65 ± 0.88
Subulina octona	0.40	0.21	3.16 ± 0.85
Allopeas clavulinum	0.20	0.26	2.84 ± 0.69
Maui versus Hawaii	Maui	Hawaii	
Cornu aspersum	0.61	0.05	4.37 ± 0.76
Deroceras laeve	0.61	0.58	4.35 ± 0.85
Tornatellidinae spp.	0.44	0.00	3.76 ± 0.69
Bradybaena similaris	0.44	0.11	3.73 ± 0.89
Allopeas clavulinum	0.33	0.26	3.49 ± 0.80
Ambigolimax valentianus	0.56	0.11	3.45 ± 0.68
Paropeas achatinaceum	0.33	0.42	3.21 ± 0.73
Deroceras reticulatum	0.56	0.16	3.07 ± 0.62
Succinea tenella	0.33	0.32	3.00 ± 0.66
Hawaiia minuscula	0.39	0.00	2.91 ± 0.69

Shiels et al. 2014). Terrestrial gastropod assemblages in high elevation nurseries were primarily composed of species from temperate regions. Non-native temperate species also dominate gastropod assemblages in high elevation areas outside nurseries (Joe and Daehler 2008; Meyer and Cowie 2010b). Several of the high elevation nurseries are near protected natural areas and forest reserves where much of the native fauna and flora persist. As such, these nurseries may be an important perennial source pool facilitating the successful establishment of non-native species, particularly those with temperate origins, in high elevation forests, which are crucial to the conservation of natural resources.

The non-native species distribution patterns support the hypothesis that the native latitudinal origin of a species can be used to predict its elevation range in nurseries. Consistent with the pattern observed by Meyer and Cowie (2010b) outside nurseries, temperate species had larger elevation ranges in nurseries

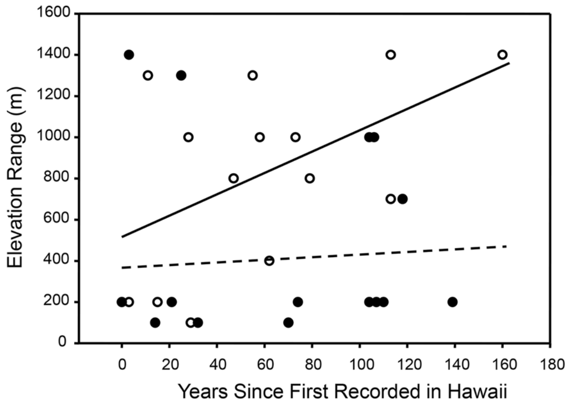

Fig. 3 Elevation range of temperate and tropical species in nurseries plotted against the number of years since first recorded in Hawaii. Best fit lines for elevation ranges of temperate and tropical species are shown to highlight that elevation ranges of temperate species are consistently larger than those of tropical species. Solid line and open dots—temperate species, dotted line and filled dots—tropical species

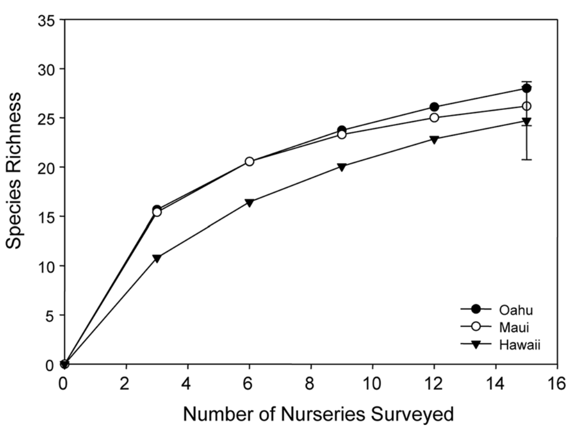

Fig. 4 Rarefaction curves of species richness as the number of nurseries surveyed increases, on Oahu, Maui, and Hawaii. Error bars represent 95% confidence intervals

than species introduced from tropical areas; they also occurred at higher elevations. Although the main Hawaiian Islands are in the tropics, temperature varies depending on elevation and location on each island (e.g. windward versus leeward), and the average temperature in the islands drops about 6.5 °C from sea level to 1000 m (Juvik and Juvik 1998). As such, temperate species have a higher probability of becoming widespread once introduced, because species from temperate regions generally experience a wider range of climatic conditions and have larger distributions in their native range (Moulton and Pimm 1986; Rapoport 1975; Stevens 1992). Combined, our results highlight that species from temperate regions are well adapted to becoming established across the elevation range, particularly at high elevations where cold temperatures may limit establishment of tropical species.

