

Invasive Temperate Species are a Threat to Tropical Island Biodiversity

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ABSTRACT

To protect the remaining biodiversity on tropical islands it is important to predict the elevational ranges of non-native species. We evaluated two hypotheses by examining land snail faunas on the eastern (windward) side of the island of Hawaii: (1) the latitude of a species' native region can be used to predict its potential elevational range and (2) non-native temperate species, which experience greater climatic fluctuations in their native range, are more likely to become established at higher elevations and to extend over larger elevational ranges than non-native tropical species. All non-native tropical species were distributed patchily among sites ≤ 500 m and occupied small elevational ranges, whereas species introduced from temperate regions occupied wide elevational ranges and formed a distinct fauna spanning elevations 500–2000 m. Most native land snail species and ecosystems occur > 500 m in areas dominated by temperate non-native snail and slug species. Therefore, knowing the native latitudinal region of a non-native species is important for conservation of tropical island ecosystems because it can be translated into potential elevational range if those species are introduced. Because temperate species will survive in tropical locales particularly at high elevation, on many tropical islands the last refuges of the native species, preventing introduction of temperate species should be a conservation priority.

Key words: alien; altitude; biogeographical patterns; Hawaii; invasion; land snails; mollusc.

TO IMPROVE THE EFFICIENCY OF CONSERVATION EFFORTS in preserving biodiversity, reliable predictors of invasion success and the impacts of non-native species must be identified and understood (Lockwood 1999, Cowie 2004, Clavero & García-Berthou 2005). Models used to predict invasion success and spread/distribution of non-native species usually incorporate some aspect of climatic matching of the invader's native range and the region invaded (Peterson 2003, Bromennimann & Guisan 2008). Study of patterns of invasion along elevational gradients, which are analogous to latitudinal climatic gradients, has the potential to provide insight into understanding the success and impact of many non-native species (Sax 2001, Pauchard & Alaback 2004, Brasher *et al.* 2006). This may be especially true on tropical islands where climatic conditions at higher elevations are more similar to those of temperate latitudes than they are to those of the adjacent warmer, more 'tropical' lower elevations.

In invasion biology, it is presumed that species with larger geographical ranges can withstand greater climatic fluctuations and generally have a higher probability of becoming established and widespread once introduced (Moulton & Pimm 1986). Therefore, non-native species from temperate climates, which have evolved to live in a wide range of climatic conditions as a result of greater seasonal fluctuations and generally larger native ranges compared to tropical species (Rapoport 1975, Stevens 1992), are more likely to become established and spread to a wide variety of habitats along an elevational range. This potentially includes not only high elevation tropical areas but also low elevation habitats often thought to be vulnerable only to species from tropical regions. Seasonally high temperatures in the native ranges of many temperate species, how-

ever, can exceed those in low elevation tropical areas. Therefore, temperate species may represent a more widespread threat to tropical islands than tropical species, particularly at higher elevations, where in many cases the majority of the remaining biodiversity is confined.

In this paper, we evaluate two hypotheses: (1) native latitudinal region (temperate or tropical) of a species can be used to broadly predict its potential elevational distribution when introduced to areas outside its native range and (2) non-native temperate species are more likely to become established at higher elevations and to extend over larger elevational ranges than non-native tropical species when introduced to tropical islands. We tested these hypotheses by examining the distribution of the terrestrial land snail and slug fauna on the tropical island of Hawaii. The Hawaiian Islands are of particular interest for studies of invasions because the highly endemic and diverse flora and fauna is renowned as a model ecosystem for studying both evolution and ecosystem processes (Vitousek 2002, Cowie & Holland 2008). Unfortunately, a majority of the native Hawaiian diversity is either extinct or threatened. The Hawaiian land snails, for instance, are recognized for their high diversity (*ca* 750 species), high levels of endemism (*ca* 99%; Cowie *et al.* 1995a), and the fact they are under extreme threat, with extinction estimates of 65–90 percent (Solem 1990, Cowie 2002, Lydeard *et al.* 2004). Estimates for plants indicate that 590 of the 1290 Hawaiian plant species are extinct or at risk of extinction (Wagner *et al.* 1999).

Non-native snails and slugs (NNSS) are recognized as a threat to the conservation of native biodiversity in Hawaii (Cowie 2005, Joe & Daehler 2008). NNSS negatively impact native plant survival (Civeyrel & Simberloff 1996, Joe & Daehler 2008) and have been implicated as a major factor in the extinction of native Hawaiian land snail species (Hadfield & Mountain 1980, Severns 1984, Hadfield *et al.* 1993, Civeyrel & Simberloff 1996, Cowie 2001a).

