THE DISTRIBUTION, SPREAD AND POTENTIAL IMPACTS OF THE INVASIVE PREDATORY SNAIL \textit{OXYCHILUS ALLIARIUS} ON TROPICAL ISLANDS

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Abstract

Island land snail species, have suffered major extinctions, partly resulting from impacts of alien species. *Oxychilus alliarius* is a widely introduced predatory European snail. This thesis includes two studies: 1) assessing its spread and impacts on native snails on Kaala, Oahu’s highest mountain; 2) modeling the environmental factors that determine its distribution in Hawaii, and applying those models to predict its potential tropical/subtropical island distribution globally. On Kaala *O. alliarius* is expanding its distribution at ~113 m per year. Abundances of native snail species on Kaala are correlated to that of *O. alliarius* in complex ways. Of 36 models developed, the four best were good predictors of *O. alliarius* distribution in Hawaii, with mean annual temperature being especially important. Globally, the models predict that some islands have areas of suitable habitat, mostly at higher elevations, and are therefore susceptible to invasion by *O. alliarius*, while others have no suitable habitat.
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Preface

Over the course of undertaking the research presented in this thesis there have been significant contributions by a number of other people. The two main chapters (chapters 2 and 3), which will be published as peer-reviewed papers and are therefore presented here as such, will both be multi-authored, with me as the lead author.

My advisor, Robert H. Cowie, is an author on both of them, as he has provided extensive guidance and editorial input and discussion. He provided similar help with the other parts of the thesis (chapters 1 and 4). Additional contributors, who will also be co-authors of the two future publications are Norine W. Yeung and Kenneth A. Hayes, who both aided in developing the ideas behind the two projects and undertaking initial survey work, In addition, Andrew D. Taylor will be a coauthor of the publication derived from chapter 2 because of the extensive advise and aid he provided with data analysis and interpretation. For both projects I was involved in development of the ideas behind the research, conducted the majority of the research, decided on the analytical methods, and wrote the manuscript with the help of my advisor.
Chapter 1

Introduction: a study of an invasive snail in the Hawaiian Islands and its potential global spread
THE BIODIVERSITY CRISIS

The earth and the Hawaiian Islands especially, are experiencing a biodiversity crisis that some are calling “the sixth great extinction” (Wake and Vredenburg 2008). Ehrlich and Ehrlich (1981) and Quammen (1996) have asserted that this crisis began around ten thousand years ago, at the beginning of the so-called Anthropocene, and that the crisis has become even worse in the last century (Soulé and Wilcox 1980). The main reasons for the global loss of biodiversity are habitat loss (Dale et al. 1994; Paulay 1994), impacts of invasive species (Wilcove et al. 1998; McKinney and Lockwood 1999), and climate change (Thomas et al. 2004). Habitat loss caused by deforestation, pollution, fire, and cultivation results in extinction of species (Henderson 1992; Stone 1995). Climate change has been cited as a reason for extinction of 67% of the 110 species in the frog genus *Atelopus* (Pounds et al. 1999, 2006). Models analyzing habitat loss and climate change together (Travis 2003) have demonstrated a synergistic increase in the threat they pose to biodiversity. Understanding the effects of invasive species, habitat destruction, and climate change on native and non-native flora and fauna is critical to understanding current and future global biodiversity loss. Invasive species are the main focus of this thesis.

INVASIVE SPECIES

The increase of human mediated dispersal of species, largely as a result of increased global trade, has brought together biota that evolved separately (D’Antonio and Vitousek 1992; Mooney and Cleland 2001). These widespread introductions are leading
to global biotic homogenization, the replacement of a diverse and geographically structured biota with a relatively small number of widely distributed species (McKinney and Lockwood 1999; Cowie 2001a; Olden et al. 2004). To conserve the world’s biodiversity, a better understanding of biotic homogenization and the impacts of invasive species is necessary.

For example, the introduction of the brown tree snake, *Boiga irregularis*, has irreparably damaged the native fauna of Guam. The snake was introduced in the 1950s and caused the extirpation of nine forest bird species, three pelagic bird species, three to five lizard species, and possibly a bat species (Savidge 1987; Rodda and Fritts 1992; Fritts and Rodda 1998).

The effects of invasive species are not limited to species losses. The invasive vine kudzu, *Pueraria lobata*, was introduced to the United States for control of soil erosion during the 1870s. It is now listed among 100 of the world’s worst invasive species (Lowe et al. 2000) and has been nicknamed “the vine that ate the south” because it will completely overgrow inanimate objects and other plants (Pappert et al. 2000; Forseth and Innis 2004).

THE HAWAIIAN ISLANDS AND THEIR BIODIVERSITY

The eight main Hawaiian Islands make up more than 99% of the exposed land in the approximately 2400 km long Hawaiian archipelago. They are one of the most isolated island groups in the world, with the nearest large land mass 3200 km away from the center of the island chain (Dejoode and Wendel 1992; Ziegler 2002; Price 2004). The Hawaiian Islands were formed as the Pacific tectonic plate moved northwestwards over a
stationary volcanic plume called a hot spot. Subsequent to the islands’ formation, erosion and subsidence result in their decline, with the islands eventually becoming low atolls, then submerged seamounts that ultimately disappear as the Pacific plate is subducted under the adjacent plates (Price and Clague 2002). Kure and Midway, in the northwest, are the oldest islands/atolls (29 Ma and 28 Ma, respectively) and the chain continues southeastwards to the youngest island, the island of Hawaii (0.5-0 Ma). The center of the Hawaiian hot spot is currently situated near the southeast coast of the island of Hawaii (Carson and Clague 1995; Fleischer et al. 1998; Ziegler 2002).

The Hawaiian archipelago was colonized by plant and animal dispersers from both sides of the Pacific (Funk and Wagner 1995). For instance, the Hawaiian silversword alliance (Asteraceae) has basal lineages in California (Baldwin and Robichaux 1995), the ground cricket genus *Thetella* is widespread in the Pacific (Shaw 1995), and the spider genus *Tetragnatha* is found worldwide (Gillespie and Croom 1995). Hawaiian Island colonization is dependent on an organism’s long-distance oceanic dispersal ability (Gillespie and Roderick 2002; Cowie and Holland 2006). The majority of the terrestrial colonizers have been invertebrates and plants (Cowie and Holland 2008). Except for birds and two species of bats (one extinct) the Hawaiian Islands lack native terrestrial vertebrates (James et al. 1987; Tarr and Fleischer 1995).

As organisms colonized the islands, some of their lineages radiated (Simon 1987; Price and Clague 2002; Cowie and Holland 2008). Many of these radiations show characteristics of the progression rule of island biogeography (Funk and Wagner 1995). This theory is based on Hennig’s (1966) progression rule, but also incorporates the geological history of sequentially formed islands. Thus the progression rule of island
biogeography posits that the most basal lineage of a clade will be found on the oldest island, more derived lineages progressively on the younger islands, and the most derived lineage on the youngest island. This pattern of diversification in the Hawaiian archipelago has led to many endemic island lineages that in some cases have gone on to form monophyletic radiations on each island (Simon 1987; Wagner and Funk 1995).

INVASIVE SPECIES IN HAWAII

Humans have been introducing species to and changing the flora and fauna of Hawaii since they first arrived (Kirch 1982; Olson and James 1982; Athens et al. 2002; Boyer 2008). The Polynesians deliberately introduced pigs (Sus scrofa), dogs (Canis familiaris), and fowl (Gallus gallus). They probably inadvertently introduced rats (Rattus exulans), many alien plant species (e.g. Ludwigia octovalvis, Oxalis corniulata, Digitaria setigera) (Kirch 1982), and snails (e.g. Allopeas gracile, Lamellidea oblonga) (Cowie 2001a). Introduction of species and alteration of landscapes by Polynesian colonizers changed vegetative communities, increased erosion, and caused the extinction of endemic species (Kirch 1982). When Europeans arrived more species were introduced and change happened at an even faster rate (Nogueira-Filho et al. 2009). Humans have rendered the ability to survive long distance dispersal across the largest oceans and landmasses unnecessary for colonization of even the remotest locations. Now species have only to establish after a boat or plane ride.

Feral pigs are one of the worst invasive species in the Hawaiian Islands. Pigs carry invasive plant seeds, for example, strawberry guava (Psidium cattleianum) and Hilo grass (Paspalum conjugatum), in their digestive tracts and on their fur (Nogueira-Filho et
Strawberry guava is a particularly serious invasive species as it establishes dense stands that out-compete native plants (Vitousek et al. 1987; Hughes and Denslow 2005). Pigs also create breeding pools for mosquitoes (Culex quinquefasciatus). These mosquitoes are vectors of avian malaria (Plasmodium relictum), which devastates native bird populations (Freed et al. 2005). Numerous species of molluscs (snails and slugs), the subject of this thesis, have also been introduced (Cowie 2001a).

MOLLUSCA

Mollusca is the second most diverse animal phylum in terms of described species. It comprises an estimated 100,000 - 200,000 species, of which about 40% are land snails (Solem and van Bruggen 1984; Gaston and Spicer 1998; Cowie 2001a). Land snails, like other macroinvertebrates, play important roles in ecosystem processes such as litter decomposition and nutrient cycling (Jones and Shachak 1990; Jones et al. 1994; Meyer et al. 2011, in review). Molluscs also play key roles as prey of mammals and birds, and even of a moth, the Hawaiian Hyposmocoma molluscivora (Dimelow 1963; Barker and Efford 2004; Rubinoff and Haines 2005). Alien snails have profound effects on agriculture (Barker 2002). For example introduced apple snails are major pests of rice (Oryza sativa) in Asia (Cowie 2002), and taro (Colocasia esculenta) in Hawaii (Tran et al. 2008). On Oahu invasive slugs cause problems for endangered plant restoration (Joe and Daehler 2008).

Since the year 1500 there have been more recorded extinctions among molluscs than in any other major taxonomic group (Lydeard et al. 2004). The International Union for Conservation of Nature (IUCN) Red List includes 302 mollusc species considered to
be extinct, compared to 271 terrestrial vertebrate species (Régnier et al. 2009). However, while 33 of these listed mollusc species are in fact extant, a comprehensive search of the literature found 566 mollusc species to be extinct (Régnier et al. 2009). Thus, although many species have been documented as extinct they are still not listed on one of the most important sources (IUCN Red List) of information for conservation action. Of the 566 extinct mollusc species recorded by Régnier et al. (2009) and Régnier (2010), only four are marine species, and of the 422 extinct terrestrial species, 225 are from the Pacific islands.

Oceanic islands tend to support high numbers of land snail species, per unit area, relative to continental landmasses (Solem and van Bruggen 1984). Lydeard et al. (2004) estimated Pacific island land snail richness to be around 4000 species. This number does not include New Zealand and New Guinea, which have an estimated 2350 species between them (Lydeard et al. 2004). Approximately 750 of these Pacific island species, representing only 11 families, are native to the Hawaiian Islands, and of these over 99 % are endemic to the Islands (Cowie 1995; Holland and Cowie 2009). In contrast, North America supports only about 850 species (Solem and van Bruggen 1984). Pacific island land snails have long been recognized for their diversity, with much attention being paid to the families Partulidae and Achatinellidae (Cowie 1996; Cowie and Cook 2001). Land snail colonization of islands is probably related to their ability to disperse passively blown by the wind (Kirchner et al. 1997) and attached to birds (Rees 1965; Vagvolgyi 1975; Gittenberger et al. 2006), particularly in the case of succineid snails (Ramsden 1914; Anonymous 1936; Cowie 1996), or even in the guts of birds (Wada et al. 2012). Their diversity and endemism is probably related to their sessile nature and ability to
persist in very small ranges for many generations, increasing the chance of genetic
divergence (Solem and van Bruggen 1984).

Unfortunately habitat loss, invasive species and, for certain groups, shell
collecting have devastated native land snail biodiversity in the Pacific (Murray et al.
estimated that 75% of the Hawaiian species had gone extinct; Cowie (2001a) suggested
that this figure was probably closer to 90%.

Pacific islands have been invaded by a large number of alien terrestrial mollusc
species; the Hawaiian Islands are home to more alien species than any other island group
(Cowie 2001a). Cowie et al. (2008) recognized 38 non-native, terrestrial snail and slug
species established in the main Hawaiian Islands, many of which are already widespread.

