

Shell shape and habitat use in the North-west Pacific land snail *Mandarina polita* from Hahajima, Ogasawara: current adaptation or ghost of species past?

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The endemic land snail genus *Mandarina* of the Ogasawara Islands provides an excellent model system to investigate adaptive radiation. Previously, it has been shown that coexisting species of the islands segregate by microhabitat, so that they are either predominantly found on the ground in relatively wet and sheltered sites, dry and exposed sites, or else are arboreal. Moreover, shell morphology correlates with microhabitat, so that species in wet and sheltered sites tend to have high-spined shells with a high aperture, and those in dry and exposed sites tend to have relatively low-spined shells with a wide aperture. We have now found that on Hahajima, *Mandarina polita* have variable shell morphology, and there is a correlation between morphology and the depth of leaf litter, as well as the presence/absence of other terrestrial species. Specifically, when high-spined terrestrial *Mandarina ponderosa* is present, *M. polita* tend to be low-spined and have a large aperture, indicative of character displacement. When *M. ponderosa* is absent, the shell shape of *M. polita* is much more variable, the overall spire is higher, individuals are found in deeper litter, and there is a strong correlation between litter depth and spire height. We argue that these patterns are due to local adaptation, but it remains possible that they are an artefact due to the 'ghost of species past'. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 91, 149–159.

ADDITIONAL KEYWORDS: adaptive radiation – character displacement – habitat segregation – shell morphology.

INTRODUCTION

Studies of geographical variation in pulmonate land snails have made a significant contribution to understanding how genetically determined morphological variability is ultimately controlled by selection due to ecological and environmental factors (Davison, 2002). Following the landmark study of Cain (1977), it was realized that land snail faunas generally have a bimodal distribution of shell shape, so that species are either high or low-spined (Cowie, 1995). Furthermore, each shell type is often associated with a particular habitat (Goodfriend, 1986; Heller, 1987; Cameron & Cook, 1989; Cook, 1997): arboreal and burrowing species tend to have a relatively high spire (Cain, 1978, 1983), whereas globular and flat-shelled species are

found on the ground. However, although there have been works on within-species shell variation in land snails such as the Mediterranean snail *Albinaria* (Wagner, 1923; Loosjes, 1955; Kemperman & Gittenberger, 1988; Schilthuizen, 1995; Welter-Schultes, 2000a), Caribbean *Cerion* (Gould & Woodruff, 1986, 1990), the North American Triodopsinae (Emberton, 1995), Arianta (Gittenberger, 1991a; Baur & Baur, 1998), and several land snail species on Gávdos island (Welter-Schultes, 1998), there have been rather few studies with a primarily ecological perspective.

In the present study, we focused on the geographical variation of shell morphology in the endemic ground-dwelling land snail *Mandarina polita* from Hahajima of the Ogasawara Islands in the north-western Pacific (Chiba, 1999a). The Ogasawara Islands consist of around 30 volcanic islands less than 25 km² in area and approximately 700 km from the

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closest neighbouring islands (Izu Islands). *Mandarina* is an endemic genus that has undergone extensive diversification within the islands into 15 or so species. The ancestor of *Mandarina* has been derived from the mainland of Japan approximately 3 Mya (Chiba, 1999a). Previously, it has been shown that coexisting *Mandarina* species segregate by microhabitat (Chiba, 1999b), so that they are either predominantly found on the ground in relatively wet and sheltered sites, or else dry and exposed sites, or they are arboreal. It has also been shown that the shell morphology of different species correlates with their microhabitat, so that taxa in wet and sheltered sites tend to have high-spired shells with small apertures, and those in dry and exposed sites tend to have relatively low-spired shells with large apertures (Chiba, 2004). Crucially, with the exception of one study on *Mandarina hahajimana* (Chiba, 1996), there are no data on within species variation. Accordingly, one aim of the present study was to investigate whether similar patterns might be present in other species, such as *M. polita*.

Mandarina polita is found only in the northern half of Hahajima, an island of approximately 20 km² in area (Fig. 1). Although the species is morphologically variable, mitochondrial sequence divergence between *M. polita* and the sister species *Mandarina aureola* is low (~1%; Chiba, 1999a), and there is even less variation within species (Davison & Chiba, 2006). Because of the limited range and low genetic diversity, we considered that *M. polita* should be an excellent model to investigate the relationship between shell morphology and environmental factors. The specific focus of this study was the relationship between shell shape, especially spire index (shell height relative to shell diameter), and environmental factors such as leaf litter depth, the vegetation type and altitude of the site, and interspecific competition.