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Although not substantiated, some native litter dwelling snail species may be declining because of competition with NNSS (Cowie 2001b, 2005). Also, there is potential for a variety of unpredicted deleterious interactions among NNSS and both native snail species and ecosystems in Hawaii (Meyer *et al.* 2008). Since many of the same NNSS on the island of Hawaii have also become established and threaten biodiversity on other Hawaiian and Pacific Islands (Solem 1964, Murray *et al.* 1988, Cowie 2002), understanding the elevational distribution patterns of these species can have wide-ranging implications for understanding invasions on oceanic islands and allow natural resource managers throughout the Pacific to better target their prevention and quarantine efforts.

METHODS

STUDY AREA.—The island of Hawaii lies within the Tropic of Cancer between $20^{\circ}16'10''$ – $18^{\circ}54'60''$ N. Surveys were conducted on the eastern (windward) side of the island along an elevational gradient from sea level to 2000 m (Fig. S1). This elevational range was chosen because native montane mesic and wet forests occur on the windward side of all the main Hawaiian Islands to an elevation of *ca* 2000 m (Gagné & Cuddihy 1990). The habitat > 2000 m is subalpine shrubland on the islands of Maui and Hawaii (the two islands that exceed this elevation) and the land snail fauna changes, at least on the island of Hawaii (Cowie *et al.* 1995b). Most site characteristics (average temperature, ecosystem type, and dominant overstory species) are correlated with elevation (Juvik & Juvik 1998). With an increase in elevation, temperatures decrease and, around 500 m elevation, the habitat changes from being dominated by human impacts and invasive plant species to being composed of more native vegetation, with trees such as ohia (*Metrosideros polymorpha*) and koa (*Acacia koa*) dominating the overstory (Juvik & Juvik 1998). In contrast, rainfall is not linearly correlated with elevation in this 0–2000 m range but varies from 1000 to 5000 mm/yr with the highest rainfall in the middle of the range (Juvik & Juvik 1998).

TRANSECT LOCATIONS.—Locations of the three transects were (1) Stainback Highway Transect (SHT), spanning Pu'u Maka'ala Natural Area Reserve, Ola'a Forest Reserve, and Mauna Loa; (2) Hawaii Volcanoes National Park Transect (HVT), spanning the Chain of Craters Road, Kilauea, Mauna Loa; and (3) Saddle Road Transect (SRT) (Fig. S1). The SHT only had sampling stations from sea level to 1250 m because access to areas higher was not permitted. The locations of the three transects were selected based on accessibility to the elevation range by car.

SAMPLING.—Nine sites (each 20×20 m) were sampled along each transect at intervals of 250 m elevation, with the exception of the SHT on which there were only six sites. All sites were *ca* 50 m from the road (the road ecotone was avoided). Each site was characterized by the origin of its flora as either native (having an overstory of ohia, koa, or both, and a high proportion of native understory) or invasive (consisting almost entirely of invasive species). Land snail/slug faunas at all sites were surveyed three times, in February, July, and

December 2004. Two sampling approaches were used: (1) a two person, 20 min, visual search of the litter focusing on as many microhabitats as possible within the 20×20 m area, and a two person, 10 min, visual search of the trees and shrubs incorporating as much plant diversity as possible (February and July only) and (2) an array of traps composed of five cups at each site (8 cm diam, 5 cm tall) filled with beer, buried in the litter so that their rims were level with the soil surface, and left in the field for 48 h (December only). Timed searching was especially important to detect species above-ground on plants, whereas beer traps were especially good at detecting slugs. Most species at each site were detected on each sampling occasion, but incorporation of the two sampling techniques and the ability to sample on multiple occasions was important to detect less abundant cryptic snail species. These sampling methods may under-sample smaller species (Ward-Booth & Dusart 2001). However, they yield many more specimens and many more species per unit person-time than more intensive methods such as sifting through litter samples in the laboratory (Emberton *et al.* 1996). Since the focus of the study was species inventory rather than relative abundance, these were deemed the most appropriate approaches. Most non-native and extant native snail species are > 10 mm in size so size-related bias may not be large (Cowie *et al.* 1995b, Cowie & Robinson 2003).

