

Selectivity of terrestrial gastropod extinctions on an oceanic archipelago and insights into the anthropogenic extinction process

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Anthropogenic impacts have led to widespread extinctions of species on oceanic islands but the nature of many of these extinctions remains poorly known. Here we investigate extinction selectivities of terrestrial gastropods from the Ogasawara archipelago in the northwest Pacific, where anthropogenic threats have changed over time, shifting primarily from the effects of habitat loss to predation by a variety of different predators. Across all of the islands, extinct species had significantly smaller geographic ranges compared with species that are still alive, but among the surviving species, ranges of those that are currently declining due to human impacts do not differ significantly from those that are not threatened. Extinctions were selective with respect to spire index (SI) of shells, a trait of potential functional importance, but the relationship between body size and extinction vulnerability varied among extinction agents, some of which were strongly size selective, whereas others were not. Overall, whereas anthropogenic impacts have resulted in nonrandom losses of phenotypic diversity, the patterns of selectivity are complex, vary among islands, and with the type of threat. As extinction agents have changed historically, so has the pattern of loss. Because of the changing nature of anthropogenic impacts, resiliency to one type of threat does not guarantee long-term survival of species and future patterns of biodiversity loss on these islands are likely to be different from those in the past.

Habitat destruction and the introduction of non-native species are the leading causes of extinction of endemic species of plants and animals on islands (1). The diverse assemblages of terrestrial gastropods on the islands in the Pacific ocean have proven to be particularly vulnerable to such anthropogenic impacts with many species already extinct, highly threatened, or declining (2). Whereas the magnitude of these losses has been documented on multiple islands (2–5), other aspects of the extinction process still remain poorly known. In particular, patterns of extinction vulnerability and selectivity of island gastropods have not been quantified, despite the fact that the vast majority of land snail species on many Pacific islands are either already extinct or declining due to human impacts (2). Whether existing knowledge of extinction selectivities, derived almost exclusively from terrestrial vertebrates (for anthropogenic extinctions) and marine invertebrates (for extinctions in the geological past) (6–8), is applicable to terrestrial gastropods remains an open question because of fundamental differences in ecology and life history. Furthermore, whereas extinctions of some species can be attributed to a single cause (e.g., a specific introduced predator), others involve a combination of different threats acting sequentially or in concert (3, 4, 9). However, relatively little is known about how the combination of such extinction filters (10) is changing the biodiversity of terrestrial gastropods on islands (but see ref. 11).

Extinction vulnerability varies among species not only as a function of their ecology and life history but also the nature of the threat—a species may be vulnerable to one type of extinction agent but resilient to another (7, 8, 12, 13). Thus, the overall pattern of extinction selectivity represents the net effect of these different agents, which may or may not operate simultaneously.

Disentangling these effects is generally difficult because information about individual agents of extinction and their effects remain scarce for virtually all extinctions in the geological past and most anthropogenic ones. One exception is species assemblages on oceanic islands where a combination of geographic isolation, high levels of endemism, and multitude of human impacts are known to have led to high levels of extinctions (1, 2), and the specific agents responsible for many of those losses are increasingly well understood (e.g., 1–5). Thus, island biotas can provide excellent model systems for better understanding how different types of threats interact to determine patterns of extinction selectivity.

Here, we use terrestrial gastropod assemblages of an isolated oceanic archipelago to quantify (*i*) extinction selectivities associated with two different types of anthropogenic impacts—habitat destruction and introduced predators—and (*ii*) their combined effects, resulting in the ongoing erosion of phenotypic diversity on individual islands as well as across multiple islands. We focus on selectivities of two different morphological traits—body size, a widely recognized correlate of extinction vulnerability in many terrestrial and marine taxa (6, 14–17), and spire index (SI), a measure of terrestrial gastropod shell shape with a functional significance (see below). In addition, we also explore the role of geographic range, another common correlate of extinction vulnerability (7, 18), in determining the vulnerability of these species.

