Mainland size variation informs predictive models of exceptional insular body size change in rodents

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Abstract

The tendency for island populations of mammalian taxa to diverge in body size from their mainland counterparts consistently in particular directions is both impressive for its regularity and, especially among rodents, troublesome for its exceptions. However, previous studies have largely ignored mainland body size variation, treating size differences of any magnitude as equally noteworthy. Here we use distributions of mainland population body sizes to identify island populations as 'extremely' big or small, and we compare traits of extreme populations and their islands with those of island populations more typical in body size. We find that although insular rodents vary in the directions of body size change, 'extreme' populations tend toward gigantism. With classification tree methods we develop a predictive model, which points to resource limitations as major drivers in the few cases of insular dwarfism. Highly successful in classifying our dataset, our model also successfully predicts change in untested cases.

Introduction

The "island rule" for mammals, a pattern of divergence in body size between insular populations of mammals and their mainland counterparts, was once deemed "an extraordinary phenomenon which seems to have fewer exceptions than any other ecotypic rule in animals" [1]. Yet as examples have proliferated—from anecdotal observations of insular mammals of unusual size [2, 3], to tabulations and tallies of taxa showing insular gigantism or dwarfism [4], to regressions on body mass of the continuous variable "size ratio" (average island / average mainland body mass

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of a species; [5])—so too have the exceptions. Shifts in the average body size of a population of insular mammals have been observed to differ in direction and in degree for different populations on different islands. And in recognition of this, the number of factors used to predict the changes has also grown. The simple scenario that Foster [4] described, in which size increase or decrease predominates within a given order of mammals, has been replaced with the description of a generally monotonic trend of decrease in size ratio with increasing body size across species [5]. This, in turn, has been refined and replaced by models of size change that apply differently in different cases and are contingent both on the phylogenetic affinity of the population and on an array of ecological, environmental, geographic, and species-specific attributes of the island + population pair [6–12; for more thorough treatments of island rule literature and theory, see 7,13,14].

Given the importance of body size in all aspects of an organism's biology [15,16], evolutionary changes in size are expected to be multifactorial and subject to contingency. And size, as a composite trait that can be obtained readily for a large and broad sampling of cases, therefore serves as a proxy for suites of other traits on which selection acts more directly. While these can eventually be the subjects of more detailed and mechanistic studies, our approach here is intentionally broad and synthetic, on the premise that important clues to causal factors emerge when predictive models identify broader patterns. Up to this point, however, broad patterns have been elusive.

In this paper we focus on rodents, the most species-rich order of mammals (with nearly half of all extant species [17]). Reports of genetic differentiation of insular populations of rodents are common (*e.g.* [18–20]) and experiments have shown divergence in insular body size to have a genetic component [21], yet this order has presented the greatest obstacle to formulation of a

general "rule" for mammalian body size change on islands. A widespread but phylogenetically circumscribed group of mammals, rodents share a distinctive and well-defined set of morphological traits. Yet despite their morphological coherence, rodents vary widely in body size, habitat, and diet. Extant insular populations of rodents exhibit higher variance in and a wider range of size ratios than any other order, and both the direction and the magnitude of size change can vary among different island populations within a single rodent species [8,9,11,13,22].

To develop a model for body-size change on islands we must first ask, what is the main variable of interest? Is it the direction of size change on an island—smaller or larger, regardless of degree? If the goal is to explain body size divergence of island populations from their mainland counterparts, size differences of a magnitude not expected on the mainland are clearly of interest. When the time of first colonization of an island and the genetic variance of the founding population are unknown, minor body-size differences can reflect either conditions that do not differ from those on the mainland or insufficient time or variation for those influences to take effect. Setting a size-difference threshold informed by body-size variation among mainland populations allows us to focus on cases in which the underlying signal is not obscured by such limitations.

Here we examine body-size divergence between conspecific island and mainland populations and address the following questions:

(i) for the purpose of discerning "rules" that govern body size evolution in insular rodents, what constitutes a meaningful difference in body sizes between populations—that is, a size difference that exceeds that commonly found among populations on the mainland?