One of the most notable of these, the giant African snail, *Achatina fulica*, is a
generalist crop and garden pest. It will consume many different plant species, rotting
vegetation, wet cardboard, dead animals, dead crushed snails, warfarin rat poison, moist
soil, and dung (Mead 1961; Meyer et al. 2008). Meyer et al. (2008) documented *A. fulica*
preying on the invasive slug species *Veronicella cubensis* in two locations on Oahu,
suggesting that *A. fulica* may also have played a predatory role elsewhere. The giant
African snail has been introduced widely, mainly purposefully, including to islands in the
Indian and Pacific Oceans, Brazil, the Caribbean, and the United States since the 1800s
(Mead 1961, 1979; Smith 2005; Thiengo et al. 2007). *Achatina fulica* has proved to be
nearly uncontrollable, except in two successful eradication efforts in Florida and
Queensland, Australia (Mead 1979; Simberloff 2003). In the Florida case a young boy
introduced two or three *A. fulica* to Miami in 1966. By 1969 42 blocks had been infested,
and another infestation had been found 40 km away. Six years and $1,000,000 later in 1975, Florida had successfully eradicated the giant African snail. Unfortunately, despite attempted control efforts, the Pacific Islands including Hawaii have not had the success of either Florida or Queensland. Pacific Island control efforts have only caused more, and arguably worse, problems (Murray et. al 1988; Simberloff and Stiling 1996). During the 1950s and 1960s, 15 species of predatory snails and 10 species of beetles were released as putative biocontrol agents in Hawaii in attempts to control *A. fulica* (Davis and Butler 1964; Cowie 2001b). Possibly the most infamous of these introduced biocontrol species is the predatory land snail *Euglandina rosea*, commonly known as the rosy wolf snail or the cannibal snail. *Euglandina rosea* was introduced widely in the Pacific for control of *A. fulica*. However, there is still no good evidence that control has been effective.

*Euglandina rosea* has been, and continues to be, a major contributor to the extinction of native snail species across the Hawaiian and other Pacific islands (Murray et al. 1988; Hopper and Smith 1992; Coote and Loève 2003). Both *E. rosea* and *A. fulica* have been included among a list of 100 of the world’s worst invasive alien species (Lowe et al. 2000).

**OXYCHILUS ALLIARIUS**

Much of the malacological research, since the mid-20th century, in the Pacific, has focused on *A. fulica*, *E. rosea* and the native Pacific Achatinellinae and Partulidae. One invasive snail, *Oxychilus alliarius* (Figure 1.1), has received almost no attention.

*Oxychilus alliarius* is a snail in the family Zonitidae that is native to North West Europe (Kerney and Cameron 1979; Giusti and Manganelli 2002). It is commonly known
as the garlic snail because it will emit a garlic like scent (Miller 1822; Taylor 1906-1914; Giusti and Manganelli 2002), as a defense mechanism (Dimelow 1963; Rudge 1968; Lloyd 1970a; Castillejo 1985; Churchfield 1990). The scent comes from a yellowish substance exuded from a gland on the snail’s mantle flap (Lloyd 1970b). The compound n-propyl mercaptan is the main smell producing component in the substance (Lloyd 1970c).

The shell of *Oxychilus alliarius* is approximately 4.5-7.0 mm in diameter and 2.5 to 3.5 mm in height with an umbilicus that is generally 1/6 of its diameter (Taylor 1906-1914; Castillejo 1985; Giusti and Manganelli 2002). The shell is somewhat translucent, glossy, faintly striated, and has 4 to 4.5 whorls when the snail is adult (Taylor 1906-1914; Castillejo 1985; Giusti and Manganelli 2002). The snail’s body is dark grey blue and has small pits and glandular structures called phylacites around the neck (Lloyd 1969; Lloyd 1970d; Giusti and Manganelli 2002). The foot is slightly lighter colored, thin, and longitudinally tripartite (Taylor 1906-1914; Giusti and Manganelli 2002).

*Oxychilus alliarius* was first described by J. S. Miller (1822) as *Helix alliaria* from “Environs of Bristol” in England. The location of the type specimen is unknown (Barker 1999).

*Oxychilus alliarius* has been introduced to the Azores (Martins 1995), Tenerife (Kappes et al. 2009), Gough Island (Jones et al. 2003), Saint Helena (Wollaston 1878), South Africa (Macdonald et al. 2003; Herbert and Kilburn 2004), Chile (Cádiz and Gallardo 2007), Colombia (Hausdorff 2002), Canada (Forsyth 1999, 2010), New Zealand (Barker 1982; Barker and Efford 2004), South Australia (Pomeroy and Laws 1967), Réunion (Griffiths and Florens 2006), Hawaii (Cowie 1997), and probably other
locations around the world. It was first found on the island of Hawaii around the town of Waimea in 1937 (Cowie 1997). By around 1945-46 it was abundant on Maui and the island of Hawaii (Cooke and Baker 1947). Severns (1984) found it widespread on Maui, including in the West Maui Mountains, on the top of Haleakala (3055 m), and on the “cinder-filled Haleakala valley floors”. He commented that *O. alliarius* was so abundant one “could scoop them up by the hundreds from the leaf litter.” It is now on the six largest Hawaiian Islands (Hayes et al. 2012).

POTENTIAL IMPACTS OF *OXYCHILUS ALLIARIUS*

*Oxychilus alliarius* is a predator of other snails and their eggs (Taylor 1906-1914; Barker 1999; Meyer and Cowie 2010a), but it will also consume non-snail and non-animal foods (Mason 1970; Barker and Efford 2004). Meyer and Cowie (2010a) found that *O. alliarius* preferentially feeds on snails of less than 3 mm in maximum dimension, although it will attack and consume much larger snails (Curry and Yeung unpublished; Figures 1.2, 1.3). Many Pacific island land snails, including most Hawaiian species, are small, less than 3 mm as adults or at least as juveniles. These include the huge diversity of species in, for example, the families Succineidae, Helicarionidae, including the genus *Philonesia* (Baker 1940), Achatinellidae, including the genus *Tornatellides* (Cooke and Kondo 1960), and Endodontidae (Solem 1976). Although the feeding rates of *Oxychilus alliarius* are much lower than those of *Euglandina rosea*, its wide elevation range in the Hawaiian Islands (Meyer and Cowie 2010b), very high densities in relatively undisturbed habitats (Severns 1984; unpublished data from surveys carried out by K.A. Hayes and collaborators) and ability to consume mollusc as well as non-mollusc food mean that it
may be having a negative impact through predation and perhaps competition on native snails, which are already effected by habitat destruction and other invasive species, especially those confined to high elevation refugia (Meyer and Cowie 2010a). Gaining a better understanding of its potential spread, constraints on its distribution, and possible mechanisms of transport to new locations is important for mitigating the threat not only to endemic island snails but also to entire ecosystems where it is introduced. Addressing these questions in detail in Hawaii will provide valuable information for controlling its spread to other locations where it has not yet been introduced.

THESIS GOALS

My research is focused on the invasive snail *Oxychilus alliarius*. This thesis addresses the following issues.

1) The spread of *O. alliarius* into the summit bog on Mt. Kaala, the highest mountain on the Hawaiian Island of Oahu.

2) The impacts of *O. alliarius* on the native snail community of the Mt. Kaala summit bog.

3) The environmental variables determining the distribution of *O. alliarius* in the Hawaiian Islands.

4) The potential suitability of 31 other tropical and subtropical islands and island groups in the Pacific, Indian and Atlantic Oceans, and the Caribbean Sea for establishment of *O. alliarius*.

Issues 1 and 2 are addressed in Chapter 2 and issues 3 and 4 are addressed in Chapter 3 of the thesis. These studies provide a quantitative assessment of the rate of spread of *O.*
alliarius and its potential impacts on native biodiversity, and a predictive model to assess its potential future range in tropical and subtropical islands globally, important information in the future management of the spread of this invasive snail species. This overall significance of the research is summarized and discussed further in the concluding Chapter 4.
Figure 1.1. *Oxychilus alliarius*.

Figure 1.2. *O. alliarius* consuming *Kaala subrutila*.

Figure 1.3. *O. alliarius* consuming a species of Hawaiian Helicinidae.
Chapter 2

Impact of the predatory snail *Oxychilus alliarius* on native Hawaiian land snails in the Mt. Kaala Natural Area Reserve
ABSTRACT

The European predatory snail *Oxychilus alliarius* has established a population on Mt. Kaala, the highest mountain on the Hawaiian Island of Oahu (1220 m above sea level). This population had been expanding its range across a bog on the summit of the mountain since before September 2008, when it was first recorded there. I hypothesized that *O. alliarius* would continue to expand its range across the summit bog, and that in areas where it established the small native snails (<3 mm in maximum dimension as adults) would decline in numbers or disappear. To assess whether the population was expanding I monitored how far it extended into habitat adjacent to a boardwalk running through the bog each month for one year. To assess whether there were differences in native snail numbers within and outside the range of *O. alliarius* I monitored the relative abundances of seven taxonomic groups of native snail species at ten sites 100 m apart along a transect represented by the board walk on a monthly basis for nine months. I found that *O. alliarius* was expanding its range, and that between September 2008 and May 2011 it moved approximately 300 m along the transect. I also found that there was a negative relationship between *O. alliarius* abundance and Succineidae abundance and a positive relationship between *O. alliarius* abundance and Tornatellidinae abundance. Other groups showed no significant trends.

INTRODUCTION

As the world sustains continuing biological invasions, and extinctions caused by those invasions, it is moving toward a state of biotic homogenization (Olden et al. 2004; Rooney et al. 2007). As many species become established over increasingly wider ranges,
there is and will be an increasing need to understand their impacts and the relationships they have with the indigenous species they encounter. Specifically it is important to know whether they are causing declines among indigenous species. Oceanic islands are particularly susceptible to biotic invasions (Baret et al. 2006; Eldredge 2006; Kraus and Duffy 2010) and island species are particularly susceptible to extinction caused by those invasions (Fritts and Rodda 1998; Lydeard et al. 2004; Donlan and Wilcox 2008). The Hawaiian Islands have seen major increases in species introductions over the last two centuries (Cox 1999). While much conservation effort in Hawaii focuses on those native species listed as endangered or threatened, the numerous unlisted native species suffer from most of the same pressures and face the same fate. Globally, conservation and restoration tends to be focused on charismatic vertebrate species, even though the often overlooked invertebrates are more in need as there is probably considerably greater loss of invertebrate and plant biodiversity (McKinney 1999; Cowie 2001a; Régnier et al. 2009; Zamin et al. 2010).

Nonetheless, some invertebrates have begun to receive conservation attention. These include in particular the tree snails of the Hawaiian islands (Achatinellinae) and of other Pacific islands (Partulidae), which are known for their colored and patterned shells, but that are threatened with extinction as a result of ill-conceived biological control programs (Clarke et al. 1984; Murray et al. 1988; Hadfield et al. 1993; Cowie 1992, Cowie 2001b; Lydeard et al. 2004; Lee et al. 2009). However, these species represent only a small portion of the native terrestrial snail diversity of the Pacific (Baker 1940; Cooke and Kondo 1960; Solem 1976), much of which is also extinct or threatened with extinction (Bouchet and Abdou 2001, 2003). In the Hawaiian Islands there were >750
native terrestrial snail species, over 99% endemic (Cowie 1995, Cowie et al. 1995), with 75-90% estimated as having already gone extinct (Solem 1990; Cowie 2001a). Concurrently with this loss through extinction, non-native land snail species have been introduced to Hawaii (Cowie 1998; Cowie et al. 2008), including the relatively well studied *Euglandina rosea* and *Achatina fulica* (Mead 1961; Kekauoha 1966; Hadfield and Mountain 1980; Hadfield et al. 1993; Meyer et al. 2008; Meyer and Cowie 2010, 2011; Sugiura et al. 2011). However, little is known about most other introduced snails.

One introduced snail that has begun to receive attention in Hawaii is *Oxychilus alliarius*, the garlic snail, so-named for its emission of a garlic-like scent when irritated (Miller 1822; Lloyd 1970). It is a predatory species (Taylor 1906-1914; Barker 1999), but also feeds on non-animal foods (Mason 1970; Barker and Efford 2004), and it is now established in many places around the world (Barker 1999; Giusti and Manganelli 2002; Herbert and Kilburn 2004). Anecdotal evidence suggests that where it is introduced *O. alliarius* negatively affects indigenous snails (Severns 1984; Barker 1999); no studies have quantified such impacts.

