Evolution and Extinction of Land Snails on Oceanic Islands

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Abstract

Nonmarine molluscs are the major animal group with the greatest number of recorded extinctions due to anthropogenic impacts, and that number is certainly a serious underestimate. Land snails, particularly endemic land snails of oceanic islands, are the group of molluscs that have sustained the most extinctions. Understanding their ecology and the evolutionary processes that have led to their extreme vulnerability is crucial if we are to be able to conserve these diverse and important species. Oceanic island snails tend to have low α-diversity and high β-diversity, and divergence of habitat use among related species is known to occur in some radiations of land snails on oceanic islands. Processes of speciation and ecological interaction are possible major drivers of these patterns. The ecological opportunities available at the initial stage of insular evolution and the scarcity of effective predators may have led to divergence of habitat use and high β-diversity in oceanic island snails. Fewer and less diverse predators on oceanic islands lead to the evolution of fewer and less diverse defense traits in oceanic island snails, which results in their high vulnerability to non-native predators. High β-diversity of oceanic island snails also results in great vulnerability to habitat loss. Accordingly, the high susceptibility of oceanic island snails to extinction reflects their evolutionary history.

1. INTRODUCTION

Since John Thomas Gulick's studies on Hawaiian land snails in the late nineteenth century (Gulick 1905), oceanic island land snails have served as excellent model systems to test hypotheses of evolution because of their high species diversity and extensive geographical variation. Various studies have addressed the issue of how new species of land snails have evolved and how diversity has arisen on the islands (e.g., Cowie & Holland 2006, Holland & Cowie 2009). Additionally, oceanic island land snails have served as model systems to understand species loss because of their high rates of extinction. Approximately 40% of the recorded extinctions of animal taxa since the year 1500 are nonmarine molluscan species (Lydeard et al. 2004), and more than 70% of molluscan extinctions have occurred on oceanic islands (Régnier et al. 2009).

Theories of island biogeography and insular radiation have provided major contributions to our understanding of the processes underlying species diversity (e.g., MacArthur & Wilson 1967, Whittaker & Fernández-Palacios 2007, Losos & Ricklefs 2009). These theories have been developed mainly in the context of oceanic islands or lakes and are based on studies of species with intrinsically high mobility, high dispersal ability, or large ranges; such species include birds, reptiles, arthropods, fish, and vascular plants. From this perspective, land snails are exceptional in the study of island biogeography and radiation processes on islands because of their extremely low active mobility, highly fragmented population structure, and limited species ranges, despite having high passive dispersal ability (e.g., Gittenberger et al. 2006).

In the first part of this article, we review patterns of land snail species diversity on oceanic islands. We discuss the processes of evolution and speciation that may operate to produce these patterns by focusing especially on the effects of predation and interspecific competition. We clarify the relative importance of the roles of these ecological factors on oceanic islands. In the second part, we address the question of why habitat alteration and predation by non-native species have become such serious threats to oceanic island land snails. We also provide an overview of natural and anthropogenic extinctions of land snails on oceanic islands. Finally, we discuss how selective pressure arises from anthropogenic extinctions and how the ecological properties and evolutionary histories of island land snails are linked to their vulnerability.

2. DIVERSITY, EVOLUTION, AND RADIATION ON OCEANIC ISLANDS

2.1. Species Diversity

Oceanic islands have long been known as hot spots of high land snail diversity and endemism (Solem 1984). For example, the Hawaiian Islands harbor more than 750 land snail species (Cowie 1995), Madeira has 237 species (Seddon 2008), and Palau approximately 200 species (Rundell 2008). Even the tiny island of Rapa in the South Pacific, only 38 km^2 in area, has more than 100 endemic species of land snails (Solem 1983), and Lord Howe Island (12.8 km^2) has at least 85 endemic species (Hickman 2009). The subtropical island of Hahajima (20.2 km^2) in the Ogasawara archipelago of Japan has 63 indigenous species (Chiba et al. 2009).

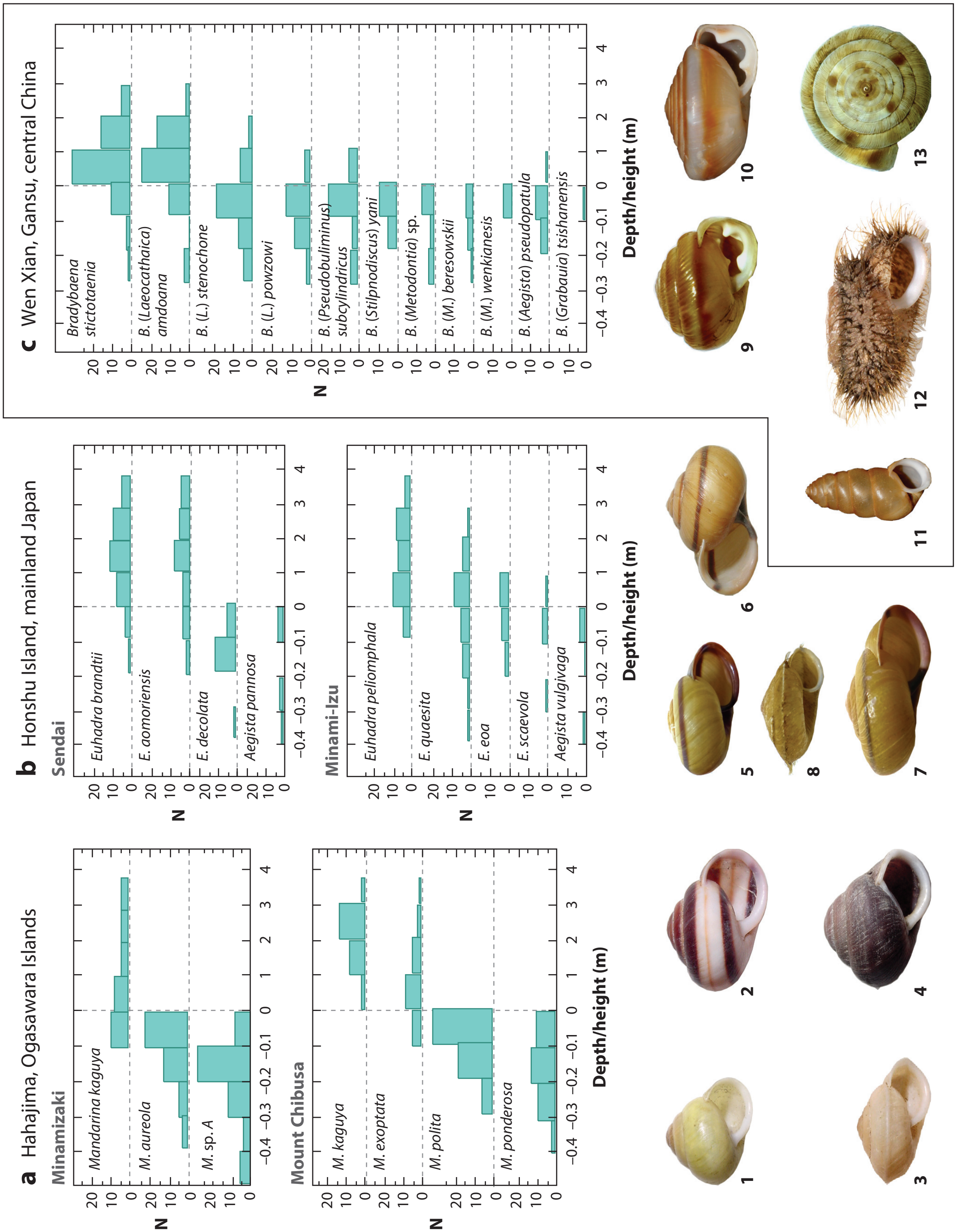
Despite this high within-island species diversity, fairly small numbers of species occur sympatrically (Solem 1984, Cook 2008). On the Hawaiian island of Oahu, which has 395 species (Cowie 1995), rarely more than 5–8 species occur sympatrically, and most Polynesian and Micronesian islands have 5–12 species at a site (Solem 1984). Rapa, with more than 100 species, has a maximum single-site diversity of only 21 species (Solem 1983). In the Ogasawara Islands, 4–23 species occur within 100 m^2 sites on Hahajima (Chiba et al. 2009) and 5–20 species on Anijima (Chiba 2007). Relatively high local species richness has been recorded on Madeira (up to 41 species per 900 m^2; see Cameron & Cook 2001) and in the Azores (up to 28 species per 400 m^2; see Cameron et al. 2012), although these numbers include non-native species introduced from Europe (Cook 2008). Accordingly, on oceanic islands, local (i.e., sympatric) diversity is low, implying that species richness on islands is more related to geographic (i.e., allopatric) diversification (Solem 1984, Cook 2008).