The Ogasawara archipelago (also known as the Bonin Islands) consists of a number of small subtropical oceanic islands in the northwestern Pacific, about 1,000 km south of the Japanese mainland (19) (Fig. 1). The terrestrial gastropod fauna of these islands is well documented with 97 recorded species, over 90% of which are endemic to this archipelago (20). Human colonization and habitat destruction began in 1830 on Chichijima Island and in 1876 on Hahajima Island, and ~60% of the forests of these two islands was cleared and converted to sugar fields or pasture by 1921 after which further forest clearing was prohibited (21). During the Second World War, most of the inhabitants of the archipelago were evacuated to mainland Japan and the US Navy occupied the islands until 1967, a period during which the islands were largely uninhabited. Because of this, the forests on Chichijima and Hahajima islands regenerated to a near preimpact state by the 1970s (21, 22). Although human settlement resumed after 1968, they were restricted to small villages on Chichijima and Hahajima, and the forested areas were protected. Nevertheless, population declines and extinctions of terrestrial gastropods have been documented on both of these islands since then, primarily due to alien species introduced after the 1940s. Okochi et al. (19) attributed the decline of gastropods on

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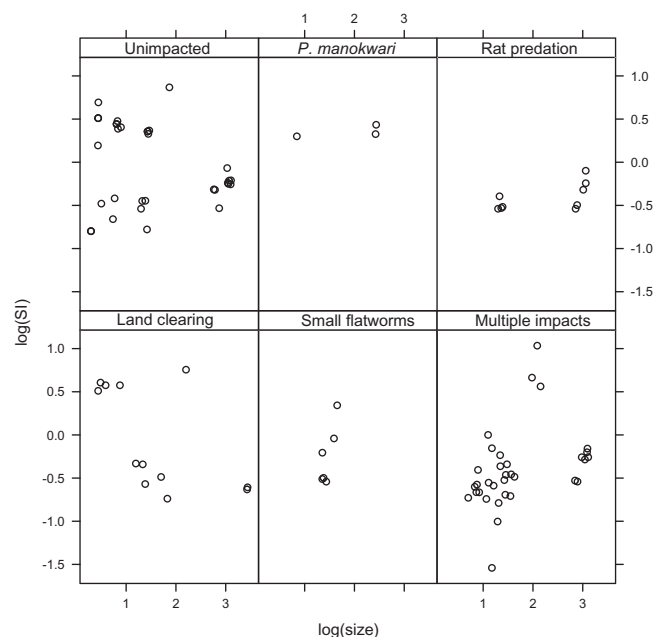


Fig. 2. Distribution of terrestrial gastropod species of the Ogasawara archipelago in the trait space defined by size and spire index (SI). Each point represents a species and the different panels show how different anthropogenic threats are selectively affecting different parts of this phenotypic space. See text for results of statistical comparisons.

Kolmogorov–Smirnov test). However, species already extinct do not differ significantly in size from those that are still living ($P = 0.5$ Kolmogorov–Smirnov test). This suggests that on Chichijima, size selectivity emerged as the extinction process unfolded and predation by the large introduced flatworm *P. manokwari*, which is the primary threat to gastropod species on the island at present, became important. SI, on the other hand, consistently differs significantly in pairwise comparisons of extinct versus living ($P = 0.004$ Kolmogorov–Smirnov test) and threatened versus the rest of the living species ($P = 0.04$ Kolmogorov–Smirnov test), suggesting that on Chichijima this trait plays an important role irrespective of the extinction agent. Although the extinction threats are different on Hahajima Island—currently predation by small flatworms is the single largest cause of decline there—extinct, threatened, and stable species significantly differ in patterns of occupation of size–SI space (Fig. S2; $P = 0.04$ MANOVA, $P = 0.03$ PERMANOVA). Size, however, does not differ significantly between extinct and living ($P = 0.12$ Kolmogorov–Smirnov test) or threatened and stable ($P = 0.3$ Kolmogorov–Smirnov test) species. For SI, pairwise comparisons reveal significant differences between living and extinct species ($P = 0.01$ Kolmogorov–Smirnov test) and between threatened and stable species ($P = 0.03$ Kolmogorov–Smirnov test). Across all of the islands, the overall pattern of selectivity (Fig. S3) is weaker than on individual islands—differences between extinct, threatened, and stable species in size–SI space is

marginally significant using MANOVA ($P = 0.06$) but not significant using PERMANOVA ($P = 0.3$). Size does not differ significantly between extinct and living ($P = 0.16$ Kolmogorov–Smirnov test) or between threatened and stable ($P = 0.08$ Kolmogorov–Smirnov test) species. SI differs significantly between extinct and living species ($P = 0.04$ Kolmogorov–Smirnov test) but not between threatened and stable species ($P = 0.1$ Kolmogorov–Smirnov test).