The goal of this study was to determine the rate of spread of an expanding population of *O. alliarius* and to assess the population’s impacts on the indigenous snail biodiversity. Because when given a choice, *O. alliarius* preferentially consumed small snails (<3 mm in maximum dimension) in experiments (Meyer and Cowie 2010), I hypothesized that the small snails would be less abundant or absent where *O. alliarius* was established, and would decline or disappear as *O. alliarius* expanded its range.
METHODS

Study area

Surveys were performed along a transect, an approximately 875 m section of trail that runs from an access road through the summit bog on Mt. Kaala (21°30'18" N, 158° 8'48" W), the highest mountain on the Hawaiian island of Oahu. The bog is approximately 1 km², has a mean annual air temperature around 16 °C, and receives approximately 1800-2000 mm of rainfall annually (Giambelluca et al. 2011). The bog’s forest is dominated by native trees (e.g., *Metrosideros polymorpha*, *Cheirodendron* spp.), ferns (*Cibotium* spp.), and shrubs (*Melicope* spp., *Broussaisia arguta*) that show stunted growth and are typically <5-6 m tall. The ground along the trail is covered by grasses, leaf litter, and in many places, a dense carpet of non-native *Sphagnum* sp. moss. The area is set aside for conservation of its relatively intact native ecosystem.

*Oxychilus alliarius* was recorded on the Mt. Kaala summit for the first time during preliminary surveys in September 2008, and subsequently in June and December 2009. At that time it was only present near the access road. In 2010 a transect was established and monitored monthly to assess the possible spread and relative abundance of *O. alliarius* and the relative abundances of other native and non-native snails. The transect consisted of ten sites established along the trail spaced 100 m apart (Table 2.1), except for the site closest to the access road, which was only 50 m from the previous site (Figure 2.1). Site elevation ranged from 1075 m to 1220 m asl.
Faunal surveys

Faunal surveys were conducted monthly from July 2010 until April 2011 (with the exception of March 2011). At each site a circular area (radius 5 m) was searched for 1 person hour by two or more experienced snail biologists. At all sites as many microhabitat types as possible were physically searched according to the methods of Cowie et al. (2008) (under leaves, in weedy vegetation, in trees, under rocks, under bark, in ground litter, etc.). All snails found were identified to the lowest taxonomic level possible in the field and recorded. Vouchers were taken to ensure accurate identification. Based on an examination of shell morphology, as well as preliminary molecular analysis (N.W. Yeung unpublished) none of these larger groups included more than two or three species.

*O. alliarius* range expansion

Additional monitoring was conducted monthly from May 2010 to May 2011 to assess the extent of the range of *O. alliarius* along the trail, beginning at the access road and heading along the transect (Figure 2.1). These additional ground surveys (in the soil, under leaves and rocks, etc.) focused solely on *O. alliarius* and were conducted based on the furthest point from the access road where it had last been found. Surveys lasted 30 person minutes or until an *O. alliarius* specimen was found, whichever was sooner, and each survey covered a circular area (5 m radius). From the furthest point of the previously established range of *O. alliarius*, surveyors moved 20 m farther along the trail and carried out an additional survey. If *O. alliarius* shells or live individuals were present, the surveyors moved another 20 m along the trail and surveyed another circular area (5 m
radius). This survey process was repeated until no *O. alliarius* shells or live snails could be found. The surveyors then returned to the last point at which live snails had been found and performed a survey 10 m farther along the transect. If shells but no live snails were found at this location, then the previous point represented the extent of the contiguous range of *O. alliarius*, and was known to within 10 m. If an *O. alliarius* range extension survey coincided with one of the main faunal surveys, the latter served as the range extension survey. On occasion a live *O. alliarius* or empty shell was found hundreds of meters further than had been previously recorded, but not as part of the contiguous range (see results and discussion).

Seven additional sites were searched for *O. alliarius* in February and April 2011 to assess its possible range extension beyond the immediate proximity of the trail transect. The additional sites were located 25 m away from the transect in a direction approximately perpendicular to the transect and on both sides of it adjacent to sites 3, 5, and 7 (Figure 2.1). An additional site 50 m south-east of site 4, in a direction perpendicular to the transect, was also surveyed, in February 2011 (Figure 2.1). Surveys at these sites lasted 30 person minutes and covered the same area (5 m radius) as the transect surveys.

**Statistical analysis**

Abundances of *Oxychilus alliarius* and the native snail groups were averaged for each site over the course of the surveys. Then simple linear regression analyses were run between *O. alliarius* average abundances and each native snail group’s average
abundance. Species richness and evenness (Pielou’s diversity index; Pielou 1966) were also calculated for each of the 10 sites.

RESULTS

*Oxychilus alliarius* was first recorded on the summit of Mt. Kaala in September 2008, on the north-east side of the summit bog (21°30'26.16"N, 158° 8'38.04"W), approximately 70 m from the access road. Between this first record and the end of the study in May 2011 (32 months) its population expanded approximately 300 m, at an average rate of around 113 m per year, so that its maximum contiguous range extended 370 m from the access road (Table 2.2). The rate of expansion varied and the population even seemed to have contracted between some survey occasions, although these instances may have been artifacts due to sampling effects. On a few occasions shells and/or live *O. alliarius* were found, in small numbers, at locations a considerable distance along the transect beyond the extent of the contiguous range and up to 450 m beyond the access road (Table 2.2). These propagules were not considered to be part of the contiguous range from the perspective of assessing the population expansion rate.

*Oxychilus alliarius* was recorded at both the extra sites adjacent to site 3 but not at those adjacent to sites 5 or 7, and not at the site 50 m south-east of site 3. At the site north-west of site 3 there were three live *O. alliarius* and 12 shells in February and six live snails and 12 additional shells in April 2011. At the site south-east of site 3 only one shell was found in February and one live snail and three shells in April 2011.

At least seven native snail taxa were recorded along the transect during the study (Table 2.3). Throughout the study *O. alliarius* abundances were highest at sites 1 and 2
(Table 2.3), where the population was first recorded. Average abundance decreased sharply at site 3, and the species was absent between sites 7 and 10. At site 6 it was absent except on one occasion, September 2010, when one live snail was found. Over the year-long study *O. alliarius* expanded its contiguous range from site 3 to site 5, which it reached in April 2011. At site 3 there was no discernible change in *O. alliarius* abundance over the course of the year (0-6 *O. alliarius* collected per hour). It was found at site 4 in January and maintained very low numbers through the rest of the study (1-3 recorded per hour). Overall native snail abundances were higher at sites 4 through 8 than at sites 1, 3, 9, and 10, although site 2 had the highest average abundance. This high overall native snail abundance at site 2 was driven by a few higher than average counts of *Elasmias* and Tornatellidinae.

The surveys indicated that the abundance of *O. alliarius* is not related to that of the various native snail taxa in the same way. Only three native snail abundances were significantly related to *O. alliarius* abundance: negatively for Succineidae (p = 0.001; R² = 74.8; d.f. = 1/9; F = 23.77) and positively for Tornatellidinae (p<0.0001; R² = 92.7; d.f. = 1/9; F = 102.29) and Pupillidae (p = 0.014; R² = 55.0 %; d.f. = 1/9; F = 9.78). Abundance of Helicarionidae and *Auriculella* species seemed to be negatively related to *O. alliarius* abundance although these relationships were not significant. *Elasmias* abundance showed no apparent trend. While average abundances of snails varied over time, there were no seasonal trends.

Species evenness varied from 0.408 (site 9) to 0.758 (site 4) (Table 2.3). None of the sites had all eight snail taxa; site 10 had five taxa, while all other sites had six or seven. Succineidae were found at every site and were the most common snails recorded.
through the study; their highest numbers were at sites 6-10. They constituted a relatively large proportion of the snails at every site except site 1 (Fig. 2.2). *Elasmias* sp., Succineidae, Helicarionidae, and Pacificellinae were either absent or very rare at site 1, but the Tornatellidinae were recorded in relatively high abundances. Pupillidae, which were rare throughout the study, were also recorded in their highest numbers at site 1. *Auriculella* spp. were also recorded at site 1, although never more than three in a single month. *Elasmias* sp. made up the largest proportion of the snails at site 2 (Fig. 2.2), where in February and April 2011 59 and 85 snails were recorded per hour, respectively. Helicarionidae were common at sites 3 through 8, and site 10, but were not recorded at sites 1 and 9. *Auriculella* spp. were less common than most of the other snails, but were recorded at their highest relative abundances between sites 4 and 8.

**DISCUSSION**

Based on almost 3 years of surveying, including a year of intensive surveying, I found that *Oxychilus alliarius* is rapidly colonizing new habitat on Mt. Kaala, the highest mountain on the Hawaiian island of Oahu. Overall, from September 2008 to May 2011, the species has moved approximately 300 m, expanding its range along the transect at a rate of approximately 113 m per year. However, this rate was not constant (Table 2.2). Specifically, between September 2008 and December 2009 *O. alliarius* moved at approximately 12.7 m per month (152 m per 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. Given the differences in rates, there is the possibility that snail propagules were accidentally transported along the
boardwalk by either natural or unnatural events. By February 2011, expansion of both the contiguous range and the isolated populations resulting from such propagules had closed the gap, resulting in a much extended contiguous range. In May and September 2010 single live *O. alliarius* individuals were found far ahead of the main population and shells were recorded at the same location in December 2010, which suggests that there was a small population at this location during 2010, probably established from a small propagule, but that the snails did not survive long enough for the main population to extend contiguously to this point during the study.

The transect followed the wooden boardwalk that runs through the summit bog and crossed the expansion front of the *Oxychilus alliarius* population, allowing the surveys to be conducted with minimal damage to the native ecosystem. However, the boardwalk may also have facilitated *O. alliarius* expansion through the bog, transported accidentally by people on clothes and footwear, perhaps as eggs in aggregate dirt clods, or on construction materials used in maintenance of the boardwalk. These mechanisms of spread may explain the occasional individuals found along the transect beyond the contiguous distribution at various times.

The additional survey sites 25 m and 50 m from the transect further support the idea that the boardwalk facilitates the advance of *O. alliarius*. In March 2011 the contiguous range extended almost to site 5, approximately 330 m from the access road (Table 2.1), but *O. alliarius* was not found 50 m south-east of site 3, which is closer to the access road. By about April 2011 the contiguous range had reached site 5, and previously, in November 2010, it had been recorded at site 5, though not as part of the
contiguous range. Yet in neither March nor April 2011 was it recorded at the extra sites north-west and south-east of site 5.

Succineidae, the abundance of which was negatively related to *O. alliarius* abundance, were found in the leaf litter more frequently than most other snail groups, such as *Auriculella*, Tornatellidinae, and *Elasmias*, which were almost never found in the leaf litter. *Oxychilus alliarius*, which is primarily a ground dwelling species, would have encountered Succineidae more frequently than these groups and presumably would have attacked them. In laboratory feeding trials *O. alliarius* consumed Succineidae and other Hawaiian snails (Meyer and Cowie 2010; Curry and Yeung unpublished). Some species of *Oxychilus* are egg predators (Barker and Efford 2004), and as Hawaiian Succineidae lay large egg masses both in the leaf litter and on the shrubs, it is possible that *O. alliarius* may have been consuming succineid eggs as well as snails.

Average Tornatellidinae abundances were low at most sites, although noticeably higher at sites 1 and 2. The habitat at these two sites is dominated by tall grasses and many Tornatellidinae were found on the grass stems. Although there was a significant positive relationship between Tornatellidinae and *O. alliarius* abundances, this relationship is probably related to their respective habitat preferences and the fact that *O. alliarius* were never found climbing the grass stems, the two taxa thereby rarely coming into contact.

*Philonesia*, which were the most commonly found Helicarionidae, live primarily in the native trees and shrubs. They were never found in grass but were occasionally found in the leaf litter. While there was not a significant relationship between *O. alliarius* abundance and Helicarionidae abundance, there were fewer Helicarionids at sites with
high numbers of *O. alliarius* than at sites with low numbers or where *O. alliarius* was absent. The exception was site 9, where no Helicarionidae were recorded, even though there were no *O. alliarius* at this site. Site 9 is on an exposed ridgeline at the south-west end of the transect. There is little leaf litter and the site is dominated by grasses and leafy herbaceous shrubs mostly less than 2 m tall (*Machaerina* sp., *Dianella sandwicensis*, *Smilax melastomifolia*; Table 2.1). The absence of Helicarionidae at this site probably has to do with the lack of woody shrubs and wet leaf litter.