2.2. Ecological Interactions

Competitive interactions between land snail species have been demonstrated under laboratory conditions (e.g., Baur & Baur 1990, Kimura & Chiba 2010). Resource competition appears to limit certain land snail distributions and cause ecological divergence (Parent & Crespi 2009), though food may not necessarily always be limiting for land snails (Barker & Mayhill 1999). Ecological divergence could also be promoted by interference competition (Pearce 1997, Kimura & Chiba 2010). In the genera *Euhadra* and *Mandarina* in Japan, habitat use by species in natural communities is affected by interspecific interference competition, and divergence of habitat use between species occurs by interference competition even in environments with unlimited resources (Kimura & Chiba 2010; S. Chiba, unpublished data). Although further studies in natural communities are needed, interference competition may limit distributions and cause divergence in habitat use among species, particularly when population density is high.

Except for the few examples mentioned above, interspecific competition has not been widely shown to play a large role in structuring natural land snail assemblages (e.g., Cameron & Cook 2001, Cook 2008). In particular, divergence in habitat use among closely related sympatric land snail species due to interspecific interactions has rarely been demonstrated (e.g., Cowie & Jones 1987). For example, studies of land snail assemblages in eastern Europe provided no evidence that the coexistence of snail species is driven by niche differences related to size or diet and indeed detected convergence in shell size between sympatric species (Schamp et al. 2010). Similarly, the North American land snails *Neohelix major* and *Mesodon normalis* exhibited greater similarity in shell morphology in sympatry than in allopatry (Emberton 1995). In assemblages of east Asian bradybaenid snails, no difference in habitat use was detected among most of the sympatric species in Gansu, central China (T. Hirano, Y. Morii, T. Sota, H. Liang & S. Chiba, unpublished data), whereas clear differences in habitat use were detected among sympatric bradybaenid (*Mandarina*) species in the Ogasawara Islands (Chiba 2004) (**Figure 1**). In addition, intermediate levels of differentiation in habitat use were observed among sympatric bradybaenid species in mainland Japan (Kimura & Chiba 2010) (**Figure 1**). Although several studies of land snails have demonstrated a positive correlation between habitat diversity and species diversity (Liew et al. 2010), many others have shown that habitat diversity does not greatly affect species diversity (e.g., Schilthuizen et al. 2013). These findings suggest little importance of interspecific competition. In general, species diversity of land snails tends to be closely associated with habitat type, as characterized by humidity, temperature, level of disturbance, soil and litter texture, and soil pH.

Nevertheless, studies that have indeed documented divergence in habitat use between sympatric species of land snails, apparently caused by interspecific interactions, come primarily from oceanic islands. For example, diversification of *Partula* species on Moorea in French Polynesia results from preferences for the position on the tree on which they are found (Murray et al. 1993). Studies of fossil snails in Bermuda suggested that ecological character displacement occurred between species of *Poecilozonites* (Schindel & Gould 1977). A similar pattern of character displacement was also observed in *Mandarina* in the Ogasawara Islands (Chiba 1996, 1999a). And in bulimulid snails in the Galapagos Islands, diversity was related to resource heterogeneity mediated primarily by competition (Parent & Crespi 2009). In Puerto Rican land snail assemblages, however, no negative correlation in population density was detected between possible competitors, suggesting that interspecific competition is weak at best (Bloch & Willig 2012).


a Hahajima, Ogasawara Islands
Minamizaki
Mandarina kaguya
M. aureola
M. sp. A
Mount Chibusa
M. kaguya
M. exoptata
M. polita
M. ponderosa
N
20 10 0
Depth/height (m)
−0.4 −0.3 −0.2 −0.1 0 1 2 3 4
b Honshu Island, mainland Japan
Sendai
Euhadra brandtii
E. aomoriensis
E. decolata
Aegista pannosa
Minami-Izu
Euhadra peliomphala
E. quaesita
E. eoa
E. scaevola
Aegista vulgivaga
c Wen Xian, Gansu, central China
Bradybaena stictotaenia
B. (Laeocathaica) amdoana
B. (L.) stenochone
B. (L.) powzowi
B. (Pseudobuliminus) subcylindricus
B. (Stilpnodiscus) yani
B. (Metodontia) sp.
B. (M.) beresowskii
B. (M.) wenkianesis
B. (Aegista) pseudopatula
B. (Grabauia) tsishanensis
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In general, because of the lack of clear evidence of competitive exclusion, it remains unclear how widespread interspecific competition is among land snail species and in particular whether it is more important on oceanic islands than in continental regions. Nonetheless, on oceanic islands, immigration of competitors is limited, because of their isolation, and this limited immigration results in many opportunities for those few species that do colonize (MacArthur & Wilson 1967, Whittaker & Fernández-Palacios 2007). The availability of multiple opportunities at the initial stage of island colonization may promote divergence in habitat use among closely related species. Thus, relatively low diversity of competitors on oceanic islands may indeed lead to divergence in habitat use among sympatric species as a result of interspecific competition. More studies are needed.