Taken together, the above results show that extinctions of Ogasawaran gastropods are strongly selective with respect to SI but not always with respect to body size. Both body size and SI tend to be phylogenetically conserved but similar sizes and/or SIs can also evolve independently in lineages with very different extinction vulnerabilities. Thus, nonphylogenetic comparisons, such as those above, can potentially miss the association between these traits and extinction vulnerability even when it exists at the level of individual lineages (16, 33). Species-level phylogeny of Ogasawaran gastropods is still unresolved so a full phylogenetic analysis of size and extinction risk is currently not possible. Instead, we used the data for the three most speciose families present on these islands to test for within-lineage size selectivity of extinction risk. Extinct species were significantly larger than living ones in the family Eoconulidae (12 extinct and 11 living species, $P = 0.02$) but did not differ significantly in the family Helicinidae (5 extinct and 13 living species, $P = 0.48$). Within Bradybaenidae, which does not have any extinct species, the threatened species did not differ significantly in size from the rest (12 threatened and 9 stable species, $P = 0.9$). Taken together, these results confirm that body size, by itself, is unlikely to be a strong overall correlate of extinction in Ogasawaran gastropods even if phylogeny is taken into account, although it is important in some lineages or on some islands (see below). Similarly, comparisons of SI did not show significant differences in any of the above comparisons ($P > 0.05$ in all cases).

Finally, a comparison of species driven to extinction by different causes on the two islands, Chichijima and Hahajima, show how the unique combination of threats on each island has led to nonrandom losses of phenotypic diversity (Fig. 5). Only a few species on Hahajima were lost by habitat destruction alone, an important cause of extinction on Chichijima, but the majority succumbed to predation by small introduced flatworms. In contrast, on Chichijima, the majority of extinctions could not be attributed to a specific agent and habitat destruction came second.

Discussion

The nature of anthropogenic threats to terrestrial gastropods in the Ogasawara archipelago has changed over time, shifting primarily from the effects of habitat loss to predation by a variety of different predators. As the extinctions resulting from these impacts unfolded, species with the most restricted geographic distributions—those occurring on few islands—preferentially went extinct, consistent with the hypothesis that geographic range is a strong predictor of extinction vulnerability of species (7, 18). However, among the surviving species, range is not a significant predictor of vulnerability; for example, whereas some of the species currently found on a single island are declining due to human impacts, a much larger proportion of single island endemics does not show any evidence of such decline. This dif-

Table 1. Summary of statistical analyses

Spatial scale	Total no. of species	Extinct species	Threatened species	MANOVA size, SI, and threats	PERMANOVA	Kruskal–Wallis test of size and threats	Kruskal–Wallis test of SI and threats
All islands together	96	25	39	$P = 0.03$	$P = 0.4$	$P = 0.4$	$P = 0.02$
Chichijima	48	27	9	$P < 0.0001$	$P = 0.003$	$P = 0.002$	$P = 0.0006$
Hahajima	58	19	3	$P = 0.002$	$P = 0.05$	$P = 0.3$	$P = 0.001$

SI, spire index.

