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**GLOBAL ADVANCES IN**  
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## **Global Advances in Biogeography**

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# Biogeographic Insights in Central American Cycad Biology

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## 1. Introduction

Cycads (Cycadophyta) are dioecious, palm-like, gymnosperm (non-flowering seed plants) trees and shrubs found broadly across the tropical belt of the world (Fig. 1). Cycads are veritable living fossils once thought to date from the Mesozoic as early as 280 million years ago (mya); however, recent reevaluation of the fossil evidence indicates they originated in the upper Paleozoic, more than 300 mya (Pott et al., 2010). They predated, and were contemporaneous with, the dinosaurs and have survived to the present. As a group, the cycads have been systematically restructured, making use of morphological and molecular characters and cladistic analysis (Caputo et al., 2004). Three families are currently considered valid (Cycadaceae, Stangeriaceae, and Zamiaceae), with a world total of about 330 described species (Osborne et al., 2012). *Cycas* and *Zamia* are the most widely distributed and researched genera.

Cycads are solely represented in Panama by the genus *Zamia*, with 16 described species and a new one soon to be described; of these 17 species, 12 are endemic. Although these 17 species are many more than were previously known and/or described by earlier workers (Stevenson, 1993; Schutzman et al., 1998), still many others are likely to be found, especially in the forested areas near the Colombian border. *Zamia*, the most widely distributed genus of cycads after *Cycas* (Fig. 2), extends the length of the isthmus, stretching from Darién Province in the east, abutting on Colombia, to Bocas del Toro and Chiriquí provinces in the west, next to the Costa Rican border (Fig. 3). Only the south-central provinces of Herrera and Los Santos lack cycad populations, and this is likely due to habitat destruction (deforestation for agricultural and cattle ranching endeavors) during past centuries, rather than a natural deficiency. Conversely, on the Atlantic slope there are many cycad populations, including *Z. pseudoparasitica*, the only known obligate gymnosperm epiphyte.

The main objective of this paper is to present data justifying the study of cycads as biogeographical subjects, taking into account their evolutionary antiquity, as well as their

extinct and extant distribution, general biology, and reproductive strategy. In this context, we present an example of tropical cycad biology, with the Isthmus of Panama as our main biogeographical framework. Much work on the biology and conservation of cycads has been carried out in this region for over 100 years, starting with many of the noteworthy European plant and animal collectors of the 19<sup>th</sup> century, up to the Panamanian national workers of today. The cycads serve as a living case of the result of island biogeography, with current distribution being limited by both biotic (pollinators, for example) and abiotic (climate, geography/orography, and habitat restrictions) factors.

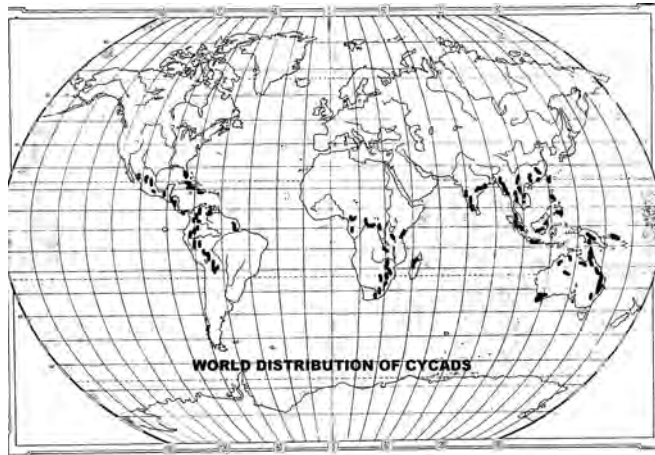


Fig. 1. World distribution of extant cycads.

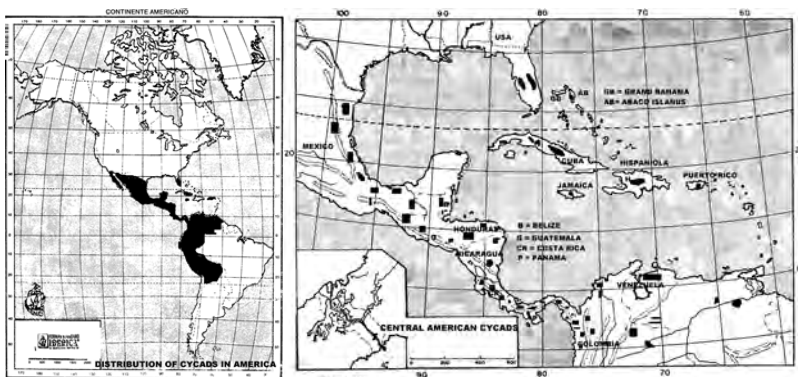


Fig. 2. Distribution of cycads (mostly *Zamia*) on the North and South American continents and in Central America and the Caribbean.

The Panama Land Bridge—definitely closed about 3-2.7 mya (Coates & Obando, 1996; Webb, 1997)—served as a physical connection to the northern and southern continents and allowed rapid and almost explosive species radiation. The Isthmus of Panama consists of about 75,500 km<sup>2</sup> of land mass (Wikipedia, 2011) and harbors about two-thirds the number of cycad species as Mexico, which is over 20 times larger in area. Panama has almost the

same number of species as Colombia, which also is nearly 20 times larger. Rising and falling sea levels and the closing of the land bridge made possible the paleontological “Great American Biodiversity Interchange,” involving the movement of animals and plants in two directions (north-south and south-north), including cycads from North and South America, into the isthmus (Fig. 4. & Table 1), where they colonized new habitats and expanded into new niches, giving rise to new species that, together with the existing flora, make this the richest cycad flora per unit area in the neotropics (Stevenson, 1993). Even though only one genus is represented, it is by far the most diverse among the cycads and has the widest distribution after *Cycas* (Fig. 2).