MATERIAL AND METHODS

Morphological divergence between *M. polita* and other ground-living species was considered in a previous study (Chiba, 1999b), but only eight populations were used, and the influence of environmental factors was not investigated. We therefore decided to examine *M. polita* in more detail. Snails of this species, as well as *Mandarina ponderosa*, *M. hahajimana* and *Mandarina exoptata* were collected in 1985–93 by searching 46 sites (approximately 100 m² per site) across the whole of the range in northern Hahajima. The sites are covered by vegetation composed of pandanus trees, palm trees, tree ferns, and broad-leaved trees. We used the discriminating factors of Okutomi *et al.* (1983) and Shimizu & Tabata (1991) to describe separate forest types, either mesic forest (dominated by *Elaeocarpus*,

Ardisina), mesic shrubby forest (*Dendrocacalia*, *Fatsia*), *Schima* forest (dominated by *Schima*, *Pouteria*), and dry forest (dominated by *Livistona*, *Pandanus*, *Rhaphiolepis*). Litter depth was measured every 2 m along the vertical and horizontal transects of a quadrat, by counting the number of leaves perforated by a stick when it was pushed down through the leaf-litter layer. We then used the average litter depth at each site for all further calculations. The litter depth has remained constant based on the measurements at three localities in the present study and those made 20 years ago. The underlying geology was also scored as either sedimentary or volcanic, using data from the geological map of Hahajima (Ujiie & Matsumaru, 1977).

In total, 785 individuals from 46 populations of *M. polita* were used in the morphological analysis (Fig. 1, Table 1). Eight measurements were taken on the adult shells using a digital micrometer (Fig. 2), which proved to be a highly reproducible (standard deviation, as determined by repeated measurements, was approximately 0.01 mm). Measurement data were then log-transformed to remove the artefact due to allometry because larger shells are also higher as a side-effect of size.

The distribution of the variation in population mean of the eight characters was examined quantitatively using principal component analysis. Principal components were extracted from the correlation matrix of variables, and scores calculated to estimate morphological differences among populations. Components with eigenvalues of less than 1.0 explain less variance than an original variable, and thus were dropped from the analysis. Shell size (shell width + shell height) and spire index (shell height/shell width) were also calculated because these characters are known to be closely associated with habitat use (Chiba, 1996); these two indices are also effective summary measures of shell shape.

The relationship between the principal component scores, the environmental variables, and coexistence with other *Mandarina* species was investigated using multiple regression. The variables used were litter depth, altitude, geology, coexistence of arboreal species, and coexistence of ground-dwelling species. Geology was a dummy variable with value 0 for sedimentary rock and 1 for volcanic rock. The presence or absence of other arboreal and ground dwelling *Mandarina* species in the sites was also a dummy variable, with value 0 for absence and 1 for presence. Differences in vegetation were not included in the multiple regression analyses because vegetation type is dependent on altitude, and litter depth is dependent upon vegetation type.

The above analysis using the principal component scores did not consider morphological variability