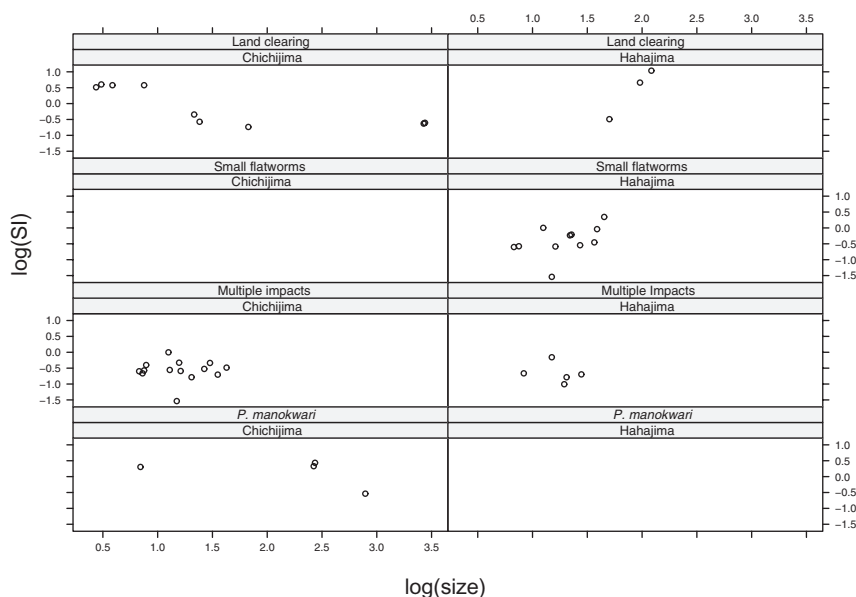


Fig. 5. Comparisons of how species driven to extinction by the different anthropogenic impacts on Chichijima and Hahajima islands are distributed in the size–SI space. Blank panels for an island denote that particular threat is absent there.

and stable species across the entire archipelago or on Chichijima or Hahajima islands ($P > 0.05$, g test, in all cases). Thus, the observed extinction selectivities in SI are not driven simply by the preferential loss of either arboreal or ground-dwelling species. Instead, finer-scale habitat partitioning that provides refugia to some species from predation or the effects of habitat loss may be important. Unfortunately the data currently available do not permit tests of this and other hypotheses.

Although strong size selectivity has often emerged as an important characteristic of anthropogenic extinctions (6, 35), body size is not a significant correlate of extinction vulnerability in many of the analyses presented here. However, our analyses also show that the relationship between size and extinction vulnerability varies substantially among extinction agents, some of which are indeed strongly size selective. This is most clearly evident on the island of Chichijima where no size bias exists in extinctions driven by habitat loss, but the species threatened by the large invasive flatworm *P. manokwari* are significantly larger compared with the other surviving species. Similarly, on the island of Anijima, species threatened by introduced rats are also significantly larger compared with the rest of the species ($P = 0.002$ Kolmogorov–Smirnov test). In fact, a comparison of species affected by predation by *P. manokwari* on Chichijima and rats on Anijima show that these two predators target species of similar sizes and SI ($P = 0.67$ MANOVA; Fig. S4). In contrast, predation by small flatworms on Hahajima Island do not show a significant size bias. These results suggest that to understand why some extinctions are strongly size selective, whereas others are not, we need better information about the underlying causes of species loss.

Overall, the loss of gastropod species on the islands of the Ogasawara archipelago follows a complex trajectory where the changing nature of threats—extinctions driven primarily by habitat loss giving way to those due to a variety of introduced predators—led to changing patterns of extinction selectivity. This suggests that for anthropogenic extinctions on islands, resilience derived from past extinction filters (10) is likely to play only a limited role in determining the current and future vulnerabilities of species. More broadly, our results show that as far as vulnerability to extinction is concerned one size does not fit all—trait(s) that can make a taxon resilient to one type of threat may not play the same role under a different type of impact. With a few exceptions (8, 12, 13), threat-specific effects have not been explicitly considered in the vast majority of analyses of how biological traits affect extinction vulnerability. The results pre-

sented here clearly show that information about how species vary in their vulnerabilities to different anthropogenic impacts (8) is essential for better predicting and preventing future extinctions. Our results also demonstrate that geographic range, a widely recognized correlate of extinction vulnerability, may be most important during the initial phase of an extinction event and much less so later on. The correlation between geographic range of species and extinction vulnerability has been shown to depend on the magnitude of extinction (36) but to our knowledge differences in the role of this trait as an extinction event unfolds have not been demonstrated before. Such a difference implies that information about past history of extinctions is particularly important for evaluating future vulnerabilities of range-restricted species. From a macroevolutionary perspective, selective advantage of large geographic range may also have varied in the geological past depending not only on the magnitude of the extinction event (36) but also the duration of the perturbation. Finally, the temporal changes in extinction selectivity documented here highlight the importance of using historical data for understanding of extinction dynamics and also the potential for using the past to better predict future vulnerabilities of species and higher taxa to various anthropogenic impacts, something that is the focus of the developing field of Conservation Paleobiology (37).