(ii) what factors are associated with such extreme—as opposed to more moderate—cases of

insular body size change?

(iii) within the set of cases that have shown extreme change, what factors differentiate

extremely small- and extremely large-bodied island populations?

To address question (i), we compare the distribution of island:mainland size ratios for insular rodents with the distribution of analogous ratios from the mainland and we develop criteria for labeling island populations as 'extreme'. In doing this we define a threshold for the magnitude of body size difference we will consider when we develop a predictive model, excluding, in the process, populations that are undergoing minor short-term fluctuations in body size or have had inadequate time (or genetic variance) for dramatic size differences to arise. For question (ii), we examine differences in the distributions of 19 organismal, climatic, and geographic variables between moderate and extreme insular rodent populations. Finally, for question (iii), we use classification trees and random forest techniques to develop a predictive model describing factors associated with extremely large and extremely small body sizes in insular populations. We then test this model on a set of cases independent from the sample used to create it.

Methods

Island Data Collection

Records of insular rodent populations were taken from the database of McClain et al. [11,23], which is an expansion of the database from Meiri et al. [8]. The size ratio for each population was calculated as the mean island body size (either mass or the cube of linear measurements when mass was unavailable [5, 8]) divided by that same measure of body size from the closest mainland population (see [8] for description of original dataset). Additional information for each

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population included organismal traits (mass, dietary data, substrate preference), six climatic

variables (temperature and precipitation, each averaged spatially across the island, their standard

deviations and their temporal variation), four measures of island productivity (the spatial mean,

maximum, minimum, and standard deviation of net primary productivity, NPP) and six

geographic variables (measures of island area, elevation, and isolation). Although several

previous studies examining the island rule have suggested that changes in predation, interspecific

competition, and population density are responsible for insular body size change (see Supporting

Information (SI) Appendix S1), accurate accounts of island population densities and community

composition are not available from primary literature for as broad a sampling of cases as we

wished to include.   Details on data collection can be found in the supplemental material for

McClain et al. [11]. Since island area and elevation can both be indicators of island terrain

heterogeneity [10], we combined measures of the two in a principle components analysis and

used PC1 as a measure of island heterogeneity (SI Table S1). A total of 306 populations of

insular rodents (67 species on 182 islands across the world) were included in the analyses.

Mainland Population Collection

We obtained mainland rodent records from the databases at the Natural History Museum of Los

Angeles County and the Smithsonian, U.S. National Museum of Natural History [24]. We

discarded all records that did not include body mass or locality information, and then grouped the

records together by species and population. Populations were defined as more than one record of

the same species obtained from exactly the same location as noted in the museum records. This

process resulted in a total of 1,076 rodent populations (mean=5.4 records/population, median=3

records/population) from across the world including species from every family that is

represented in the island database. We took the mean mass for each population, and divided it

by the mean mass for the species as defined in the masses of mammals database [17], to obtain a population:species body size ratio for each population analogous to (albeit distinct from) the size ratios between island and mainland populations described above. The averages of populations by species that we assembled did not differ significantly from the values in MoM (Wilcoxon rank sum, p = 0.169, r^2 = 0.942). (In SI Appendix S2 we show that small sample size exacerbated by sexual size dimorphism is unlikely to have distorted our size-ratio distribution, and that raising the minimum number of individuals required for a population to n=3 -- for a median of n=5 -- or n = 4 -- for a median of n=6 -- leaves our interpretations and conclusions unchanged.)

Defining 'Meaningful' Size Change

To test for a difference between the size ratio distributions of mainland and island populations (each standardized, because sample sizes differed, to total 100% in a probability density function), we used the *Matching* package in R [25,26] to perform a bootstrapped Kolmogorov-Smirnov (K-S) test on the two groups.

We then defined 'normal' size differences for the mainland as any size ratio that fell between the lowest and highest 2.5% of all mainland size ratios. Anything falling outside those boundaries (in the tails) was defined as 'extreme' size difference. The same numerical size-ratio cutoffs (values of the ratios, as opposed to percentage) were then applied to the island populations to identify insular body size ratios that were 'normal' and 'extreme' with respect to variation on the mainland. The extreme island populations were further categorized as either extremely big ('Big') or extremely small ('Small').

