Species Diversity and Conservation of *Mandarina*, an Endemic Land Snail of the Ogasawara Islands

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Abstract

The endemic land snails, genus *Mandarina* of the Ogasawara Islands, have diversified into arboreal, semi-arboreal and ground ecotypes.   Shell morphologies of *Mandarina* species have a clear relationship with their respective ecotypes.   In addition, marked geographical variations in morphology and genes are found within species.   Phylogenetic relationships based on mitochondrial DNA (mtDNA) sequences suggests that *Mandarina* evolved from *Euhadra*, a genus distributed on the mainland of Japan.   The inferred phylogeny suggests that similar morphologies and ecotypes appeared independently and rapidly in different lineages and islands at different times.   This rapid evolution produced some incongruities among phylogenetic relationships, morphology, species taxonomy, and the level of reproductive isolation.   Interspecific hybridization occurs between sympatric species due to environmental change, resulting in an admixture of genetic and morphological characteristics.   These findings reveal the importance of *Mandarina* as a model system for evolutionary study.   However, a predatory land snail and flatworm have recently been introduced into the Ogasawaras.   These predators may rapidly cause the extinction of *Mandarina,* and thus, a conservation program is needed for *Mandarina*.   In the conservation program for *Mandarina*, species taxonomy should not be used as a criterion for selection of populations for captive breeding because of incongruence among the phylogeny, morphology, ecology, species taxonomy and reproductive isolation.   In addition, the danger of interspecific hybridization should be considered when captive-bred snails are reintroduced into restored or secure habitat.

Key words: adaptive radiation, conservation, hybridization, *Mandarina*, Ogasawara Islands

1. Introduction

Organisms in small isolated locations have great potential in evolutionary studies.   Adaptive radiation in endemic organisms inhabiting isolated islands and lakes have been used as general evidence for major evolution.   Examples of such adaptive radiations include Darwin's finches in the Galapagos Islands, Hawaiian honey creepers, and African cichlids (*e.g.*, Lack, 1947; Grant, 1986; Freed *et al*., 1987; Schliewen *et al*., 1994).   Detailed studies of the processes and causes of adaptive radiation of island organisms have provided excellent data for understanding the process of character divergence.

The endemic *Mandarina* land snails of the Ogasawara Islands offer an exceptional example of character divergence.   *Mandarina* has diversified into taxa occupying many habitats, (*e.g.* arboreal, semi-arboreal, terrestrial, dry, and wet habitats) and shows remarkable diversity in shell and genital morphology (Emura, 1943; Habe, 1969; Minato, 1978;

Chiba, 1996).   Shell diameters range from 15 mm to 80 mm, and 17 species including five extinct species have been described.

The Ogasawara Islands are located in the northwest Pacific, about 1,000 km south of Japan, and they consist of about 30 small volcanic islands.   The biggest island among them is only 25 km^2 in area.   The Ogasawara Islands have been entirely isolated from other regions, and the biota of these islands (plants, birds, insects and land snails) are characterized by several peculiarities as are the biota in other oceanic islands.

In the last 10 years there have been several studies on the population genetic structure, community structures, the evolutionary history and the process of speciation of *Mandarina*.   These studies suggest that large ecological and morphological differences among the species of *Mandarina* have evolved despite a small genetic differentiation among these species.   However, these ecological and morphological differences easily disappear when hybridization occurs

between different species. Reproductive isolation among the species is easily broken in *Mandarina*, resulting in complex geographical variations in morphology and genetics. In this article, I show how morphologically and ecologically divergent species have evolved during a relatively short time, and how morphologically distinct species have hybridized. In addition, I describe how rapid diversification and hybridization is causing a problem with regard to the conservation of island organisms such as *Mandarina*.

2. Divergences in Habitat Preference and Morphology

The Ogasawara Islands are composed of three groups of islands, the Mukojima, Chichijima, and Hahajima groups. Four extant species and five extinct species have been recorded in the Chichijima Group, one extant species has been recorded in the Mukojima Group and six extant species have been recorded in the Hahajima Group. These species are all endemic to each group of islands (Fig. 1). Each species is composed of many local populations with distinctive shell or genital morphologies. In addition, some parapatric species are producing hybrid zones (Chiba, 1997), and thus, geographical variations of *Mandarina* species are markedly complex.