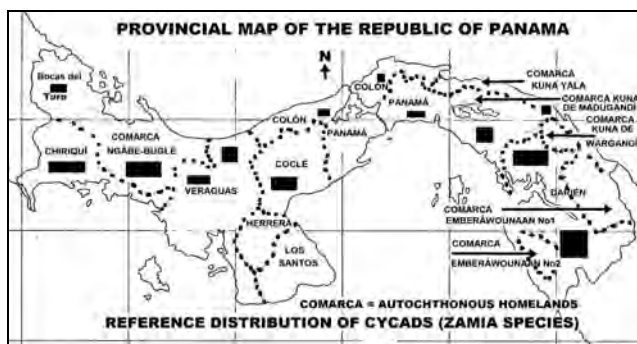


Fig. 3. Generalized distribution of cycads (*Zamia*) across the Isthmus of Panama.



Fig. 4. Interchange of *Zamia* species on the Isthmus of Panama and new types that evolved there. 1-4. *Zamia* species from Colombia; 5-7. *Zamia* species from Central America.

*Zamia* includes the only known obligate gymnosperm epiphyte (*Z. pseudoparasitica*). There are types with underground stems (e.g., *Z. ipetiensis*, *Z. cunaria*, *Z. dressleri*) and others with large, above-ground trunks (e.g., *Z. elegantissima*, *Z. nesophila*, *Z. obliqua*); types with leaflets ranging from quite small (*Z. acuminata*) to very large (e.g., *Z. hamannii*, *Z. imperialis*); lowland types sporadically inundated with seawater (*Z. nesophila*, *Z. hamannii*) to upland types above 1,500 masl (e.g., *Z. lindleyi*, *Z. pseudomonticola*); and types pollinated by only one pollinator (e.g., *Pharaxonotha* in *Z. manicata*) to those pollinated by two different genera of pollinators (e.g., *Pharaxonotha* and *Rhopalotria* [or *Rhopalotria*-like weevil] in *Z. obliqua* and *Z. fairchildiana*).

CYCAD SPECIES	COUNTRY OF ORIGIN		
	PANAMA	COSTA RICA	COLOMBIA
<i>Z. acuminata</i> *	Yes	Yes	No
<i>Z. cunaria</i>	Yes	No	No
<i>Z. dressleri</i>	Yes	No	No
<i>Z. elegantissima</i>	Yes	No	No
<i>Z. fairchildiana</i>	Yes	Yes	No
<i>Z. hamannii</i>	Yes	No	No
<i>Z. imperialis</i>	Yes	No	No
<i>Z. ipetiensis</i>	Yes	No	No
<i>Z. lindleyi</i>	Yes	No	No
<i>Z. manicata</i>	Yes	No	Yes
<i>Z. nesophila</i>	Yes	No	No
<i>Z. neurophyllidia</i>	Yes	Yes	No
<i>Z. obliqua</i>	Yes	No	Yes
<i>Z. pseudomonticola</i>	Yes	Yes	No
<i>Z. pseudoparasitica</i>	Yes	No	No
<i>Z. skinneri</i>	Yes	No	No
<i>Zamia</i> cf. <i>elegantissima</i>	Yes	No	No

\* Considered not synonymous with the described species from Nicaragua.

Table 1. Relationship between the cycad flora of Costa Rica, Panama, and Colombia.

## 2. Methods

More than 40 populations including all 17 species of isthmian cycads were studied between 1998 and 2010. We collected data on plant size and reproductive strategy, including coning cycles, sex ratios, time of dehiscence and receptivity of cones, pollination and pollinators, ripening of seed cones, and disarticulation of cones. Efforts were made to find dispersal agents of cycads, and data on herbivory were collected on almost every visit. Data were also collected pertaining to biogeographic and taxonomic issues of the plicate-leaved species, which have puzzled botanists for more than a century. A concise phylogeny of the genus, distribution among forest types, and conservation threats rounded out the data gathered. Trips were made on foot, by car, by special all-terrain vehicles, by train, boat, and plane, and even on horseback. Different detection methods for pollinating beetles were employed, including exclusion experiments, the use of greased microscope slides tied to petioles near pollen and ovulate cones, and baiting pollinators outside of the normal coning period using dehiscing cones from garden plants.

### 2.1 Study area

The Isthmus of Panama occurs in the tropics of the western hemisphere with the following coordinates: 7°12'07" to 9°38'46" North and 77°09'24" to 83°03'07" West. It is limited to the west by Costa Rica, to the north by the Caribbean Sea, to the east by Colombia, and to the south by the Pacific Ocean. The isthmus emerged through volcanic activities and elevation of the sea floor (Coates, 2003), and is presently traversed by two cordilleras: one extending

from Nicaragua to the western side of the canal (the Talamanca range), and the other from the east side of the canal into Colombia (which is related to the Andean system of South America; Wikipedia, 2012). The result is a typically montane and irregular topography with peaks to 3,300 masl. Moreover, there are narrow coastal plains and, in certain zones, contracted alluvial terraces. The cordillera rocks are volcanic in origin. In the central part of the isthmus where the Panama Canal is found, the topography is sinuous, being formed by rocks from the rising sea beds (Instituto Geográfico Nacional Tommy Guardia, 2007).

Because of its geography, Panama has a typical tropical climate. Average temperature is 21.0°C at the lowest and 34.5°C at the highest, with an annual average of 27.7°C. April has the highest temperature readings, and the lowest are found in December and March. Rainfall varies according to region, with values from 1,000-7,000 mm annually, and there are two distinct seasons: a rainy season from the end of April until November, and a dry season from December to April. Panama's rainfall pattern is governed by the seasonal displacement of tropical Pacific air pockets and subtropical ones of the Atlantic and is modified by local orography, although there is a fairly uniform pattern of rainfall distribution throughout the year on the Caribbean slope (ANAM, 2006).