The Mt. Kaala endemic helicarionid, *Kaala subrutila*, was most often found in the leaf litter. Live *K. subrutila* were not found at sites 1-4, where *O. alliarius* was already established, or expanded into during the study. However, a *K. subrutila* shell was found near site 3 indicating that previously its range had probably extended at least this far. Generally the highest numbers of *K. subrutila* were found at site 5, which is approximately 350 m from the access road. By the end of the study *O. alliarius* had reached this site, at which time *O. alliarius* was recorded consuming a *K. subrutila* in the field (Curry and Yeung unpublished). While there was no significant relationship between overall Helicarionidae abundance and *O. alliarius* abundance, it is possible that these species are being detrimentally impacted by *O. alliarius* predation.

Abundance of *Auriculella* spp., which were nearly always found in shrubs or trees, seemed more related to habitat than to the presence of *O. alliarius*. They were relatively abundant between sites 4 and 8, but not at others. At site 1, where the highest abundances of *O. alliarius* were recorded, there were about four *Auriculella* living in a single isolated *Metrosideros polymorpha*, no taller than 2 m, through the course of the study. Furthermore, I found relatively few at sites 9 and 10, which had no *O. alliarius*
through the study. As tree and shrub dwellers they are probably rarely encountered by *O. alliarius*.

*Elasmias* were generally found on vegetation about a meter or more off the ground. Their abundance did not seem to be related to that of *O. alliarius*, their average abundances being fairly similar across sites. However, their highest abundances, 59 and 85 snails recorded per hour in January and April 2011, respectively, were at site 2, where there were high abundances of *O. alliarius*. Nonetheless, at site 1, where *O. alliarius* was even more abundant, *Elasmias* occurred at its second lowest abundance (0.89 per hour). Site 1 may simply not be suitable habitat for *Elasmias*.

*Pacificellinae* were rare, and did not show any real trends in relation to *O. alliarius* abundance, but were always found in shrubs or tall grass. *Pupillidae* were also rare, but were unusual in that they were in the ground cover (grass and the herb *Plantago major*) even at site 1, where there were the most *O. alliarius*. Because of their small size (1-2 mm as adults), and presumably low overall abundance, they were extremely difficult to find during the surveys. Nonetheless their abundance did not seem to be related to that of *O. alliarius*, as evidenced by their presence on the ground at site 1.

In conclusion, *Oxychilus alliarius* is expanding its range in the Mt. Kaala bog. This is especially apparent along the boardwalk where it seems to be being transported by natural or unnatural events. The expanding population along the boardwalk may also serve as a source for *O. alliarius* to expand outwards into the bog. To prevent hitchhiking by live *O. alliarius* or its eggs people should brush all dirt and debris off their boots and clothes regularly, possibly in designated areas, and especially before going off the boardwalk trail. Equipment going to or from Mt. Kaala should be cleaned before it is
moved, and possibly most importantly, out-plantings should be searched for any snails before taking them to or from Mt. Kaala. The _O. alliarius_ population is expanding out from the Kaala access road, which indicates that the original colonizers probably came up the road on vehicles rather than being accidentally brought up to the bog by hikers accessing Kaala from the trail at the opposite end of the study area.

Native snail species abundances were related to the abundance of _O. alliarius_ in different ways, negatively in the case of Succineidae and probably Helicarionidae, although more data are needed to confirm or refute the latter relationship. Tornatellidinae and _Elasmias_ abundances seemed unrelated to that of _O. alliarius_, and they were always found off the ground. However, at sites other than Mt. Kaala, Tornatellidinae (perhaps other species) are found in the leaf litter (N.W. Yeung personal communication). Habitat and microhabitat preference are probably very important in determining whether the native snails will encounter _O. alliarius_. It is also possible that reproductive strategy plays a role. While the Succineidae lay eggs that may be preyed upon by _O. alliarius_ if laid on the ground, many other Hawaiian snails do not lay eggs but give birth to live young (e.g. _Achatinella_ spp.; _Kaala subrutila_, and possibly other Hawaiian Helicarionidae, are probably ovoviviparous (Baker 1940). This means that if _O. alliarius_ predates a snail that is gravid, the mother and all offspring will be affected.

The relationships between _O. alliarius_ and native snail species in areas it invades are important to understand. It is likely that _O. alliarius_ populations expanded in a similar way in other places to which it has been introduced, not only in the Hawaiian Islands (Cowie 1997; Cowie et al. 2008), but in other islands and locations around the world (e.g., Barker 1999; Giusti and Manganelli 2002; Herbert and Kilburn 2004). It may have
had similar possible impacts on the native snails of those areas. Preventative measures are the best ways to minimize its establishment and spread. But for effective management aimed at conserving the native land snail faunas there will not only need to be an understanding of the ecology of *O. alliarius* but of the ecology of each of the native species potentially affected. Knowing which species are most vulnerable is important for the development of conservation plans.
Table 2.1. Descriptions of the habitat at the ten transect sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Habitat description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Immediately next to the access road, ~70% short grass with sparse <em>Plantago major</em> herbs, ~30% tall grass (&gt;1 m), one small <em>Metrosideros polymorpha</em> sapling</td>
</tr>
<tr>
<td>2</td>
<td>Beginning of boardwalk, patches of <em>M. polymorpha</em>, <em>Brossaisia arguta</em>, <em>Melicope</em> sp., <em>Cibotium</em> sp., and other shrub, tree, and herb species between short and tall grass, exposed leaf litter under shrubs and trees</td>
</tr>
<tr>
<td>3</td>
<td>Dense forest of shrubs and trees, mainly <em>M. polymorpha</em>, <em>B. arguta</em>, <em>Melicope</em> sp., <em>Cibotium</em> sp., and some <em>Cheirodendron</em> spp., ground covered in leaf litter and some <em>Sphagnum</em> sp. moss, wooden boardwalk running through the site</td>
</tr>
<tr>
<td>4</td>
<td>Dense forest of shrubs and trees, mainly <em>M. polymorpha</em>, <em>B. arguta</em>, <em>Melicope</em> sp., <em>Cibotium</em> sp., and some <em>Cheirodendron</em> spp., ground covered in leaf litter, but more <em>Sphagnum</em> sp. moss than site 3, wooden boardwalk running through the site</td>
</tr>
<tr>
<td>5</td>
<td>Dense forest of shrubs and trees, mainly <em>M. polymorpha</em>, <em>B. arguta</em>, <em>Melicope</em> sp., <em>Cibotium</em> sp., and some <em>Cheirodendron</em> spp., ground covered in leaf litter, and <em>Sphagnum</em> sp. moss, wooden boardwalk running through the site</td>
</tr>
<tr>
<td>6</td>
<td>Open area mainly covered in <em>Sphagnum</em> sp. moss, but also some leaf litter, surrounded by forest of shrubs and trees, mainly <em>M. polymorpha</em>, <em>B. arguta</em>, <em>Melicope</em> sp., <em>Cibotium</em> sp., <em>Cheirodendron</em> spp., and a few large <em>Machaerina angustifolia</em>, wooden boardwalk running through the site</td>
</tr>
<tr>
<td>7</td>
<td>Dense forest of shrubs and trees, mainly <em>M. polymorpha</em>, <em>B. arguta</em>, <em>Melicope</em> sp., <em>Cibotium</em> sp., and some <em>Cheirodendron</em> spp., ground covered in leaf litter, and <em>Sphagnum</em> sp. moss, wooden boardwalk running through the site</td>
</tr>
<tr>
<td>8</td>
<td>Dense forest of shrubs and trees, mainly <em>M. polymorpha</em>, <em>B. arguta</em>, <em>Melicope</em> sp., <em>Cibotium</em> sp., and some <em>Cheirodendron</em> spp., ground covered in leaf litter, less <em>Sphagnum</em> sp. moss, wooden boardwalk running through the site</td>
</tr>
<tr>
<td>9</td>
<td>Exposed ridgeline, much drier than forested sites, ground mainly covered in short grass, the shrubs and trees are <em>M. angustifolia</em>, <em>Dianella sandwicensis</em>, <em>B. arguta</em>, and <em>M. polymorpha</em>, although there is little canopy, dirt trail runs through the site</td>
</tr>
<tr>
<td>10</td>
<td>Relatively wet muddy site, less dense forest with taller trees (&gt;3 m), <em>Cheirodendron</em> spp., <em>Cibotium</em> sp., <em>B. arguta</em>, <em>Melicope</em> sp., and other shrubs and trees, approximately 10 m off of dirt trail, southwest most site</td>
</tr>
</tbody>
</table>
Table 2.2. *Oxychilus alliarius* range expansion along the transect.

<table>
<thead>
<tr>
<th>Date</th>
<th>Months since first record</th>
<th>Extent of contiguous range from access road (m)</th>
<th>Expansion of contiguous range since previous survey (m)</th>
<th>Distance of unconnected propagules from access road (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sep 2008</td>
<td>0</td>
<td>70</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Jun 2009</td>
<td>9</td>
<td>150</td>
<td>80</td>
<td>-</td>
</tr>
<tr>
<td>Dec 2009</td>
<td>15</td>
<td>200</td>
<td>50</td>
<td>-</td>
</tr>
<tr>
<td>May 2010</td>
<td>20</td>
<td>180</td>
<td>-20</td>
<td>450</td>
</tr>
<tr>
<td>Jun 2010</td>
<td>21</td>
<td>205</td>
<td>25</td>
<td>-</td>
</tr>
<tr>
<td>Jul 2010</td>
<td>22</td>
<td>195</td>
<td>-10</td>
<td>-</td>
</tr>
<tr>
<td>Aug 2010</td>
<td>23</td>
<td>200</td>
<td>5</td>
<td>270</td>
</tr>
<tr>
<td>Sep 2010</td>
<td>24</td>
<td>210</td>
<td>10</td>
<td>450</td>
</tr>
<tr>
<td>Oct 2010</td>
<td>25</td>
<td>210</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Nov 2010</td>
<td>26</td>
<td>250</td>
<td>40</td>
<td>330, 350</td>
</tr>
<tr>
<td>Dec 2010</td>
<td>27</td>
<td>240</td>
<td>-10</td>
<td>350</td>
</tr>
<tr>
<td>Jan 2011</td>
<td>28</td>
<td>250</td>
<td>10</td>
<td>330</td>
</tr>
<tr>
<td>Feb 2011</td>
<td>29</td>
<td>330</td>
<td>80</td>
<td>-</td>
</tr>
<tr>
<td>Mar 2011</td>
<td>30</td>
<td>330</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Apr 2011</td>
<td>31</td>
<td>360</td>
<td>30</td>
<td>-</td>
</tr>
<tr>
<td>May 2011</td>
<td>32</td>
<td>370</td>
<td>10</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 2.3. Species richness (number of species recorded at each site over the course of the study), species evenness (Pielou’s evenness index) and mean abundance (± standard deviation) of each taxon at each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Richness</th>
<th>Evenness</th>
<th>O. alliusrius</th>
<th>Auriculella spp.</th>
<th>Elasmias sp.</th>
<th>Pacificellae</th>
<th>Helicarionidae</th>
<th>Pupillidae</th>
<th>Succinea</th>
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Figure 2.1. Map of the transect along the boardwalk at the summit of Mt. Kaala and the location of Mt. Kaala on the island of Oahu.
Chapter 3

The potential tropical island distribution of a temperate invasive snail, *Oxychilus alliarius*, modeled on its distribution in Hawaii
ABSTRACT

Globalization has led to increases in rates of biotic homogenization around the world in the last few centuries. Therefore, understanding the locations that species can be spread to has become increasingly important. Species distribution modeling is a method of estimating what habitat types and hence which areas around the world are most likely to be affected by a particular invading species. Oceanic islands typically have very high levels of indigenous snail biodiversity when compared with continental land masses. The predatory snail *Oxychilus alliarius*, which has already been introduced to many places around the world, including some island groups, may have the potential to cause major declines in indigenous snails where it is established. Here I present the four best of 36 models that use *O. alliarius* presence and absence data from the Hawaiian Islands of Maui and Hawaii to estimate habitat suitability on the six largest Hawaiian Islands, validating the estimates based on known distributions of *O. alliarius* on the other four islands (Molokai, Lanai, Oahu, and Kauai). These models were further validated with data from four other islands around the world to which *O. alliarius* has been introduced. They were then applied to 31 tropical and subtropical islands and island groups around the world, on which *O. alliarius* has not been recorded, to predict the extent of suitable habitat on those islands and thus the potential for *O. alliarius* establishment should it be introduced. The results showed that there are islands with suitable *O. alliarius* habitat in the Pacific, Indian and Atlantic Oceans, and in the Caribbean Sea, and that the four models make slightly different predictions based on which environmental variables they use. The models indicate that there is still a large amount of area on islands supporting indigenous snail species that is suitable for establishment of *O. alliarius*. 
INTRODUCTION

Throughout the past half millennium, globalization has caused a dramatic increase in the spread of non-native species around the world (Hulme 2009). Rapid introductions of novel species have been linked to loss of biodiversity (Wilcove et al. 1998; McKinney and Lockwood 1999), which leads to biotic homogenization, as diverse and geographically structured biotas are replaced by a small number of widely distributed species (Cowie 2001a; Olden et al. 2004). Endemic island species, many of which have naturally small and confined populations, are particularly susceptible to extinctions compared to species on larger land masses (Vitousek et al. 1987; Lydeard et al. 2004; Baret et al. 2006; Régnier et al. 2009). Furthermore, island populations may have evolved for millions of years in the absence of predation or competition, leading to loss of the defenses necessary to resist the detrimental effects of invaders (Paulay 1994).