Habitat preference of *Mandarina* was examined for each species in previous studies and the species were divided into arboreal, semi-arboreal and ground ecotypes (Fig. 2) (Minato, 1978; Chiba, 1996). The arboreal ecotypes were found only in trees. These

included *M. suenoae* from the Chichijima Islands and *M. hahajimana* from the middle to northern parts of Hahajima. Most of the arboreal species were found at a height of more than 1 m from the ground. Semi-arboreal ecotypes are found both in trees and on the ground, and rest between the trunk and leaf or in the space between thick leaves of pandanus trees or palm trees when they are inactive. These include *M. hirasei* from the Chichijima Islands and *M. exoptata* from Hahajima and *M. hahajimana* from the southern parts of Hahajima, Anejima and Mukoujima. The ground ecotypes are found on the ground and are never found in trees. These include three species from the Chichijima Islands (*M. chichijimana*, *M. mandarina* and *M. anijimana*), four species from the Hahajima Islands (*M. ponderosa*, *M. conus*, *M. aureola* and *M. polita*), *M. hahajimana* from Imotojima and Meijima, and *M. trifasciata* from the Mukojima Islands. There are also differences in preference of microhabitat among the ground ecotypes. The species that have the exposed-ground ecotype prefer to rest or forage in more exposed, thinner, dryer litter than the species that have the hidden-ground ecotype (Chiba, 1999b). For example, *M. anijimana*, which coexists with *M. mandarina* in the central part of Anijima, was found in bushes or in forest litter that was dominated by leaves of pandanus trees and broad-leaved trees, but not in litter dominated by leaves of palm trees. *M. mandarina* was found in all kinds of habitat, but it was relatively rare in bushes or in forest litter that was dominated by leaves of broad-leaved trees when it coexisted with *M. anijimana*.
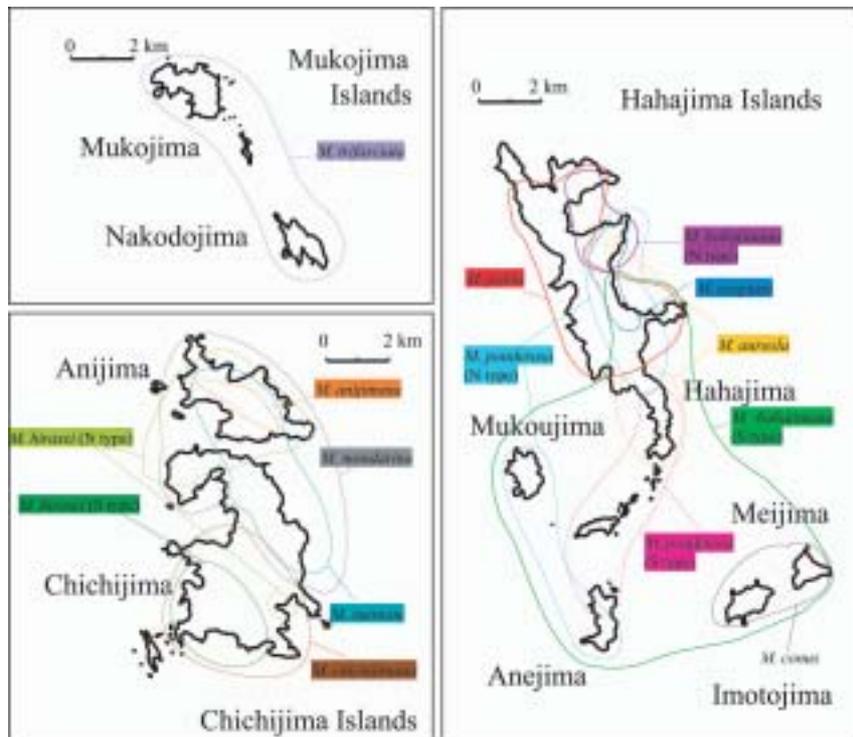

Fig. 1   The Ogasawara Islands, with distributions of species of *Mandarina* indicated.