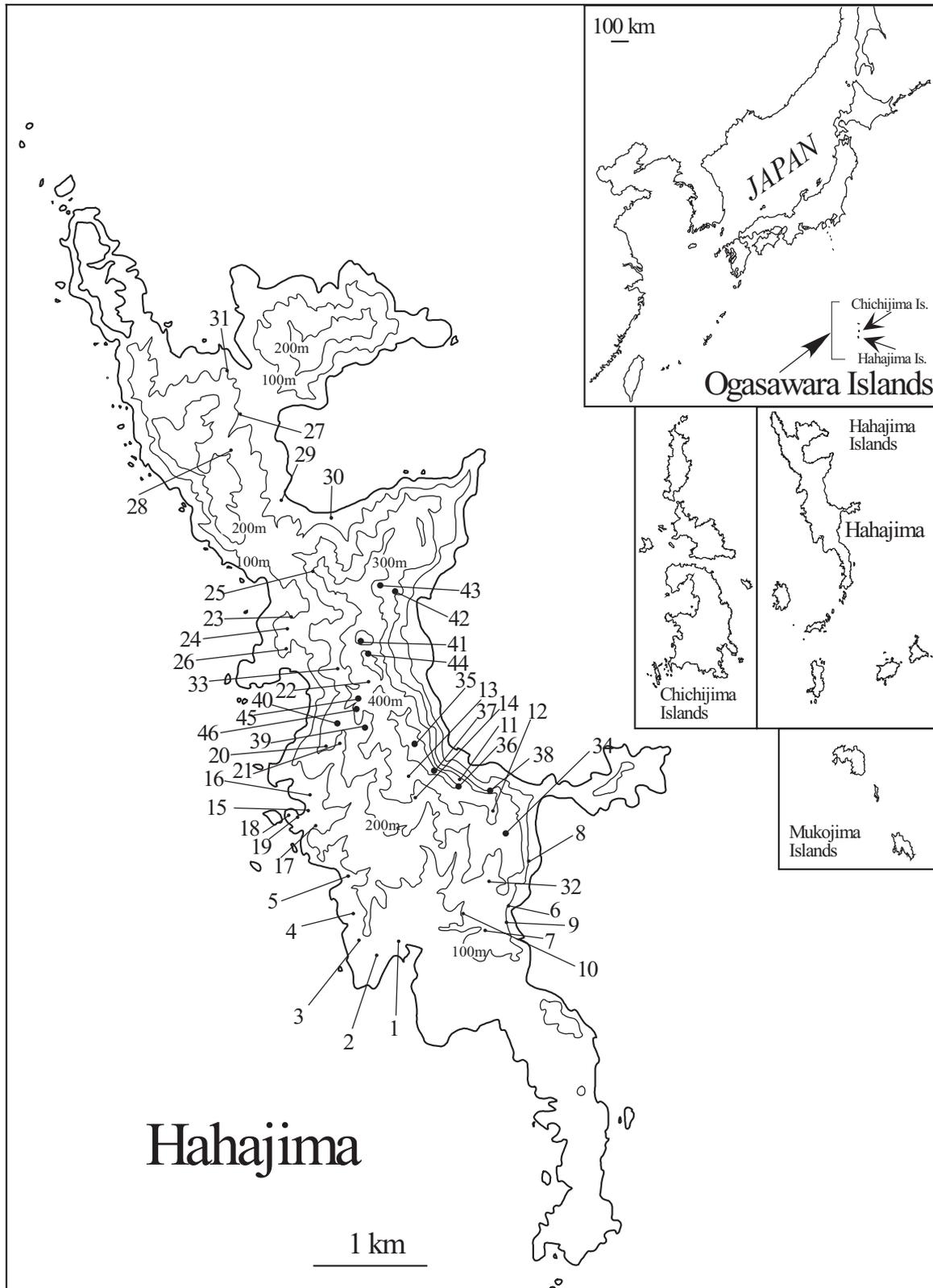


Figure 1. A map of the island of Hahajima of the Ogasawara Islands showing the numbered sample locations. Large dots indicate localities where *Mandarina polita* and *Mandarina ponderosa* live together, and small dots indicate localities where *M. polita* does not coexist with *M. ponderosa*.

Table 1. A list of samples used, showing the altitude of sampling site, litter depth mean, vegetation, geology, and species coexisting with *Mandarina polita* at the site

| Samples | Sample size | Altitude (m) | Leaf litter depth | Vegetation | Geology | Coexistence |
|---------|-------------|--------------|-------------------|---------------|---------|-------------|
| 1 | 27 | 20 | 3.63 | Dry | Sed | |
| 2 | 18 | 10 | 4.20 | Dry | Sed | |
| 3 | 28 | 80 | 2.47 | Dry | Sed | |
| 4 | 19 | 60 | 3.17 | Dry | Sed | |
| 5 | 28 | 30 | 3.55 | Dry | Sed | ha |
| 6 | 15 | 90 | 2.15 | Dry | Vol | ha |
| 7 | 13 | 140 | 3.80 | Dry | Vol | ha |
| 8 | 8 | 85 | 3.67 | Dry | Vol | ha |
| 9 | 10 | 95 | 1.05 | Dry | Vol | ha |
| 10 | 12 | 110 | 2.76 | Dry | Vol | |
| 11 | 19 | 360 | 2.56 | Mesic shrubby | Vol | ha, ex |
| 12 | 24 | 310 | 2.05 | Mesic shrubby | Vol | ha, ex |
| 13 | 19 | 350 | 4.05 | Mesic shrubby | Vol | ha, ex |
| 14 | 15 | 290 | 2.25 | Mesic shrubby | Sed | ha, ex |
| 15 | 25 | 0 | 1.25 | Dry | Sed | |
| 16 | 17 | 25 | 1.58 | Dry | Sed | |
| 17 | 30 | 90 | 3.03 | Dry | Sed | |
| 18 | 12 | 35 | 0.85 | Dry | Sed | |
| 19 | 14 | 15 | 3.36 | Dry | Sed | |
| 20 | 24 | 220 | 2.75 | Mesic | Vol | |
| 21 | 22 | 170 | 2.33 | Mesic | Vol | |
| 22 | 16 | 330 | 2.49 | Mesic shrubby | Vol | ha, ex |
| 23 | 15 | 100 | 2.80 | Dry | Vol | ha |
| 24 | 12 | 175 | 4.63 | Dry | Vol | ha |
| 25 | 18 | 280 | 3.33 | Dry | Vol | ha |
| 26 | 10 | 130 | 3.48 | Dry | Vol | |
| 27 | 9 | 90 | 2.78 | Dry | Vol | |
| 28 | 8 | 180 | 1.72 | Dry | Vol | |
| 29 | 10 | 65 | 4.06 | Dry | Vol | ha |
| 30 | 15 | 50 | 3.90 | Dry | Vol | ha |
| 31 | 8 | 100 | 0.92 | Dry | Vol | ha |
| 32 | 17 | 185 | 1.63 | Dry | Vol | |
| 33 | 11 | 250 | 3.88 | Mesic | Vol | |
| 34 | 13 | 280 | 1.90 | Mesic shrubby | Vol | pn, ha, ex |
| 35 | 12 | 430 | 2.86 | Mesic shrubby | Vol | pn, ha, ex |
| 36 | 17 | 405 | 2.32 | Mesic shrubby | Vol | pn, ha, ex |
| 37 | 20 | 410 | 2.57 | Mesic shrubby | Vol | pn, ha, ex |
| 38 | 24 | 320 | 2.22 | Mesic shrubby | Vol | pn, ha, ex |
| 39 | 25 | 270 | 2.73 | Mesic | Vol | pn |
| 40 | 20 | 270 | 3.36 | Mesic | Vol | pn |
| 41 | 23 | 400 | 2.95 | Mesic shrubby | Vol | pn, ha, ex |
| 42 | 15 | 220 | 2.25 | Mesic | Vol | pn, ha, ex |
| 43 | 19 | 265 | 2.58 | Mesic | Vol | pn, ha, ex |
| 44 | 17 | 405 | 3.10 | Mesic shrubby | Vol | pn |
| 45 | 15 | 330 | 2.80 | Mesic | Vol | pn |
| 46 | 17 | 310 | 2.75 | Mesic | Vol | pn |

Sed, sedimentary rocks; Vol, volcanic rocks; ha, *Mandarina hahajimana*; ex, *Mandarina exoptata*; pn, *Mandarina ponderosa*.