However, since nursery conditions can be highly modified to support optimal growth, survival and flowering conditions of various plant species, whether the above pattern is similar on other tropical islands is likely to depend in part on the reasons for establishing nurseries at high elevation. If high elevation nurseries focus on growing similar plants as are grown in low elevation nurseries, then high and low elevation nurseries might have similar non-native terrestrial gastropod assemblages. Conversely, if high elevation nurseries were developed to support plant species that thrive in conditions similar to those immediately outside the nursery, terrestrial gastropod communities in high elevation nurseries would be likely to differ from those in low elevation nurseries. In Hawaii, the latter possibility seems to describe the situation. Some high elevation nurseries have been designed to propagate native Hawaiian plants for restoration of protected natural areas, thereby increasing the probability of successful establishment of non-native species associated with out-planting in such areas.

While highlighting the threat that high elevation nurseries pose, we do not downplay the impact of low elevation nurseries, as these nurseries also harbor many temperate species that are common in high elevation natural forests. For example, *D. laeve* and *O. alliarius*, both species native to temperate regions, are widespread in nurseries at all elevations and are common in high elevation forests on the islands of Hawaii and Oahu (Meyer and Cowie 2010b, 2011). Therefore, low elevation nurseries represent key sources responsible for the widespread establishment of non-native species in Hawaii, especially as most produce plants for gardens and some grow native plants for out-planting in protected forest and natural area reserves. While it is unclear to what extent different nurseries influence establishment outside the actual facilities and ultimately in areas of conservation importance, it seems probable that high elevation nurseries represent a more direct pathway for non-native species to become established in native forests and areas where native species persist.

In addition to understanding species assemblages in low and high elevation nurseries, knowing introduction and dispersal pathways of non-native species is necessary to decrease future establishment. Cowie et al. (2008) identified Oahu as the main port of entry of non-native gastropods to the Hawaiian Island as it had higher species richness, and gastropod assemblages on other islands were subsets of the Oahu assemblages. However, our inclusion of high elevation nurseries in a combined analysis with the low elevation nurseries of Cowie et al. (2008) decreased overall support for this model of Oahu as a hub because species richness on the three islands did not differ and high elevation nurseries on Maui and Hawaii harbored species not found in Oahu nurseries (i.e. *A. valentianus* and *C. aspersum*). As such, our results indicate that high elevation nurseries on Maui and Hawaii are probably receiving shipments from multiple sources and not only via nurseries on Oahu; this may also be the case for low elevation nurseries. With multiple horticultural pathways responsible for introducing non-native species to various islands, the difficulty in controlling their spread increases. However, there are clear indications of pathways that could be targeted for control. Robinson (1999) and McCullough et al. (2006) reported that cut flowers, plants, and associated products (e.g. soil, cuttings, plant parts, seeds) transported in the horticultural trade account for about 29–40% of all gastropod interceptions. Unfortunately, Robinson (1999) also pointed out that in the U.S., as a result of inadequate funding, less than 5% of horticultural products can be inspected by quarantine personnel, such that many of these non-native species may yet be introduced and become established. While these studies clearly point to the major role of the horticultural trade in the spread of "traveling species", further detailed studies of the movement of plants and supplies into specific nurseries would shed light on the pathways and vectors involved in the import of non-native species into Hawaii as well as their movement between nurseries and within and between islands.

The environmental consequences of the introduction and spread of non-native species are severe. While the purposeful introduction of the predatory *Euglandina* species has received the most attention (Meyer et al. 2017; and references in the introduction), impacts of other non-native species, particularly those from temperate locations, are significant and exacerbating the impacts on an already imperiled biota. For example, the unintentional introduction of *O. alliarius*, an abundant facultative predator, is likely also to be contributing to population declines, and in extreme cases, population extirpation and possibly even extinction, of native Hawaiian terrestrial gastropod species (Meyer and Cowie 2010a; Curry et al. 2016). Non-native terrestrial gastropods from temperate regions are abundant in high elevation forests in Hawaii (Meyer and Cowie 2010b, 2011). They negatively influence native shrub survivorship (Joe and Daehler 2008) and thereby may modify or destroy the habitat on which native snails depend. In our surveys, only *Euglandina* spp. and *O. alliarius* are predators but many of the other species, both temperate and tropical, are in fact considered major plant pests (e.g. Godan, 1983; Barker 2002; Cowie et al. 2009). Cowie (2001) hypothesized that non-native snails may outcompete native species, but further research is needed to confirm the importance of competition, as the ecological role of many of these species is still largely unknown (Meyer and Yeung 2011).