Climatic conditions in Panama are adequate for forest development. However, at present only 44% of the surface has a natural forest covering. Deforested sites are being used for agriculture and cattle ranching (ANAM, 2006). Extant forests are found north and east in Panama, and the process of forest destruction began with the arrival of the first settlers and has henceforth continued. At present, the continued destruction of natural forests is due to the advancing agricultural and cattle ranching frontier in different regions and to the development of surface mining activity (ANAM, 2006).

## 2.2 Forest types & cycad populations

During the Great American Biodiversity Interchange, a great many species of plants migrated across the isthmus, some of which have become adapted to the local climate, forming the structure of the natural vegetation observed today. In the case of forests, species biodiversity is from different sources. High-altitude forests have Mesoamerican influence, while in the lowlands, conditions have been influenced by neotropical species and migration from the Chocó region (Louis Berger Group, 2003). The differences between lowland vegetation and those from the highlands are due principally to temperature changes concordant with changes in altitude.

Panamanian cycads are associated with different forest types, and can be found alongside natural montane vegetation and with localized forests in the lowlands. Moreover, it is possible to find cycads in association with human-altered forests. In general, Panamanian cycads grow in three general types of forests: lowland evergreen forest, lowland semideciduous forest, and submontane evergreen forest (although the geographic distribution of most species coincides with the lowland forest types) (Fig. 5, Table 2).

**Lowland evergreen forests:** These are found below 700 masl; annual rainfall is above 3,000 mm, and temperature varies between 24-30°C. Tree tops bear leaves year-round, which leads to the understory being relatively sparse. These forests have densities of around 600 individual trees per hectare, representing approximately 100 distinct species (Mendieta, unpubl.). Thirteen species of native cycads are found here, representing 76% of described isthmian species (Fig. 5, Table 2).

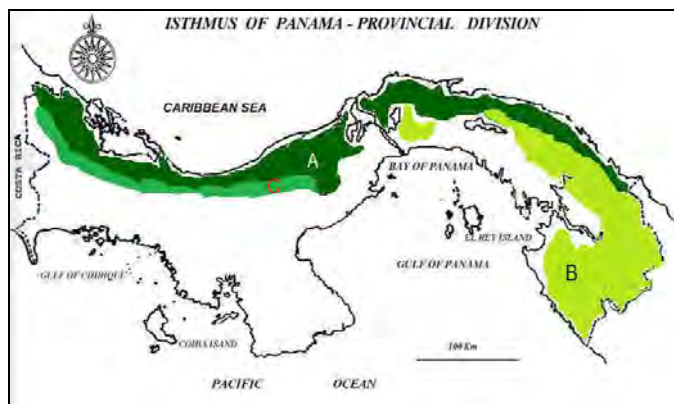


Fig. 5. Distribution of isthmian cycads according to forest type. A. Lowland evergreen forest; B. Lowland semideciduous forest; C. Submontane evergreen forest.

Species	Lowland evergreen forest	Evergreen submontane forests	Lowland semideciduous forests
<i>Z. acuminata</i>	X		
<i>Z. cunaria</i>	X		
<i>Z. dressleri</i>	X		
<i>Z. elegantissima</i>	X		
<i>Z. fairchildiana</i>	X		
<i>Z. hamannii</i>	X		
<i>Z. imperialis</i>	X		
<i>Z. ipetiensis</i>	X		X
<i>Z. lindleyi</i>		X	
<i>Z. manicata</i>	X		
<i>Z. obliqua</i>	X		X
<i>Z. pseudomonticola</i>		X	
<i>Z. pseudoparasitica</i>		X	
<i>Z. nesophila</i>	X		
<i>Z. neurophyllidia</i>	X		
<i>Z. skinneri</i>	X		
<i>Z. cf. elegantissima</i>			X
<b>Totals</b>	<b>13</b>	<b>3</b>	<b>3</b>

Table 2. Presence of isthmian cycads in natural forest types.

**Lowland semideciduous forests.** These are found below 700 masl, with annual rainfall between 2,000-3,000 mm, and with temperatures ranging between 24-30°C. Under these conditions, 30-40% of tree species are deciduous, and understory species are generally evergreen year round. Tree densities are on the order of 430 individual trees per hectare, representing approximately 100 distinct species (Mendieta, unpubl.). Three native cycad species are found in this forest type, representing 17% of described isthmian species (Fig. 5, Table 2).



**Submontane evergreen forests.** These are found between 700-1,200 masl, with annual rainfall above 3,000 mm. Altitude modifies these forests, so the temperature varies between 21-24°C during the year. Tree tops are evergreen year round. Tree densities are on the order of 700 individual trees per hectare, representing 110 distinct species (Louis Berger Group, 2000). Three native cycad species are found in this forest type, representing 17% of described isthmian species (Fig. 5, Table 2).

### 3. Isthmian cycad flora

Cycads abound throughout the neotropics and even in warm temperate areas of the globe, but they are much more abundant in tropical and subtropical sites with high humidity and temperatures (Fig. 1). Considering its relatively small size and abundance of cycad species, the Isthmus of Panama is an ideal locale for their study, and cycad populations across the isthmus have been examined by the authors over the past three decades. The following is a brief summary of the Panamanian cycad flora:

1. *Zamia cunaria* (Fig. 6A) - a plant with no above-ground stem and with very few leaves in mature specimens; its habit and morphology are similar to that of *Z. ipetiensis*; it is a narrow Panamanian endemic, found only along a road encompassing national land and part of the Kuna or Dule homeland in eastern Panama, where it grows at 400-650 masl.
2. *Z. dressleri* (Fig. 6B) - another species with no above-ground stem and with very few leaves in mature specimens (1-3 generally). This is a Panamanian endemic found on the Atlantic side of the isthmus in Colón Province. It is very hardy and will withstand rough handling, drought, and some direct sunlight.
3. *Z. obliqua* (Fig. 6C) - a shrub to large tree with distinctive leaflets indicative of its specific epithet, although there are variations on the theme; it is found in separate sites in Darién Province, and there are disjunct, remnant populations abutting on the Atlantic coast, near the Panama Canal area, and in northwestern Panamá Province, growing in extended sympatric association with *Z. imperialis* and *Z. pseudoparasitica* in north-central Panama. It almost rivals *Z. pseudoparasitica* in distribution and is the only widely-disjunct cycad in Panama.