Fig. 2 Diversity of morphology and habitat use in *Mandarina*.   1: *M. hahajimana* N type (Mt. Sakaigatake, Hahajima),   2: *M. aureola* (Minamizaki, Hahajima),   3: *M. polita* (Chibusa-yama, Hahajima),   4: *M. hahajimana* S type (Minamizaki, Hahajima),   5. *M. exoptata* (Chibusa-yama, Hahajima),   6: *M. mandarina* (Yoake-yama, Chichijima),   7: *M. ponderosa* N type (Chibusa-yama, Hahajima),   8: *M. suenoae*, (Anijima),   9: *M. hirasei* S type (Takayama, Chichijima).

There is a clear association between ecotypes and shell morphologies (Fig. 3). The shells of ground-dwelling snails are consistently thicker and heavier, and have a smaller aperture than those of arboreal or semi-arboreal populations.   Populations with a similar habitat have similar shell morphology.   The remarkable divergence in shell morphology in *Mandarina* is associated with the differences in its habitats (Chiba, 1996).   The thinner, larger aperture shells of the arboreal and semi-arboreal populations are possibly adapted for living in trees because they allow the snails to adhere better to trunks and leaves.   The species with the exposed-ground ecotype possess flatter and brighter shells than the species with the hidden-ground ecotype.   Shells of species with the arboreal and semi-arboreal ecotypes are also brighter than shells of species with the ground ecotype. This relationship between shell color and particular habitats is consistently found in all of the pairs of ground species in *Mandarina*.   Bright shells would be expected to have an advantage in sites where snails are largely exposed, because they do not heat up as much as dark shells in the sunlight.   Snails with bright shells would be able to avoid overheating in the sun.

## 3. Parallel Adaptive Radiation of *Mandarina* in the Ogasawara Islands

A comparison between (i) the ecotype and (ii) the phylogenetic relationship of *Mandarina* species estimated by mitochondrial 16SrRNA and 12SrRNA gene sequences suggests that radiation and divergence of arboreal, semi-arboreal, ground ecotypes have occurred repeatedly at different times and in different areas and lineages (Chiba, 1999a).   The consistent topology between the 16SrRNA and 12SrRNA trees suggests that radiation and divergence of arboreal and terrestrial species first occurred in the Chichijima Islands.   The species migrated to the Hahajima and Mukojima Islands from the Chichijima Islands and diversified on Hahajima, leading to a second radiation. Divergence of different lineages of arboreal, semi-arboreal and terrestrial species occurred repeatedly in the Hahajima Islands.

Although details of the mitochondrial DNA (mtDNA) tree and the population tree may differ because of hybridization between different species, the mtDNA tree suggests that there has been repeated divergence of arboreal and ground ecotypes, because no examples have been found of hybridization between species with the ground ecotypes and those

with the arboreal ecotypes. Species with similar shell morphologies appear repeatedly in different lineages (Fig. 3) because shell morphologies are closely related to life habits (Chiba, 1996). Extreme ecological and morphological differences have been found between the arboreal *M. hahajimana* (N type) and the ground-dwelling *M. aureola* (Chiba, 1996). Phylogenetically, however, these populations are very close. Large differences in shell forms and life habits have also been found between (i) phylogenetically close lineages such as *M. exoptata* and *M. ponderosa* and (ii) populations of *M. hahajimana* (S type) from Imotojima and Mukoujima (Fig. 3). Remarkable differences in genitalia occur between

genetically and phylogenetically close species. For example, the size of the penis of *M. chichijimana* is no more than 1/5 that of *M. mandarina*, but the genetic distance between these species is only 1.4%. This suggests that shell morphology, genital morphology and the ecotypes of *Mandarina* have all evolved rapidly.