All live specimens collected were deposited in either the Bishop Museum (Honolulu) malacological collections (accession number 2008.125, catalog numbers BPBM 270200–270272) or in the Hawaii Volcanoes National Park collections (accession number HAVO-624, catalog numbers HAVO 15521–15552).

DATA ANALYSIS.—All species collected alive were identified and categorized as native or non-native. All non-native species were categorized as either tropical or temperate (Table 1) based on their native ranges, following Kerney and Cameron (1979), Pflieger and Chatfield (1988), and Cowie (1997). Species were considered tropical if the majority of their native range is bounded by the tropics of Capricorn and Cancer; otherwise they were considered temperate.

Two rarefaction curves were created using the program EcoSim 7.0 (Gotelli & Entsminger 2001) to examine patterns in species richness as (1) the number of individuals collected increased and (2) the number of sampling sites increased. Before carrying out further statistical analyses, a presence/absence matrix of all species by site was assembled, collapsing the data from the three sampling times. This was done for two reasons: (1) the timed search sampling method was aimed at assessing species richness not relative abundances (so maximizing the number of different microhabitats sampled was the focus) and (2) all species present at a site were unlikely to be detected on a single sampling occasion. Three sites, those in HVT from sea level to 500 m elevation, were excluded from the analyses because no live snails were found there on any occasion, and all species collected at only one site were excluded from the analyses because the information provided by these sites and species is not informative in developing an index of similarity (see below). Non-native faunas were grouped by cluster analysis using PRIMER v.5.2.9 (Clarke & Gorley 2001). The Bray–Curtis index was chosen as the similarity coefficient because it avoids grouping sites

TABLE 1. *The non-native species recorded in the study. Year of introduction and native range were obtained from Kerney and Cameron (1979), Pfleger and Chatfield (1988), Cowie (1997), and references therein.*

Family species	Year introduced	Native range
Tropical species		
Achatinidae		
<i>Achatina fulica</i>	1936	East Africa
Philomycidae		
<i>Meghimatium striatum</i>	1846	Southern Asia
Subulinidae		
<i>Allopeas clavulinum</i>	1906	East Africa
<i>Allopeas gracile</i>	1846	Neotropics
<i>Opeas hannense</i>	1906	Tropical Central America
<i>Paropeas achatinaceum</i>	1904	Australasia, Java, Sumatra
Veronicellidae		
<i>Veronicella cubensis</i>	1985	Cuba
Temperate species		
Arionidae		
<i>Arion intermedius</i>	1981	Western Europe
Limacidae		
<i>Deroceras laeve</i>	1987	Holarctic
<i>Limax maximus</i>	1931	Europe and North Africa
Spiraxidae		
<i>Euglandina rosea</i> ^a	1955	Florida and neighboring states, U.S.A.
Zonitidae		
<i>Oxychilus alliarius</i> ^a	1937	Western Europe

^aPredatory snail species. The rest are presumed primarily herbivorous or detritivorous (including fungivorous).

according to species absence, *i.e.*, absences are not taken as an indication of similarity (Legendre & Legendre 1983). The unweighted pair group method using arithmetic averages (UPMGA) was applied to cluster the sites. Clusters were mapped at 75 percent dissimilarity. Analysis of similitude (ANOSIM) was used to detect differences in faunal composition of NNSS among three elevation categories defined a priori by dividing the nine elevations into three groups of three (low elevation, sites at 0, 250, 500 m; mid elevation, sites at 750, 1000, 1250 m; high elevation, sites at 1500, 1750, 2000 m) and between the two habitat types (native and invasive).

To test if species introduced from temperate areas had wider non-native elevational ranges than did species introduced from tropical areas, a Mann–Whitney *U* test was employed because the data violated the assumption of equal variances (Sokal & Rohlf 1995). Since we had a small number of species and wanted to be certain that one species' elevational range was not alone responsible for statistically significant differences between the observed elevational ranges of non-native temperate and tropical species, we re-ran the Mann–Whitney *U* test multiple times, each time with one observation removed until we had run all possible tests. If all results were significant we could be confident that the differences were not driven by one particular species (Manly 1991). The number of

years since the species became established could be a confounding factor affecting the ability to detect differences in elevational range among species from temperate and tropical regions, because species that have been established longer may have been able to colonize a larger elevational range. To visualize this pattern the elevational range of NNSS from both temperate and tropical areas were plotted against the number of years since the species was first recorded in the Hawaiian Islands.

