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Title: Can cycads persist in disturbed habitats? A study of local adaptation of *Zamia fairchildiana* populations to disturbed forests in Costa Rica.

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Organisms are constantly changing in ecological and evolutionary time, as individuals adjust to novel conditions and eventually populations adapt to new habitats. That is what cycads have been doing for millions of years. However, the current rate of degradation of ecosystems is extremely high, as a result of human-related activities transforming entire landscapes. Many plant species are now disappearing at alarming rates from fragmented forests and other disturbed habitats. We know that many cycad populations are extremely endangered; nevertheless, we have very little information about the natural history of cycads in their native habitats and much less about their ability to cope with habitat changes. This information is essential for developing effective conservation strategies. If we want to protect cycads, we need to understand the mechanisms behind population decline and identify the stages or the processes that are critical for population viability in the short and long term.

With my dissertation project I am evaluating the effects of anthropogenic disturbances on the population viability of *Zamia fairchildiana* in Costa Rica. This species is not currently endangered (it is cited as Near Threatened by the IUCN) and, thus is suitable for large-scale studies about cycad responses to habitat changes. I have been monitoring eight colonies of *Z. fairchildiana* in two localities in the Osa Peninsula of Costa Rica for two years. To carry out my fieldwork, I have been lucky enough to receive funding and logistical support from the Cycad Society and Montgomery Botanical Center. Through the support of its members, the funding from the Cycad Society has allowed me to gather the field data I need to test my research hypotheses and have the amazing opportunity of studying up close some marvelous populations of rainforest cycads. Here, I present some of the results from my dissertation work and discuss their potential implications for the conservation of cycad populations.

Zamia fairchildiana **in Costa Rica.**

Zamia fairchildiana is a species typical of the understory of tropical rain forests in southern Costa Rica and western Panama (Gomez 1982). It has an aerial stem that can reach 2 m and can bear up to 20 leaves. The leaves can reach more than 2 m long and can have up to 60 leaflets. In the Osa Peninsula (Costa Rica), plants produce a flush of 1-5 new leaves at the beginning of the rainy season (April-May). By the peak of the rainy season (September), males and females start the production of cones. Males produce 1-3 cones, while females produce only one cone. Pollination occurs at the beginning of the dry season (December), and seeds develop through the following year and are released by the end of the rainy season (November). The seeds are red when immature and bright orange when dispersing. I have collected samples of the pollinator beetles, but have not yet identified them. Unfortunately, I have not been able to observe any potential seed disperser in the field—although Dr. Luis-Diego Gomez from OTS has observed jays dispersing seeds in a botanical garden setting in Costa Rica (Gomez 1993).

Effect of habitat changes on population life history.

In Costa Rica, *Zamia fairchildiana* inhabits large tracts of undisturbed tropical wet forest in the Osa Peninsula, mostly within Corcovado National Park and its buffer zones (Fig. 1). In the eastern part of the Osa Peninsula and other places in southern Costa Rica (Puntarenas province), populations of *Z. fairchildiana* are found in forest patches that are affected by logging, hunting, and other human activities. The environmental conditions in the understory in these disturbed forests can be quite different from the conditions in the old-growth forest. In particular, light availability is higher and soil moisture is lower due to reduced canopy cover resulting from logging and changes in species composition.

Populations of *Zamia fairchildiana* in disturbed forests differ significantly in several life-history traits from populations in native habitats. In the disturbed habitats, individuals have higher growth rates, i.e. they produce more leaves/year. In addition, both males and females are able to reproduce at a smaller size, reproduce more often, and produce more cones in a given season. Finally, and very interestingly, the trade-off between reproduction and growth that is common in other rainforest cycads (i.e. a decrease in leaf production after coning (Clark and Clark 1988)) is not observed in this species in disturbed habitats. This suggests that individuals in disturbed habitats are not as resource-limited as in their native habitats, likely because of higher light availability.

However, it seems that elevated growth and reproductive rates in disturbed habitats may have some costs in terms of offspring size. Seeds and seedlings are smaller in disturbed habitat, resulting in a lower germination rate and likely in lower seedling survival (I am still monitoring seedlings to estimate their survival rate). In addition, it is plausible that faster development and higher reproductive effort in disturbed habitats will result in reduced adult longevity, which, in turn, could significantly affect the population growth rate. In the near future, I will use the data I am gathering to determine whether reductions in seed germination and seedling survival or potential shorter longevity will negatively affect population growth, despite the increase in adult growth and reproduction. These analyses will allow me to evaluate the impact of life-history differences between habitats on the short-term viability of populations in disturbed habitats.

