Investigating the Role of a Cryptic Life Stage in Fern Community Assembly

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Introduction

Ferns have a **unique life cycle**, alternating between morphologically distinct sporophyte (diploid) and gametophyte (haploid) generations. The majority of the life span of each generation is nutritionally and physically independent from the other. This characteristic makes ferns unique; although bryophytes and seed plants also have alternation of generations, in these plants one life phase is completely dependent on the other. Fern **gametophytes**, as the sexual phase of the life cycle, are particularly significant to fern evolution. However, due to their highly cryptic nature (typically <1 cm in size and lacking morphological characters for species-level identification), the ecology of fern gametophytes is virtually unknown.

The **goal** of this project is to analyze ecological traits of fern gametophytes and sporophytes in a phylogenetic context to elucidate the processes driving community assembly and evolution in an island fern flora.

Study Site and Methods

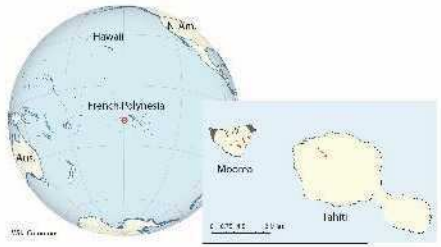

Figure 1: World map centered on French Polynesia. Red circle indicates location of Tahiti.
Inset: Moorea and Tahiti. Red triangles indicate sampling sites.

Moorea and Tahiti are part of the Society Island archipelago, one of the most isolated island chains in the world (Fig. 1). The islands harbor several habitat types, including coastal strand, low elevation rainforest, and cloud forest. The Tahitian fern flora comprises ca. 150 species (Nitta et al. 2011), and is phylogenetically diverse, including 20/37 families of Smith et al. (2006). These encompass a variety of habitat preferences (e.g., epiphytic, epipetric, terrestrial), sporophyte morphologies, and gametophyte morphotypes.

- We constructed DNA libraries using chloroplast *rbcL* to use for phylogenetic analysis and identification of field-collected cryptic gametophytes.
- We conducted field surveys along an elevational gradient to investigate species ranges of both sporophytes and gametophytes. Sporophyte diversity was sampled in 10x10 m plots, and gametophytes in 50 x 50 cm subplots. Sampling plots were located at ca. 200m intervals along an elevational gradient from 200m to 2000m.
- We analyzed physiological (e.g., desiccation tolerance) and morphological traits (e.g., morphotype, frond anatomy) in a phylogenetic framework to investigate how characteristics of both the gametophyte and sporophyte influence fern community assembly.

Results

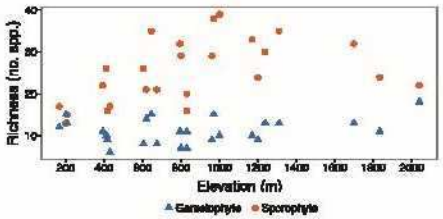

Figure 2: Observed species richness of fern gametophytes (blue triangles) and sporophytes (red dots) along an elevational gradient from 200 to 2000m. $n = 25$ sites total.

Over 1600 fern gametophytes were collected across the gradient; of these, 1374 (85%) were successfully identified to species using the DNA barcode marker. Species richness was higher for sporophytes (total 124 spp all plots; mean 25.3 ± 7.6 spp per plot) than gametophytes (total 73 spp all plots; mean 9.8 ± 2.1 spp per plot). Sporophytes reached maximum richness at mid-elevations; however, this humped distribution was not observed in gametophytes (Fig. 2).

Most gametophytes occurred near conspecific sporophytes. However, gametophytes of 42 species were observed growing in plots that lacked conspecific sporophytes ("x" in Fig. 3). Furthermore, gametophytes of two species, *Antrophyum sp.* and *Vaginularia* **cf.** ***angustissima***, were found which appear to completely lack sporophytes on Moorea or Tahiti (arrows in Fig. 3).