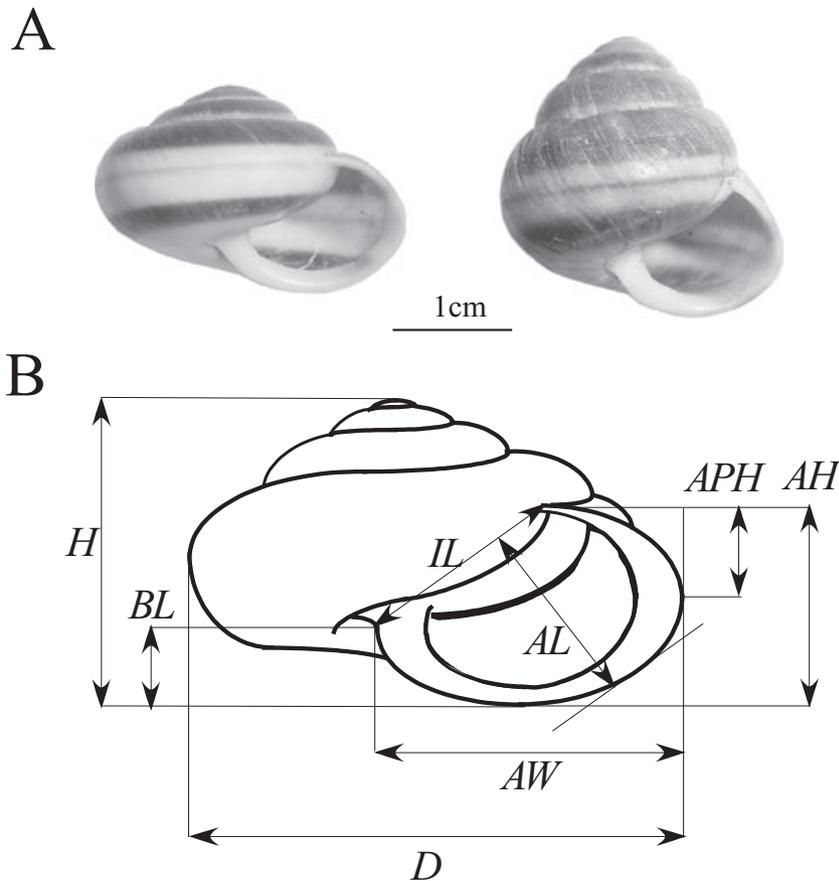


Figure 2. A, two different *Mandarina polita* shells. B, measurements of the shell of *M. polita* used in the principal component analysis. D, shell diameter; H, shell height; AW, apertural width; AH, apertural height; AL, broadness of aperture; IL, length of inner lip; BL, height of basal lip; APH, height from the uppermost part of the aperture to the periphery.

between the populations, so differences in the spire index and shell size among the populations due to environmental factors were examined statistically. Correlations of shell size and spire index with litter depth and altitude of the sampling sites were examined by regression analysis, using a Mantel test to assess significance. Whether morphological characters vary by vegetation type was tested using nested-analysis of variance (ANOVA), with probabilities adjusted by the Bonferroni method. Morphological differences between populations of *M. polita* with/without competing *M. ponderosa* were also examined using nested-ANOVA. The coefficient of variation (CV) for population mean shell size and spire index was calculated to describe the morphological variability of *M. polita*. The CV of *M. polita* was then compared against the same coefficient in *Euhadra quaesita*, *Euhadra peliomphala* and *Euhadra eoa*, using previously published data (Hayashi & Chiba, 2000, 2004; Watanabe & Chiba, 2001).

RESULTS

Markedly divergent shell morphologies were found within the same species (Fig. 2), so that *M. polita* shells tend to be either relatively low or high-spired, with a corresponding wide or high aperture. Together, the first two principal components explained 80.6% of the variance in the morphological measurements (Table 2), and were the only two with eigenvalues greater than 1. The first principal component (PC1) was interpreted as size, with higher scores meaning larger shells (all variables exhibited positive loadings on PC1). Higher scores on the second principal component (PC2) indicated shells with low spires (positive D and negative H), and an elongated aperture (positive AW, AL and negative BL, APH). A high level of geographical variation was found in the scores of both the principal components: the scores changed drastically between sample points, and clines were not observed for either shell size or shape (Fig. 3), at least

Table 2. Variable loadings, eigenvalues, and percentage of the variation in the first two principal components for all samples of *Mandarina polita*

| Variables | Variable loadings | |
|---|-------------------|--------|
| | PC1 | PC2 |
| Shell diameter (D) | 0.888 | 0.366 |
| Shell height (H) | 0.587 | -0.737 |
| Apertural width (AW) | 0.899 | 0.331 |
| Apertural height (AH) | 0.961 | 0.041 |
| Length of inner lip (IL) | 0.887 | 0.248 |
| Broadness of aperture (AL) | 0.767 | -0.060 |
| height from the uppermost part of the aperture to the periphery (APH) | 0.817 | -0.145 |
| Height of basal lip (BL) | 0.712 | -0.398 |
| Eigenvalue | 5.42 | 1.03 |
| Percent of total variance explained | 67.7 | 12.9 |

on the scale that we sampled. However, there was an obvious association in that most of the flat-shelled populations of *M. polita* were collected from a single central location, part of the high northern mountain ridge (Fig. 3B), which is also the same region from which *M. ponderosa* were collected.