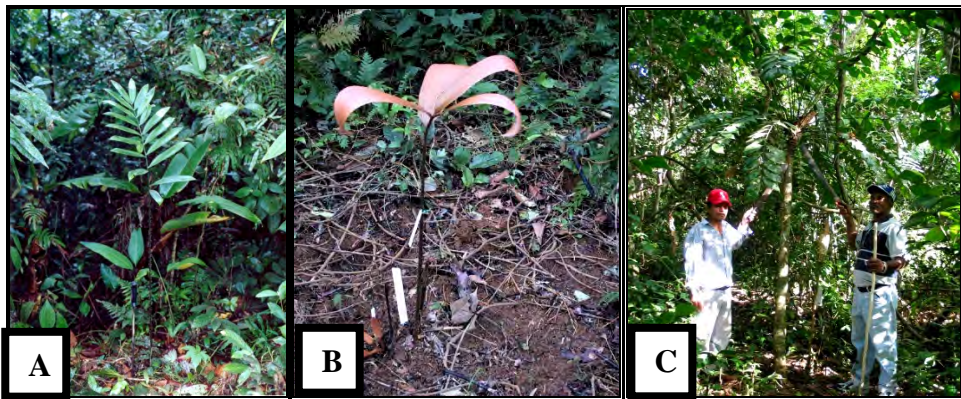


Fig. 6. Biodiversity of Panamanian cycads. A. *Zamia cunaria*, with underground stem; B. *Z. dressleri*, idem, with pollen cones near soil level; C. *Z. obliqua* with huge, arborescent trunk.

4. *Z. pseudoparasitica* (Fig. 7A) – this obligate tree-dwelling cycad, while a Panamanian endemic, is perhaps the widest ranging species in Panama, being found on high, and sometimes lower, tree branches from Bocas del Toro Province in the west to Colón Province near the northern end of the Panama Canal; germinated seeds have been found on the ground, but these apparently are eaten by unknown animals, and neither juvenile nor adult plants are ever seen growing terrestrially.
5. *Z. acuminata* (Fig. 7B) – a plant with no above-ground stem in habitat (potted plants may show aboveground stems). It is found above 500 masl in east-central Coclé Province. This species is small, with many long-acuminate leaves; it has been treated as synonymous with another plant along the Río San Juan in southern Nicaragua, but it likely is a different species (Schutzman, 2004; Lindström, pers. comm.). The long-acuminate leaves are distinctive in the genus.
6. *Z. imperialis* (Fig. 7C-D) – previously known as the “red leaf *skinneri*,” it is quite attractive with crimson-colored leaves seen all over the forest when the leaves are emerging. The plants are generally short-stemmed with a few large leaves (1-3 generally) and huge leaflets. It is an endemic species of the central Atlantic versant.

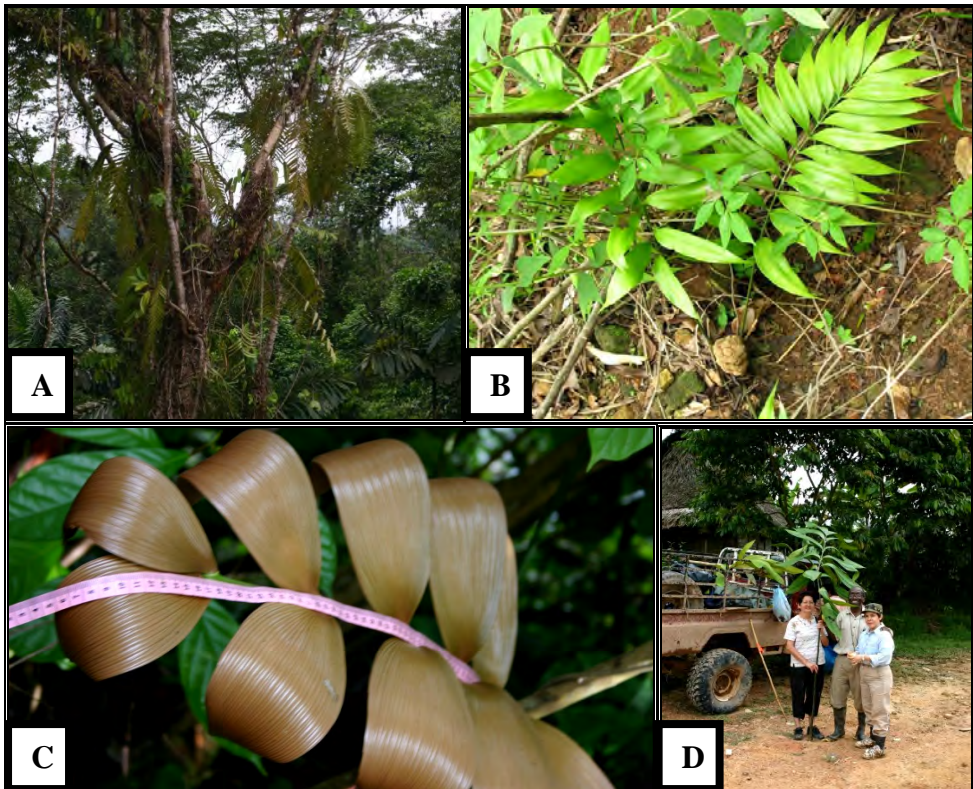


Fig. 7. Biodiversity of Panamanian cycads (cont'd.): A. Specimens of *Zamia pseudoparasitica* hanging from tree branches in north-central Panama; B. *Z. acuminata*, a small-leaved species with underground stems; C-D. *Z. imperialis*, one of the large-leaved, plicate-leaved species.