Materials and Methods

Sampling of Species and Designation of Vulnerability. The terrestrial gastropod fauna of the Ogasawara archipelago has been examined since early surveys during 1839–1907 (38–42), followed by work in 1930–1940 (43, 44), 1973, 1977 (45–47), and 1987–1991 (48–51). We used these baseline data along with more recent surveys in 2004–2009 (11, 23, 52, 53) to identify local and global extinctions as well as conservation status of species. We used a standardized taxonomic framework developed for these islands, and a species was categorized as threatened if its average population density during the latest surveys was less than one-half of that estimated from the previous surveys (Fig. S5 and *SI Materials and Methods*). Because of the overall correlation between density and geographic distribution, geographic ranges of many threatened species are also smaller now than in the past. Despite such reductions, we found that geographic range is a poor predictor of current extinction vulnerability, which makes our result conservative. For species that are extinct or are declining in abundance, we used the information from different surveys along with field observations and published studies to infer the cause of decline or loss. If the data were insufficient to identify a specific cause or suggested multiple causes, the species was categorized as impacted by multiple agents (*SI Materials and Methods*).

Shell length and diameter were measured from specimens collected during the field surveys and from those in the collections of the Kyoto University Museum and National Science Museum, Tokyo. For a few species not found in the museum collections, we used shell length and diameter of subfossil specimens from the Holocene dune and cave deposits of Chichijima and Hahajima (54). Shell sizes of subfossil and living specimens of a species from the same localities do not differ significantly so this procedure is unlikely to introduce any appreciable bias. Each specimen was photographed in a standard orientation and the measurements were taken from the photographs. For species with multiple specimens, we used the average of each measured trait. Following previous studies, body size is defined here as the geometric mean of the length and width of a shell, a metric widely used for mollusks (14, 55, 56). Note that our choice of morphological traits is determined

by measurements that are currently available for all of the species present in the Ogasawara archipelago. Other aspects of the ecology of terrestrial gastropods, such as diet, may also be relevant for understanding extinction vulnerability and can be inferred for living and fossil specimens using stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$) (57). However, the isotopic information currently available for Ogasawara species (58) is too limited for any meaningful analysis.

Statistical Analyses. Descriptions of the statistical methods used are provided in *SI Materials and Methods*.

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Supporting Information

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SI Materials and Methods

Species Sampling and Determination of Vulnerability and Extinction.

The islands used in this paper were sampled for gastropods during 1987–1991 and again during 2004–2009 (see *Materials and Methods*), when a number of new sites were also added. Each island was divided into 0.25×0.25 km grids for preliminary surveys, which were used to select a number of sites (9–20 per area during 1987–1991 and 10–35 during 2004–2009) for more intensive sampling. At each site, we first searched for arboreal species on the trees and large ground-dwelling species, such as Mandarinina (20–30 mm diameter), in the leaf litter in a 10×10 m quadrat. Subsequently, we searched more thoroughly for small species (<10 mm) by placing twenty 0.5×0.5 m quadrats randomly within each 10×10 m quadrat. Leaves were carefully removed and searched for gastropods. In addition, litter samples (2 L each) were taken from 5 quadrats, dried, and sorted by hand, to recover microsnails and fragments of dead individuals.