RESULTS

In total, 19 land snail and slug species (719 individuals) were collected (Fig. 1). The majority (12) are non-native, of which five were from temperate and seven from tropical latitudes (Table 1). Many of the non-native species were more abundant than the native species (W. M. Meyer, pers. obs.). The native species consisted of Succineidae (2 species), Helicarionidae (1), and Achatinellidae (subfamilies Tornatellidinae and Tornatellininae; 4). These numbers may be conservative as molecular data have revealed that the *Succinea* species may be complexes of multiple cryptic species (W. M. Meyer, unpubl. data) and it is not known how widespread such complexes might be in other families of Hawaiian land snails. We assigned individual achatinellids to four unidentified species based on differences in shell morphology. The group is extremely diverse (Cowie *et al.* 1995a) and the taxonomy very difficult; we were unable to conclusively assign individuals to named species. Five of the seven native species were collected at mid elevations only (750–1250 m), while the other two, both achatinellids, were only collected at one site at 250 m elevation (Fig. 1).

The rarefaction analysis indicates that a high proportion of the species present at the sites was collected, *i.e.*, if more individuals had been collected few additional species would be recorded (Fig. 2A). However, the rarefaction curve of cumulative species richness as the number of sites increased indicates that increasing the number of sampling sites would have yielded more species (Fig. 2B). This result is indicative of the presence of additional rare or patchy species, so our sampling does not allow an accurate estimate of overall species richness across the entire study area. Our objective, however, was to understand the distribution of the most abundant and widespread species, because it is these that are more likely to be currently having significant impacts.

The non-native species were partitioned along the elevational gradient according to their native temperate or tropical origins (Fig. 1). Cluster analysis of sites according to the presence of non-native species shows four distinct faunal groupings at 75 percent dissimilarity (Fig. 3). Three groups (A, B, D) occur at low elevation sites (0–500 m) and include species primarily from tropical regions, although three temperate species (*Euglandina rosea*, *Limax maximus*, *Oxychilus alliarius*) were occasionally found at low elevations. The other group (C) consisted entirely of temperate species in sites at higher elevations (500–2000 m; Fig. 3). ANOSIM revealed significant overall differences in faunal composition among elevations ($R=0.331$, $P < 0.001$) and between habitat types ($R=0.916$, $P < 0.001$). These two factors (elevation and habitat type) are highly correlated, with native habitat found primarily at sites

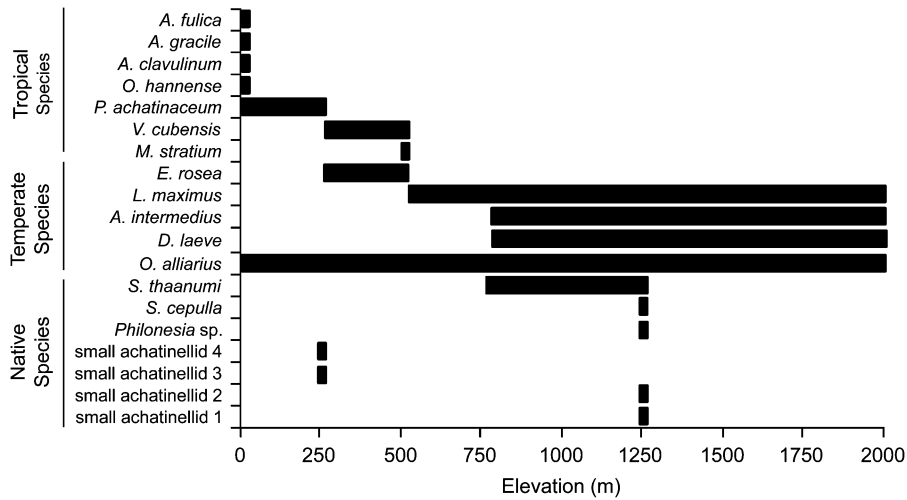


FIGURE 1. Elevation ranges of native and non-native snails and slugs on the eastern part of the island of Hawaii. The achatinellids could only be identified as belonging to either/both of two genera, *Tornatellides* and *Tornatellaria*.

> 500 m (Fig. 3). Pairwise ANOSIM results indicated that faunas at low elevation sites (0–500 m), which consisted entirely of invasive habitat, were significantly different from those at mid ($R=0.616$, $P < 0.001$) and high ($R=0.412$, $P=0.002$) elevation sites where all the native habitat occurred (Fig. 3). There was no significant difference in faunal structure between mid and high elevations ($R=-0.054$, $P=0.73$).