7. *Z. hamannii* (Fig. 8A) – a shrubby to large, arborescent, island-dwelling plant that often grows near the sea in Bocas del Toro Province. Emergent leaves are rosy red to orange. This species is similar to *Z. imperialis* in overall appearance, but has a silver tomentum on emerging leaves, bears many more leaves, and has different seed cones.
8. *Z. nesophila* (Fig. 8B) – shrubby to arborescent, with leaves green (emergent and mature) and leaflets and cones differing from those of other plicate-leaved species. It is found near beaches, withstanding sea spray and occasional inundation by seawater. Like *Z. hamannii*, it is an island-dweller in the Bocas del Toro region.
9. *Z. skinneri* – long confused with other plicate-leaved taxa but recently recharacterized (Taylor et al., 2008; 2012), it grows large, arborescent trunks, bears green-emergent leaves, and is widely distributed throughout coastal mainland Bocas del Toro Province.
10. *Z. neurophyllidia* – similar to *Z. skinneri* (and similarly confused for many years), but much smaller and with a different form of seed cone. It is distributed in extreme northwestern Panama and may occur in Costa Rica.
11. *Z. elegantissima* – a small shrub to very large tree (Fig. 8C), it is found near eastern and northern Colón Province on the Atlantic versant and is sympatric with *Z. cunaria*, where it grows a stem to almost 3 m high. Populations are very small, numbering less than 50 plants, and emergent leaves are cream-colored.
12. *Z. cf. elegantissima* – known among cycad workers as “blanco,” or white, because of the snow-white appearance of its new leaves, this species appears to be a diminutive variant of *Z. elegantissima*. However, this is the only Panamanian species with this type of emergent leaf. The shape and size of the cones and seeds, as well as the overall size and number of leaves, and the diameter and height of the trunks of mature specimens also are smaller in every respect. Reproductive plants range from nearly acaulescent to 1.5 m high, and this species is endemic to Panamá Province.
13. *Z. pseudomonticola* – this species is very similar to *Z. fairchildiana* (see below) and is distributed in far western Panama.
14. *Z. fairchildiana* – described by Luis Diego Gómez, the same author as *Z. pseudomonticola*, plants apparently are also found in Costa Rica and are somewhat similar in overall appearance to *Z. elegantissima*, but the pointed leaflets have a raised surface on the upper or adaxial side; the size and form of cones and the emergent leaves also differ. It is found in western to southwestern Panama.
15. *Z. lindleyi* – a shrubby to arborescent, narrow-leafleted plant in the high-altitude, humid forests of Chiriquí Province, northwestern Panama (Fig. 8D).
16. *Z. ipetiensis* – a small to medium-sized plant with branching underground stems and leaves to approximately 1 m tall (Fig. 8E). It is endemic to eastern Panama in one of the homelands of the Emberá tribal group. This is the only species in Panama in which the pollen cones in natural populations can number up to 13 on an individual plant.
17. *Z. manicata* – found only in Darién Province, it is the only Panamanian *Zamia* (and one of only two zamias, the other of which is in Peru) having a petiolule, or leaflet stalk, near the base of which is a small, gland-like protuberance (Fig. 8F-G).

## 4. Reproductive biology, sex ratio & herbivory in isthmian cycads

### 4.1 Reproductive biology

Most Panamanian cycads in natural populations, when coning, do so only once a year. Four months are required for cone maturation, 1-2 months for pollen dehiscence and receptivity,