There are some incongruities between phylogenetic patterns of mtDNA and species taxonomy (Fig. 3). The species taxonomy of *Mandarina* is based mainly on differences in genital morphology (Emura, 1943; Minato, 1978). Therefore, some incongruities between species taxonomy and the phylogenetic relationship observed in *Mandarina* can be attributed
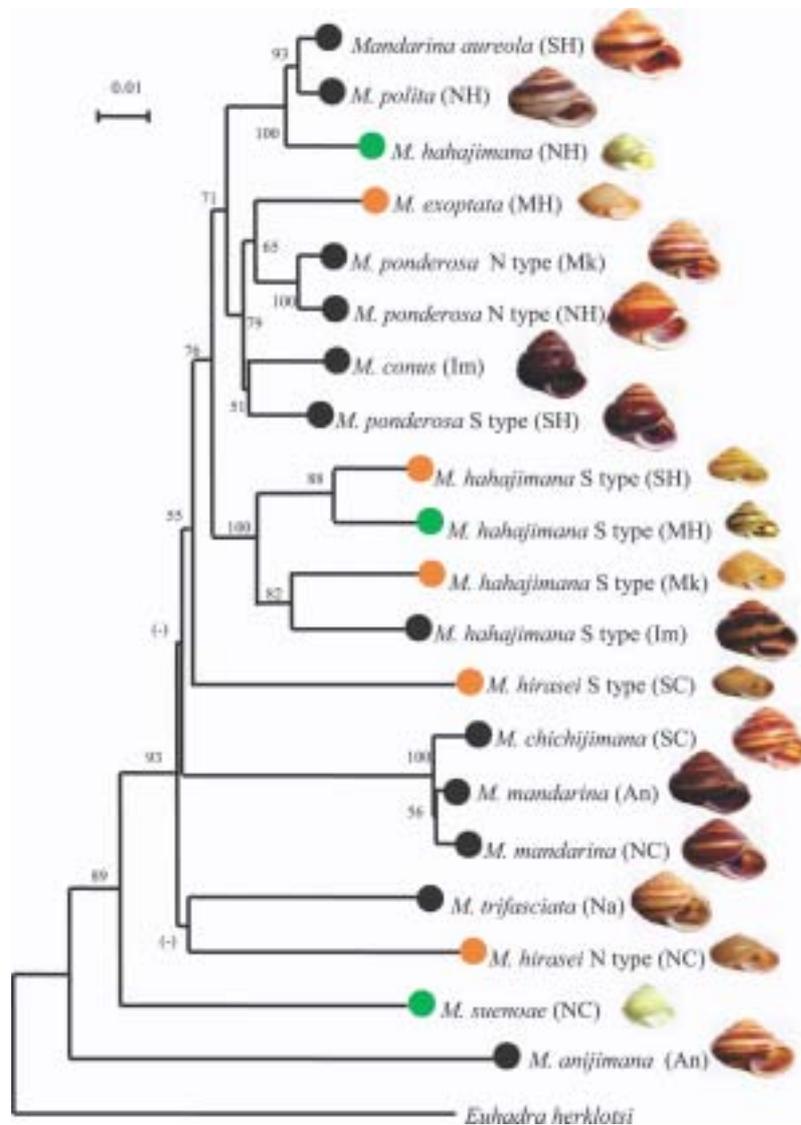
Fig. 3 A neighbor-joining tree for 18 populations of *Mandarina* on combined sequences of 16SrRNA and 12SrRNA genes. Numbers above selected nodes are percentage of times in 500 bootstrap replications that populations occurred in these clades. Bootstrap values lower than 50% were exhibited by (-). Populations with the arboreal ecotype, semi-arboreal ecotype and ground-dwelling ecotype are indicated by green, yellow and black circles respectively. Distribution of each population are also shown in parentheses (NH: north Hahajima, MH: middle Hahajima, SH: south Hahajima, Mk: Mukoujima, Im: Imotojima, Na: Nakodojima (Mukojima Islands), SC: south Chichijima, NC: north Chichijima, An: Anijima. (Modified from Chiba, 1999a).

to the rapid morphological evolution of this species and to convergent evolution. *M. hahajimana* (N type) from the northern part of Hahajima is phylogenetically closer to *M. aureola* and *M. polita* than other populations of *M. hahajimana*. A similar case is found in the northern and southern populations of *M. hirasei*. The southern populations of *M. hirasei* are phylogenetically closer to the Hahajima species than to other species of Chichijima, and thus, the northern and southern populations of *M. hirasei* should be separated as different species. In addition, the mtDNA tree shows that *M. ponderosa* (N type) from the northern part of Hahajima is phylogenetically closer to *M. exoptata* than to *M. ponderosa* (S type) from the southern part of Hahajima, and these populations of *M. ponderosa* also may be separated as different species. However, these populations of *M. ponderosa* are producing a hybrid zone in the middle range of Hahajima without assortative mating (Chiba, 1993). The incongruence among the morphology, phylogeny, and condition of reproductive isolation makes it difficult to determine the taxonomic positions of these populations.