Non-native species from temperate regions have a significantly greater average elevational range than do non-native species from tropical regions ($Z=2.72$, $P=0.007$), and all Mann–Whitney U tests with one observation missing were significant ($P=0.012-0.007$), but in neither group was the elevational range statistically significantly related to number of years since introduction (Fig. 4).

DISCUSSION

Our study examined the distributions of 12 NNSS, which represents ca 30 percent of the established non-native land snail and slug species in Hawaii (Cowie *et al.* 2008). These distributions support

the concept that the native latitudinal origin of a species can be used to predict its elevational range in a tropical location. NNSS from tropical regions only occurred at elevations of 500 m or below (Figs. 1 and 3) and had smaller elevational ranges than temperate species (Fig. 4), contrasting with the NNSS fauna that dominates sites > 500 m, which consists entirely of temperate species (Fig. 3). This non-native mid and high elevation fauna consists of *Deroceras laeve*, *O. alliarus*, *Arion intermedius*, and *L. maximus*, with *E. rosea* at just one site at 500 m. All the species in the high elevation fauna are from temperate regions and most (not *E. rosea*) are widespread at elevations > 500 m (Fig. 1). *Euglandina rosea*, although classified here as a temperate species, is in fact subtropical, occurring in Florida and neighboring regions of the southeastern United States, which probably explains its absence from upper elevations. The two other temperate species (*L. maximus* and *O. alliarus*) that were also occasionally found at lower elevation sites (Fig. 1) have large native ranges. The native range of *L. maximus* extends from northern Europe to North Africa (Pfeleger & Chatfield 1988) and *O. alliarus* is found in western Europe from Scandinavia to southwest France (Kerney & Cameron 1979). Despite their classification as

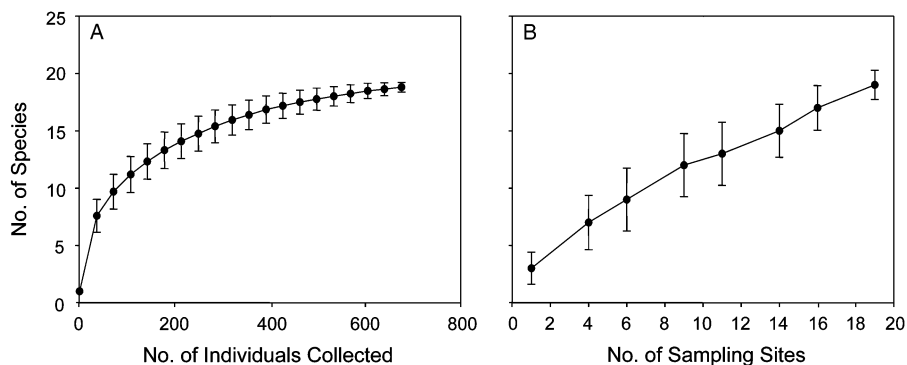


FIGURE 2. Rarefaction curves of species richness as (A) the number of individuals collected increases and (B) the number of sampling sites increases.

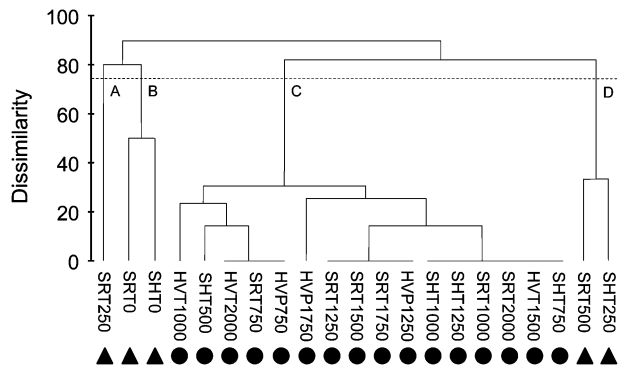


FIGURE 3. Dendrogram representation of the cluster analysis that grouped sites according to species presence. The numbers following each transect represent the elevation (m) of the site, and the symbols indicate whether the site was in native (circles) or invasive (triangles) habitat. Four faunal groupings were found at 75 percent dissimilarity, denoted by A–D. Group C is dominated by temperate species while the other groups are dominated by tropical species.

temperate species, native ranges of such species may include regions where seasonally high temperatures are similar to or higher than those at lower elevations in Hawaii, suggesting that temperate species have may be tolerant of the climatic variation throughout the elevational range surveyed.