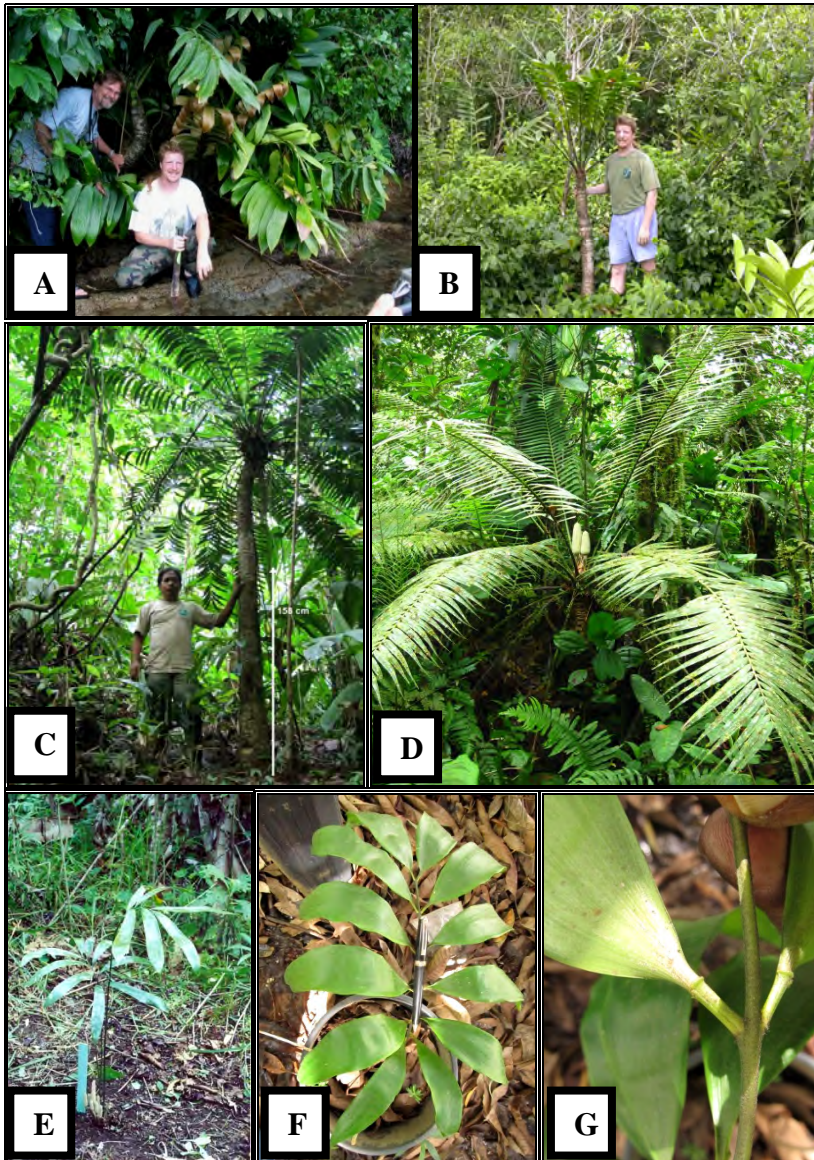


Fig. 8. Biodiversity of Panamanian cycads (cont'd.). A. *Zamia hamannii*, a species sometimes inundated by seawater; B. *Z. nesophila*, a species mostly growing on sand and sometimes inundated by seawater; C. *Z. elegantissima*; D. *Z. lindleyi*, a high mountain species, with two pollen cones; E. *Z. ipetiensis*, a species similar to *Z. cunaria* but which produces many more pollen cones per plant; F-G. *Z. manicata*, showing the petiolules and associated gland at the base of the leaflets.

and 1-2 years for seed ripening. There are exceptions (e.g., *Zamia acuminata* seeds ripen in about eight months after pollination), but this is the general rule for almost all of the populations studied. Outside the natural environment (gardens, landscapes, or isolation due to habitat destruction), coning can occur at any time and sometimes occurs many times during a year. We have not observed any stress-triggered reproduction—coning after disturbance as a do-or-die strategy—in Panamanian *Zamia* species, although examples of having mature cones many times a year in natural populations have been observed in *Z. nesophila* in the Bocas del Toro archipelago and in *Z. hamannii* somewhere far away in the same political jurisdiction. *Zamia nesophila* has been observed having dehiscent pollen cones and receptive ovulate cones three times during a given year and *Z. hamannii* twice.

The grandfather of cycad studies, Charles Joseph Chamberlain, thought that cycads were wind pollinated just like other gymnosperms, even knowing that insects were found in, upon, and about pollen cones at the time of pollination (Chamberlain, 1919; 1935), and that others (Pearson, 1906; Rattray, 1935) had, indeed, observed beetles on pollen cones and written about the possibility of insect pollination in the South African cycads *Encephalartos altensteinii* and *E. villosus*. Pollination by insects is now strongly supported for cycads as a group (Norstog & Nicholls, 1997; Wilson, 2002; Proches et al., 2009), and pollinators have been found for all populations studied on the Isthmus of Panama with the exception of *Zamia neurophyllidia*. Pollinators represent weevils that are morphologically similar to *Rhopalotria*, as well as the erotylid pleasing fungus beetle, *Pharaxonotha* (Fig. 9D). *Pharaxonotha* is always found in dehiscent pollen cones and is sometimes accompanied by *Rhopalotria*, suggesting that *Pharaxonotha* is the primary pollinator of isthmian zamias. The insects enter the pollen cones and ovulate cones guided by aromatic chemicals emitted by the cones (Stevenson et al., 1998; Taylor, 2002).

The exact form of pollination and the reward offered to pollinators have been variously discussed by others, and Terry et al. (2007) put forth an odor-mediated “push-pull” pollination mechanism in which the volatiles emitted by dehiscent pollen cones and receptive ovulate cones are increased at certain times in a diel cycle. When the dehiscent cone temperature becomes quite high above ambient, the pollinators are “pushed” out of the cone and move toward available receptive ovulate cones. When the temperature is reduced, the volatile concentration also declines, and the insects are once more “pulled” into the pollen cones. In a preliminary experiment accompanied by the senior author in 2006, Terry and Roemer (unpublished) observed only a slight increase in pollen cone temperature above ambient in an excised cone in the lab that was maintained in a water-absorbent material. The extremely rainy period and no available assistance and infrastructure to safeguard the instruments, however, made it impossible to undertake the field experiment; this will be taken up in the future. Suinyuy et al. (2012) have confirmed the relationship between volatile emissions and insect attraction to dehiscent pollen cones and receptive ovulate cones of *Encephalartos villosus* in South Africa. Thermogenesis exists, but the confirmation of the “push-pull mechanism” of Terry et al. (2007) still remains to be supported in other cycad species, including those of *Encephalartos*.

Another question to consider is the mutualistic reward offered to the plant by pollinator destruction of pollen cones, which, according to Marler (2010), is not only the conveying of pollen to receptive ovulate cones, but also a cryptic benefit of cone tissue disposal which translates into an increase in ultimate lifetime reproductive effort or events. In fact, any event, natural or accidental, that rapidly disposes of cycad cones in a given reproductive cycle will hasten the onset of the next reproductive cycle. This has been observed by the

senior author in at least one of the isthmic species (*Zamia* cf. *elegantissima*) in which the destruction of an almost mature ovulate cone by larvae of the lepidopteran *Eumaeus godarti* brought about the onset of a new reproductive cycle in a short time (about a year). When this does not happen, the reproductive cycle takes many years to be repeated in this species. A point should be made here that cone disposal by non-pollinating insects or natural destruction and abscission of pollen cones in isthmic cycads takes place even without the benefit of the pollinators, both in natural populations and in garden-grown plants.