Comparing Conditions associated with 'normal' vs 'extreme' Island Populations

To examine the factors influencing extreme insular body size change, we plotted as probability density functions the frequency distributions for the 'normal' and 'extreme' cases with respect to each of the geographic, climatic and productivity variables, and then compared these distributions using bootstrapped K-S tests. The pairwise comparisons included 'normal' vs Big, 'normal' vs Small, 'normal' vs Big + Small combined, and Big vs Small. In all instances the threshold for significance was taken as $p < 0.05$. No correction was made for multiple comparisons, as we viewed these comparisons as descriptive and exploratory.

Classification Tree Analyses

In addition to comparing frequency distributions for each variable, we used classification trees to create a predictive model for the directionality of extreme insular body size change (Big or Small). CART (classification and regression tree, jointly called "decision tree") methods identify a succession of predictor variables to group samples so as to minimize within-group heterogeneity while maximizing the between-group heterogeneity of a response variable. Both classification and regression trees have been implemented with some success in previous studies, by the current authors and others, on insular mammalian body size change. See refs. [9] and [10] for more extensive discussions of CART methods.

For the island rodent samples deemed 'extreme' according to the criteria noted above, we constructed a fully-grown classification tree using the *rpart* package in R [25,27] using all of the variables in our insular population dataset to predict the direction of extreme size change. The fully grown tree was pruned to obtain the optimal tree (cross-validated error rate within 1 SE of minimum error tree; as discussed in ref. [9]). To test the stability of our classification tree, we also built a random forest model consisting of 5,000 trees built from bootstrapped subsets of the

data using the *randomForest* package in R [28]. A relatively stable classification tree will have a predictive accuracy similar to that of the related random forest model.

Earlier studies that applied CART methods to identify variables associated with insular body size change [9,10] were largely descriptive and inferential, constructing the decision trees and examining the chosen variables for their biological relevance. However, CART methods, especially classification trees, are widely used in other disciplines not only to describe the data used to build the tree, but to build a model to predict values of the response variable for samples independent of those used to construct the tree [29]. Recent work by Lomolino et al. [12] provided size ratios and locality data for almost 100 insular rodent populations for which we had island information (obtained earlier for purposes of studying insular mammals other than rodents; ref. [11]) but had not included in our "model-training" data set. Of those populations, 39 of them qualified as extreme according to our definition. We ran these 39 samples through our classification tree and random forest to assess the efficacy of our models as predictive tools.

Results

Defining 'Meaningful' Size Change

According to the K-S test, size ratio distributions for island and mainland rodent populations differed significantly (p<0.001; see Fig 1a). On the mainland, the lower 2.5% quantile for size ratios was 0.80 while the upper 97.5% quantile was 1.09. We took these as the boundaries for 'normal' body size, and the 5% of mainland samples falling outside these boundaries were considered 'extreme' mainland populations (see Fig. 1a). Applying the same boundaries to the island samples, 54% of the samples were classified as 'extreme' insular populations. Of these extreme populations, 78% (deemed 'Big') had increased in size, while 22% (deemed 'Small')

decreased in size. Although there were no consistent patterns within species or more inclusive

clades (see SI Appendix S3) in the tendency to produce insular populations of extreme body size,

for species that produced extreme populations on multiple islands the tendency was strong for

those extreme changes to occur in the same direction (Big or Small). The lack of a consistent

tendency for changes within species to be extreme or not could reflect the genetic or time

constraints mentioned above; the intraspecific consistency in direction of extreme changes

echoes earlier findings from analyses of insular body size change of any magnitude [9]. There

was also some inclination for more than one species of rodent on a single island to be either

normal or extreme, but the tendency was slight and the extreme populations had not necessarily

changed in the same direction. The extent to which size changes documented in our data set are

associated with particular islands or particular species is an additional indication that

characteristics of species and of islands are relevant for predicting when and in which direction

extreme body size change should occur.