Mandarina has been generally included in the Camaenidae and is believed to have evolved from Camaenid ancestors distributed in southeast China (Minato, 1978). However, a recent study has suggested that *Mandarina* is not phylogenetically close to Camaenid genera but is closer to Bradybaenid genera (Chiba, 1999a). Phylogenies based on mtDNA showed that *Mandarina* is closest to *Euhadra*, a genus from the mainland of Japan (Chiba, 1999a). The shell and genital morphologies and mating behavior of *Euhadra* distinctly differ from those of *Mandarina*. For example, *Euhadra* possess a dart sac, a mucus gland and complex courtship, all of which are absent in *Mandarina*. *Mandarina* lays a small number of large eggs (one to three eggs larger than 1/5 of adult shell size, see Fig. 4), while *Euhadra* lays a larger number of smaller eggs (more than 20 eggs smaller

than 1/10 of adult shell size). *Mandarina* has an extremely solid shell. This suggests that *Mandarina* has changed its reproductive organs, mating behavior, egg size, and morphology to such an extent that it has been placed in a different family. This is also supported by the occurrence of an extinct species, *M. luhuana*, which has a shell morphology similar to that of *Euhadra* from Pleistocene deposits on Chichijima.

Although the 16SrRNA sequences of the *Mandarina* species diverge considerably among the species of *Mandarina*, this does not imply that the diversifycation of *Mandarina* has a long history, because the divergence rate of the mitochondrial 16SrRNA gene of land snails is extremely fast, approximately 10% per Ma (Hayashi & Chiba, 2000; Thacker & Hadfield, 2000).

Sequence divergences among sympatric species of *Mandarina* from Hahajima (2% - 6%) were mostly smaller than those among local populations within species of *Euhadra* (1% - 14%) (Hayashi & Chiba, 2000; Watanabe & Chiba, 2001). The mean genetic distance of 16SrRNA between *Mandarina* and *Euhadra* (0.188) (Chiba, 1999a) is much smaller than the maximum level of intraspecific genetic distance in *Cepaea nemoralis* (0.25) (Thomaz *et al.*, 1994) and *Ainohelix editha* (0.23) (Teshima *et al.*, 2003). These results imply that the morphological and ecological evolution of *Mandarina* has been accelerated in the Bonin Islands.

Studies of organisms from remote islands such as the Galapagos and Hawaii (Carson & Kaneshiro, 1976; Schluter, 1988, 2000) suggest that morphological and ecological divergence is accelerated in depauperate environments where competitors and predators are fewer. A rapid morphological and ecological evolution of *Mandarina* in the Ogasawara Islands, where competitors and predators are fewer than on the mainland, is consistent with this view. A rapid ecological divergence has also been reported in Hawaiian land snails (Thacker & Hadfield, 2000). These findings suggest that a scarcity of sympatric species soon after the establishment of an island species of land snail will accelerate its ecological divergence.

4. Interspecific Hybridization

Recent studies have shown that the loss or partial loss of reproductive isolation between sympatric species of animals is not as rare an event as was previously thought (Grant & Grant, 1992; Dowling & DeMarais, 1993; Chiba, 1993; Falniowski *et al.*, 1993; Byrne & Anderson, 1994; see a review by Arnold, 1997). Furthermore, such hybridization may have severe effects on genetic variation in island populations (Johnson *et al.*, 1993; Clarke *et al.*, 1998). The influence of sympatric hybridization is especially serious for organisms with geographically limited gene flow.
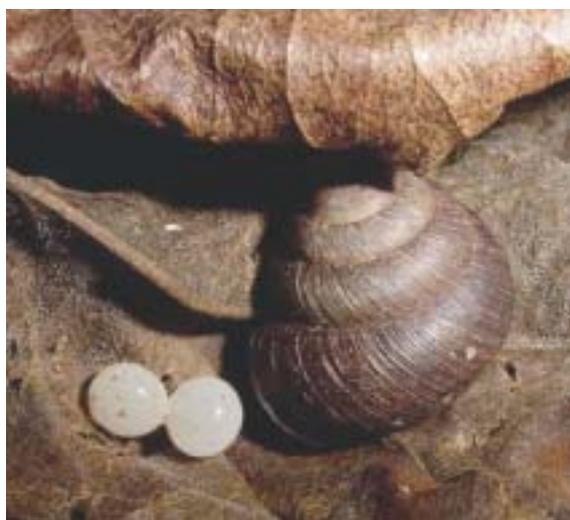
Genetic and morphologic analyses of populations