Oceanic islands tend to support high numbers of land snail species, per unit area, relative to continental landmasses, and the faunas exhibit high endemicity (Solem and van Bruggen 1984; Cowie 1995, 1996). The high diversity and endemism are probably related to the sessile nature of snails and their ability to persist in very small ranges for many generations, thereby increasing the chance of genetic divergence (Solem and van Bruggen 1984). In the Pacific islands alone, including New Zealand and New Guinea, there are an estimated 6,350 known species of land snails (Lydeard et al. 2004).

Land snails are particularly vulnerable to invasions. Since 1500 there have been more recorded extinctions among molluscs than in any other major taxonomic group (Lydeard et al. 2004; Régnier et al. 2009; Régnier 2010). Of these extinctions, the highest proportions are among snails on Pacific islands (Régnier et al. 2009). Traditionally,
conservation has focused on charismatic megafauna and vertebrate species (Ponder and Lunney 1999), although recent efforts in the Pacific, notably in Hawaii (Hadfield et al. 2004; Hall and Hadfield 2010), Tahiti and Moorea (Coote et al. 2004; Lee et al. 2007), and New Zealand (Stringer and Parrish 2008; Trewick et al. 2008; Walker et al. 2008) are beginning to target land snails.

In many cases introduced snails are among the most harmful predators and competitors of indigenous snails (Clarke et al. 1984; Hadfield et al. 1993; Cowie 2001b; Carlsson et al. 2005). Control and eradication of invasive snails is extremely difficult (Mead 1979; Cowie 2001b; Barker 2002; Joshi and Sebastian 2006), so it is critical to prevent the introduction of these potentially damaging species in the first place (Leung et al. 2002).

*Oxychilus alliarius*, commonly called the garlic snail for its ability to emit a garlic-like scent as a defense (Miller 1822; Lloyd 1970), is an invasive predatory snail native to Western Europe. It is now established in many places around the world, including Greenland (Giusti and Manganelli 2002), the Azores (Martins 1995), Tenerife (Kappes et al. 2009), Gough Island (Jones et al. 2003), Saint Helena (Wollaston 1878), South Africa (Macdonald et al. 2003; Herbert and Kilburn 2004), United States (Pilsbry 1946), Canada (Forsyth 1999, 2010), Colombia (Hausdorf 2002), Chile (Cádiz and Gallardo 2007), Juan Fernandez Island (Giusti and Manganelli 2002) New Zealand (Barker 1982; Barker and Efford 2004), South Australia (Pomeroy and Laws 1967), Reunion (Griffiths and Florens 2006), Hawaii (Cowie 1997), and probably other locations as well, and has been designated a “travelling species” by Robinson (1999), as it is readily transported accidentally associated with human activities. It is a predatory
species that feeds on other snails and possibly their eggs (Taylor 1906-1914; Barker 1999; Barker and Efford 2004; Meyer and Cowie 2010a), although it also consumes non-animal foods (Mason 1970; Barker and Efford 2004). As a predator it has been thought to threaten native land snails (Severns 1984; Barker 1999; Forsyth 1999).

The first record of *O. alliarius* in Hawaii dates to 1937 (Cowie 1997), although it has probably been present in the islands for longer. In the 1940s it was found on the islands of Maui and Hawaii (Cooke and Baker 1947), and since then it has also been recorded on the islands of Oahu, Kauai, Molokai (Meyer and Cowie 2010a) and Lanai (Hayes et al. 2012).

Here I use a species distribution modeling approach to identify the most important environmental factors determining the distribution of *O. alliarius* in the Hawaiian Islands and then select the best fitting models to project the extent of suitable habitat for *O. alliarius*. Using these best fitting models, I further validate them on four other tropical islands to which *O. alliarius* has been introduced. Finally, I use the models to predict the potential distribution of *O. alliarius* to tropical islands globally.

**METHODS**

**Survey methods and sites**

The data are from 231 sites surveyed between 2004 and 2011 across the six largest Hawaiian Islands (Figure 3.1). The sites covered a broad a range of habitat types, from ungulate degraded grasslands to dry windblown ridgelines to nearly pristine cloud forests. Site elevations ranged from sea level to 2,831 m. Constraints on site locations were access permission, physical accessibility, and safety. Surveys generally lasted two
person hours. During each survey as many microhabitat types as possible were physically searched according to the methods of Cowie et al. (2008): under leaves, in weedy vegetation, in trees, under rocks, under bark, in ground litter, etc. GPS coordinates were recorded for all site locations, then mapped in a geographic information system (GIS) using ArcGIS (version 10.0; ESRI, 2010).

To assess the importance of a range of environmental factors in determining the distribution of *Oxychilus alliarius* in the Hawaiian Islands, values for these variables at each site location were extracted from GIS data layers for each variable obtained as follows. Mean, mean minimum, and mean maximum temperature data at 250 m$^2$ resolution were obtained from Thomas Giambelluca (unpublished). Annual precipitation data for the Hawaiian Islands, also at 250 m$^2$ resolution, were obtained from Giambelluca et al. (2011). Vegetation data (Townshend et al. 2011), consisting of yearly average percent tree cover detected by the Moderate Resolution Imaging Spectroradiometer (MODIS), a device mounted on NASA’s Terra satellite and subsequently ground truthed, were obtained from NASA’s publicly available satellite data resource.

**Model building and validation**

I used a logistic regression framework to build a habitat suitability model based on *Oxychilus alliarius* presence and absence data from the islands of Hawaii and Maui (98 sites). Hawaii and Maui are the two Hawaiian Islands where *Oxychilus alliarius* was first recorded and where it has been present longest and therefore is most likely to have reached equilibrium in terms of colonizing all or most suitable habitat. The model was validated using the data from the islands of Molokai, Lanai, Oahu and Kauai (133 sites).
Only environmental variables with complete worldwide datasets were evaluated for use in the model. In the case that the environmental variables had very high collinearity, one was chosen and the rest were excluded based on preliminary assessment of fit using Akaike information criterion (AIC) scores. Of the 36 models that included the variables, their interactions, and their quadratic terms, I excluded models without the quadratic term for temperature, as these models indicate increasing habitat suitability for *O. alliarius* at increasingly low temperatures, which is not biologically logical as these animals will have a low temperature limit below which they cannot survive. In general, to determine which model has the best fit to the data, validation data sets are used (Harrell et al. 1996). However, because the validation dataset in the present case did not include areas of very high elevation, very low vegetation, or low rainfall, the building dataset was also used to assess the best model fit. Therefore, from these 14 models (Table 3.1) the two models with the highest scores for area under the receiver operating characteristic curve (AUC) for the building and validation data sets and the two with the lowest AIC scores for the building and validation data sets were used to project maps of estimated habitat suitability for *O. alliarius* in the Hawaiian Islands using ArcGIS Desktop 10.0 (ESRI 2011). The four models were further validated using reports of *O. alliarius* from other tropical islands (Sri Lanka, Tenerife, Saint Helena, Réunion).

**Model projecting**

The four habitat suitability models were projected to 31 islands and island groups around the world between latitudes 30° N and 30° S (Table 3.2). The Hawaiian Islands are climatically diverse enough to support tropical and temperate species, but they are
located in the tropics (the eight main islands lie approximately between latitudes 19° and 23° N) and therefore are not subject to the wide seasonal variation of temperature in temperate areas.

Temperature and precipitation data for all non-Hawaiian islands were obtained from WorldClim at a spatial resolution of ~1 km² (Hijmans et al. 2005). For all islands vegetative data at a spatial resolution of 250 m squares were obtained from MODIS (Townshend et al. 2011), then re-projected to the same spatial resolution as the WorldClim data. Total area on each island was broken into four suitability categories: unsuitable (0-25%), low suitability (25-50%), suitable (50-75%), and highly suitable (75-100%).

RESULTS

Model performance

The results for the 14 models are summarized in Table 3.3. The best models were model 1 (lowest AIC score for the validation data set), model 2 (highest AUC score for the validation data set), model 11 (lowest AIC score for the model building data set), and model 14 (highest AUC score for the model building data set and highest average AUC score for the two data sets). The false negative rate, or number of sites where *O. alliarius* was predicted to be absent (habitat suitability less than 50 %) but was actually present differed among the four models (combined value for building and validation datasets). Models 1 and 2 had false negative rates of 0.078, model 11 had the best false negative rate of 0.029, and model 14 had a rate of 0.058. Model 11 therefore had the lowest false negative rate of the four models, and the lowest AIC score for the model building data set.
(Table 3.3). The coefficients for the terms in the four best models are listed in table 3.4. This model takes into account temperature, precipitation, and vegetation, but excludes quadratic terms for precipitation and vegetation. It seems less likely to be over fitting the data than model 14, which includes these terms, as evidenced by its lower false negative rate and lower AIC score.

Model validation

On Hawaii (Figure 3.2a) and Maui (Figure 3.2b) most of the land above approximately 500 m was suitable or highly suitable, although on Hawaii the lava flows with the least vegetation and lowest rainfall were <50 % suitable, as were the highest elevations, where the temperature is too cool and there is little rainfall. On Lanai (Figure 3.2c) and Molokai (Figure 3.2d) the suitable habitat and location of all O. alliarius records are at the upper elevations. On the highly populated island of Oahu (Figure 3.2d) O. alliarius was present in the suitable and highly suitable habitat in both mountain ranges. Only a few O. alliarius populations were recorded on Kauai (Figure 3.2f), generally within highly suitable habitat.

Oxychilus alliarius has been reported in the literature from very few tropical/subtropical islands, Records could be found from only four: Tenerife (Canary Islands), Sri Lanka, Réunion and Saint Helena. On Tenerife, it has been recorded in the Orotava valley and the Anaga Mountains (Kappes 2009; Heike Kappes personal communication), all sites being above 750 m elevation. All were in areas of >75 % habitat suitability (Figure 3.3a). In Sri Lanka, Naggs et al. (2003; F. Naggs, personal communication) found a single O. alliarius specimen outside the town of Agarapathana
in the highlands where there is relatively more rain and temperatures are cooler. Although
the models indicate that a very small percentage of Sri Lanka is suitable for *O. alliarius*,
the single record is in this small area that had a habitat suitability >75 % (Figure 3.3b).
On Réunion, *O. alliarius* “seems to be restricted to high-altitude areas” (Griffiths and
Florens 2006), and the models predict that a large amount of the island is indeed suitable
for *O. alliarius* (Figure 3.3c). Finally, on the south Atlantic island of Saint Helena,
Wollaston (1878) reported occasional findings of *O. alliarius* above about 550 m, and
stated that *O. alliarius* was “universal above the altitude of about 2000 feet [610 m]”. The
models predicted that areas above about 350 m were suitable habitat for *O. alliarius*
(Figure 3.3d).