Comparing Normal and Extreme Islands

The distributions of seven variables were found to differ significantly between insular

populations of Big and 'normal'-sized rodents (see Fig. 1b-g). Among these seven variables,

values were generally lower for heterogeneity of island terrain (a composite measure of area and

elevation), mean temperature (averaged spatially), and the spatial standard deviation in annual

precipitation for the Big populations, while distance to continent, minimum net primary

productivity (NPP), and mean annual precipitation tended to be higher. Three variables were

distributed significantly differently between island populations of 'normal'-sized rodents and

Small insular populations, which, by contrast, tended to experience high mean annual

temperature, a high standard deviation of NPP, and lower mean precipitation.

Big and Small insular populations differed significantly in four variables. Mean precipitation was higher for Big populations, mean temperature and the spatial standard deviation of NPP were both higher for Small populations, and Big populations were found at higher latitudes than Small ones.

Classification Tree Analyses

The classification tree based on our original dataset (Fig 2a) correctly classified 90% of its extreme cases of insular body size changes (98% of the Big and 62% of the Small populations correctly predicted, Cohen's $\kappa = 0.671$, $P < 0.001$) while the random forest correctly predicted 87% of the size changes (97% of the Big and 52% of the Small, Cohen's $\kappa = 0.559$, $P < 0.001$). The first split on the classification tree distinguishes between different dietary categories. While populations in most diet categories overwhelmingly tend to become Big on islands (102 populations becoming Big, 10 becoming Small), frugivores and granivores vary (30 Big, 27 Small). Size change in frugivores and granivores appears to depend on the mean productivity of the islands they inhabit, the tendency being to become Small on low productivity islands (1 Big, 13 Small populations). Frugivore and granivore populations on high productivity islands are subdivided a final time on the basis of the heterogeneity of the productivity landscape on the island. Islands that vary in productivity spatially (i.e., with high spatial productivity standard deviations) tended to produce Small body sizes (2 Big, 10 Small populations) whereas those with low standard deviations produced Big body sizes (27 Big, 4 Small).

When applied to a new dataset derived from ref. [12], the classification tree was able to correctly classify 33 of the 39 'extreme' populations (85%: 94% of Big populations, 20% of Small

populations correctly predicted) while the random forest correctly predicted 90% of the new populations (100% of Big populations, 20% of Small populations correctly predicted).

Discussion

From this examination of extreme insular body size evolution, it is clear that island rodents exhibit some striking differences from their mainland counterparts. Not only do the distributions of size ratios differ between island and mainland populations, but over half of the insular rodent populations fall outside the boundaries encompassing 95% of the size variation ordinarily found among mainland populations—a pattern unlikely to have arisen through founder effects alone.

We found a greater than expected proportion of insular rodent populations of extremely small body size (12% of all island populations, 4.8 times the frequency observed on the mainland), but the great majority of extreme sized island rodents were extremely big (42% of all island populations, 16.8 times the frequency on the mainland). The predominance of extremes of larger size could suggest that a form of 'immigrant selection' was at work [30], with greater success of large-bodied individuals surviving dispersal over water; however, these percentages stand in stark contrast to the broader pool encompassing all island rodents in our dataset (including non-extreme and extreme body size), where it is a virtual coin toss whether a population will increase or decrease in body size relative to the closest mainland population (58% are relatively big, 42% relatively small). This strong trend for 'extreme' populations to be of larger body size suggests that this is the general pattern for rodents on islands, whereas populations in which body size becomes extremely small represent notable exceptions. (This tendency is evident even if cutoff points for Big and Small are chosen to be symmetrical about a value of 1; see SI Appendix S4.)