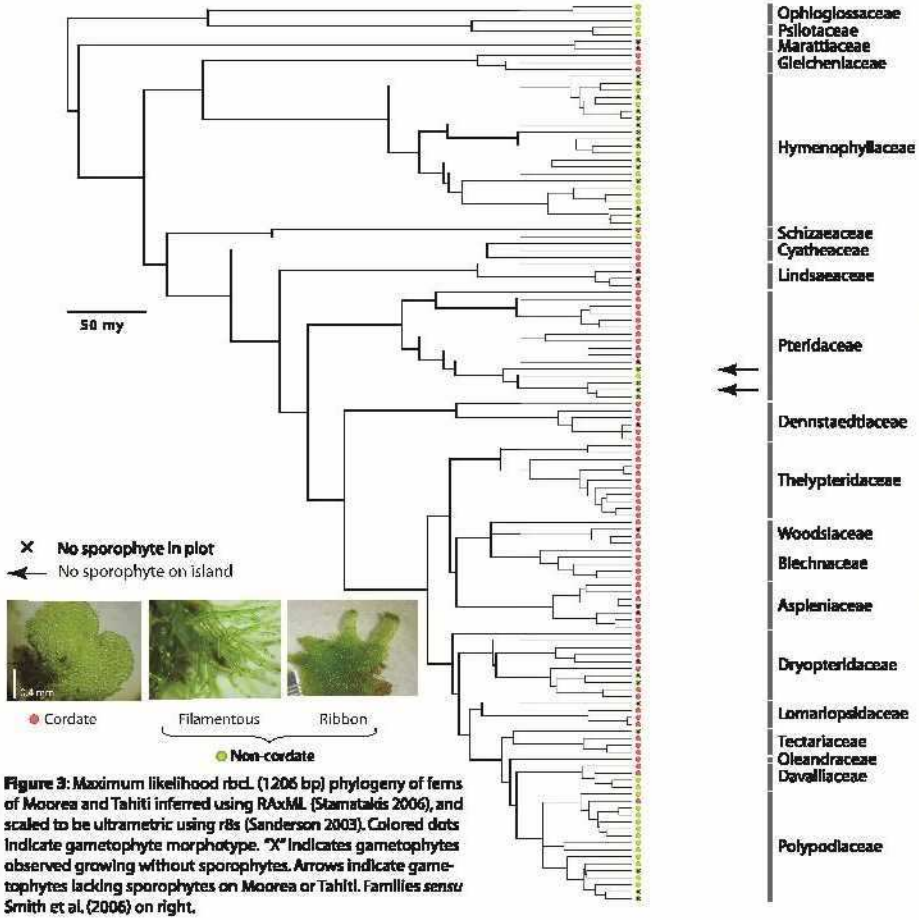

Figure 3: Maximum likelihood rbcL (1206 bp) phylogeny of ferns of Moorea and Tahiti inferred using RAxML (Stamatakis 2006), and scaled to be ultrametric using r8s (Sanderson 2003). Colored dots indicate gametophyte morphotype. "X" indicates gametophytes observed growing without sporophytes. Arrows indicate gametophytes lacking sporophytes on Moorea or Tahiti. Families *sensu* Smith et al. (2006) on right.

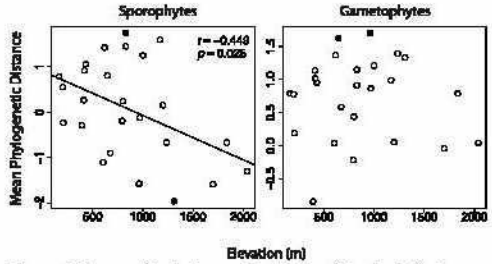

Figure 4: Community phylogenetic structure (standard effect size of MPD) of gametophytes (left) and sporophytes (right) along an elevational gradient from 200 to 2000m. Positive SES values indicate overdispersion; negative values indicate clustering. Significant Pearson correlation of SES with elevation shown for sporophytes. Communities significantly different from null distribution in black. $n = 22$ sites total.

We used Pagel's (1994) method to test for correlated evolution between gametophyte morphotype and occurrence beyond conspecific sporophytes; a model of correlated evolution was found to be more likely (log likelihood -99) than one in which the two traits were independent (log likelihood -107).

Phylogenetic structure of each gametophyte and sporophyte community was characterized using Mean Phylogenetic Distance (MPD) and Mean Nearest Taxon Index (MNTD) with the Picante package (Kembel et al. 2010) in R (R Core Team 2012). Sporophyte communities decreased in MPD with increasing elevation, but no correlation between phylogenetic community structure was observed in gametophytes (Fig. 4).

Conclusions

The results of our study suggest that, despite the developmental link between fern sporophytes and gametophytes, community assembly dynamics may differ between these two generations. Although phylogenetic community structure of gametophytes does not change with elevation, sporophytes become more clustered at higher elevations. Furthermore, we found gametophytes of multiple fern species that exist beyond the ranges of their sporophyte counterparts, and that these gametophytes tend to have non-cordate morphologies. The ability of fern gametophytes to persist in favorable microhabitats even when the conditions do not allow growth of the sporophyte may be important for the evolutionary success of ferns.

Acknowledgements

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