The absence or scarcity of effective predators of land snails such as mammals and ants on many oceanic islands (Paulay & Starmer 2011) could also contribute to the divergence in habitat use of land snails. Although controversies still exist, recent meta-analyses suggest that increasing diversity of predators (predator richness) enhances prey suppression, particularly when the taxonomic distinctness of the predators is high (Griffin et al. 2013). Higher diversity of predators in continental habitats than on oceanic islands (Walter 2004) suggests that continental habitats are likely to have greater predation rates (Vermeij 2004), which could decrease population densities and weaken the effects of interspecific competition (Bloch & Willig 2012). On the oceanic Ogasawara Islands, the only predators of bradybaenid snails are birds and crabs, whereas in mainland Japan, predators of bradybaenids include birds, carabid beetles (one species), mammals, slugs, and flatworms and in central China, they include birds, carabid beetles (four species), mammals, flatworms, snakes, slugs, and carnivorous snails (Chiba et al. 2009; S. Chiba, unpublished data). In addition, continents may have harsher environments with higher stochasticity, leading to less abundant populations or greater fluctuation in population density, which can mitigate the effects of interspecific competition. Indeed, population abundance is commonly very low in continental tropical rainforests (Solem 1984, Schilthuizen et al. 2013) except for communities of microsnails feeding on the microvegetated limestone surfaces (Clements et al. 2006), though these communities have similar levels of regional species diversity. In some tropical rainforests, land snails may also suffer from high predation pressure by other, carnivorous snails (Schilthuizen et al. 2013).

Although further studies are needed to assess the generality of the relationships, the availability of multiple ecological opportunities, at least at the initial stage of colonization, and the low predator richness and/or scarcity of effective predators on oceanic islands potentially promote divergence in

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Figure 1

Variation in the depth (in the litter) and height (on the plants) of resting sites of sympatric species of (*a*) *Mandarina* in the Ogasawara Islands (data from Chiba 2004), (*b*) *Euhadra* and *Aegista*, the close relatives of *Mandarina*, in Honshu Island of mainland Japan (data from Kimura & Chiba 2010 and S. Chiba, unpublished data), and (*c*) *Bradybaena*, their continental relatives in central China (Y. Morii, T. Hirano, H. Liang, T. Sota & S. Chiba, unpublished data). The areas of the study sites were 100 m^2 for Hahajima (*a*, Minamizaki and Mount Chibusa) and 400 m^2 for both Honshu Island of Japan (*b*, Sendai and Minami-Izu) and central China (*c*, Wen Xian, Gansu). Significant differences in habitat use among sympatric *Mandarina* species were found (*a*) (see Chiba 2004), but no differences were found among *Bradybaena* species, except for two species showing preferences for an arboreal lifestyle (*c*). Consistent patterns of habitat use are seen for other habitat parameters (e.g., substrate preference). The images at the bottom show representative species occurring at each study site. Diversity in shell morphology of *Mandarina* (*a*) reflects adaptation to different habitat use (i.e., adaptive radiation). In *Bradybaena* (*c*), aperture modification (9–11), aperture teeth (9, 10), tightly coiled whorls (11, 13), and spines on the shell (12) appear to reflect adaptation against attacks by predators, particularly by malacophagous beetles, slugs, and snails. These species from central China are morphologically highly divergent but phylogenetically closely related (Hirano et al. 2014), and this pattern suggests predation-induced radiation. 1, *Mandarina kaguya*; 2, *Mandarina polita*; 3, *Mandarina exoptata*; 4, *Mandarina ponderosa*; 5, *Euhadra peliomphala*; 6, *Euhadra quaesita*; 7, *Euhadra eoa*; 8, *Aegista vulgivaga*; 9, *Bradybaena* (*Metodontia*) *beresowskii*; 10, *Bradybaena* (*Metodontia*) *wenkianesis*; 11, *Bradybaena* (*Pseudobuliminus*) *subcylindricus*; 12, *Bradybaena* (*Grabauia*) *tsishanensis*; 13, *Bradybaena* (*Laeocathaica*) *powzowi*.

habitat use through interspecific competition. No evidence of ecological release in the land snails colonizing oceanic islands has been found, perhaps because of weaker interspecific competition in continental habitats than on oceanic islands. However, because release from predation may occur at the initial stage of colonization of oceanic islands to yield ecological release, better insights into this issue would require focusing on newly formed islands and comparing islands of different ages.

2.3. Evolution of Life History Traits

Carlquist (1974) suggested that land snails on remote oceanic islands have smaller shells than those on continents or on islands close to continents. This tends to be the case if shell size is compared among overall assemblages because the snail faunas of remote islands tend to be derived from small species with high passive dispersal ability, which is somehow constrained phylogenetically. However, if comparisons are made within lineages, oceanic island species are not necessary smaller than their continental relatives. For example, most of the species of *Ogasawarana*, a genus endemic to the Ogasawara Islands, are larger than species of their closest continental relative *Aphanoconia* (S. Webster, unpublished data). The large size of certain species on oceanic islands almost certainly arose through evolution in situ from a smaller colonizing propagule. For example, tree snails in the endemic Hawaiian subfamily Achatinellinae are larger than the achatinellid taxa of other Pacific islands from which they presumably evolved (Holland & Hadfield 2004).