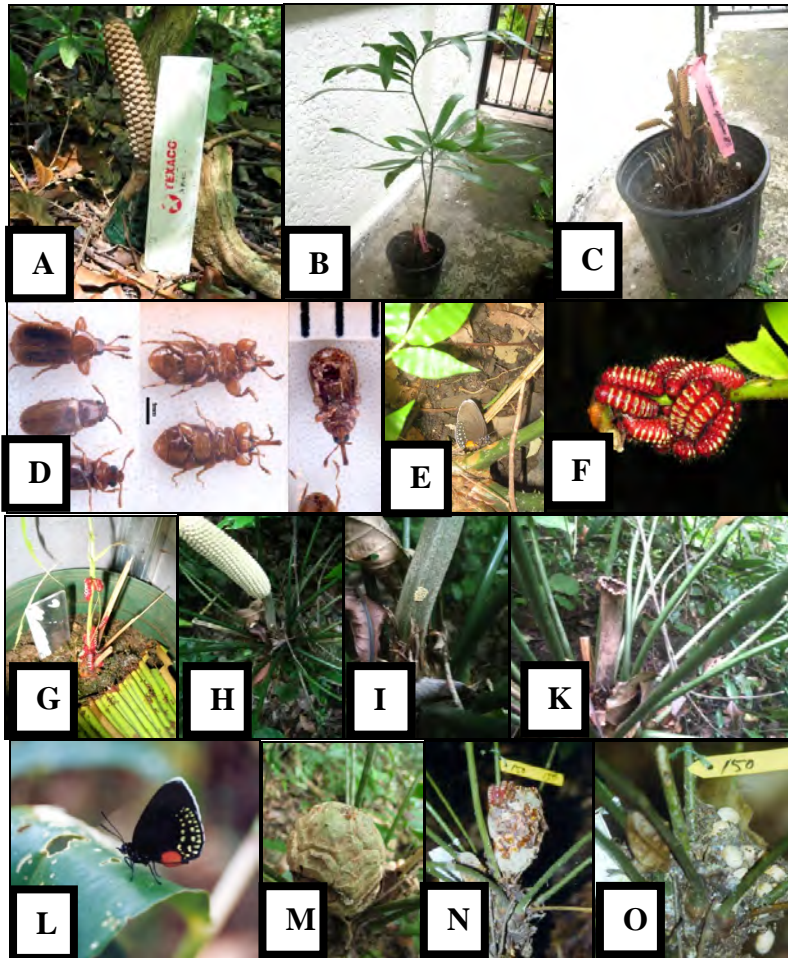


Fig. 9. Pollination and herbivory in Panamanian cycads. A. Pollen bait cone of *Zamia* cf. *elegantissima*; B. Small potted pollen plant of *Z. ipetiensis* used as bait; C. Pollen cones of B; D. Cycad pollinators: *Pharaxonotha* beetles (left middle and left bottom) and *Rhopalotria*-like weevils (center and right); E. *Eumaeus godarti* butterfly laying eggs; F. *E. godarti* larvae on *Z. lindleyi* leaf; G. *Zamia* germling destroyed by *E. godarti* larvae; H-K. Destruction of *Z. elegantissima* pollen cones by *E. godarti* larvae; L. *E. godarti* mature butterfly; M-O. Attacked seed cone of *Z. cf. elegantissima* with liberation of seeds (these seeds later germinated).

A method devised by the senior author known as the “pollen bait method” makes use of *ex situ* dehiscent pollen cones of the same or related species taken to a natural population, with the pollen cone peduncle in a water-absorbent material and held in an appropriate receptacle (Fig. 9A). Small potted plants with dehiscent pollen were also used (Fig. 9B-C). After two days, the bait cone is retrieved and, if it was effective (bait cones of the same species are always effective), pollinators (weevils and/or beetles) are captured even outside of the normal coning period for the species. This, of course, means that the pollinators in some form (perhaps as dormant pupae) are present in the populations and are always ready for a dehiscent or receptive cone. Because cones of different species have been effectively used as bait, it follows that some pollinators are either not species-specific or different cycad species emit the same or similar aromatic attractants. This interspecific attraction is not found in all isthmian species. Pollinators are found in large numbers throughout the Isthmus of Panama. However, because the same insect species sometimes pollinates different cycad species, and different pollinators can pollinate the same species, it appears to be relatively easy for isthmian cycads to extend their ranges. This probably explains the broad distribution of *Zamia obliqua* and *Z. pseudoparasitica* across the isthmus.

#### 4.2 Coning cycle & sex ratio

Timing of coning is different for the various species of *Zamia* in Panama; in most populations, individuals do not cone every year, or those that do generally represent a small percentage of the total population (Table 3). However, in the case of *Z. ipetiensis* and two populations of *Z. cunaria*, most individuals that appeared mature, judging from leaf size, bore cones. In populations of other species (e.g., *Z. cf. elegantissima*), most individuals observed in the population studied bore cones, but in one coning cycle (year 2000) most plants did not cone. One must consider that ovulate plants use more resources in cone building than pollen plants. While most species appear to have a nearly 1:1 sex ratio, the ratio may vary markedly from one coning cycle to the next. In the case of *Z. ipetiensis*, it is almost certain that there is a bias toward ovulate plants. Pollen plants, however, produce many more cones per plant (up to 13) than other species, and this apparently results in the population being quite vigorous, for there is always enough pollen during a coning cycle to account for the greater number of ovulate plants.

#### 4.3 Herbivory

*Eumaeus godarti* (Lepidoptera: Lycaenidae) (Figs. 9E & L) is the principal cycad herbivore in Panama, but only in a very small number of cases has it adversely affected the populations infested, and most plants recover rapidly after being attacked. The life cycle of the insect has been worked out by the senior author for isthmian populations. Even in cases in which the larvae of the butterfly eat most of the mature ovulate cone parenchyma, the seeds are left intact, and these germinate sooner than if the cone is left to disintegrate naturally (Fig. 9M-O). In this case, the herbivore can be considered an opportunistic semi-mutualist *Zamia* symbiont, at least part of the time (Taylor, 1999), and an aid to limited seed dispersal, especially if seed cleaning occurs on plants near natural embankments or cliffs.