The idiosyncratic nature of insular rodent populations of extremely reduced body size is also reflected in the groups identified by the classification tree. Figure 2b shows the differences in body mass between sets of populations predicted to be extremely big and others predicted to be extremely small. The two terminal nodes in which body size was predicted to be extremely big comprise a large number of populations (112 and 31, respectively, together representing 84.7% of all extreme populations) and have a wide range of masses, with each encompassing almost the entire range of rodent body sizes considered in this analysis (6-304 grams; populations for which the predictions of size increase were accurate spanned the same range). In contrast, the terminal nodes for which size was predicted to have decreased consist of fewer samples (12 and 14, 15.3% of extreme populations) and have much narrower body size ranges, and these narrow ranges lie at opposite ends of the size spectrum for rodents, separated by an order of magnitude. In one set, and noting the cases in which the prediction of size decrease was accurate, all but two of the populations were large rodents (mean=357 grams, median=322 grams) that had become extremely smaller (comparatively "Small") on islands; in the other set, 13 out of 14 populations were small rodents (mean=24 grams, median=16 grams) that had become extremely small. Based on these patterns, it appears that rodents on islands are generally extremely big; that extreme insular body size decreases represent a deviation from the more typical pattern, and that each group of size-reduced insular populations requires a distinct set of variables to explain its deviation. On the classification tree, populations of extremely reduced rodents were dispersed among several terminal nodes, suggesting that different insular circumstances lead distinct subgroups to evolve substantially smaller size. Yet despite differences among these subgroups in the specific sets of relevant variables, resource availability may be an underlying factor that influences all of them. All groups that were successfully predicted to be extremely reduced in

size are fruit and grain specialists found on islands with productivity that is either low or spatially heterogeneous (*i.e.* 'complex') – a finding aligned with predictions from previous studies [31,32] – whereas the fruit and grain specialists that were predictably greatly enlarged are found on islands with homogeneous productivity landscapes. Since resource availability declines much faster with decreasing area for fruit/grain specialists than for more generalist species [32,33], small frugivore/granivores on low productivity islands may not be able acquire the resources necessary for maintaining populations of a 'normal' body size. Likewise, large frugivore/granivores on islands with a heterogeneous productivity landscape may be similarly limited due to their inability to access patchy resources across an island.

The factors identified as significant by the Kolmogorov-Smirnov tests largely agree with the classification tree, suggesting that resource-related variables are major drivers of extreme size change. The concordance between the classification tree and the K-S tests is particularly noteworthy, given that some island populations classified as 'normal' might, with additional time or genetic variation, have diverged significantly in size. Also noteworthy is the transitivity of the K-S results—differences between 'Small' and 'normal' were in the same direction as differences between 'Small' and 'Big'—which need not have been the case. Terrain heterogeneity, temperature precipitation, and productivity differ in their distributions for islands that produce 'extreme' rather than 'normal' body sizes in their rodent inhabitants: Greatly enlarged rodents tend to be found on small, homogeneous islands with above-average precipitation and high, relatively consistent resource availability; extremely reduced rodents are typically found on hot, dry islands where availability of resources is spatially variable.

While the classification tree and random forest both excelled in classifying the data used to build the models, their success at predicting independent data is perhaps even more impressive. Of the

34 cases of insular rodent populations in the independent dataset that exhibited extreme size

increase, the classification tree successfully predicted all but one while the random forest

correctly classified all of them. Although the classification rate for populations of small body

size from that dataset was less successful (1 of 5 correctly classified), all four of the misclassified

populations reached the same terminal node as the largest group of misclassified populations

from the original data: extremely reduced non-frugivorous/granivorous rodents. Since

measurements such as net primary productivity and diet are imprecise proxies for factors like

resource availability, we might anticipate that predictions would improve with the inclusion of

more detailed diet and resource availability data.

The results of our analyses underscore the importance of taking variation that is commonly found

on the mainland into account when identifying factors that produce unusual body sizes on

islands. Striking differences exist between mainland and island populations, but many of the

factors associated with changes in body size in insular rodents come into focus only when the

statistical noise produced by variation ordinarily found also on the mainland is removed.

Specifically, it becomes clear that some version of the island rule holds true for rodents, with the

great majority of insular populations that undergo extreme changes increasing in size. While

exceptions to this rule still exist, and while additional data not currently available for all

populations we considered might clarify trends and further enhance our understanding of them

(e.g. SI Appendix S1), we have developed a simple yet highly successful predictive model of

insular body size change based largely on diet and resource availability that correctly classifies

over 90% of extreme populations, remains robust when classifying novel samples, and suggests

future avenues for more mechanistic studies of this phenomenon. Although previous authors

have despaired of finding generalities that could predict the response of populations to novel

insular environments, using models designed to handle the very factors and contingencies that frustrated previous work, we find that significant patterns do emerge. These patterns and the resulting predictability of size change found in this study represent a major step in the description and understanding of an ecotypic "rule" half a century in the making, and they open the way for further work at the population level to examine the mechanisms and processes that affect body size and its correlates.