Thus, both in Hawaii and on these other four widely separated tropical/subtropical
islands *Oxychilus alliarius* occurred in areas that the models predicted as being suitable
or highly suitable and was absent from areas predicted to be less suitable. The predictive
power of the models was thus shown to be excellent.

**Model predictions**

The four models were then used to predict areas of suitable habitat on a large
selection of islands between latitudes 30 ° N and 30 ° S on which *Oxychilus alliarius* has
not been recorded. All four models predict that the majority of Oceania between latitudes
30 ° N and 30 ° S is not appropriate habitat for *O. alliarius*, and there have been no
records of it on Pacific islands other than the Hawaiian Islands (Cowie 2000, 2001a).
Nonetheless, some of the larger, higher islands did have some suitable habitat. New
Caledonia has suitable, although patchily distributed, areas along the mountains in the
center of the main island (Figure 3.4a). Vanuatu has suitable habitat on the largest island, Espiritu Santo (Figure 3.4b). Fiji has a large amount of suitable area in the center of Vitu Levu (Figure 3.4c). The central mountain on Rapa Nui (Easter Island) is predicted to be suitable for *O. alliarius* (Figure 3.4d). Samoa (Figure 3.4e) and American Samoa (Figure 3.4f) both have suitable habitat, although there is far more on the larger, higher Samoan islands, especially Savaii, than on the American Samoan islands. Except for a few small patches on Tahiti, no habitat in French Polynesia appeared suitable (Figure 3.5a), although all four models predicted the same areas to be suitable on Tahiti. Model 11 actually predicted the largest amount of suitable habitat on Tahiti, and model 14 predicted the smallest amount (Table 3.5). There were a few patches of suitable habitat around craters on the Galápagos Islands (Figure 3.5b). All models predicted the same general areas to be suitable for *O. alliarius*, but models 1 and 2 predicted a larger extent of those area than either models 11 or 14 (Table 3.5).

In the Indian Ocean, the four models predict that there is suitable habitat for *O. alliarius* in the Comoros archipelago (Figure 3.6a), which lies in the channel between Madagascar and mainland Africa, with the largest amount on Ngazidja (Grand Comore) and a small patch also on Nzwani (Anjouan). According to models 1, 2 and 11, there was only a very small amount of suitable habitat on Mauritius (none according to model 14), and *O. alliarius* has not been reported from there, although it does occur on neighboring Réunion, where all models predict that a large amount of the island is suitable (Table 3.5, Figure 3.6b).

In the Atlantic Ocean there is a large amount of suitable habitat in the Canary Islands according to models 1 and 2, but much less according to models 11 and 14 (Table
3.5), which predict most of the suitable habitat to be on the islands further from Africa (Figure 3.7a, b); *Oxychilus alliarius* has been recorded only from Tenerife. São Tomé has some suitable habitat in the center of the island but *O. alliarius* has not been recorded there (Figure 3.7c). The models also predict that Bioko (formerly Fernando Po) has two patches of suitable habitat in the center of its northern and southern parts, but *O. alliarius* has not been recorded there either (Figure 3.7d). The islands of Cape Verde present a special case; they have many areas with <200 mm of annual rainfall, which is outside the rainfall range of the model building data set. Models 11 and 14 incorrectly predict that the driest, least vegetated islands, which are closest to the African continent, have the highest amount of suitable habitat (Figure 3.8c, d). In contrast, model 1, which is based on temperature only, and model 2, which does not include the interaction between temperature and precipitation, predict that the islands furthest from the African continent, with the coolest mean annual temperatures, have the highest amount of suitable habitat (Figure 3.8a, b).

All models predicted little suitable habitat in the Caribbean, and *O. alliarius* has not been recorded there. Cuba has a small patch of suitable habitat near its highest peak (Figure 3.9a). On Hispaniola (Haiti and the Dominican Republic) (Figure 3.9b), suitable habitat occurred along the mountain ranges. Puerto Rico has small areas of patchily distributed suitable habitat on the mountains in the center of the island and a very small area at the eastern end (Figure 3.9c). The predictions of the four models differ primarily in the level of suitability in Puerto Rico (Table 3.5). Models 1 and 2 do not differ from each other but model 11 predicts a considerably larger proportion of suitable habitat than any other model. Where models 1 and 2 predict that the habitat is between 25 and 50 %
suitable model 11 predicts that the habitat is above 50% suitable, and model 14 predicts that the majority of the habitat is less than 25% suitable. Jamaica has a small amount of suitable habitat in the eastern and central parts of the island (all models; Figure 3.9d). All models predict very small patches of suitable habitat in Guadeloupe, Dominica and Martinique, in the Lesser Antilles (Figure 3.9e). Model 11 predicts that no other islands had habitat of 50% suitability or more.

Overall for most islands and island groups, models 1 and 2 predict very similar amounts of suitable habitat and models 11 and 14 predict similar amounts of suitable habitat to each other, in general less than models 1 and 2. However, model 14 generally predicts somewhat less suitable habitat than model 11, possibly as a result of over fitting (Figure 3.10).

DISCUSSION

In the Hawaiian Islands there is a good correspondence between the predicted suitable *O. alliarius* habitat and *O. alliarius* presence for all four of the best fit models. The models performed very well (Table 3.3) despite their reliance on only three environmental variables, their interactions, and their quadratics. The excellent performance of the models indicates that *O. alliarius* has probably had the opportunity to establish in most locations across the Hawaiian Islands, and that pressures such as competition and predation may not be important in determining its overall Hawaiian distribution. It is more abundant than any other snail species at elevations above 500 m in the Hawaiian Islands (K.A. Hayes et al. unpublished).

Temperature and the quadratic term for temperature were the most important explanatory variables in all four models. However, the temperature only model, model 1,
made unrealistic predictions of suitable habitat in barren regions. For example recent lava flows were considered to be as suitable as heavily vegetated forests on the island of Hawaii. Model 2, which included rainfall as a term, predicted almost the same results as model 1 (Table 3.5). Rainfall played a minimal role in model 2 and merely succeeded in increasing the AUC score by 0.000017, but also increasing the AIC score by 2.031. For practical purposes model 2 is no better a predictor than model 1. Models 11 and 14 incorporated rainfall, vegetation, and interaction terms, and in the case of model 14, quadratic terms for rainfall and vegetation. These terms tightened model projections, and made the models more realistic, especially when applied to areas other than the Hawaiian Islands. Model 11 generally predicts a higher amount of area to be suitable than does model 14 (Table 3.5); model 14 may have involved some over fitting.

For most Pacific islands, temperature seems to be the key variable. However, for islands like the Canary Islands, which are located off the coast of the Sahara desert, vegetation and precipitation terms changed the results drastically (Table 3.3). The *O. alliarius* populations on Tenerife, in the Canary Islands, occur in areas that receive approximately 500 mm of rainfall annually (Kappes et al. 2009). These areas were modeled as suitable by all four models, but models 1 and 2 also show each island to be almost completely covered by suitable habitat, even the areas with very little rainfall and vegetation. Models 11 and 14 only show the islands further from the African continent (Gran Canaria, Tenerife, La Gomera, El Hierro, and La Palma) to have suitable habitat.

The only islands in this study lacking large areas with >500 mm of annual rainfall are the two Canary Islands closest to Africa (Lanzarote, Fuerteventura) and most of the Cape Verde islands. The Cape Verde islands have many areas with <200 mm of annual
rainfall, which is less than anywhere on the islands of Maui or Hawaii (the model building dataset). Because of this lack of congruity, the interactions between rainfall and the other variables in the models lead to major shifts in the range of the variables exhibited by the areas predicted as being suitable habitat, especially for temperature. This can be seen in Figure 3.8 in which models 11 and 14 predict that the hottest, driest islands have the most suitable *O. alliarius* habitat. This emphasizes the need to rely on the models that have variable ranges similar to those of the building dataset, as using them to predict habitat suitability on islands with ranges outside those of the building dataset can lead to incorrect predictions. All other islands modeled have large areas with >500 mm of annual rainfall, so low precipitation would not be limiting. Similarly, regarding vegetation, only extremely barren areas, such as Hawaiian lava flows, are clearly unsuitable because of the lack of vegetation. The suitability of habitat on many oceanic islands in the Pacific and Indian Oceans, and in the Caribbean is primarily determined by mean annual temperature, at both the upper and lower limits, and secondarily precipitation and vegetation index. For some islands far more than others precipitation and vegetation index play a major role. The inclusion of all three variables results in more precise predictions.

Similar problems may arise if the magnitude of seasonality of the island for which a prediction is being made is much greater than that of the building dataset. The Canary Islands exhibit higher seasonal temperature variation than any other island group modeled. The models assume that the variation around the response curve for any one combination of variables in a particular location is the same as it is on the islands of Maui and Hawaii (the islands on which the models were based). If the seasonal temperature
range for a particular location is much larger than the seasonal temperature range on Maui and Hawaii then the models may not accurately predict habitat suitability in that location. The seasonality, defined as the standard deviation of mean annual temperature (Bioclim variable 4), on Maui and Hawaii is between 7.5 and 15 °C; on Lanai, Molokai, Oahu, and Kauai it is quite similar, between 10 and 17.5 °C. However, on Tenerife, seasonality reaches nearly 50 °C at the highest elevations. This means that, although the models have correctly predicted the area in which *O. alliarius* occurs on Tenerife, prediction of the overall area that is suitable on Tenerife may not have been predicted accurately, underscoring the importance of restricting the model’s predictions to islands within the 30° N to 30° S band. The Canaries fall only just within this band.

Many islands have highly suitable habitat for *O. alliarius*, yet it has only been recorded on a small number of them, or only in certain locations on these islands. There may be a number of reasons for this. First, *O. alliarius* may indeed be present but there have been no adequate surveys or reviews of museum collections to detect them (Cowie 2000, 2001a). For example, *O. alliarius* was first recorded on the highly populated Hawaiian island of Oahu only in 2008 (Cowie et al. 2008), despite having been present for a long time and in abundance on the islands of Maui and Hawaii. It was probably present much earlier on Oahu but just not recorded. Second, the snail must be transported to the island alive and the chance of this happening may have been low in the past. However, increased globalization of commerce and tourism mean that transport of invasive species is increasing, and the chance that *O. alliarius* will be introduced to these islands is no doubt also increasing. Third, the snails must find suitable habitat. Human population density is much higher in the lowlands of many islands, where the majority of
the human population spends its time. Because the lowlands and coastlines on islands between 30° N and 30° S are generally too hot for *O. alliarius* this lessens the chances of introduction to appropriate habitat. Finally, to be recorded, *O. alliarius* must establish a population that survives and is large enough to be found.

*Oxychilus alliarius* is readily transported around the world. Study of publicly available United States Department of Agriculture lists of quarantine interceptions reveals that *O. alliarius* was intercepted, usually in the soil with plants that were being transported for horticulture or agriculture, on average 2.3 times per year between 1955 and 1959 from Scotland, Ireland, Iceland, Germany, the Netherlands and South Africa (Hunt 1957, 1958, 1959; Mumford 1960, 1961). From 1960 through 1970 it was intercepted 3.1 times per year, from Italy, France, Portugal, England, Ireland, Scotland, Belgium, the Netherlands, the Azores, Brazil, Costa Rica, Mexico, Canada, Hawaii, and New Zealand (Mumford 1962, 1963, 1964, 1965, 1966, 1967; Girard 1968, 1969, 1971,1972). Globalization of trade probably means that transport of *O. alliarius* will have increased, and therefore such interceptions will also have increased (Cowie et al. 2009), or if interceptions have not increased, this means that *O. alliarius* escapes interception more frequently as only a very small proportion of commerce is inspected for snails (Cowie et al. 2008). This indicates that it may have far more opportunities for introduction to these many islands than at any time in the past, and that it will continue to have more opportunities until quarantine measures are increased.

If *O. alliarius* does establish in all of the suitable habitats on tropical islands it could seriously threaten indigenous snail species around the world through predation and competition for resources (chapter 2). Its garlic scent defense could make it unpalatable
and therefore resistant to potential predators. Because it is already established so widely around the world the likelihood of its transport and introduction to other places is even greater. Prevention of its even wider introduction can only be achieved by control of \textit{O. alliarius} outside its native range and by stricter and more widely applied quarantine measures. Once established, and if given the correct conditions, a population of \textit{O. alliarius} can expand, spatially, more than 100 m per year (chapter 2).

