Evaluating Chamaedorea alternans

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1. Los Tuxtlas Biological Station is home to 11 palm species.

Chamaedorea alternans is endemic to Veracruz, Mexico. Delimitation from the related widespread *Chamaedorea tepejilote* distributed from southern Mexico to western Colombia is assessed in this paper.

Understanding species limits has been a problem for systematists working in many plant groups, including palms. First of all, there are several different species concepts that apply to plants, each having a different philosophical basis. Second, classification of plants can be inherently difficult because of hybridization and polyploidy, plastic phenotypes and variable morphology, as well as technical issues including field collection and herbarium work. In certain groups of palms, systematists have only partial knowledge of species variation. Molecular evidence has improved research from classic morphological studies in many cases because of its power in resolving difficult taxonomic problems. An example where species-level taxonomic confusion prevails is in the genus *Chamaedorea*. *Chamaedorea* has traditionally been a difficult group in which to work due to issues with dioecy, sympatry and complex morphological variation (Hodel 1992).

One example of historical confusion in Chamaedorea that has received particular attention is that of Chamaedorea alternans H.Wendl. and C. tepejilote Liebm. These two species are sympatric in the Los Tuxtlas Biological Station in Veracruz, Mexico, where C. alternans is endemic and listed as a threatened taxon. Chamaedorea tepejilote is morphologically variable and is distributed from southern Mexico to western Colombia. This article will review recent work involving the assessment of species boundaries between these species using molecular markers and supporting evidence from morphological characters (Bacon & Bailey 2006). Lastly, the aim is also to illustrate how problems in taxonomy can impede conservation efforts for threatened and endangered taxa.

La Estación Biología Tropical Los Tuxtlas (Fig. 1) is located at the northern limit of the tropical rainforest ecosystem, in the state of Veracruz, between 150 and 700 m (492–2296 ft.) in altitude. The Los Tuxtlas region is phytogeographically interesting as elements of Caribbean, Central American, and mainland Mexican flora mix in a relatively restricted geographic area. Annual rainfall averages 450 cm (177 in.), and the mean annual temperature is 24°C (75°F). The substrate in the preserve is volcanic in origin. A detailed account of the Los Tuxtlas field station can be found in Gonzalez Soriano et al. (1997).

Although the Los Tuxtlas area has been largely deforested for pastureland, the station itself encompasses some areas of virgin tropical rain forest that contain approximately 820 vascular plant species (Ibarra-Manriquez & Sinaca-Colin 1987). Of the 11 species of palms found within the preserve, six are members of *Chamaedorea* (*C. alternans, C. elatior, C. ernesti-augusti, C. oblongata, C. pinnatifrons, C. tepejilote* and *C. woodsoniana*) and five are from other genera (*Astrocaryum, Bactris, Geonoma, Reinhardtia* and *Desmoncus*). All palms in Los Tuxtlas are subcanopy plants that do not exceed 10 m (32 ft) in height.

Some of the past debate over the recognition of *Chamaedorea alternans* appears to be caused by the paucity of quality herbarium specimens. Many botanical collections lack informative characters that would facilitate positive identification, and therefore numerous collections are likely misidentified. At the herbarium at the Los Tuxtlas Biological Station, specimens have been annotated numerous times and generally alternate between designations.

The debate has impacted some recent and older ecological studies on *Chamaedorea* that have recognized just one species, *C. tepejilote*, rather than both (Oyama & Dirzo 1988, Pompa et al. 1988, Oyama 1990, Oyama & Mendoza 1990, Oyama et al. 1992, Oyama & Dirzo 1991, Oyama et al. 1992, Oyama 1993, Gonzalez Soriano et al. 1997), while others have accepted *C. alternans* as distinct from *C. tepejilote* (Otero-Arnaiz & Oyama 2001). If the latter classification is accurate, then the former approach has mixed divergent species within studies designed to address intraspecific variation.

It is also likely that the great morphological variation found across the range of *Chamaedorea tepejilote* has confused past comparisons with *C. alternans*. Given that *C. tepejilote* is a widespread and poorly understood taxon, the pertinent comparisons are from those *C. tepejilote* that occur in sympatry with *C. alternans*. Based on field observations of *C. tepejilote* outside of this region, future research on this species may demonstrate that this taxon, now understood to be highly variable, will warrant splitting it into additional taxa.