In various animal taxa, lineages on oceanic islands tend to lay smaller numbers of larger eggs and require a longer time for maturation than their mainland relatives because of increased competition and decreased predation pressure (Whittaker & Fernández-Palacios 2007). In land snails, however, whether such differences in life history traits exist between oceanic islands and continents is unclear. In the Ogasawara Islands, *Mandarina* species lay 2–10 eggs that are larger than 1/5 of the adult shell diameter, and they take 2 years to reach maturity, whereas species of their mainland relative, *Euhadra*, lay more than 20 eggs that are smaller than 1/10 of the adult shell diameter, and they take 1–1.5 years to reach maturity. Similarly, species of the Pacific island genus *Partula* and of the endemic Hawaiian subfamily Achatinellinae exhibit an extremely slow rate of reproduction, as well as ovoviviparity (Hadfield 1986, Cowie 1992, Hadfield & Saufler 2009). However, great variation in egg size is also found in continental land snails because various environmental factors including temperature and moisture affect egg size; ovoviviparity is also found in some continental land snail species (Baur 1994).

2.4. Speciation and Radiation

Dispersal is an important biogeographical phenomenon, and its role in shaping distributions of island, particularly oceanic island, lineages should not be underestimated (Cowie & Holland 2006), especially in land snails (Holland & Cowie 2009, Lee et al. 2014). The origins of the biotas of oceanic islands that were never connected to a continent are necessarily a result of dispersal, as are the origins of the biotas of islands that were never connected to each other within an archipelago. However, because such dispersal events are rare, species richness on oceanic islands is mainly a result of speciation within an island or archipelago and not of an equilibrium between immigration and extinction (Cowie 1995, 1996; Lee et al. 2014).

Within a fauna, evolutionary radiation often gives rise to ecologically and morphologically similar land snail species that are distributed allopatrically in a mosaic pattern of numerous congeneric species. Examples of such diversification, termed nonadaptive radiation (Gittenberger 1991, Rundell & Price 2009), commonly occur on oceanic islands (e.g., Cameron et al. 1996) as well as in continental regions. For example, in Hawaiian Achatinellinae, diversification across ecologically similar ridges and valleys arose (presumably) as a result of rare chance dispersal events, as was noted more than a century ago (Gulick 1905). Nonadaptive radiation occurs if there is isolation in the absence of any novel ecological opportunity.

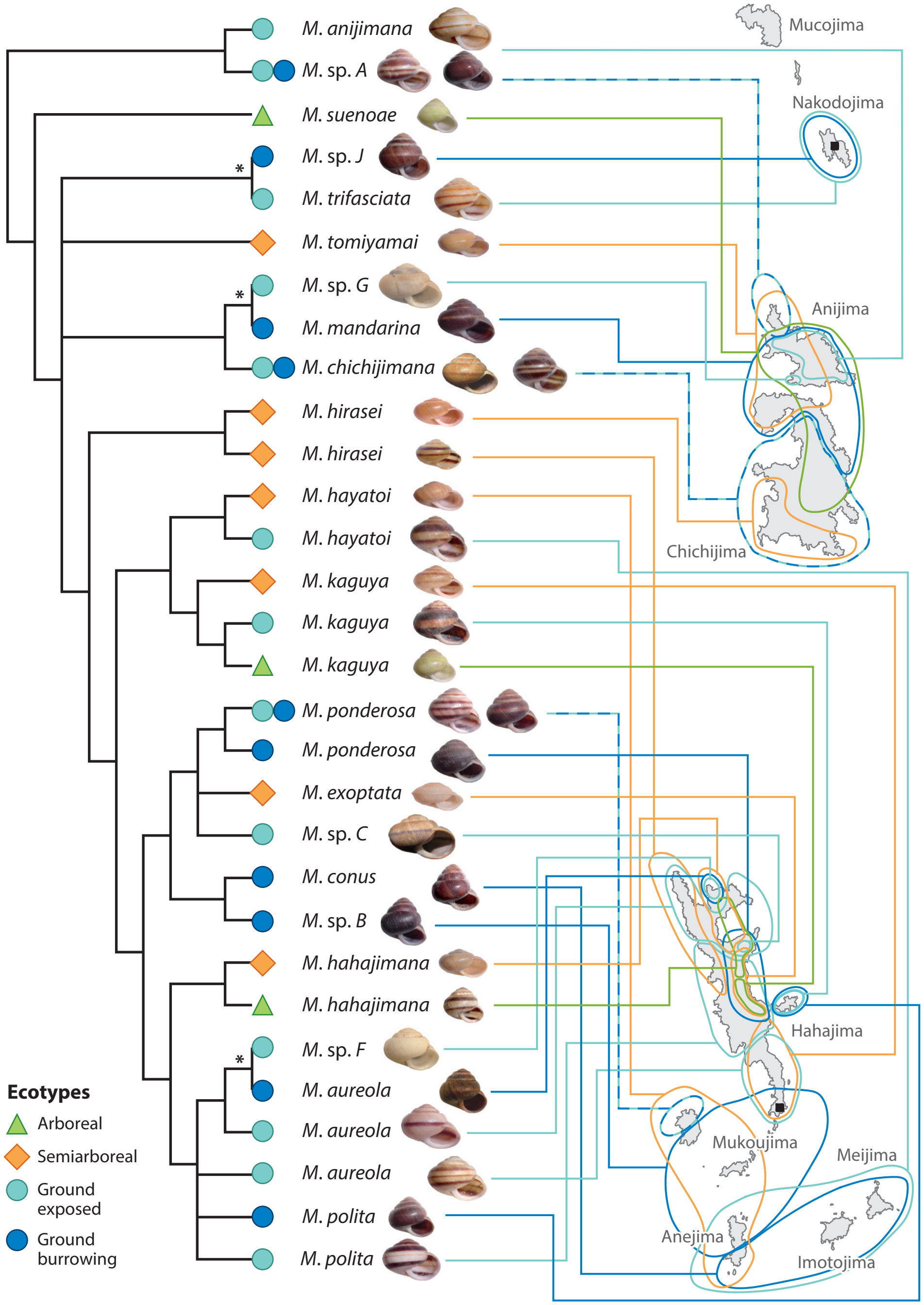
When species that have diversified allopatrically meet, adaptive divergence of habitat use may occur as a result of interspecific competition (manifested as ecological character displacement) or reproductive interference. Thus, coexistence of species within a lineage does not occur during nonadaptive radiation but is a primary stage of adaptive radiation (Rundell & Price 2009). This suggests that both nonadaptive radiation and diversification associated with habitat heterogeneity may play a role in the generation of land snail species richness on oceanic islands.