At each site, we recorded live individuals as well as empty shells. To ensure better sampling of the rare species, we included empty shells with periostraca (the outer proteinaceous layer of the shell that erodes once the animal dies) in our samples. We experimentally measured how long it takes for the periostracum on a shell to completely disappear after death and although there was substantial variation among species and sites, the periostraca of all species were lost after three years. Thus, if either living individuals or empty shells with periostraca were found in 2004–2009 and 1987–1991, the species was described as “extant” in 2004–2009 and 1987–1991, respectively (i.e., we used a single time-averaging window of 3 y for all species). Population density (number of individuals/m²) of each species during each sampling interval was calculated using both live individuals and empty shells with periostraca. These values were used to calculate the average population density of species on each island and also across all islands. We used the ratio of average population density during 2004–2009 and 1987–1991 to determine the threat status for each species. If a species was alive during the last sampling period but the ratio of the population density between the two periods was lower than 0.5, the species was categorized as threatened/impacted. We chose this cutoff on the basis of the frequency distribution of the ratios (Fig. S5), which was bimodal across all islands as well as on individual islands.

Extinctions of species before 1987–1991 on each island were inferred by comparing species compositions of our samples from 1987 to 1991 and faunal records from 1901 to 1977 (see *Materials and Methods*). If no live individuals or empty shells with periostraca of a species found in earlier surveys were present in our samples, the species was categorized as extinct. Thus, the differences in species composition between 1987–1991 and 1901–1940 (the previous sampling interval; see *Materials and Methods*) reflect extinctions during this time. If live individuals or empty shells with periostraca were found in 1987–1991 but not in 2004–2009, the species was categorized as extinct after 1987–1991.

Causes of Extinction. Determining the specific cause(s) of extinction of a species is clearly difficult due to the lack of direct observations. We inferred the cause(s) of decline or extinction of each species using field observations and published information about how different anthropogenic impacts are affecting Ogasawaran gastropods. In addition, the general timing of extinctions, determined by comparing the results of different surveys, also provides important information about the likely causal agent because the types of impacts have changed over time. Overall,

four different kinds of anthropogenic impacts are known to have caused declines or extinctions of gastropod species in Ogasawara. They are (i) habitat loss due to land clearing, primarily for agriculture; (ii) predation by small malacophagous flatworms; (iii) predation by the large flatworm *Platydemus manokwari*; and (iv) predation by introduced rats.

Both Chichijima and Hahajima islands were cultivated until World War II (main text), and the resulting habitat loss has been identified as a cause of early extinctions there (1). No invasive flatworms were recorded on these islands before World War II; therefore, it is very unlikely that they were a major cause of extinctions during that period. Thus, we attributed extinctions before the 1940s to habitat loss.

The extinctions on Hahajima Island occurring after 1980 can be attributed to predation by small malacophagous flatworms, because (i) there is a clear association between the distributions of these flatworms and gastropods and (ii) there are no other major threats to gastropods known on this island (2). Recent extinctions on Chichijima Island are attributable to predation by *P. manokwari*, which was introduced on this island in the early 1990s. At present there are no other known threats to gastropods on Chichijima and predation by *P. manokwari* is considered to be the primary cause of decline of native gastropods on this island (3).

On Anijima Island, cultivation and habitat loss have never been a major factor and no declines or extinctions of gastropods were documented until the 2000s. Rats were not recorded from the Ogasawara archipelago before the 1930s, and they have increased in density only on Anijima since the year 2000. A recent study (4) shows that predation by black rats (*Rattus rattus*) is the primary cause of the decline of gastropod species on this island.

For a number of species, the available information is not sufficient to attribute their decline or extinction on a specific island to one of the four known anthropogenic impacts and so they were coded as affected by “multiple” impacts. These are the cases where we simply do not know exactly what caused the declines or extinctions.

Statistical Analyses. Because the distribution of body size is highly skewed and that of spire index (SI) is bimodal, we used non-parametric statistics for individual analyses of these two traits. For the analyses requiring a multivariate approach, we log transformed the data to reduce skewness and used a multivariate analysis of variance (MANOVA). As is common with ecological data, the distributions deviated from normality even after such transformation, violating the assumptions of parametric statistics. Although MANOVA is known to be robust to such violations (5, 6), we also repeated the analyses using a nonparametric test—permutational multivariate analysis of variance (PERMANOVA, also known as NPMANOVA) (7). In this case we used untransformed data and Euclidean distances and estimated the *P* values using 10,000 iterations. Whereas PERMANOVA, like other randomization approaches, has the advantage of being “distribution free,” the power of this test appears to be sensitive to the shape of the underlying distribution (8). Furthermore, the power of PERMANOVA relative to MANOVA for small sample sizes, such as those involved in some of our comparisons, remains poorly known, especially when the underlying distributions deviate from normality. Clearly each approach has limitations and so we present the results of both tests. Also, because of small sample sizes, we have not attempted post hoc tests for either the MANOVA or the PERMANOVA results. Finally, we did not adjust the individual *P* values presented here for multiple comparisons. First,