Data Accessibility

Both the island and mainland body size databases will be accessible on Dryad following publication of this manuscript.
Island Database: Dryad doi:10.5061/dryad.1b736 (http://dx.doi.org/10.5061/dryad.1b736)
Mainland Body Sizes: Dryad doi:10.5061/dryad.sd6nj (http://dx.doi.org/10.5061/dryad.sd6nj)

Author Contributions

P.A.P.D. initiated the project, assembled the data, conducted analyses, prepared the figures, and drafted the manuscript; V.L.R. participated in project design, interpretation of findings, and writing the paper.

Competing Interests

We have no competing interests.

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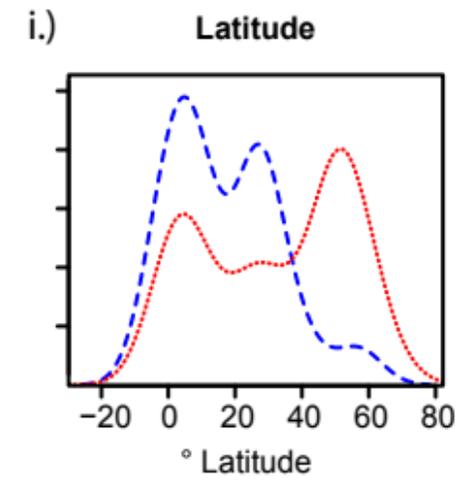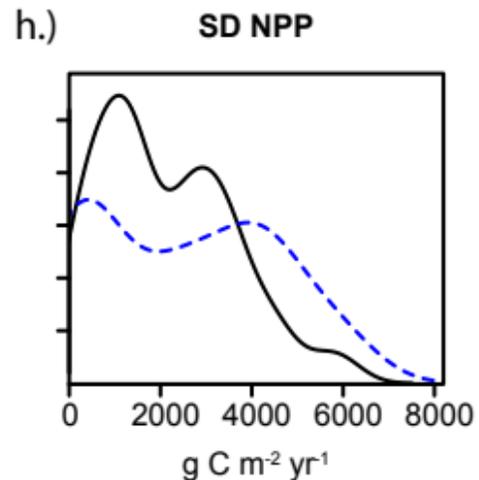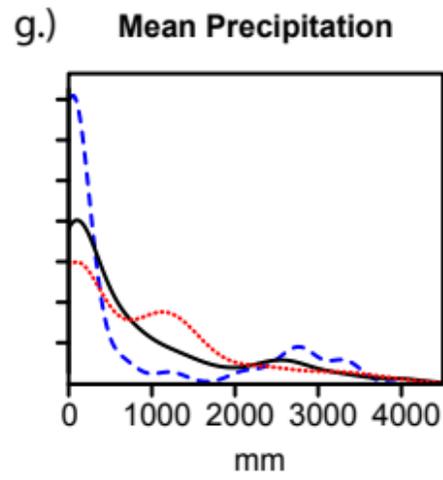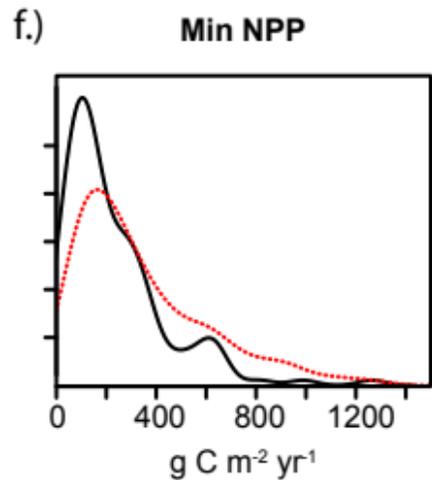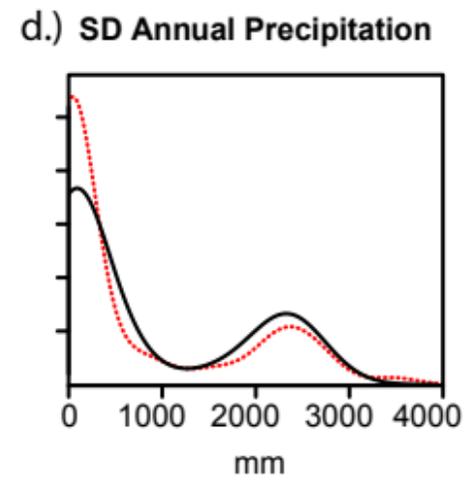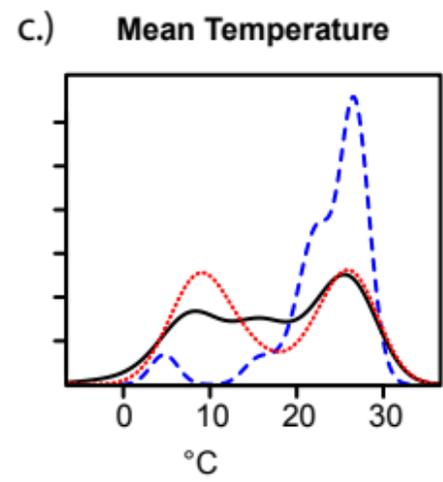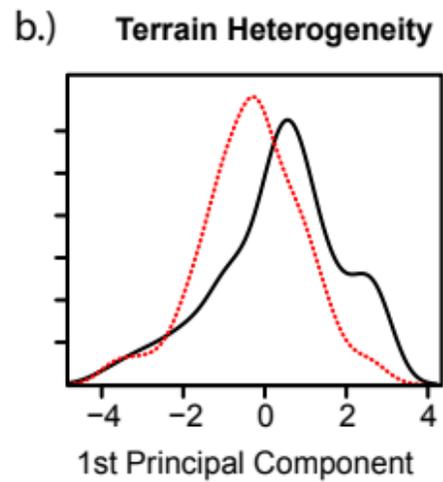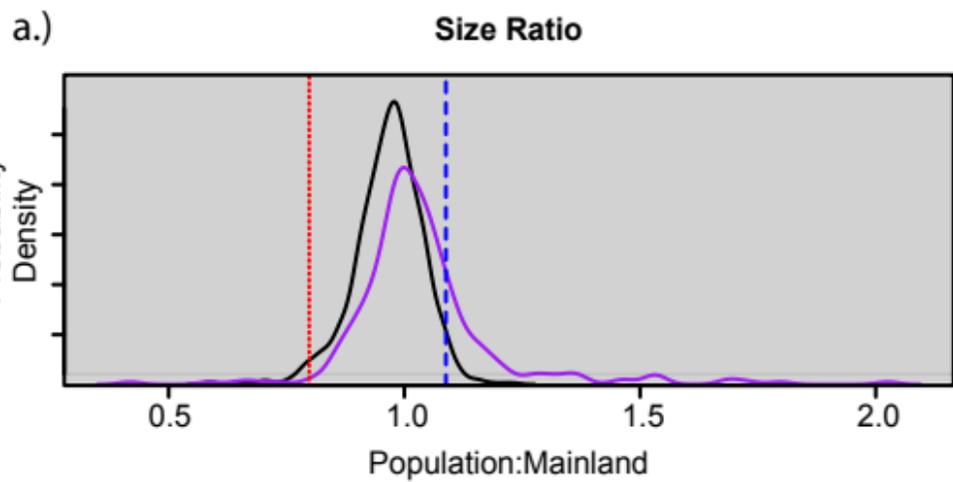
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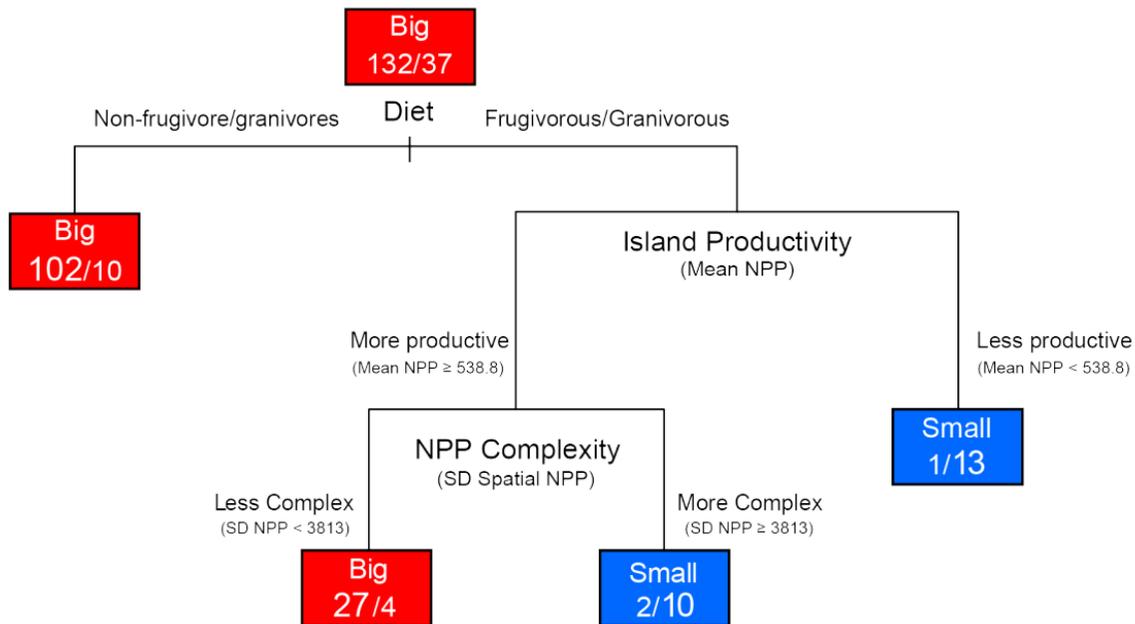
Figure 1. Density plots comparing distributions of numbers of island populations (y-axis) for