Species richness of Galapagos bulimulid land snails resulting from within-island speciation is mainly determined by habitat heterogeneity (Parent & Crespi 2009, Parent 2012). Hawaiian land snail species richness, also primarily a result of within-island speciation following initial colonization, is determined primarily by island area, island age, and habitat diversity (Cowie 1995). More generally, Cameron et al. (2013) showed that for a number of Pacific and Atlantic island groups, both island age and area (a correlate of available habitat diversity) determine species richness. However, the relationship between species richness and island age is complex (Cowie 1995, Cameron et al. 2013). Thus, geographical isolation in combination with nonadaptive radiation and adaptive divergence into different habitats contributes to species and phenotypic diversity on oceanic islands. Indeed, adaptive radiation has occurred in a number of lineages of oceanic island snails (Murray et al. 1993, Chiba 1999b, Parent & Crespi 2006).

Divergence of phenotypic traits associated with habitat use is likely to occur mainly through three processes: (*a*) as a result of interactions (i.e., interspecific competition or reproductive interference) among species that initially diverged by geographical isolation and whose ranges subsequently came to overlap; (*b*) via allopatric speciation with adaptive divergence; and (*c*) by ecological sympatric speciation in which genetic differentiation is enhanced by divergent selection in different microhabitats, resulting in rapid divergence of species using different microhabitats (Schluter 2000, Nosil 2012). These processes may all lead to adaptive radiation.

Speciation events due to a mixture of nonadaptive speciation via geographical isolation and adaptive speciation have been documented in the endemic species of the genus *Theba* in the Canary Islands (Greve et al. 2012). The phenotypic evolution of *Cavernacmella* species in the Ogasawara Islands is characterized by a pattern of long-term stasis among allopatric species over 2 million years with periodic bursts of change among sympatric species approximately every 10,000 years (Wada et al. 2013). Diversification of *Mandarina* in the Ogasawara Islands includes both adaptive radiation and divergence without ecological differentiation (Chiba 1999b, 2004; Davison & Chiba 2006a,b, 2008). Species of *Mandarina* have diversified into arboreal, semiarboreal, ground exposed (i.e., they prefer to rest in exposed sites), and ground burrowing (i.e., they prefer to rest in sheltered sites) ecotypes that differ in shell shape and size. Divergence of these four ecotypes has occurred repeatedly and independently in different lineages and in different islands and areas of the Ogasawara archipelago (**Figure 2**); thus, these species have exhibited so-called replicated adaptive radiation (Schluter 2000). Species in the same ecotype are distributed allopatrically and never coexist. Divergence of these ecotypes of *Mandarina* is promoted not only by interspecific competition or reproductive interference after allopatric speciation but also by genetic differentiation resulting from divergent selection in different microhabitats (S. Chiba, unpublished data). Populations of *Mandarina* from Nakodo Island and small peninsulas of Hahajima and Anijima include variants with different shell shapes and sizes. Gene flow among these ecotypes is partially restricted, thereby suggesting an initial stage of speciation. The differences in size and shape between ground exposed and ground burrowing ecotypes reflect adaptation to their preferred habitat. In fact, assortative mating based on size occurs in the bradybaenids *Bradybaena pellucida*

(Kimura et al. 2015) and *Euhadra quaesita* (K. Shibuya, K. Kimura & S. Chiba, unpublished data), the closest mainland relative of *Mandarina*. Therefore, divergence among ecotypes by adaptation to distinct microhabitats automatically results in the evolution of reproductive isolation. This sort of speciation is greatly facilitated when traits subject to divergent selection also contribute to nonrandom mating (i.e., magic traits) (Gavrilets 2004).



In contrast, adaptive radiation is less likely to occur if the effects of competition are mitigated by predation and/or unstable environments. Instead, ecological speciation due to adaptation against predation (Nosil 2012) is more likely to occur in such circumstances. Divergence in shell morphology of land snails can occur as a result of adaptation against divergent strategies of predator attack (Schilthuizen et al. 2006, Konuma & Chiba 2007, Hoso & Hori 2008). Vermeij (1987) suggested that the appearance of novel predators facilitates the morphological diversification of prey lineages. Morphological divergence as a response to predation may promote evolution of reproductive isolation through ecological speciation. For example, if shell morphology is involved in mate recognition, reproductive isolation may evolve when traits such as spines on a shell are selected for because they aid in prevention of attack by predators, as in the case of *Opisthostoma* species preyed on by slugs in Borneo (Schilthuizen et al. 2006). In mainland Southeast Asia, adaptation against predation by malacophagous snakes causes differentiation in the coiling direction of shells, which automatically results in reproductive isolation (Hoso et al. 2010). In mainland Japan, coevolution between snails and malacophagous beetles has caused divergence in the body size of *Euhadra* species (Konuma et al. 2011), which appears to have facilitated the evolution of reproductive isolation because of size-assortative mating. Also, adaptation to differential predation strategies of malacophagous beetles has resulted in the evolution of distinctive behaviors and shell morphology, accompanied by the evolution of reproductive isolation, in species of the bradybaenid genera *Ainohelix* and *Ezohelix* in Russia and Japan, respectively (Y. Morii, L. Prozorova & S. Chiba, unpublished data). These observations suggest that predation promoted both morphological diversification and speciation without divergence in habitat use. High morphological and species diversity of *Bradybaena* in central China appears to represent such an example of predation-induced radiation (T. Hirano, Y. Morii, T. Sota, H. Liang & S. Chiba, unpublished data) (**Figure 1**).

Although morphological evolution promoted by predation has been reported on oceanic islands (e.g., in *Poecilozonites* species in Bermuda) (Olson & Hearty 2010), so far no instance of possible predation-induced radiation has been reported in oceanic island land snails. Greater diversity of predators and therefore of predation strategies may provide more opportunities for predator-driven diversification in continental habitats. In general, therefore, rapid radiation with morphological divergence occurs both on oceanic islands and in continental habitats. Although the majority of the diversification on islands is likely to be a result of nonadaptive radiation and adaptive radiation associated with habitat, a greater proportion of predation-induced radiation may be found in continental habitats.

Figure 2

Phylogenetic relationships among populations of *Mandarina* in the Ogasawara Islands. Diversification of *Mandarina* into four ecotypes (arboreal, semiarboreal, ground exposed, ground burrowing) occurred repeatedly and independently in different lineages and in different islands and areas. The phylogeny was constructed from previous molecular phylogenetic analyses of *Mandarina* based on mitochondrial DNA sequences (Chiba 1999b; Davison & Chiba 2006a,b; Chiba & Davison 2008) supplemented by additional unpublished data (S. Chiba, unpublished data). Occurrence of each population at each representative site is shown by a line connected to the site on the map. The symbol placed before the species name indicates the ecotype of the population. Various levels of segregation by ecotype and species are shown. Asterisks indicate instances in which two species (e.g., dark *M. aureola* and pale *M.* sp. *F*) are morphologically and genetically (microsatellites and/or allozymes) distinct but cannot be separated by phylogenetic analyses (S. Chiba, unpublished data). The populations indicated with two different symbols (e.g., *M.* sp. *A*) not only have phenotypes associated with the different ecotypes but also have intermediate phenotypes, indicating no restriction in gene flow between phenotypes (Davison & Chiba 2008).