Species distribution models are versatile tools that can be used in many ways to aid conservation. They can potentially be used to locate rare species (Guisan et al. 2006), or, as in this study, to analyze the potential impacts of invasive species (Arriaga et al. 2004; Smith 2005). In the case of the Hawaiian Islands the models were used as explanatory tools, but when applied to islands where \textit{O. alliarius} has not established, they function as predictive tools. Predictive modeling may be of great use both from conservation and economic perspectives as it allows resource managers to focus control and conservation efforts instead of using a much less targeted approach (Cayula et al. 2009). Furthermore, species distribution models can be used to predict the effects of climate change (Thomas et al. 2004; Lv et al. 2011).

The endemic snail faunas of oceanic islands are at risk because of the impacts of invasive species. This modeling study helps to identify islands and parts of islands that are most at risk from the introduction or potential introduction of \textit{O. alliarius}. These native snail faunas may already be restricted to the areas most at risk of \textit{O. alliarius} invasion (mostly higher elevations) because of habitat destruction and invasion of other species at lower elevations (Meyer and Cowie 2010b). \textit{Oxychilus alliarius} may therefore
represent an additional pressure on indigenous snail faunas that are already severely threatened.

Preventative measures offer the best solution to the potential establishment of *O. alliarius* around the world. Horticultural and agricultural shipments have been the commonest pathway of introduction of many invasive species of snails (Robinson 1999; Cowie and Robinson 2003; Cowie et al. 2008). *O. alliarius* is a potentially serious invasive species and should be high on the list of species targeted by quarantine measures.
Table 3.1. The 14 models used to model *O. alliarius* habitat suitability. HS - habitat suitability, T - mean annual temperature, P - annual precipitation, V - vegetation index.

<table>
<thead>
<tr>
<th>Model</th>
<th>Model Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>HS = T + T²</td>
</tr>
<tr>
<td>2</td>
<td>HS = T + P + T²</td>
</tr>
<tr>
<td>3</td>
<td>HS = T + V + T²</td>
</tr>
<tr>
<td>4</td>
<td>HS = T + P + (T x P) + T²</td>
</tr>
<tr>
<td>5</td>
<td>HS = T + V + (T x V) + T²</td>
</tr>
<tr>
<td>6</td>
<td>HS = T + P + V + T²</td>
</tr>
<tr>
<td>7</td>
<td>HS = T + P + V + (T x P) + (T x V) + (P x V) + T²</td>
</tr>
<tr>
<td>8</td>
<td>HS = T + P + V + (T x P) + (T x V) + (P x V) + T² + P²</td>
</tr>
<tr>
<td>9</td>
<td>HS = T + P + V + (T x P) + (T x V) + (P x V) + T² + V²</td>
</tr>
<tr>
<td>10</td>
<td>HS = T + P + V + (T x P) + (T x V) + (P x V) + T² + P² + V²</td>
</tr>
<tr>
<td>11</td>
<td>HS = T + P + V + (T x P) + (T x V) + (P x V) + T² + (P x V x T)</td>
</tr>
<tr>
<td>12</td>
<td>HS = T + P + V + (T x P) + (T x V) + (P x V) + T² + P² + (P x V x T)</td>
</tr>
<tr>
<td>13</td>
<td>HS = T + P + V + (T x P) + (T x V) + (P x V) + T² + V² + (P x V x T)</td>
</tr>
<tr>
<td>14</td>
<td>HS = T + P + V + (T x P) + (T x V) + (P x V) + T² + P² + V² + (P x V x T)</td>
</tr>
</tbody>
</table>
Table 3.2. Islands and island groups modeled.

<table>
<thead>
<tr>
<th>Island(s)</th>
<th>O. alliarius</th>
<th>Ocean</th>
<th>Geographic Coordinates</th>
<th>Maximum Elevation (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawaii Island</td>
<td>Present</td>
<td>Pacific</td>
<td>19°34′N 155°30′W</td>
<td>4205</td>
</tr>
<tr>
<td>Maui</td>
<td>Present</td>
<td>Pacific</td>
<td>20°48′N 156°20′W</td>
<td>3055</td>
</tr>
<tr>
<td>Lanai</td>
<td>Present</td>
<td>Pacific</td>
<td>20°50′N 156°56′W</td>
<td>1026</td>
</tr>
<tr>
<td>Molokai</td>
<td>Present</td>
<td>Pacific</td>
<td>21°08′N 157°02′W</td>
<td>1512</td>
</tr>
<tr>
<td>Oahu</td>
<td>Present</td>
<td>Pacific</td>
<td>21°28′N 157°59′W</td>
<td>1220</td>
</tr>
<tr>
<td>Kauai</td>
<td>Present</td>
<td>Pacific</td>
<td>22°05′N 159°30′W</td>
<td>1598</td>
</tr>
<tr>
<td>Galápagos</td>
<td>Absent</td>
<td>Pacific</td>
<td>0°49′N 91°5′W</td>
<td>1707</td>
</tr>
<tr>
<td>Rapa Nui</td>
<td>Absent</td>
<td>Pacific</td>
<td>27°9′S 109°25′W</td>
<td>507</td>
</tr>
<tr>
<td>Society Islands</td>
<td>Absent</td>
<td>Pacific</td>
<td>17°12′S 150°27′W</td>
<td>2241</td>
</tr>
<tr>
<td>American Samoa</td>
<td>Absent</td>
<td>Pacific</td>
<td>14°20′S, 170°00′W</td>
<td>964</td>
</tr>
<tr>
<td>Samoa</td>
<td>Absent</td>
<td>Pacific</td>
<td>13°50′S 171°45′W</td>
<td>1857</td>
</tr>
<tr>
<td>Tonga</td>
<td>Absent</td>
<td>Pacific</td>
<td>21°08′S 175°12′W</td>
<td>1033</td>
</tr>
<tr>
<td>Wallis and Futuna</td>
<td>Absent</td>
<td>Pacific</td>
<td>13°17′S 176°11′W</td>
<td>524</td>
</tr>
<tr>
<td>Fiji</td>
<td>Absent</td>
<td>Pacific</td>
<td>18°10′S 178°27′W</td>
<td>1324</td>
</tr>
<tr>
<td>Vanuatu</td>
<td>Absent</td>
<td>Pacific</td>
<td>17°45′S 168°18′E</td>
<td>1879</td>
</tr>
<tr>
<td>New Caledonia</td>
<td>Absent</td>
<td>Pacific</td>
<td>21°30′S 165°30′E</td>
<td>1628</td>
</tr>
<tr>
<td>Pohnpei</td>
<td>Absent</td>
<td>Pacific</td>
<td>6°31′N 158°13′E</td>
<td>791</td>
</tr>
<tr>
<td>Mariana Islands</td>
<td>Absent</td>
<td>Pacific</td>
<td>16°20′N 145°18′E</td>
<td>965</td>
</tr>
<tr>
<td>Palau</td>
<td>Absent</td>
<td>Pacific</td>
<td>7°21′N 134°28′E</td>
<td>242</td>
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<tr>
<td>Sri Lanka</td>
<td>Present</td>
<td>Indian</td>
<td>6°54′N 79°54′E</td>
<td>2524</td>
</tr>
<tr>
<td>Maldives</td>
<td>Absent</td>
<td>Indian</td>
<td>4°10′N 73°30′E</td>
<td>3</td>
</tr>
<tr>
<td>Seychelles</td>
<td>Absent</td>
<td>Indian</td>
<td>4°37′S 55°27′E</td>
<td>905</td>
</tr>
<tr>
<td>Mascarene Islands</td>
<td>Present</td>
<td>Indian</td>
<td>20°43′S 56°37′E</td>
<td>3069</td>
</tr>
<tr>
<td>Comoros Islands</td>
<td>Absent</td>
<td>Indian</td>
<td>12°08′S 44°15′E</td>
<td>2361</td>
</tr>
<tr>
<td>Bioko Island</td>
<td>Absent</td>
<td>Atlantic</td>
<td>3°30′S 8°42′E</td>
<td>3012</td>
</tr>
<tr>
<td>São Tomé and Principe</td>
<td>Absent</td>
<td>Atlantic</td>
<td>0°20′N 6°44′E</td>
<td>2014</td>
</tr>
<tr>
<td>Saint Helena</td>
<td>Present</td>
<td>Atlantic</td>
<td>15°56′S 5°43′W</td>
<td>819</td>
</tr>
<tr>
<td>Ascension Island</td>
<td>Absent</td>
<td>Atlantic</td>
<td>7°56′S 14°22′W</td>
<td>859</td>
</tr>
<tr>
<td>Canary Islands</td>
<td>Present</td>
<td>Atlantic</td>
<td>28°06′N 15°24′W</td>
<td>3718</td>
</tr>
<tr>
<td>Cape Verde Islands</td>
<td>Absent</td>
<td>Atlantic</td>
<td>15°06′N 23°37′W</td>
<td>2829</td>
</tr>
<tr>
<td>Dominica</td>
<td>Absent</td>
<td>Caribbean</td>
<td>15°18′N 61°23′W</td>
<td>1447</td>
</tr>
<tr>
<td>Guadeloupe</td>
<td>Absent</td>
<td>Caribbean</td>
<td>16°15′N 61°35′W</td>
<td>1467</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>Absent</td>
<td>Caribbean</td>
<td>18°27′N 66°06′W</td>
<td>1338</td>
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<tr>
<td>Hispaniola</td>
<td>Absent</td>
<td>Caribbean</td>
<td>19°00′N 71°00′W</td>
<td>3175</td>
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<tr>
<td>Jamaica</td>
<td>Absent</td>
<td>Caribbean</td>
<td>18°10′N 77°19′W</td>
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</tr>
<tr>
<td>Cuba</td>
<td>Absent</td>
<td>Caribbean</td>
<td>22°00′N 79°30′W</td>
<td>1975</td>
</tr>
</tbody>
</table>
Table 3.3. Fit results for the 14 models of *O. alliarius* habitat suitability. The four models selected are highlighted in bold, and the underlined values are the best scoring values for each statistic. The building data set scores are denoted by B, the validation data set scores by V. Average AUC is the average of the AUC values for the building and validation data sets.

