

Another one bites the leaf: Heterophylly of Mascarene plants as an adaptation to giant tortoise herbivory

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Background

Heterophylly is a widespread phenomenon found in many different plant families and outstandingly prominent in the Mascarene islands, especially on Mauritius and Rodrigues. Here, many endemic plants have two leaf types (juvenile and adult) that are strikingly different in size, shape and colour. The change in leaf type is quite abrupt in most species, and typically occurs between 0.8–1.5 m above the ground. This feature has been proposed to be an adaptation to herbivory by recently extinct giant tortoises (*Cylindraspis* spp.), the largest of which could browse up to ~1.3m and flightless birds. Indeed, in Mauritius, non-native Aldabra giant tortoises (*Aldabrachelys gigantea*) could distinguish between the two leaf morphs, strongly preferring the adult leaves^[1]. An analysis of secondary leaf compounds didn't show a clear pattern^[2], leaving the mechanism behind this choice pattern unresolved. We here 1) examine the generality of tortoises' response to Mascarene heterophylly, by studying the feeding response of Aldabra giant tortoises to nine endemic heterophyllous woody species from Rodrigues (Fig. 1, Table 1), and 2) investigate the response of young, naïve tortoises to heterophylly.

Cafeteria experiment I

Individual tortoises could choose between two small branches of the same heterophyllous species, one of each leaf type (juvenile and adult). Both branches had similar total leaf area (Fig. 2). During each 5 min trials we recorded which sample was approached first and the total number of bites.

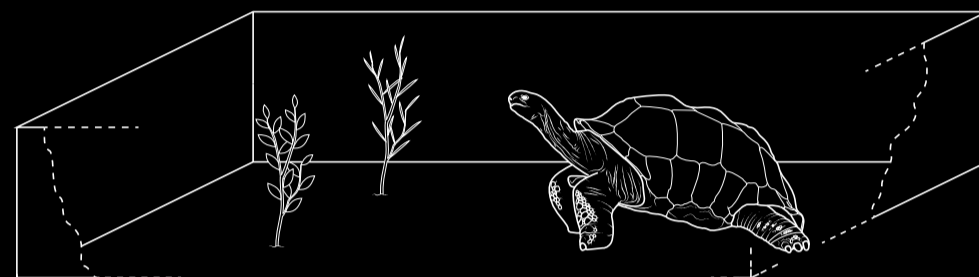


Figure 2: Experimental design for the first cafeteria experiment.

Cafeteria experiment II

Here we used three groups of three adult tortoises, kept separately in stone wall enclosures (8 x 8 m). Four branches (2 juvenile, 2 adult leaf type) were presented simultaneously, arranged in a 2 x 2 m square. The branches were placed in water to prevent them from drying out. We recorded biomass and number of leaves before and after each trial, which lasted 24 hours. Tortoises had *ad libitum* access to water and their staple food (*Leucaena leucocephala*) during the trials.

Results

Both choice experiments demonstrated that both naïve and non-naïve *A. gigantea* could distinguish between the two leaf types, with adult-type leaves being clearly preferred over juvenile leaves (Figs 3, 4).

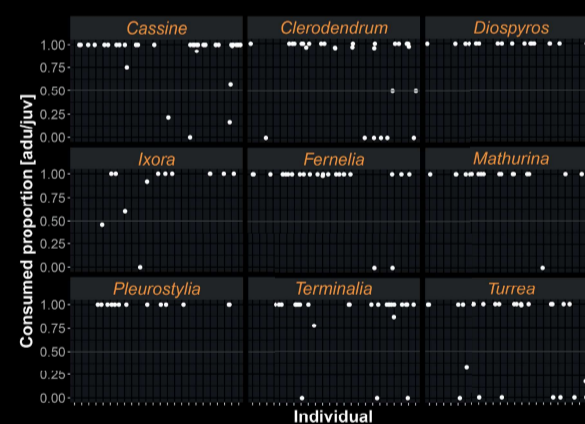


Figure 3: Proportions of bites (adult*juvenile⁻¹) from the first cafeteria experiment. The 50% limit was used to convert the proportion into a binary response variable of preference for the leaf type (1 = adult, 0 = juvenile).

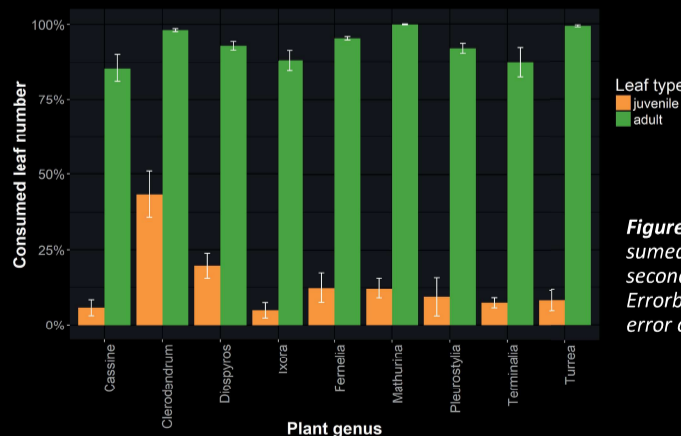


Figure 4: Proportions of consumed leaf numbers from the second cafeteria experiment. Errorbars indicate the standard error of the mean.