2.5. Patterns of Diversity

Differences in the major processes that cause speciation and radiation may result in differences in species diversity patterns between oceanic islands and continents. On oceanic islands, the presence of relatively low predator richness and abundance combined with stable environments leads to high land snail population density and, hence, high β-diversity as a result of speciation due to geographical isolation (i.e., nonadaptive radiation). Higher population density may result in greater interspecific competition, thereby promoting divergence of habitat use (i.e., ecological character displacement). Ecological speciation via divergence in habitat use is also likely to occur under such conditions. The number of species that can coexist appears to be limited if island age is not old enough to permit ecological divergence. Thus, relatively low α-diversity and high β-diversity are expected for land snails on oceanic islands. Characteristics of diversity and the evolution of land snails on oceanic islands appear in part to reflect the type of interspecific interaction that is dominant in an ecosystem.

3. EXTINCTIONS ON OCEANIC ISLANDS

Species diversity is affected not only by evolutionary processes (i.e., speciation) but also by processes of species loss (i.e., extinction). Before the arrival of humans, climatic changes were a major cause of land snail extinctions on oceanic islands. Since human colonization, however, habitat loss due to human activity and the impacts of non-native species have been the major causes of extinction.

3.1. Natural Extinctions

The species richness of organisms on islands is often described, following MacArthur & Wilson (1967), as a dynamic balance between immigration and extinction. However, this theory of island biogeography was essentially an ecological theory set in an ecological timescale. For many groups of organisms and especially for land snails, species richness on islands seems better described as a balance between extinction and speciation, that is, framed by an evolutionary timescale (Cowie 1995, 1996; Cameron et al. 2013). Climatic changes during the Quaternary have greatly affected environments, habitat conditions, and the malacofaunas of oceanic islands (e.g., Cook et al. 1993, Goodfriend et al. 1996, Yanes et al. 2011). Paleontological data on the land snails of Madeira suggest that climatic change during the Pleistocene altered the island's vegetation, which subsequently caused changes in faunal composition and the distribution of species as a result of the association between the distributions of particular snail species and particular types of vegetation (Cook et al. 1993, Cameron et al. 2006). In the Pacific region, fossil land snails in the Ogasawara Islands also exhibited a pattern of stable community composition interrupted by alterations in species composition due to climatic change (Chiba 1998). Climatic change results in extinctions of local populations and species via habitat loss, which fragments the distributions of species into geographically isolated populations (Cameron et al. 2006).

3.2. Anthropogenic Extinctions

As mentioned earlier, among all animal groups, land snails have suffered the greatest number of species extinctions as a result of anthropogenic impacts (Lydeard et al. 2004; Régnier et al. 2009, 2015a). Despite the relative lack of data on invertebrates compared with vertebrates, almost as many molluscs (310) are listed as extinct by IUCN (2015) as all chordates combined (338); most (281) are gastropods, with the great majority being land snails of oceanic islands and more than half of these (144) being Pacific island snails. Régnier et al. (2009) reevaluated the mollusc species and subspecies then listed as extinct by IUCN through bibliographic research and consultation with experts; some species were in fact extant, but an additional 288 taxa were assessed as extinct. Of the 566 extinct taxa, 400 (71%) were from oceanic islands. The total global number of land snail extinctions is undoubtedly much higher than this: 10% of all land snail species may in fact be extinct (Régnier et al. 2015a). However, this overall global extinction rate does not highlight the major difference between continental regions and oceanic islands, with many island faunas having lost far more than 10% of their land snail species (Régnier et al. 2015b).

The main cause of extinction of land snails on oceanic islands is primary habitat loss due to deforestation, cultivation, mineral extraction, and urbanization. In the Pacific region, subfossil records of land snails suggest that some extinctions occurred during the initial stages of colonization of the islands by Pacific Islanders (e.g., Burney et al. 2001, Sartori et al. 2013). In the Hawaiian Islands, considerable habitat destruction was caused by Polynesians, before European arrival in 1778, and undoubtedly caused local extirpations and some extinctions (Régnier et al. 2015b).

In addition to these direct impacts of early human activities, intentionally or unintentionally introduced non-native species may have affected island land snails, both directly and indirectly. Polynesians introduced the Polynesian rat (*Rattus exulans*), which may have caused destruction of lowland forests (Athens 2009) and the snails they supported, although snails now seem not to be an important part of its diet (Régnier et al. 2015b). Polynesian pigs have been thought by some to have remained closely domesticated, causing little ecological harm, although highly damaging modern feral pigs are predominantly descended from Polynesian rather than European pigs (Régnier et al. 2015b). Such early impacts were similar on many Pacific islands (Steadman 2006). These land snail species that went extinct prior to European colonization of the islands may have been the species that were most sensitive to environmental change.

However, in many cases, especially in the absence of archaeological investigation of the faunas and/or dating of shells, it is difficult to be sure of the timing of extinctions, either before or after the colonization of the islands by Westerners (Sartori et al. 2013). Nonetheless, following the arrival of Westerners, the rate of extinction probably increased substantially, primarily in the late eighteenth and during the nineteenth centuries and even more so during the twentieth century (Régnier et al. 2015a). Thus, habitat loss appeared to affect numerous groups of land snails, such as the Endodontidae (Sartori et al. 2014), Euconulidae (Bouchet & Abdou 2001), Assimineidae (Bouchet & Abdou 2003), Helicinidae (Richling & Bouchet 2013), and the Hawaiian endemic family Amastridae (Régnier et al. 2015b). Many of these species went extinct before they were recognized scientifically (Richling & Bouchet 2013). Many such species, not just land snails, are no doubt still undiscovered and undescribed, which has significant implications for estimates of true overall anthropogenic extinction rates (Hawksworth & Cowie 2013).