There was no correlation between litter depth and altitude ($r = 0.01$, $P > 0.05$), so these variables were regarded as independent, at least for this analysis; litter depth changes over a short distance (Fig. 4). The multiple regression analysis (Table 3) showed that altitude was significantly associated with the PC1 score (standard coefficient = -0.482 , $P < 0.05$), explaining 21.2% of the variance, although the correlation was weak. The interpretation is that *M. polita* are significantly larger at lower altitude. Altitude, litter depth, and coexistence of ground-dwelling species were significantly associated with the PC2 scores (Table 3; Fig. 5). These variables together explained 90.7% of the variance in the scores, with litter depth

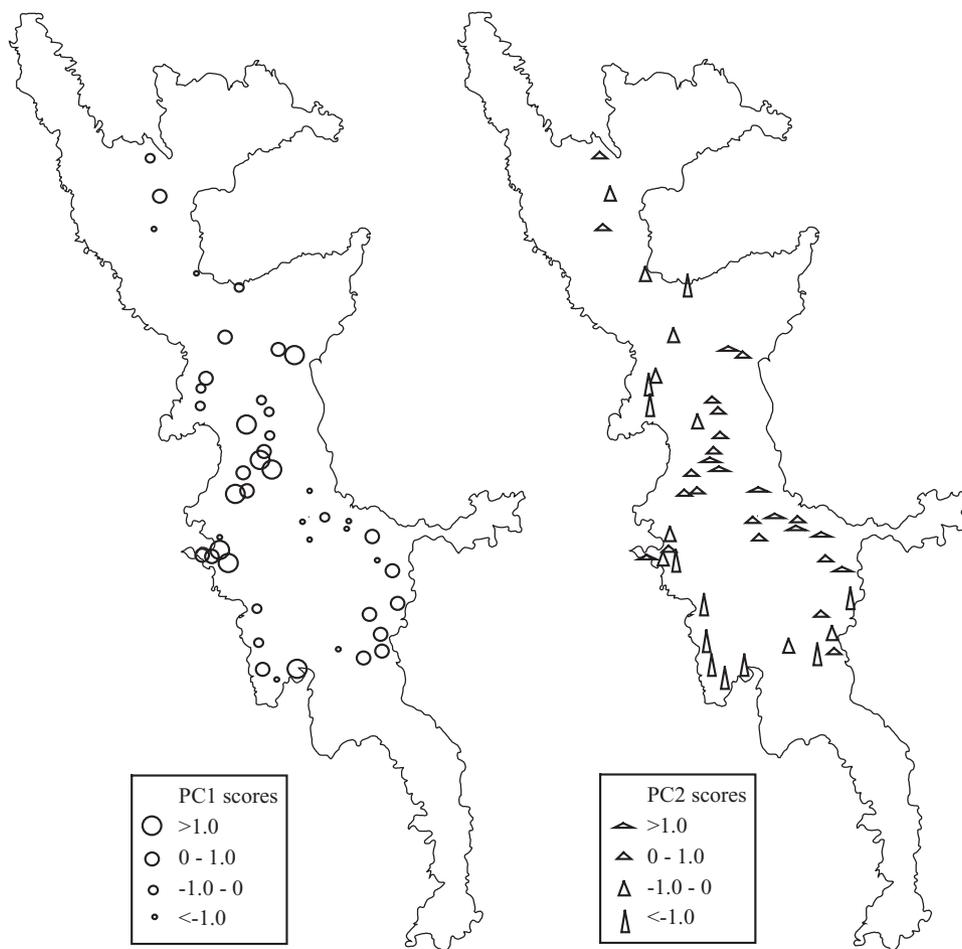


Figure 3. Geographical variation in the scores on PC1 (shell size, large values indicate large shells) and PC2 (shell shape, large values indicate low spire and large aperture).