The lack of a consensus on the status of *Chamaedorea alternans* has implications that reach beyond basic taxonomy. The Los Tuxtlas region has been largely devastated by deforestation over the last 20 years (e.g., Dirzo & Garcia 1992). While the Mexican government currently treats *C. alternans* as a threatened taxon, the uncertain taxonomic status of *C. alternans* puts the putative species in a delicate position with regard to its conservation status. Thus the ongoing debate and confusion over *C. alternans* has direct impacts for conservation in southern Mexico.

In a review of the literature, a number of systematists have in fact recognized *Chamaedorea alternans* as a distinct taxon from *C. tepejilote* (Hemsley 1885, Standley 1920, Burret 1933, Glassman 1972, Hodel 1992, Quero 1992, Govaerts & Dransfield 2005). Taxonomic treatments recognizing a single highly variable *C. tepejilote* are primarily attributable to Ibarra-Manriquez (1988) and Henderson et al. (1995).



2. *Chamaedorea alternans* has multiple inflorescences at the node.

Using data derived primarily from field observations, Hodel (1992) concluded that Chamaedorea alternans, which was first described by the German botanist Hermann Wendland in 1880, represents a taxon distinct from C. tepejilote. He distinguished C. alternans primarily by the presence of white leaf sheaths distinct venation and multiple with inflorescences at a node (Fig. 2). More recently, Henderson et al. (1995) addressed the status of C. alternans using observations from available herbarium specimens. They concluded that specimens that were identified as C. alternans were insufficiently distinct from those of C. tepejilote. Subsequently, they treated all representatives of this group as C. tepejilote, a name that has nomenclatural priority over C. alternans.

The goal of this study (Bacon & Bailey 2006) was to investigate whether *Chamaedorea alternans* and *C. tepejilote,* as morphologically defined by Hodel (1992), are genetically distinct in the Los Tuxtlas region, meaning they are behaving as separate species. Populations of both putative species were analyzed using Amplified Fragment Length Polymorphism (AFLP) markers (Vos et al. 1995). AFLP is a highly sensitive method for detecting DNA polymorphisms. AFLP data can be informative at and below the species level, and these data have been useful in addressing species complexes in several plant groups.

A total of 249 samples of leaf material suitable for AFLP was collected (127 of *Chamaedorea tepejilote* and 122 of *C. alternans*). Upon AFLP analysis (Bacon & Bailey 2006), the samples separated into distinct clusters that closely correspond to the morphologically defined *C. alternans* and *C. tepejilote* (*sensu* Hodel 1992). AFLP analysis provides results that are consistent with genetic differentiation between species and shows no evidence of gene flow occurring between taxa, suggesting that they are distinct under most currently accepted concept of species.

Taxonomically useful characters that were previously unused in the classification of the two species of *Chamaedorea* were noted in the field by Bacon (Bacon & Bailey 2006). These include *Chamaedorea alternans* having a solitary, single-stemmed life form, larger fruit and seed size, as well as delayed fruit maturation and possibly flowering time, compared to *C. tepejilote*. In contrast, *C. tepejilote* has multiple stems and has smaller fruits and seeds, which mature earlier than *C. alternans*. These morphological characters support the differentiation of *C. alternans* and *C. tepejilote* as distinct species.

Apparent ecological differentiation was also observed between the species. In general, *Chamaedorea alternans* is common in the eastern half of the reserve in association with well-developed soils. In contrast, *C. tepejilote* is nearly absent from the eastern portion of the reserve but dominates the rocky forests in the western half. It is important to note that the morphological and ecological characters of *C. tepejilote* in this study apply only to individuals within the Los Tuxtlas field station. There appears to be considerable morphological variation in *C. tepejilote* across its greater distribution, but nowhere does it approach *C. alternans* in similarity.

Evidence supporting the distinctiveness of *Chamaedorea alternans* from *C. tepejilote* is important for both conservation biology and ongoing research on these taxa. Our results (Bacon & Bailey 2006) demonstrate *C. alternans* should remain a priority for conservation biology in southern Mexico. *Chamaedorea alternans* is found within a rapidly disappearing type of vegetation, and it is not currently known to exist outside of the Los Tuxtlas region. Recognition of this species should create an impetus for its conservation and the proper management of this area.

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