Fig. 4 An adult snail of *M. ponderosa* and its huge eggs.

of *Mandarina* suggest that hybridization between sympatric species has occurred on different islands. In the middle range of Hahajima Island, hybridization between *M. ponderosa* and *M. aureola* has occurred and a complex admixture of genes of these species has been created (Fig. 5) (Chiba, 1993). Although most of these populations are described as *M. aureola* based on their genital morphology, the shells have intermediate characteristics between *M. aureola* and *M. ponderosa*. However, such intermediate shells are not found in the fossil samples (2,000 - 13,000 years ago) collected from Hahajima except for one locality, and thus hybridization between these species has occurred recently (Fig. 6). The past distribution and geographic variation of *M. ponderosa* can be traced from the distribution of *M. ponderosa*-derived genotypes (Chiba, 1993). For example, populations of *M. aureola* in the eastern parts of the middle range of Hahajima possess marker alleles of *M. ponderosa*. *M. ponderosa* is not distributed in this area at present. However, fossils of *M. ponderosa* occur in this area. Thus, the *M. ponderosa* alleles in the populations of *M. aureola* in this area are derived from *M. ponderosa* that has become extinct (Chiba, 1993).

Another example of hybridization is found between the two sympatric species *M. mandarina* and *M. anijimana* on Anijima Island (Chiba, 1998). Intermediate shells and the coexistence of marker alleles between these species are found in populations occupying transitional zones between forest and shrub.

These findings suggest that some ecological factors are causing a partial breakdown of the reproductive isolation between these species. One plausible scenario is "frequency-dependent" hybridization (Chiba, 1998). If one species is rare at a given site and cannot find individuals to mate with, it would mate with individuals of the other sympatric species.

This hypothesis seems to be supported by the fact that hybrids have been found in high frequencies in the transitional zone between shrub and forest where *M. anijimana* becomes rare but *M. mandarina* is abundant. Although the exact mechanism of reproductive isolation between sympatric species of *Mandarina* is not clear, it may depend on pre-zygotic isolation by a simple ecological difference as has been shown to be the case with the land snail *Partula* (Johnson *et al*., 1977; Murray *et al*., 1982). This kind of isolation would be easily broken and fertile offspring would be produced.

5. Endangerment of *Mandarina* and its Conservation

Human colonization of the islands affects native wildlife both through habitat destruction and through the introduction of domesticated animals and other nonindigenous species. The most prominent cases of the influence of introduced animals are the extinction of *Partula* in Tahiti and the marked decline of endemic land snail faunas of Hawaii and Mauritius due to predation by an introduced carnivorous land snail *Euglandina rosea* (Clarke *et al*., 1984; Hadfield, 1986; Murray *et al*., 1988; Griffiths *et al*., 1993; Wells, 1995). *E. rosea* was introduced (Fig. 7) to control a giant African snail (*Achatina fulica*), a serious agricultural pest. Although *E. rosea* was not the sole cause of the extinction of native snail species, it was a critical factor.