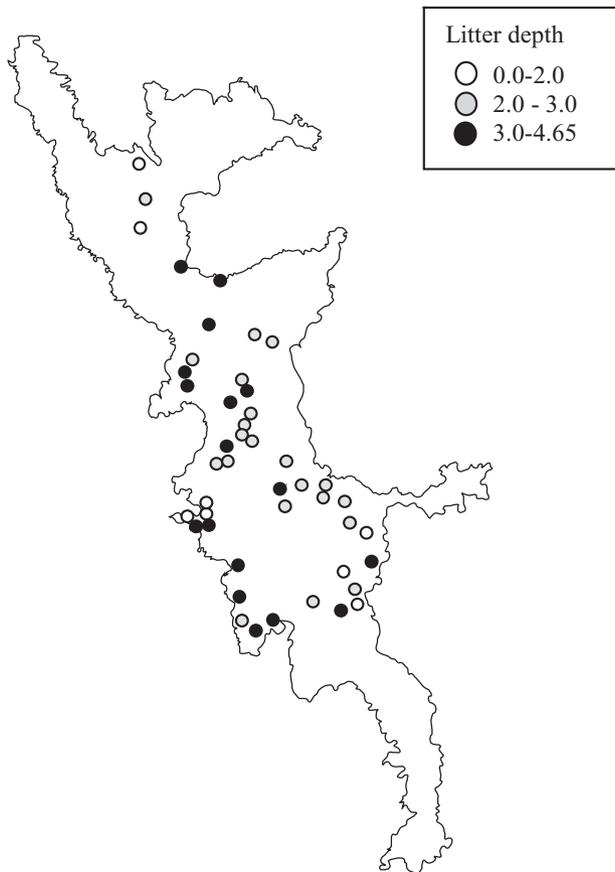


Figure 4. Litter depth of each population. Open circles, 0.0–2.0; grey circles, 2.0–3.0; black circles, 3.0–4.65.

having the largest effect (37.8%). The standardized correlation coefficients were positively significant for altitude (0.387, $P < 0.001$) and were negatively significant for litter depth (-0.538 , $P < 0.001$). The interpretation is that *M. polita* is relatively high-spired and has a short aperture at low altitude (Fig. 5B). Moreover, high-spired/short aperture populations tended to be found where there is deep litter, and vice versa (Fig. 5A). No significant effect was found for geology.

Mandarina polita coexisted with the arboreal species *M. hahajimana* and *M. exoptata* at 24 sites. However, there was no evidence that arboreal species affected the shell morphology of *M. polita*, based on the principal component analysis (Table 3). *Mandarina polita* coexisted with the terrestrial species *M. ponderosa* at sites 34–46 (Table 1). By contrast to the situation with arboreal species, coexistence with *M. ponderosa* was significantly associated with a higher PC2 score (standard coefficient = 0.367, $P < 0.001$). Thus, *M. polita* had lower spires and longer apertures in the sites where they coexisted with *M. ponderosa*, which is a high-spired snail with a short aperture (Fig. 5). Most of the sites where *M. polita* coexisted with *M. ponderosa* were at a high altitude (Table 1; Fig. 5B). Although the range in litter depth was greater for *M. polita* living alone, the mean litter depth did not differ significantly regardless of whether *M. ponderosa* were present (range = 1.9–3.36, mean = 2.65) or not (range = 0.85–4.63, mean = 2.78) (Fig. 5A).

Differences in shell size and spire index among the populations were highly significant. Spire index was significantly correlated with depth of the litter ($r = 0.47$, $P = 0.000$) and negatively correlated with altitude (Fig. 5). At high altitude (> 250 m), spire

Table 3. Multiple regression analysis of the scores on PC1 and PC2 against five environmental factors

| Factors | Coefficient | Standard error | Standard coefficient | <i>t</i> | <i>P</i> |
|------------------------|-------------|----------------|----------------------|----------|----------|
| PC1 | | | | | |
| Constant | 1.02 | 0.584 | 0 | 1.75 | 0.087 |
| Altitude | -0.004 | 0.002 | -0.484 | -2.19 | 0.035 |
| Litter depth | -0.086 | 0.159 | -0.077 | -0.54 | 0.590 |
| Coexistence (ground) | 0.85 | 0.423 | 0.387 | 2.01 | 0.055 |
| Coexistence (arboreal) | -0.479 | 0.411 | -0.127 | -0.72 | 0.478 |
| Geology | -0.294 | 0.307 | -0.242 | -1.56 | 0.126 |
| PC2 | | | | | |
| Constant | 0.964 | 0.256 | 0 | 3.76 | 0.001 |
| Altitude | 0.003 | 0.001 | 0.387 | 3.99 | 0.000 |
| Litter depth | -0.604 | 0.070 | -0.538 | -8.68 | 0.000 |
| Coexistence (ground) | 0.805 | 0.186 | 0.367 | 4.34 | 0.000 |
| Coexistence (arboreal) | -0.091 | 0.135 | -0.046 | -1.12 | 0.500 |
| Geology | -0.202 | 0.180 | -0.087 | -0.68 | 0.269 |