Hahajima Island

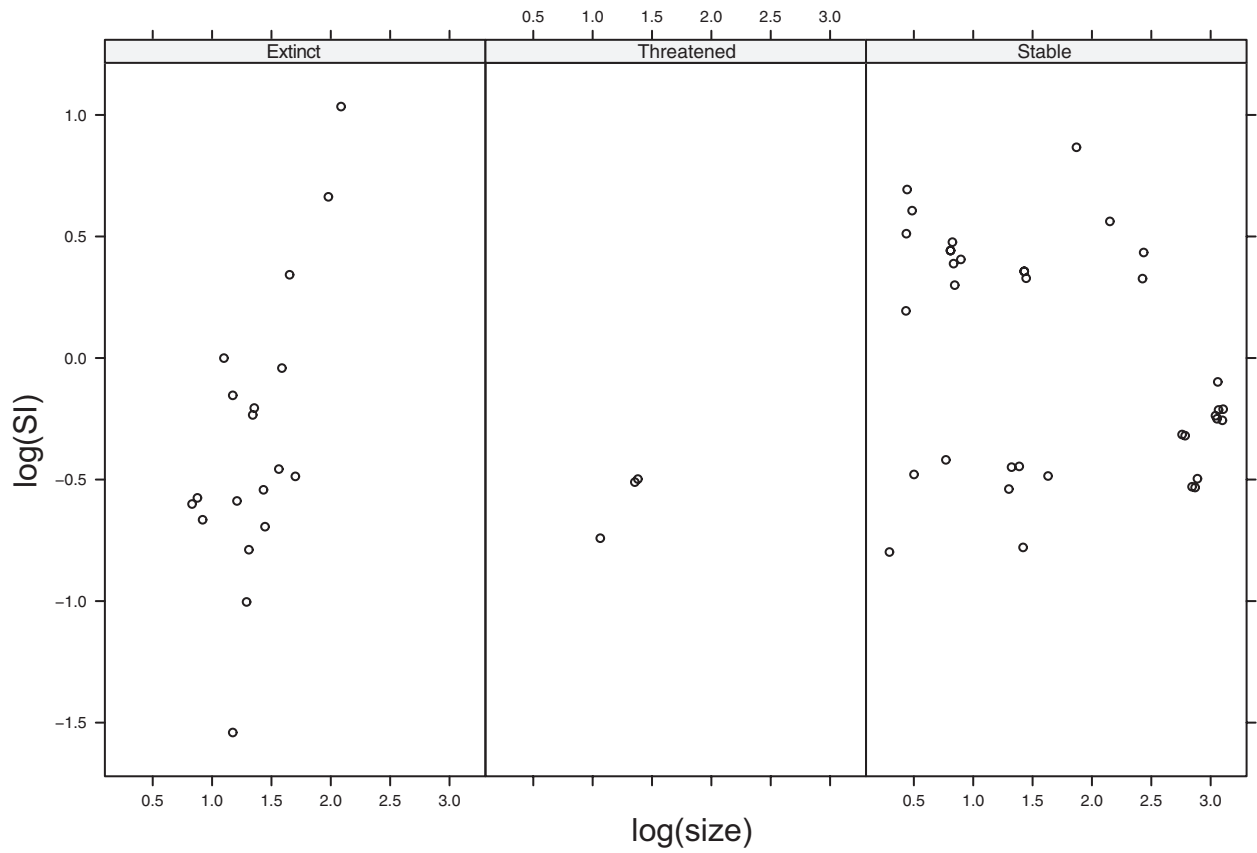


Fig. S2. Distributions of extinct, threatened, and stable species of gastropods on Hahajima Island in the size-SI space. Each point represents a species (see *Results*).