The conservation implications of this and other studies are that non-native gastropod species from temperate areas represent a significant threat to Hawaiian and other Pacific island biodiversity, as they are likely to become established in areas where native species persist—high elevation habitat (Gargominy 2008; Brook 2012; Hirano et al. 2018; Yeung et al. 2018; Yeung and Hayes 2018). Nurseries, particularly those at higher elevations, are potentially key sources for the introduction of temperate species, which are a threat to remaining forest, especially in nearby conservation areas that support much of the remaining native and endemic biodiversity.

There is undoubtedly a legacy effect of non-native snail species introduced a long time ago, but additional species continue to be introduced (e.g., Hayes et al. 2007, 2012). However, we now have a better understanding of how nurseries may play a role in terrestrial gastropod invasion of oceanic islands. We hope this will spur conservation action especially towards better quarantine measures to prevent import of snails into nurseries in the first place, and better control of non-native gastropods in nurseries, particularly those at higher elevations; many nurseries practice no control and many nursery staff are unaware of snail infestations, especially of small species. Nurseries have a relatively small footprint, so snail control would not only be much easier and less environmentally destructive than trying to control snails once they are established outside nurseries, but would also potentially limit further ecological damage to the already imperiled Pacific flora and fauna.

Acknowledgements We thank Meaghan Parker, Skippy Hau, Penny Levin, Pam Hayes, Ginny Cowie, Jennah Bedrosian, Siggi Arnason, Brenden Holland, Shinji Sugiura and Patrick Curry for assistance in the field and David Robinson and Gary Barker for help with identifications. Thank you to Regina Kawamoto and Carl Christensen for help in the collections of the Bishop Museum, and the various horticultural/agricultural facility staff for facilitating access. We appreciate Justin Gerlach for comments on a draft of the manuscript. This work was supported by the U.S. Department of Agriculture, Cooperative Agricultural Pest Surveys (CAPS) program, via grants to RHC, and we especially thank Yolisa Ishibashi of the CAPS program for her support. DNA based identification of snails was supported by U.S. National Science Foundation Grants DEB-0316308 to RHC, DEB-1120906 to KAH, and DEB-1656254 to NWY. Contribution number 10625 of the University of Hawaii School of Ocean and Earth Science and Technology and Bishop Museum's Hawaii Biological Survey 2019-002.

References

Barker GM (2002) Molluscs as crop pests. CABI, Wallingford

Benning TL, LaPointe D, Atkinson CT, Vitousek PM (2002) Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. Proc Natl Acad Sci 99:14246–14249

Bergey EA, Figueroa LL, Mather CM, Artin RJ, Ray EJ, Kurien JT (2014) Trading in snails: plant nurseries as transport hubs for non-native species. Biol Invasions 16:1441–1451

Brook F (2012) Report on the landsnail fauna of Upland Savai'i. In: Atherton J, Jefferies B (eds) Rapid biodiversity assessment of Upland Savai'i, Samoa. Secretariat of the Pacific Regional Environmental Programme, Apia, pp 139–173

Chiba S, Cowie RH (2016) Evolution and extinction of land snails on oceanic islands. Annu Rev Ecol Evol Syst 47:123–141

Clarke KR, Gorley RN (2001) PRIMER v5: user manual/tutorial. Primer-E Ltd., Plymouth

Coote T, Loève E (2003) From 61 species to five: endemic tree snails of the Society Islands fall prey to an ill-judged biological control programme. Oryx 37:91–96

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

Cowie RH (2001) 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, Robinson DG (2003) Pathways of introduction of nonindigenous land and freshwater snails and slugs. In: Ruiz G, Carlton JT (eds) Invasive species: vectors and management strategies. Island Press, Washington, pp 93–122

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 Manage 54:267–276

Cowie RH, Dillon RT Jr, Robinson DG, Smith JW (2009) Alien non-marine snails and slugs of priority quarantine importance in the United States: a preliminary risk assessment. Am Malacol Bull 27:113–132

Curry PA, Yeung NW, Hayes KA, Meyer WM, Taylor AD, Cowie RH (2016) Rapid range expansion of an invasive predatory snail, *Oxychilus alliarius* (Miller 1822), and its impact on endemic Hawaiian land snails. Biol Invasions 18:1769–1780

Gargominy O (2008) Beyond the alien invasion: a recently discovered radiation of Nesopupinae (Gastropoda: Pulmonata: Vertiginidae) from the summits of Tahiti (Society Islands, French Polynesia). J Conchol 39:517–536