various characteristics (x-axis). (a) Size ratios for mainland (black) and island (purple)

populations; vertical dashed lines delimit tails of the distributions showing extreme size

reduction (left) or increase (right). (b-i) Various attributes whose distributions differ

significantly (K-S test, p<0.05) between 'normal' (solid black), Small (dashed blue) and/or Big

(dotted red) island populations.

Figure 2. Classification tree, showing predicted direction of size change for insular rodent

populations, and body size ranges corresponding to its terminal nodes. (a.) Classification tree

showing variables and the ranges of values used in the classification process and the numbers of

cases showing size increase / decrease at each node. In the terminal nodes, the number of cases

correctly predicted are in a larger font. (b.) Box-and-whisker plot showing the distribution of

species masses for each of the four terminal nodes in the tree. The box extends from the first to

the third quartile with the bold line indicating the median mass for the box.

a.) **Size Ratio**

Probability Density

Population:Mainland

b.) **Terrain Heterogeneity**

1st Principal Component

c.) **Mean Temperature**

°C

d.) **SD Annual Precipitation**

mm

e.) **Distance to Continent**

Probability Density

Log10(km)

f.) **Min NPP**

g C m^{-2} yr^{-1}

g.) **Mean Precipitation**

mm

h.) **SD NPP**

g C m^{-2} yr^{-1}

i.) **Latitude**

° Latitude

a)

Big
132/37

Diet

Non-frugivore/granivores — Frugivorous/Granivorous

Big
102/10

Island Productivity
(Mean NPP)

More productive
(Mean NPP ≥ 538.8)

Less productive
(Mean NPP < 538.8)

Small
1/13

NPP Complexity
(SD Spatial NPP)

Less Complex
(SD NPP < 3813)

More Complex
(SD NPP ≥ 3813)

Big
27/4

Small
2/10

b)