Mandarina has suffered serious destruction of habitat due to cultivation since 100 years ago (Kurozumi, 1988; Tomiyama, 1994). However, the most serious problem is predation by introduced species. For example, a predatory flatworm, *Platydemus monokwari* (Fig. 4) was introduced to the
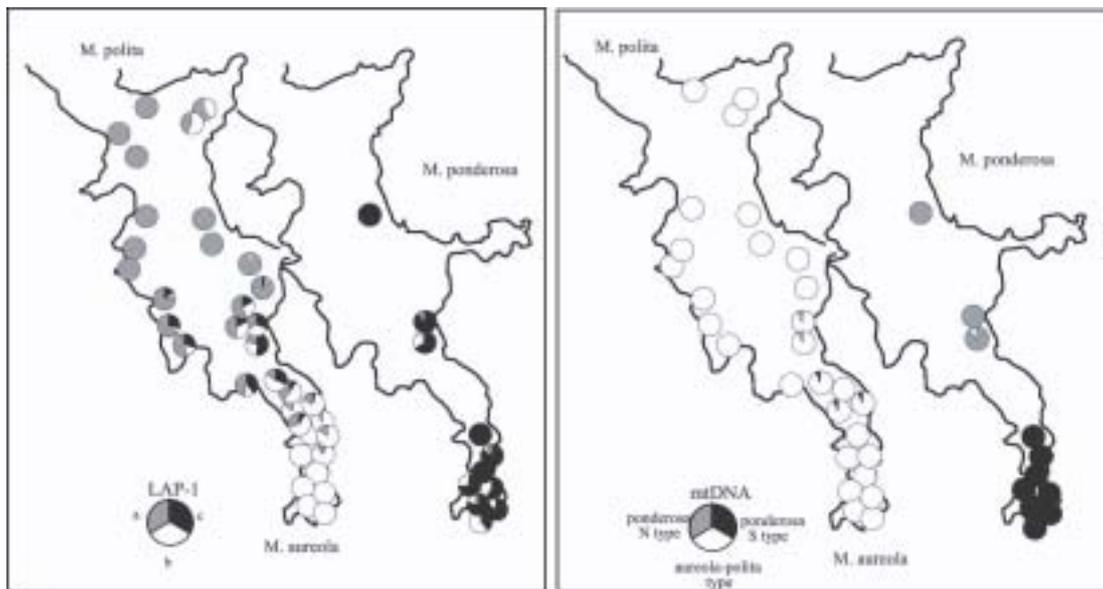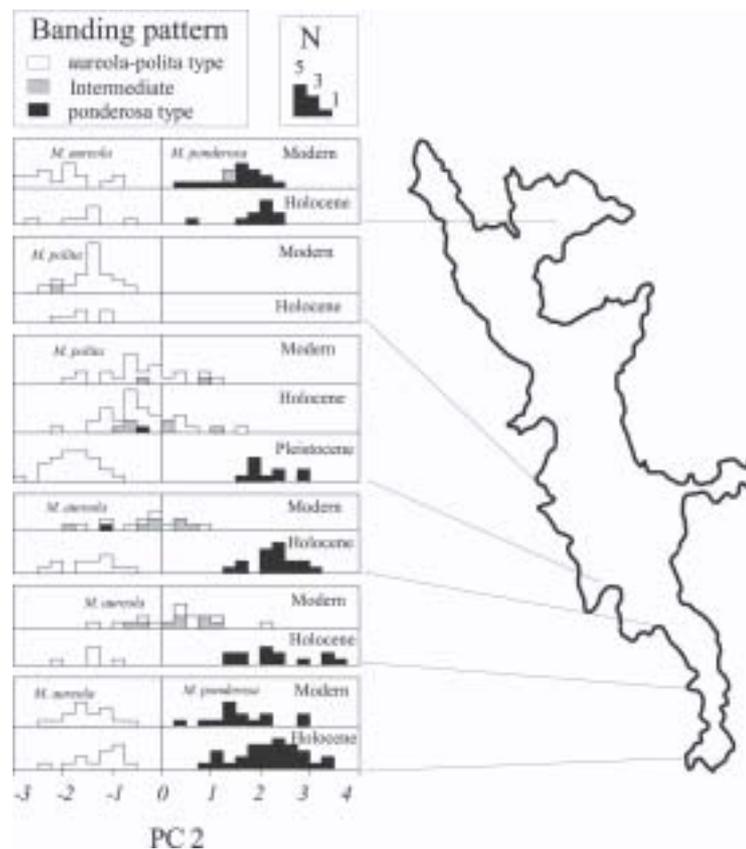

Fig. 5 Geographical variation in an allozyme locus, *Lap-1* and mtDNA (16SrRNA) for *M. aureola-M. polita* (left) and M. ponderosa (right).

Fig. 6 Historical changes in shell morphologies in living and fossil samples of *M. aureola*, *M. polita* and *M. ponderosa*. The horizontal axis indicates principal component scores on the second principal component. The scores on the principal component were obtained by principal component analysis using 13 shell characters. (Modified from Chiba, 1993).

Fig. 7 Introduced predators: a predatory land snail, *Euglandina rosea* (upper), and a predatory flatworm, *Platydemus monokwari* (lower).