Following European arrival, the introduction of ungulates, notably goats and European pigs (Cox 1999), extended the habitat destruction more widely inland and to higher elevation areas. The introduction and rapid spread of *Rattus norvegicus* and *Rattus rattus*, which readily feed on snails, probably caused negative population-level impacts (Hadfield 1986, Hadfield & Saufler 2009, Régnier et al. 2015b). More recently, introduced chameleons (*Trioceros jacksonii*) may be having similar impacts (Chiaverano & Holland 2014).

Along with rats, the carnivorous snail *Euglandina rosea* has probably been the most important introduced predator of land snails. It was introduced from Florida to the Pacific Islands and islands of the Indian Ocean starting in the 1950s as a biological control agent for the giant African snail, *Achatina fulica* (Griffiths et al. 1993; Cowie 2001a,b). Predation by *E. rosea* caused extinctions of *Partula* species in French Polynesia (Murray et al. 1988, Cowie 1992, Coote & Loève 2003, Lee et al. 2014) and resulted in serious impacts to the land snail faunas of many oceanic islands, including the Hawaiian Islands (Hadfield 1986, Hadfield & Saufler 2009) and perhaps also American Samoa (Cowie 2001b, Cowie & Cook 2001), Guam (Hopper & Smith 1992), and Mauritius (Griffiths et al. 1993). *E. rosea* has been introduced to other Pacific islands, and although surveys have not been undertaken, its impacts may be similar (Cowie 2001a,c). Régnier et al. (2009) noted that among the 400 land snail species they assessed as extinct on oceanic islands, 234 species were on islands where *E. rosea* had been introduced and 134 of these extinctions were highly likely to have ultimately been caused by *E. rosea*. In contrast, no clear decrease in *A. fulica* can be attributed to predation by *E. rosea* (Cowie 2001a). Other predatory land snail species have also been introduced as putative biocontrol agents, most notably *Gonaxis* species, but their impacts appear to be much less than those of *E. rosea* (Cowie 2001a).

The predatory flatworm *Platydemus manokwari* is another species, native to New Guinea, that has been introduced as a putative biological control agent for *A. fulica* (e.g., Muniappan et al. 1986). It preys heavily on land snails, including arboreal species (Sugiura et al. 2006, Sugiura & Yamaura 2010, Ohbayashi et al. 2007). It has become a serious threat to the native snail faunas of the Mariana Islands (Hopper & Smith 1992, Eldredge & Smith 1995, Régnier et al. 2009) and Samoa (Cowie & Robinson 2003), and it is present on many other islands and archipelagos, including Palau (Eldredge & Smith 1995), Pohnpei in the Federated States of Micronesia (Eldredge & Smith 1995), the Philippines (Muniappan et al. 1986), Tonga and Vanuatu (Anonymous 2002), Fiji (Brodie et al. 2014), and Mangareva in French Polynesia (Winsor et al. 2004). Although it has been introduced to the Hawaiian Islands (Eldredge & Smith 1995), it has not become widespread or abundant (S. Sugiura, personal communication), and its impacts on the native snail fauna may not as yet have been great.

In the 1980s *P. manokwari* invaded the Ryukyu Islands, and in the early 1990s it was introduced to Chichijima in the Ogasawara Islands (Ohbayashi et al. 2007). Since then, the distribution of *P. manokwari* has expanded rapidly and now encompasses the whole island, and most of the native land snail species of Chichijima have gone extinct except in two small peninsulas in the southernmost part of the island, where the flatworm has not yet invaded (**Figure 3**). Among the 25 native snail species recorded on Chichijima in the 1980s, 16 went extinct on the island within 25 years because of predation by *P. manokwari*, and only 3 native species survive in the areas where *P. manokwari* occurs. In contrast, no extinction has occurred among the 13 non-native snail species recorded in the 1980s, and the distribution of some of the non-native snail species has increased since approximately 1990 (S. Uchida & S. Chiba, unpublished data). The agents that have caused the decline of the endemic land snails differ from island to island among the Ogasawara archipelago (Chiba & Roy 2011). On Hahajima, cultivation and deforestation combined with associated habitat disturbance first impacted the fauna during 1880–1940; subsequently, non-native carnivorous flatworms (mainly *Bipalium muninense*, originally from the Ryukyu Islands) have caused a decline in land snail populations (Chiba et al. 2009). On Anijima, predation by *R. rattus* became a serious problem after the late 2000s, and the land snail fauna of the island declined rapidly (Chiba 2010a).

A possible additional novel threat to island snail faunas is the introduction of the nematode parasite *Angiostrongylus cantonensis*; when transmitted to humans, this parasite can cause angiostrongyliasis, a potentially fatal illness that manifests as eosinophilic meningitis (Cowie 2013). The definitive hosts are rats (Yong & Eamsobhana 2013), and the intermediate hosts are diverse snail species that vary greatly in infectivity competence (Kim et al. 2014). Humans are infected as accidental hosts (in which the parasite dies before completing its life cycle) after eating infected snails. *A. cantonensis*, which appears to be a tropical and subtropical species, is spreading from its putative Southeast Asian origin to other areas including the Hawaiian Islands, French Polynesia, American Samoa, parts of the Caribbean, North America, and South America (Cowie 2013, Stockdale-Walden et al. 2015). Climate change may allow it to spread to higher latitudes (J.R. Kim,