Gargominy O, Fontaine B, Prié V (2011) Focus on alien land snails. In: Bouchet P, Le Guyader H, Pascal O (eds) The natural history of Santo. Muséum national d'Histoire naturelle, Paris, IRD, Marseille, Pro-Natura international, Paris, pp 495–500

Gerlach J (2001) Predator, prey and pathogen interactions in introduced snail populations. Anim Conserv 4:203–209

Godan D (1983) Pest slugs and snails. Biology and control. Springer, Berlin

Gotelli NJ, Entsminger GL (2001) Swap and fill algorithms in null model analysis: rethinking the knight's tour. Oecologia 129:281–291

Hadfield MG (1986) Extinction in Hawaiian achatinelline snails. Malacologia 27:67–81

Hayes KA, Tran CT, Cowie RH (2007) New records of alien Mollusca in the Hawaiian Islands: nonmarine snails and slugs (Gastropoda) associated with the horticultural trade. Bishop Mus Occas Pap 96:54–63

Hayes KA, Cowie RH, Thiengo SC, Strong EE (2012) Comparing apples with apples: clarifying the identities of two highly invasive Neotropical Ampullariidae (Caenogastropoda). Zool J Linnean Soc 166(4):723–753

Hirano T, Wada S, Mori H, Uchida S, Saito T, Chiba S (2018) Genetic and morphometric rediscovery of an extinct land snail on oceanic islands. J Molluscan Stud 84:148–156

Horsák M, Dvořák L, Juřičková L (2004) Greenhouse gastropods of the Czech Republic: current stage of research. Malakol Tájék 22:141–147

Joe SM, Daehler CC (2008) Invasive slugs as under-appreciated obstacles to rare plant restoration: evidence from the Hawaiian Islands. Biol Invasions 10:245–255

Juvik SP, Juvik JO (1998) Atlas of Hawai'i, 3rd edn. University of Hawai'i Press, Honolulu

Kerney MP, Cameron RAD (1979) Field guide to the land snails of Britain and north-west Europe. Collins, London

Legendre L, Legendre P (1983) Numerical ecology. Elsevier Scientific, New York

Loope LL, Giambelluca TW (1998) Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawaii. Clim Change 39:503–517

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 nonmarine mollusks. Bioscience 54:321–330

McCullough DG, Work TT, Cavey JF, Liebhold AM, Marshall D (2006) Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biol Invasions 8:611–630

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

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

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, Yeung NW (2011) Trophic relationships among terrestrial molluscs in a Hawaiian rain forest: analysis of carbon and nitrogen isotopes. J Trop Ecol 27:441–445

Meyer WM III, Yeung NW, Slapcinsky J, Hayes KA (2017) Two for one: inadvertent introduction of *Euglandina* species during failed bio-control efforts in Hawaii. Biol Invasions 19:1399–1405

Moulton MP, Pimm SL (1986) Species introductions to Hawaii. In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii. Springer, New York, pp 231–249

Pfleger V, Chatfield JE (1983) A guide to snails of Britain and Europe. Hamlyn, London

Rapoport EH (1975) Areografia: estrategias geografias des las especies. Fondo de Cultura Economica, Mexico City

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

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

Robinson DG (1999) Alien invasions: the effects of the global economy on non-marine gastropod introductions to the United States. Malacologia 41:413–438

Rolett B, Diamond J (2004) Environmental predictors of pre-European deforestation on Pacific islands. Nature 431:443–446

Shiels AB, Ennis MK, Shiels L (2014) Trait-based plant mortality and preference for native versus non-native seedlings by invasive slug and snail herbivores in Hawaii. Biol Invasions 16:1929–1940

Sokal RR, Rohlf FJ (1995) Biometry. The principles and practice of statistics in biological research, 3rd edn. W.H. Freeman and Co., New York

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

Stevens GC (1992) The elevational gradient in altitudinal range, an extension of Rapoport's latitudinal rule to altitude. Am Nat 140:893–911

Yeung N, Hayes K (2018) Biodiversity and extinction of Hawaiian Land snails: how many are left now and what must we do to conserve them—a reply to Solem (1990). Integr Comp Biol. https://doi.org/10.1093/icb/icy043

Yeung NW, Bustamente KM, Sischo DR, Hayes KA (2018) Rediscovery of *Newcombia canaliculata* (Baldwin, 1895) (Gastropoda: Achatinellidae) and *Laminella venusta* (Mighels, 1845) (Gastropoda: Amastridae). Bishop Mus Occas Pap 123:31–36