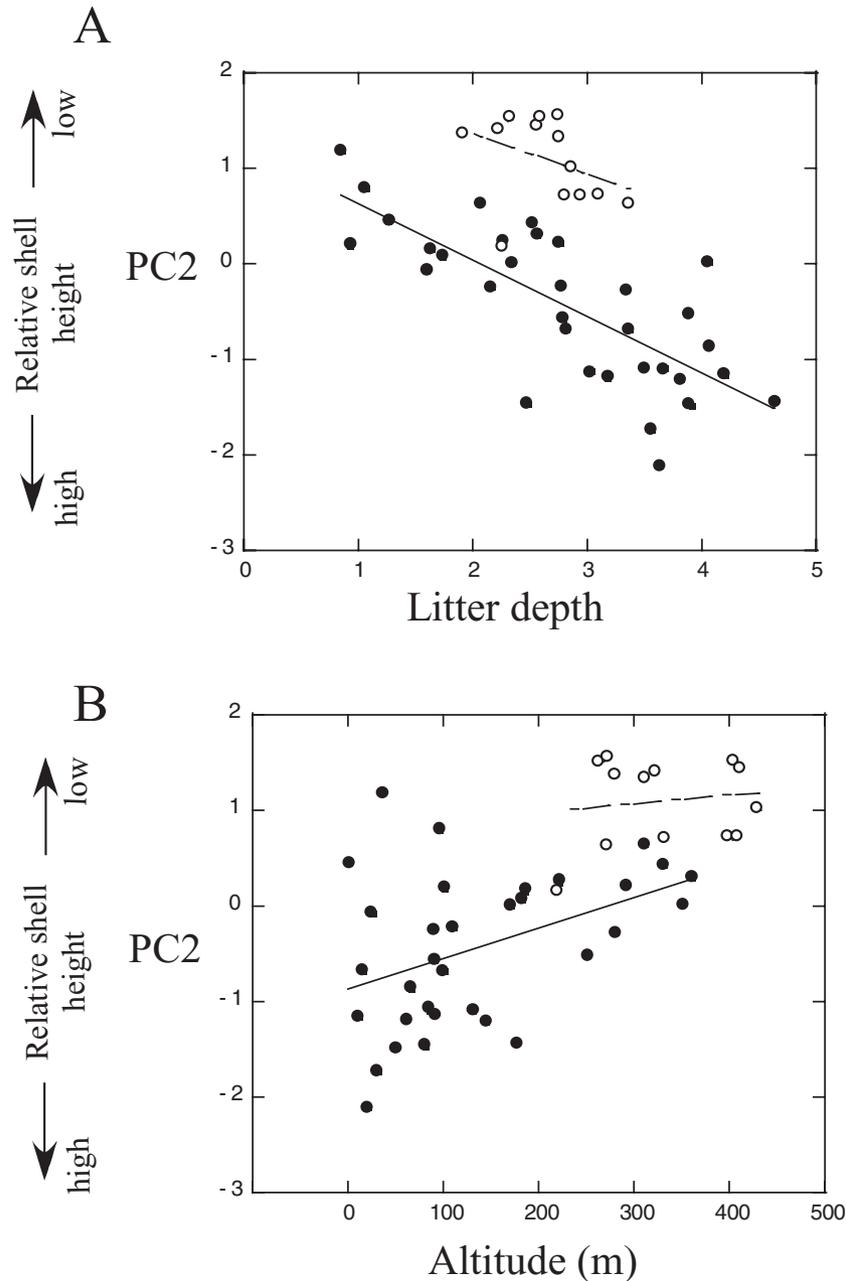


Figure 5. Score on PC2 against litter depth (A) and altitude (B) of each population. Open circles, *Mandarina polita* populations that coexist with *Mandarina ponderosa*; closed circles, populations that do not coexist with *M. ponderosa*. Regression lines are also shown.

index was significantly larger in the populations coexisting with *M. ponderosa* than in the populations living alone (Table 4). Therefore, although *M. polita* with the lowest spire index coexisted with *M. ponderosa*, and tended to be at high altitudes, *M. polita* with the highest spires lacked competing species, and were more often found at low altitudes. *Mandarina polita* with somewhat intermediate shell

indices and PC2 scores of around zero were found in shallow litter (Fig. 5A). Finally, there was a possible association of shell size with habitat: the largest shells were found in populations from mesic forest, and the smallest from the mesic shrubby forest ($F = 18.2, P < 0.001$).

The CV for population means of spire index was 0.065 (Table 5), indicating that spire index is much

Table 4. A result of nested analysis of variance for comparison of populations coexisting, or not, with other ground dwelling species

| Source | Sum of squares | d.f. | Mean square | F-ratio | P |
|--------------------------|----------------|------|-------------|---------|-------|
| Coexistence | 32.5 | 1 | 32.5 | 19.2 | 0.000 |
| Population (coexistence) | 892.3 | 17 | 52.5 | 31.0 | 0.000 |
| Error | 549.0 | 324 | 1.69 | | |

Populations from highland (located at an altitude higher than 250 m) were used for the comparison.

Table 5. The coefficient of variations for population means of shell size and spire index for *Mandarina polita* and its mainland relatives *Euhadra*

| Species | Coefficient of variations | | |
|----------------------------|---------------------------|-------------|--------------|
| | Shell size | Spire index | Altitude (m) |
| <i>Mandarina polita</i> | 0.041 | 0.065 | 0–410 |
| <i>Euhadra quaesita</i> | 0.095 | 0.027 | 10–1030 |
| <i>Euhadra peliomphala</i> | 0.039 | 0.014 | 10–960 |
| <i>Euhadra eoa</i> | 0.045 | 0.034 | 30–880 |

The maximum and minimum altitude of the populations treated are shown as an indication of environmental heterogeneity.

more variable in *M. polita* than in *Euhadra* (range = 0.014–0.034).