Heterophylly

"Concurrent variation in leaf form within a single plant, or environmentally induced switches between either of two (or more) leaf morphologies."

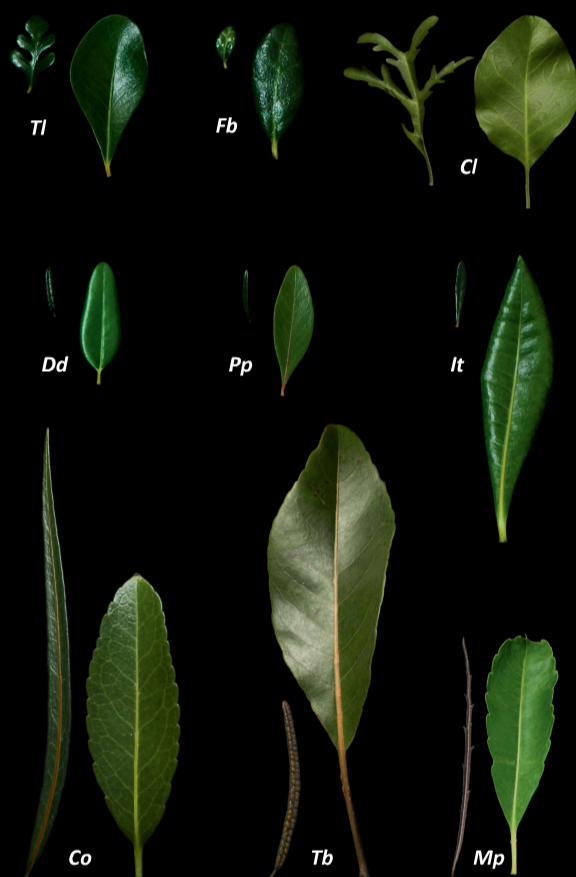


Figure 1: The two life-size leaf types (juvenile left, adult right) of the heterophyllous plant species. Initials of the species from table 1 are indicated. TI and Fb are magnified x2. The Aldabra giant tortoise can reach up to ~1m when stretching.

Study site

The study took place in the François Leguat Giant Tortoise and Cave Reserve on Rodrigues Island (Mauritius). The 20-hectare reserve is the site of a reforestation project that began in 2006, where more than 200,000 endemic seedlings have since been planted.

Table 1: The nine heterophyllous plant species used in the experiments.

Genus Species	Family	Endemism
<i>Cassine orientalis</i> (Co)	Celastraceae	Mascarenes
<i>Clerodendrum laciniatum</i> (Cl)	Lamiaceae	Rodrigues
<i>Diospyros diversifolia</i> (Dd)	Ebenaceae	Rodrigues
<i>Fernelia buxifolia</i> (Fb)	Rubiaceae	Mascarenes
<i>Ixora trilocularis</i> (It)	Rubiaceae	Rodrigues
<i>Mathurina penduliflora</i> (Mp)	Passifloraceae	Rodrigues
<i>Pleurostyliya putamen</i> (Pp)	Celastraceae	Rodrigues
<i>Terminalia bentzoe ssp. rodriguesensis</i> (Tb)	Combretaceae	Rodrigues
<i>Turraea lanceolata</i> (TI)	Meliaceae	Rodrigues

Study species

Aldabra giant tortoises (*Aldabrachelys gigantea*) have been introduced in the reserve to restore ecosystem functions, e.g., herbivory, seed dispersal, and nutrient cycling, that would have been provided by the recently extinct endemic giant tortoises (*Cylindraspis vosmaeri* and *C. peltastes*). We used three different tortoises age classes for the experiments, 20 one-year-old ("yearlings"), 7 two-to-three-year-old ("young"), and 9 adults ("adults"). The "yearlings" and "young" tortoises were kept in a nursery and never had contact with the study plants (naïve). The adult tortoises roam the reserve freely and have had contact with the study plants (non-naïve).

Conclusion

Our findings provide strong support to the hypothesis that heterophylly has evolved multiple times independently as an anti-herbivory strategy of Mascarene plants. The specific mechanism(s) remain unknown.

In preparation

Scent samples for a chemical analysis of the dynamic headspace were collected from two plant species to evaluate possible candidate deterring compounds. These may have a key role in herbivore defence.

References

[1] Eskildsen, L.I., J.M. Olesen, and C.G. Jones, Feeding response of the Aldabra giant tortoise (*Geochelone gigantea*) to island plants showing heterophylly. *Journal of Biogeography*, 2004. 31(11): p. 1785-1790.; [2] Hansen, I., L. Brimer, and P. Mølgaard, Herbivore-deterring secondary compounds in heterophyllous woody species of the Mascarene Islands. *Perspectives in Plant Ecology, Evolution and Systematics*, 2004. 6(3): p. 187-203.