<table>
<thead>
<tr>
<th>Model</th>
<th>B AIC</th>
<th>B Δ AIC</th>
<th>B AUC</th>
<th>V AIC</th>
<th>V Δ AIC</th>
<th>V AUC</th>
<th>Average AUC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>62.142</td>
<td>11.207</td>
<td>0.94040</td>
<td>72.378</td>
<td>0.000</td>
<td>0.96038</td>
<td>0.95039</td>
</tr>
<tr>
<td>2</td>
<td>64.141</td>
<td>13.206</td>
<td>0.94042</td>
<td>74.409</td>
<td>2.031</td>
<td>0.96085</td>
<td>0.95063</td>
</tr>
<tr>
<td>3</td>
<td>62.797</td>
<td>11.863</td>
<td>0.94417</td>
<td>80.961</td>
<td>8.584</td>
<td>0.95566</td>
<td>0.94991</td>
</tr>
<tr>
<td>4</td>
<td>66.032</td>
<td>15.097</td>
<td>0.94000</td>
<td>76.211</td>
<td>3.833</td>
<td>0.96061</td>
<td>0.95031</td>
</tr>
<tr>
<td>5</td>
<td>64.783</td>
<td>13.848</td>
<td>0.94458</td>
<td>83.399</td>
<td>11.021</td>
<td>0.95543</td>
<td>0.95000</td>
</tr>
<tr>
<td>6</td>
<td>63.706</td>
<td>12.771</td>
<td>0.94708</td>
<td>95.378</td>
<td>23.000</td>
<td>0.93632</td>
<td>0.94170</td>
</tr>
<tr>
<td>7</td>
<td>61.646</td>
<td>10.712</td>
<td>0.96542</td>
<td>160.455</td>
<td>88.077</td>
<td>0.93090</td>
<td>0.94816</td>
</tr>
<tr>
<td>8</td>
<td>63.508</td>
<td>12.574</td>
<td>0.96708</td>
<td>154.198</td>
<td>81.820</td>
<td>0.93609</td>
<td>0.95158</td>
</tr>
<tr>
<td>9</td>
<td>63.633</td>
<td>12.698</td>
<td>0.96542</td>
<td>167.074</td>
<td>94.696</td>
<td>0.92689</td>
<td>0.94615</td>
</tr>
<tr>
<td>10</td>
<td>65.508</td>
<td>14.573</td>
<td>0.96708</td>
<td>157.092</td>
<td>84.714</td>
<td>0.93538</td>
<td>0.95123</td>
</tr>
<tr>
<td>11</td>
<td>50.935</td>
<td>0.000</td>
<td>0.98292</td>
<td>294.505</td>
<td>222.127</td>
<td>0.93750</td>
<td>0.96021</td>
</tr>
<tr>
<td>12</td>
<td>52.690</td>
<td>1.755</td>
<td>0.98333</td>
<td>288.440</td>
<td>216.062</td>
<td>0.93715</td>
<td>0.96024</td>
</tr>
<tr>
<td>13</td>
<td>52.738</td>
<td>1.804</td>
<td>0.98375</td>
<td>264.954</td>
<td>192.576</td>
<td>0.94222</td>
<td>0.96298</td>
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<tr>
<td>14</td>
<td>53.108</td>
<td>2.173</td>
<td>0.98625</td>
<td>184.611</td>
<td>112.233</td>
<td>0.95094</td>
<td>0.96860</td>
</tr>
</tbody>
</table>
Table 3.4. The coefficients for the 4 best models. T - mean annual temperature, P - annual precipitation, V - vegetation index.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Model 1</th>
<th>Model 2</th>
<th>Model 11</th>
<th>Model 14</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-25.9942</td>
<td>-26.0552</td>
<td>-88.6849</td>
<td>-100.5</td>
</tr>
<tr>
<td>T</td>
<td>4.0593</td>
<td>4.0695</td>
<td>6.9445</td>
<td>7.6978</td>
</tr>
<tr>
<td>P</td>
<td>-6.12E-06</td>
<td>-0.0607</td>
<td>0.0726</td>
<td></td>
</tr>
<tr>
<td>V</td>
<td></td>
<td>2.4067</td>
<td>2.58</td>
<td></td>
</tr>
<tr>
<td>(T x P)</td>
<td>-</td>
<td>-</td>
<td>-0.00312</td>
<td>-0.00381</td>
</tr>
<tr>
<td>(T x V)</td>
<td>-</td>
<td>-</td>
<td>-0.1162</td>
<td>-0.1142</td>
</tr>
<tr>
<td>(P x V)</td>
<td>-</td>
<td>-</td>
<td>-0.00122</td>
<td>-0.00129</td>
</tr>
<tr>
<td>(T x P x V)</td>
<td>-</td>
<td>-</td>
<td>6.2E-05</td>
<td>7.2E-05</td>
</tr>
<tr>
<td>T²</td>
<td>-0.1409</td>
<td>-0.1412</td>
<td>-0.1314</td>
<td>-0.1426</td>
</tr>
<tr>
<td>P²</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-7.03E-07</td>
</tr>
<tr>
<td>V²</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-0.00638</td>
</tr>
</tbody>
</table>
Table 3.5. Area (km$^2$) of suitable (> 50 % suitability) habitat for *O. alliarius* in the Hawaiian Islands and other islands or island groups for which the predictions of the four models differ substantially (see text).

<table>
<thead>
<tr>
<th>Model</th>
<th>Hawaii</th>
<th>Mauritius and Réunion</th>
<th>Tahiti</th>
<th>Galápagos</th>
<th>Canaries</th>
<th>Puerto Rico</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>6740.0</td>
<td>1315.3</td>
<td>22.9</td>
<td>440.1</td>
<td>5072.1</td>
<td>44.2</td>
</tr>
<tr>
<td>2</td>
<td>6747.5</td>
<td>1315.3</td>
<td>22.9</td>
<td>440.1</td>
<td>5072.1</td>
<td>44.2</td>
</tr>
<tr>
<td>11</td>
<td>6004.8</td>
<td>1597.2</td>
<td>65.5</td>
<td>384.3</td>
<td>1148.5</td>
<td>220.1</td>
</tr>
<tr>
<td>14</td>
<td>5467.4</td>
<td>1296.7</td>
<td>29.5</td>
<td>304.7</td>
<td>1125.6</td>
<td>97.4</td>
</tr>
</tbody>
</table>
Figure 3.1. The survey locations on the Hawaiian Islands, and presence and absence of *Oxychilus alliarius*. 
Figure 3.2. *Oxychilus alliarius* habitat suitability in the Hawaiian Islands. The colors representing suitable habitat are used in all subsequent figures.
Figure 3.3. *Oxychilus allarius* habitat suitability on islands where it has already been recorded other than the Hawaiian Islands.
Figure 3.4. *Oxychilus alliarius* habitat suitability in New Caledonia, Vanuatu, Fiji, Easter Island (Rapa Nui), Samoa, and American Samoa which are in the South Pacific Ocean.
Figure 3.5. *Oxychilus alliarius* habitat suitability on the Society Islands and the Galápagos Islands, which are in the Pacific Ocean.
Figure 3.6. *Oxychilus alliarius* habitat suitability on the Comoros Archipelago and the Mascarene Islands, which are in the Indian Ocean.
Figure 3.7. *Oxychilus alliarius* habitat suitability on the Canary Islands, São Tomé and Bioko, which are in the Atlantic Ocean.
Figure 3.8. The four best *Oxychilus alliarius* habitat suitability models for the Cape Verde islands.
Figure 3.9. *Oxychilus alliarius* habitat suitability on islands of the Caribbean Sea.
Figure 3.10. The four best *Oxychilus alliarius* habitat suitability models on the island of Hawaii.
Chapter 4

Conclusion
THESIS RESEARCH GOALS

The potential impacts and distribution of the invasive predatory snail *Oxychilus alliarius* were the topics of my thesis research. I addressed the questions: 1) is the population of *O. alliarius* on Mt. Kaala expanding its range, 2) what are the potential impacts *O. alliarius* will have on the native snails it encounters as it expands its range on Mt. Kaala, 3) what determines the distribution of *O. alliarius* in the Hawaiian Islands, and 4) do other islands and island groups around the world, between 30° N and 30° S latitudes, have suitable habitat for *O. alliarius*?

THE SPREAD OF *O. ALLIARIUS*

The *Oxychilus alliarius* population, living on Mt. Kaala did expand its established range between the time of its first record, in September 2008, and the end of the monitoring study, in May 2011 (chapter 2). It moved approximately 300 m over this time period, a rate of around 113 m per year, although this movement was not constant. I recorded individuals that had broken away from the source population and moved up to 270 m ahead further along the boardwalk (chapter 2). Furthermore, between January and February of 2011 it seemed that the source population, and a propagule population actually coalesced, effectively moving the furthest extent of the source population to the furthest extent of the propagule population. To determine whether *O. alliarius* was moving through the forest on either side of the boardwalk at the same rate, I surveyed sites that ran in parallel to the boardwalk, but were 25 m away on either side in February and April 2011. I found *O. alliarius* had not expanded its range on either side of the
boardwalk as much as it had along the boardwalk. The salutatory expansion along the boardwalk, along with the slower movement of the snail through the forest on either side of the boardwalk, suggests that *O. alliarius* movement was either less hindered along the board walk, or that it was aided by some biotic or abiotic factor. However, these are hypotheses that remains to be tested.

**IMPACTS OF *O. ALLIARIUS* ON NATIVE HAWAIIAN SNAILS**

I found a significant negative relationship between *O. alliarius* abundance and the abundance of Succineidae (p = 0.001; $R^2 = 74.8\%$; d.f. = 1/9; F = 23.77) and a significant positive relationship of the abundance of *O. alliarius* and of Tornatellidinae (p < 0.0001; $R^2 = 92.7\%$; d.f. = 1/9; F = 102.29) and of Pupillidae (p = 0.014; $R^2 = 55.0\%$; d.f. = 1/9; F = 9.78) in the Mt. Kaala summit bog (chapter 2). There were no other significant relationships between *O. alliarius* abundance and the abundance of Mt. Kaala native snail taxa. However, when the *O. alliarius* source population reached approximately 350 to 370 m from the access road, an *O. alliarius* individual was found consuming an individual of *Kaala subrutila*, a species of Helicarionidae endemic to Mt. Kaala. Although there was no significant relationship between Helicarionidae abundance and *O. alliarius* abundance, this confirms that *O. alliarius* is directly impacting *K. subrutila* at an individual level, and that if *O. alliarius* continues to expand its range on Mt. Kaala, over time it may have a negative impact on *Kaala subrutila*.  

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ENVIRONMENTAL DETERMINANTS OF THE DISTRIBUTION OF *O. alliarius* IN THE HAWAIIAN ISLANDS

Logistic regressions using temperature, precipitation, and vegetation index turned out to be very good predictors of the presence and absence of *O. alliarius* in the Hawaiian Islands. Four of 36 models that were built performed very well. Each of the four models included the quadratic temperature term that modeled the decline in habitat suitability at temperatures that were both too hot and too cold for *O. alliarius* to establish. The four models all predicted that *O. alliarius* was restricted to the higher parts of the islands, but they differed in detail, essentially depending on whether precipitation and vegetation index were included or not. Models 1 and 2, which were based on temperature, and, to a very small degree, precipitation predicted almost exactly the same result, except that model 1 predicted approximately 7.5 km$^2$ more suitable habitat for *O. alliarius* in the Hawaiian Islands than model 2. Models 11 and 14 differed from models 1 and 2 in that they incorporated precipitation, vegetation, and the interactions between the variables, and model 14 also included quadratic terms for precipitation and vegetation. These two models seemed to make more conservative estimates of the suitable habitat in the Hawaiian Islands compared to models 1 and 2. They differed from each other most noticeably on the islands of Oahu and Kauai, where model 14 predicted a much tighter fit of the suitable habitat to the mountain ranges than did model 11. Of all the models model 11 had the lowest false negative rate of only three incorrectly predicted absences out of the 103 real *O. alliarius* presences, whereas model 14 incorrectly predicted five and both models 1 and 2 incorrectly predicted eight. Models 1 and 2 offer only slightly different predictions from each other, but greatly from models 11 and 14, and models 11 and 14
differed slightly from each other but to a greater degree than models 1 and 2. However, models 11 and 14 are much more realistic in predicting *O. alliarius* absence in arid areas and provide good explanatory tools for the predicting the distribution of *O. alliarius* in the Hawaiian Islands.

**PREDICTION OF HABITAT SUITABILITY FOR *OXYCHILUS ALLIARIUS* ON OTHER ISLANDS**

I found that the four *O. alliarius* habitat suitability models correctly predicted the locations where *O. alliarius* had already been recorded on Tenerife, Saint Helena, Sri Lanka, and Réunion, thereby further validating the models. In using these four models to predict suitable habitat on other islands in the North and South Pacific, Atlantic and Indian Oceans, and in the Caribbean Sea, their performance was similar to their performance in Hawaii, with the four models being generally congruent but predicting slightly different areas for each of the islands with suitable habitat. Again, models 1 and 2 made almost exactly the same predictions as each other, and, generally, predicted the largest amounts of suitable habitat on the islands. Models 11 and 14 predicted more restricted ranges than models 1 and 2, and in most cases, model 14 predicted a more restricted range than model 11. In two cases model 11 predicted the largest amount of suitable habitat (Puerto Rico and Mauritius). The models did not work well on islands with <200 mm of rainfall per year (notably the Cape Verde Islands), and seasonal temperature variation that is much greater than that in the Hawaiian Islands used to build the models (notably the Canary Islands). Essentially, the models will only produce accurate predictions in locations with similar ranges of temperature, precipitation and
vegetation index to the locations used to build the models in the first place. Given these constraints, these models could be used as tools to predict the potential range expansion of *O. alliarius* if it is introduced to new island locations around the world.

This thesis, then, has demonstrated that the invasive European predatory snail *Oxychilus alliarius*, when introduced to suitable habitat can expand its range rapidly, that it may have negative impacts on native land snail faunas through predation, that its distribution is constrained primarily by temperature but also to some extent by precipitation and vegetation cover, and that it is possible to model these constraints to predict its potential distribution should it be introduced to tropical/subtropical islands worldwide.
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