DISCUSSION

On Hahajima, *M. polita* has a variable shell morphology at different sites, and there is a correlation between morphology and the depth of leaf litter in which the species is found, as well as the presence or absence of competing terrestrial species. Specifically, when high-spined terrestrial *M. ponderosa* is present, *M. polita* tend to be low-spined and have a large aperture. When *M. ponderosa* is absent, the shell shape of *M. polita* is much more variable although, overall, the spire is higher and individuals are found in deeper litter. Crucially, the spire-height of *M. polita* is strongly correlated with litter depth in sites that are free from competition, and the same relationship is seen, although not statistically significantly so, in sites where *M. ponderosa* was present. We therefore believe that the morphology of *M. polita* is a consequence of character displacement, owing to competition from *M. ponderosa*, and especially character release when *M. ponderosa* is absent. The close association between shell morphology and especially litter depth is suggestive of local adaptation. Although a significant corre-

lation was found between shell size and altitude, the interpretation of this association is unclear. Because the correlation is weak, it may reflect associations with other factors that are coincidentally attached to certain altitudes (Goodfriend, 1986) or simply be an artefact of sampling (Welter-Schultes, 2000a).

It has been shown previously that differences in relative spire height correlate with the inclination of the surface on which the snails live, which itself is related to the mechanics of carrying a shell of a certain shape (Cain & Cowie, 1978; Cameron & Cook, 1989; Cowie, 1995). The positive correlation between shell height and litter depth that we discovered suggests that burrowing ability is a function of shell height. *Mandarina polita* usually aestivates within the litter during the daytime and, where more than one species is present, the higher-spined species is frequently found in deeper litter during the day (Chiba, 1992). This is consistent with the belief that species with globular shells are better able to burrow in soft substrates compared with flat-shelled taxa (Cain, 1978, 1983). The advantage for *Mandarina* is that high spined individuals in deeper litter are protected from extremes of temperature and desiccation. However, at the sites with thin litter, there is no advantage to having a high spire, so that species foraging on horizontal ground tend to be low-spined (Cain, 1978, 1983; Emberton, 1994).

Schluter (2000) has previously listed six criteria that are necessary evidence for character displacement to be a good hypothesis for morphological change. There is good evidence available indicating that *M. polita* (as well as the other *Mandarina*; Chiba, 1999b) have been affected by character displacement because the only criterion lacking is direct evidence for interspecific competition. Although the results are preliminary, eggs that are transported to the laboratory hatch and grow into juveniles with the same shape as their parental population (S. Chiba & A. Davison, unpubl. observ.). In addition, there is a high heritability to both shell size and shell shape in species that have been characterized genetically (e.g. *Partula*, Murray & Clarke, 1968; *Albinaria*, Welter-Schultes, 2000b). Therefore, although some of the dif-

ferences between populations may be due to phenotypic plasticity, the majority of the differences must be genetic, and thus due to character displacement.

Spatial variation in land snail shell morphology is not necessarily adaptive (Gittenberger, 1991b; Welter-Schultes, 2000a). Our findings of associations between shell height and habitat and the presence or absence of sympatric species, however, suggests that the marked morphological diversity within *M. polita* has resulted from adaptation at a fine spatial scale, for which there are two complementary causes. First, local adaptation may occur in spite of gene flow between populations. Second, because morphological variation within *M. polita* is greater than in *Euhadra*, then a lack of other competing genera on Hahajima may mean that the adaptive radiation is continuing to this day. By contrast, in *Euhadra* from mainland Japan, fewer empty niches may enhance habitat specialization. Although further investigation is required, it is possible that phenotypic diversity in island endemics is often increased due to enhanced local adaptation.

As discussed above, the evidence for character displacement affecting morphology in *M. polita* and other *Mandarina* species is strong. In theory, the correlations between litter depth and shell shape (Fig. 5A) could have an artefactual explanation. Specifically, the shell shape of *M. polita* in some populations could reflect the 'ghost of species past': species that were present until recently have affected the shell shape of *Mandarina polita*, but now they cannot be detected. It is striking that most *M. ponderosa* were recovered from high altitude sites, so it is possible that the high altitude sites without *M. ponderosa* have only recently lost this species, due to cultivation and forest clearance before World War II.

We therefore reanalysed the data under this scenario. As expected, *M. polita* in '*M. ponderosa* absent' sites still had significantly higher spires than *M. polita* in '*M. ponderosa* present' sites, but the relationship between PC2 scores and litter depth/altitude was weaker (Fig. 5). However, for several reasons, we argue that particularly the relationship between relative shell height and litter depth is not an artefact. First, there was a negative correlation between *M. polita* PC2 scores and litter depth at sites with *M. ponderosa*, although it was not statistically significant (Fig. 5A). Second, the bimodal distribution that separates the two kinds of sites in Figure 5A suggests a qualitative difference between them (i.e. *M. ponderosa* present/absent). Finally, several low altitude sites, where there is no suspicion of *M. ponderosa* ever having been present, contain low- or high-spired populations, depending upon a thin or thick litter, respectively. Thus, although we cannot absolutely rule out a 'ghost of species past' effect, the results are consistent with our original interpretation.

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