In general, the majority of the remaining native Hawaiian biodiversity is restricted to higher elevations, as observed here for native land snails (Fig. 1) and ecosystems (Fig. 3). The majority of the native land snails found were at elevations of 750–1250 m (Fig. 1). Non-native species that colonize higher elevation habitats are therefore likely to have a greater impact on native biodiversity than those that remain at lower elevations. Since the NNSS fauna that dominates the mid and high elevation areas (750–2000 m) consists entirely of temperate species, it is these temperate NNSS that may impact the native snails and ecosystems negatively through competition and/or predation/herbivory (Fig. 2). Temperate slug species

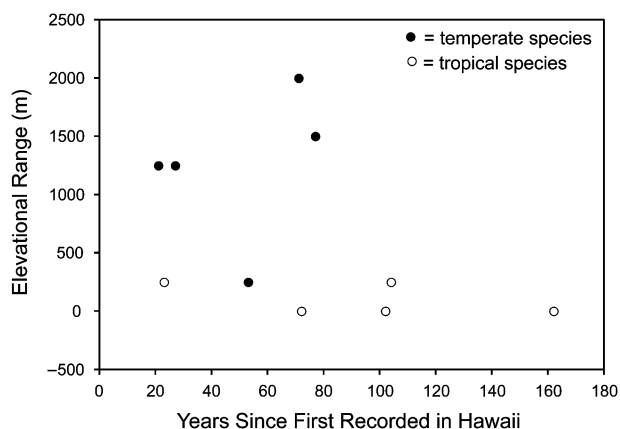


FIGURE 4. Elevational range of temperate and tropical species plotted against the number of years since they were first recorded in Hawaii.

(*D. laeve* and *L. maximus*) negatively affect native plant seedling survivorship in Hawaii (Joe & Daehler 2008) and *O. alliarius* can consume small snails (3 mm or less in maximum shell dimension) (Severns 1984, W. Meyer & R. Cowie, unpubl. data). Therefore, in an already highly modified tropical region like Hawaii, where native biodiversity is now confined primarily to higher elevation refugia, non-native temperate species may be more likely to negatively impact the native biota. Our study demonstrates that just knowing a species' latitudinal origin may be a good predictor of potential elevational range in the invaded region. Our study also indicates that the potential invasiveness of temperate species when introduced to tropical locations should receive more attention.

Patterns of invasion described here for NNSS are also found in other groups of organisms. For example, there is an increasing proportion of non-native temperate plant species at higher elevations in Hawaii (Wester & Juvik 1983, Daehler 2005). While the ecotone for plants is more gradual and occurs at higher elevations (Daehler 2005), Hawaii's roadside weeds are predominately of European origin at an elevation of 1000 m (Wester & Juvik 1983). Moulton and Pimm (1986) showed that introduced passerine bird species with larger native ranges were more likely to succeed in Hawaii but that there was no difference in invasion success between tropical and temperate bird species.

It has been suggested that after introduction, NNSS remain in anthropogenically modified environments and do not spread to more natural surrounding areas (Harry 1966). There is no doubt that successful invaders are often well adapted to human disturbed environments (McKinney 2002, Gurevitch & Padilla 2004). In temperate systems, most non-native species do occur in low elevation human disturbed habitats (Hobbs 2000, McKinney 2002), although higher elevation areas with more intact environments are also impacted (Noss & Cooperrider 1994). In Hawaii, many NNSS (mostly from temperate regions) have spread into high elevation natural areas and have had deleterious impacts on native biodiversity (Hadfield *et al.* 1993; Cowie 1998, 2001a, 2004, 2005; Joe & Daehler 2008). We hope that this paper provides some impetus for detailed surveys examining the elevational distributions of many non-native taxa on more islands. In Hawaii, we suggest researchers focus also on other groups that include higher numbers of non-native species, such as insects (*e.g.*, 50 introduced species of ants) and plants (Eldredge & Evenhuis 2003). Tropical invasive species are often thought to represent the greatest threat to tropical island ecosystems. However, we emphasize that temperate species, in our case snails and slugs, also pose a threat, perhaps greater in some cases, to tropical oceanic island biodiversity and that every effort should be taken to limit temperate species from being introduced to these islands.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Map of the eastern part of the island of Hawaii showing the locations of the three transects.

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