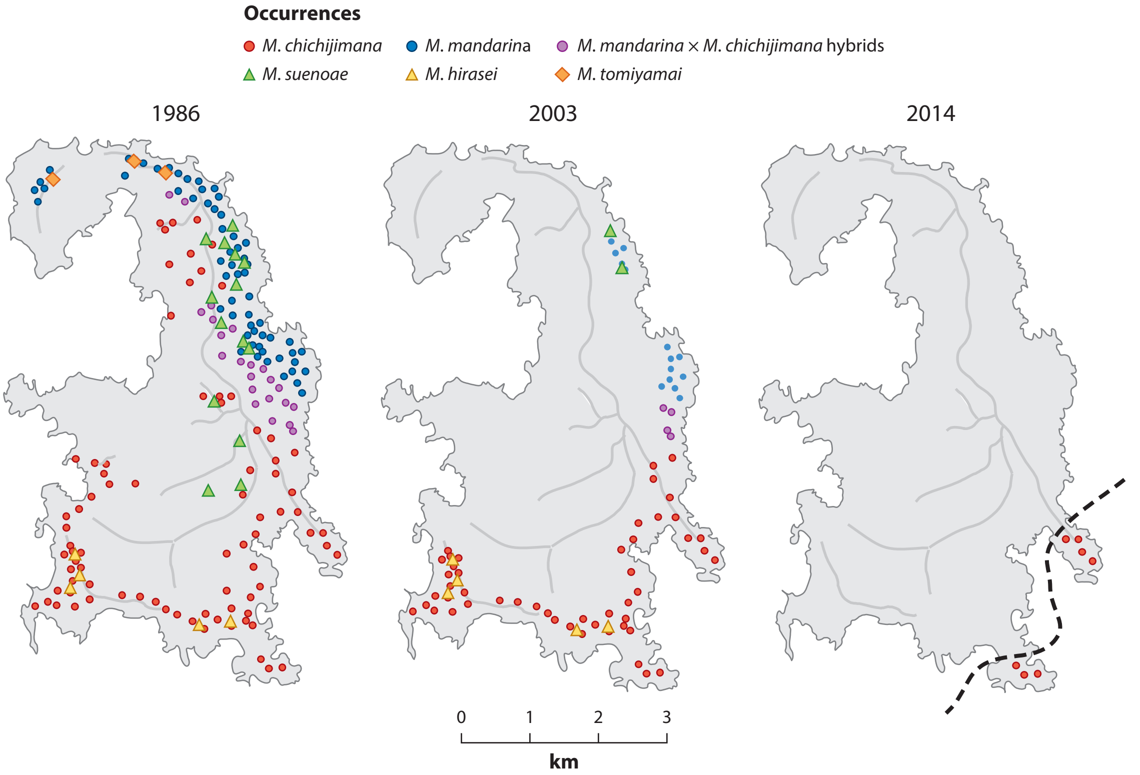


Figure 3

Temporal changes in the occurrence of five species of *Mandarina* on Chichijima in the Ogasawara Islands since 1986. This decline of *Mandarina* was caused by predation by the predatory flatworm *Platydemus manokwari*. By 2014, only *Mandarina chichijimana* had survived, and its distribution was restricted to two small peninsulas. The dashed line indicates the *P. manokwari* invasion front.

T.M. Wong, P.A. Curry, N.W. Yeung, K.A. Hayes & R.H. Cowie, unpublished draft manuscript). However, the impact of the parasite on its snail hosts is almost unknown, despite the presence of nearly 3 million larvae in some individuals (Kim et al. 2014). The hyperdiverse (>750 species) and highly endemic (>99%) native Hawaiian land snail fauna (Cowie 1995) has already suffered from habitat destruction and impacts of alien species, as described above, and 50–90% of the species may be extinct (Lydeard et al. 2004, Régnier et al. 2015b). Some native Hawaiian snail species can become infected by *A. cantonensis* (Kim et al. 2014), but the potential impact of this parasite on these and other already threatened and endangered island species is unknown at present.

In general, the multiple factors described above have contributed to extinction of island snails. These factors do not necessarily act in isolation—they are associated. For example, habitat alteration as a result of cultivation may provide preferred habitat for rats, thereby intensifying the impact of rats. Introduction of *A. fulica* led to the development of biological control programs, which introduced *E. rosea* and *P. manokwari*, resulting in extinction of a number of island snail species. Indirect effects among non-native and native species are complex, and some non-native species can mitigate the impact of other non-native species on native snail species (Chiba 2010b). However, cascades of a series of multiple anthropogenic effects could cause serious declines in island snail faunas (Chiba & Roy 2011). Further surveys are required to clarify the processes of extinction of island snails and especially to demonstrate causality rather than simply correlation.

3.3. Evolution and Extinction

Why are species on oceanic islands more vulnerable to anthropogenic extinction than those of continental regions? In the case of land snails, vulnerability of oceanic island species appears to be explained primarily by two processes.

First, habitat loss is likely to affect island snails more severely than continental snails. As land snail species on oceanic islands have relatively high β-diversity but very localized distributions, the probability of extinction caused by an equivalent level of habitat loss (or stochastic events such as hurricanes or fires) is higher in the former than in the latter.

Second, impacts of invasive predators are more serious on oceanic islands, especially for some species, than in continental habitats, as discussed above. In the case of land snails, island species are likely to be less preadapted to predator attacks than continental species because predators are naturally lower in abundance and diversity on oceanic islands and the snails have evolved in the absence of high predation pressure. For instance, achatinelline tree snails (and other snails) in the Hawaiian Islands and partulid tree snails elsewhere in the Pacific region have evolved to produce low numbers of large, crawl-away (by ovoviviparity) offspring that mature slowly but live much longer than most continental species (Cowie 1992). They are therefore highly vulnerable to predation by alien predators because it would take a long time for a population to recover from a single predation episode that destroys a significant portion of the population or for a population to withstand a consistent, lower level of predation (e.g., Hadfield 1986, Cowie 2001a, Lee et al. 2014). Other species with more rapid reproduction and higher fecundity may be able to withstand predation, but this suggestion has not been confirmed by comparative studies. Nonetheless, the idea is supported by the fact that the invasion of *P. manokwari* in the Ogasawara Islands has not led to any extinction of non-native land snail species introduced from continental Asia. In addition, no evidence of a decline of native land snail species on the continental Ryukyu Islands following the invasion of *P. manokwari* in the 1980s has been found (S. Uchida & S. Chiba, unpublished manuscript).

Accordingly, the high susceptibility of oceanic island snails to extinction reflects their ecology, which results from their evolution in situ on the islands. These observations lead to the expectation that anthropogenic extinction of land snails will be more serious on older, more isolated, and more environmentally stable islands, which will also be those that support the faunas exhibiting the highest levels of narrow island or even more local endemism. Empirical studies are required to test this hypothesis.

4. CONCLUSION

Invertebrates, and land snails in particular, are suffering far higher rates of extinction than previously thought and bear the brunt of the current biodiversity crisis (Régnier et al. 2009, 2015a). Many extinctions of land snails on islands have been due to habitat destruction and the impacts of non-native species. Island land snails have provided excellent model systems to study evolutionary processes because of their high species diversity within small areas resulting from within-island radiation. However, these processes and resulting patterns make island land snails especially prone to extinction. In addition, adaptation to island environments with low diversity of predators is likely to result in the evolution of species that are vulnerable to attack by novel predators introduced from continental regions. The vulnerability of oceanic island land snails to anthropogenic extinction therefore reflects, at least in part, the outcomes of their evolution on the islands. Thus, clarifying how species interactions affect species diversity and how endemic species have originated on oceanic islands is crucial for their conservation. Our knowledge regarding the ecology and evolution of island snails remains limited, and much greater conservation effort is required if these diverse but especially vulnerable species are to survive.

DISCLOSURE STATEMENT

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