Local adaptation to disturbed habitats.

To evaluate the potential for long-term persistence of populations in disturbed habitats, it is necessary to consider not only the demographic viability of populations in the short term (i.e. whether population size is increasing or not), but also the 'evolutionary viability' of populations. In the long term, populations will persist in a novel habitat only if they are able to locally adapt and increase population fitness under the new environmental conditions. To explore local adaptation, one can perform a reciprocal transplant experiment between habitats. If populations are locally adapted to each habitat, the prediction is that individuals will perform better in the habitat they originated from compared to the alternative habitat. I have done such an experiment with two populations of *Z. fairchildiana* from mature and disturbed habitats.

The results from this experiment (Fig. 2) suggest that populations of *Z. fairchildiana* are indeed locally adapting to the environmental conditions in disturbed habitats, at least in terms of seed germination. Seeds from disturbed habitats germinate better in the disturbed forest than in the mature-forest habitat. This is a very interesting result, because it implies that local adaptation to the disturbed habitat is happening very quickly, i.e. in a matter of a few generations (human disturbance has been significant for only five or six decades). We now have increasing evidence that rapid evolution may be common in nature, especially when environmental changes are drastic, as in the case of human-dominated landscapes. Another part of my research deals with the potential for rapid evolution in populations of *Z. fairchildiana* and the mechanisms involved in the process. I still have much work to do in that aspect of my dissertation.

Relevance to cycad conservation.

Habitat destruction and degradation is the main threat for cycad populations worldwide. Therefore, understanding the effects of habitat changes on population viability is critical for cycad conservation. By analyzing the effects of habitat disturbance on the life-history and demographic properties of populations, it is possible to identify traits or stages in the life cycle that are critical for population growth. This information can then be used to target particular aspects of the biology of populations to either avoid population decline or try enhancing or restoring population viability. Finally, this type of information can be used to develop demographic models to simulate how different conservation scenarios or management practices can affect population viability (e.g. see Raimondo and Donaldson 2003).

Unfortunately, this may not be enough for many cycad species that have little remaining of their native habitat, such that populations persist mostly in disturbed habitats. These species will survive in the long term only if they are able to adapt to these degraded conditions in human-dominated landscapes. Understanding the potential for local adaptation to disturbed habitats is, therefore, another aspect of cycad conservation in need of consideration. Local adaptation will increase population fitness in disturbed habitats, but it could also result in the loss of genetic variability relevant to survival in the native habitats or in the ability of a population to respond to future environmental changes. Finally, genetic divergence (due to natural selection or other evolutionary forces) between populations needs to be considered in defining units of conservation. Evaluating the potential for local adaptation involves studies of natural selection and genetic variability, so they also provide additional and interesting information on cycad biology.

It is my goal to continue doing research on the effects of habitat destruction and modification on cycad population viability. I think this research can contribute a great deal of information for guiding conservation programs and unraveling the mysteries of this fascinating group of plants. By joining efforts with other people addressing other aspects of cycad conservation, I believe we can enhance their survival in nature. Thanks again to the members of the Cycad Society for making these efforts possible.

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LEGENDS FOR GRAPHICS

Figure 1. Map showing the forest cover in the Osa Peninsula and the location of the two study sites.

Figure 2. Results from a reciprocal transplant experiment where 19 families of seeds (from the same female cone) were split and planted in disturbed and mature forest patches. The significant interaction between family and habitat indicates that seeds from the disturbed habitat germinate better in the disturbed habitat than in the mature habitat and vice versa.

Picture 1. *Z. fairchildiana* in habitat, the understory of tropical wet forest in Costa Rica

Picture 2. Adult individual of *Z. fairchildiana*

Picture 3. Mature female cone of *Z. fairchildiana*

Picture 4. Mature male cone of *Z. fairchildiana*

Picture 5. Adult individuals of *Eumaeus minyas*, a specialist predator of *Z. fairchildiana*

Picture 6. Larvae of *Eumaeus minyas*, a specialist predator of *Z. fairchildiana*