Ogasawaras. This predatory flatworm was introduced to several islands in the Pacific and Indian Oceans as a biological control agent for *Achatina fulica*, and has become a serious threat to the native gastropod fauna of Guam. Some other predatory flatworms were also found in the Ogasawaras, and these flatworms may be one of the causes of the recent decline in land snail species in the Ogasawaras (Kawakatsu *et al.*, 1999; Ohkouchi *et al.*, 1999; Tomiyama, 2002). In addition, the carnivorous land snail *Euglandina rosea*, that led to the extinction of the Tahitian snails, was also introduced to Chichijima. The effect of these introduced predators on native land snail fauna is so serious that they may rapidly cause the extinction of many of the native land snails in the Ogasawaras. The history of disasters caused by these snails to the land snails of Hawaii, Tahiti and other Pacific islands strongly suggest that the same sort of disaster will occur with *Mandarina* in the near future. A conservation program is needed to avoid the extinction of *Mandarina*.

Protection of the native habitat is not enough to avoid the influence of introduced predators such as flatworms and *Euglandina rosea*. The best way to protect *Mandarina* and other endemic land snail species would be to remove all flatworms and *Euglandia rosea* from the Ogasawaras. However,

the cases of extinction of land snails in the Pacific islands show that it is very difficult to destroy these alien predators. One approach to avoid the extinction of *Mandarina* would be captive breeding. Reintroduction of captive-bred snails into restored or secure habitats may be one way of preserving *Mandarina*. In the case of *Partula*, more than thousand of these snails are being bred in captivity. The London Zoological Society released the first captive-bred *Partula* into a protected area on the island of Moorea in 1994 (Pearce-Kelly *et al.*, 1995).

However, the captive breeding and re-introduction of *Mandarina* species face several problems. First, each species of *Mandarina* is segregated into many genetically and morphologically different local populations. In addition, these local populations produce hybrid zones with complex geographical patterns in morphology and genetics. The best way to recover the present geographical variation is to collect all of the populations living in the islands for captive breeding, and after removing the predators, re-introduce the captive-bred snails to exactly the same sites where the snails were collected. Although this program is not impossible, it is not feasible. Second, the incongruence among morphology, phylogeny, and condition of reproductive isolation make it difficult to identify units for captive breeding and select suitable source populations. For example, taxonomic species should not be used as a unit of conservation, because a species of *Mandarina* includes populations that are genetically and phylogenetically distant from other populations of the same nominal species. In addition, a population reproductively isolated from other populations is not necessarily more distantly related to these populations than a population that is not reproductively isolated from these populations (see section 4). Third, reproductive isolation among sympatric species of *Mandarina* is easily broken by environmental change. Human alterations of environmental conditions and habitats have been shown to have resulted in hybridization in several animals (McDonnell *et al.*, 1978; Harrison & Arnold, 1982; Hillis, 1988). Changes in habitat conditions and population density through the re-introduction of captive-bred snails may result in hybridization among species, and thus, the genetic and morphological characteristics of each species may be lost as a result of this program. What is most urgent at this time is research on the breeding of *Mandarina* snails in captivity and at the same time, research on how individuals and populations differ genetically from each other. If we have genetic information for all populations on the islands, we can reconstruct the genetic diversity of *Mandarina* after their extinction in nature, even if we can save only a small part of these populations.

6. Conclusion

Mandarina provides an excellent natural laboratory in which we can test various ecological theories because of its high phenotypic diversity and accelerated evolution. In addition, a high level of geographical variation in *Mandarina* provides an excellent model system for the study of population genetics and speciation processes. The divergence of habitat preference among sympatric species and independent diversification in arboreal, semi-arboreal and ground ecotypes in different lineages at different times on different islands reveal importance of ecological factors in species coexistence and speciation. Hybridization among genetically and phenotypically divergent species suggests that the reproductive isolation of *Mandarina* depends on pre-zygotic isolation by simple ecological differences. These findings should contribute largely to understanding the process of adaptive radiation and evolution. However, at the same time, these findings reveal that it will be difficult to conduct conservation programs for *Mandarina*. Detailed ecological and genetic information as well as captive breeding is needed to keep the loss of genetic diversity of *Mandarina* to a minimum.

Acknowledgments

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