Species & Year	Pop. Size (approx.)	Plants Observed	# Coning		% Coning	Sex Ratio (♀/♂)
			♀	♂		
<i>Z. acuminata</i> 1999-2002	>400	170	65	73	81.2	0.9
<i>Z. acuminata</i> 2002	>400	170	24	22	27.0	1.1
<i>Z. cunaria</i> 2007	>100	31	3	5	25.8	0.6
<i>Z. cunaria</i> 2007	>100	28	14	2	57.1	7.0
<i>Z. cunaria</i> 2008	>100	36	32	3	97.2	10.7
<i>Z. cf. elegantissima</i> 1998-2000	>100	60	3	14	28.3	0.2
<i>Z. cf. elegantissima</i> 1999	>300	223	9	17	11.7	0.5
<i>Z. cf. elegantissima</i> 1999-2001	>300	223	57	42	44.4	1.4
<i>Z. cf. elegantissima</i> 2000-2001	>700	362	32*	61**	25.7	0.52
<i>Z. cf. elegantissima</i> 1999-2001	>700	362	90	110	55.2	0.8
<i>Z. ipetiensis</i> 1999-2001	>300	150	75	29	69.3	2.6
<i>Z. ipetiensis</i> 2000	>300	55	33	21	98.2	1.6

Table 3. Coning events in Panamanian cycads during different coning cycles. (\* Plants that had coned the year before were still bearing old cones [19]; \*\* some of these [24] had also coned the year before).

## 5. Dispersal of isthmian cycads

Cycad seeds are formed by two layers: an outer pulpy layer known as the sarcotesta – which harbors toxins in some cycads and is attractive to many biotic dispersers (Fig.10A-B) – and an inner hard layer known as the sclerotesta (Fig. 10C). Cycad seeds range from relatively large to relatively small, according to species (Fig. 10), varying in isthmian species from 2.8-3.0 cm long and 1.6-1.8 cm wide in *Zamia elegantissima* (on the large side), to 1-1.5 cm long and 0.5-0.8 cm wide in *Z. manicata* (medium-sized), down to 1.6-1.9 cm long and 0.4-0.5 cm wide in *Z. acuminata* (the smallest). Most cycad seeds require an after-ripening period, after seed cone disarticulation, to germinate. This period can range from a few weeks, as in most *Zamia* species – including those from Panama – to more than a year, as in some *Encephalartos* species in South Africa. In a year-long experiment at the University of Panama (unpublished), the germination rates for *Z. cf. elegantissima*, *Z. acuminata*, and *Z. ipetiensis* seeds decreased during the year, and germination was negligible after that.



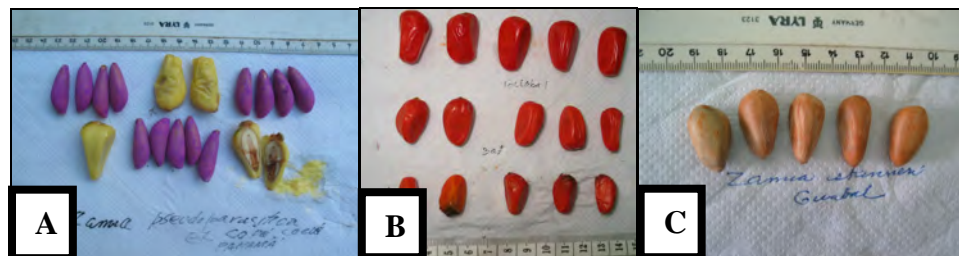


Fig. 10. Isthmian cycad seeds. A. *Zamia pseudoparasitica* with yellow sarcotesta (violet color is due to antifungal solution on the sclerotesta); B. *Z. imperialis* (above) and *Z. nesophila* (below) with red sarcotesta; C. *Z. imperialis*, showing the stony sclerotesta.

Palatability of the sarcotesta is known for many cycad species (Norstog & Nicholls, 1997; Jones, 2002), and this should also stand for isthmian species such as *Zamia pseudoparasitica*, the sarcotesta of which exudes a gummy substance when ripe (Fig.10A). The sarcotesta of all isthmian species is red, except for that of *Z. pseudoparasitica*, which is yellow. It generally becomes soft and quite pulpy during after-ripening. At the moment, there are no known long-distance dispersal agents for any cycad species in Panama, except gravity when seeds fall near cliff sides or on the sides of steep hills. Ants and other insects and also crabs have been seen moving seeds over short distances. Perhaps the animals that dispersed seeds no longer exist, or perhaps there has just not been enough monitoring time or effort put into studying and discovering the dispersers. In the case of *Z. pseudoparasitica*, bats and toucans have been reported by a few of our field supporters in western Panama to transport seeds, but definitive proof is still needed. Two of us have seen the toucans flying in the area where the species is growing, and there are bats in the area and lots of anecdotal statements, but no real proof—although the seeds have been seen germinating on the branches of different trees not containing cycads, and the most likely dispersers would be birds, bats, or mammals. Traps with mature seeds were set in preliminary trials and will be repeated, because of both negative results and the field observance of the senior author and one of his field assistants of the overnight consumption of one third of a mature *Z. pseudoparasitica* cone in north-central Panama in an area with toucans and bats.

Janzen (1981a; 1981b), in his seminal studies of the *guanacaste* tree in neighboring Costa Rica (*Enterolobium cyclocarpum*: Mimosoideae), hypothesized that equids the size of contemporary Costa Rican range horses were present in Costa Rica in the late Pleistocene. Removed by evolutionary forces for about  $10^6$  years, they were again introduced as modern horses (*Equus caballus*) by the Spaniards after the European colonization of the Americas. Examples of these horses are Costa Rican free ranging horses that eat and then excrete the *guanacaste* (also known as Corotu or curutu in Panama) seeds in their dung, with most of these germinating later. The equids, then, are the ideal dispersers of the tree, although they were absent for so many thousand years. Other approaches to this problem of apparent missing dispersers (Hunter, 1989) consider that no animal interaction is necessary to explain the spread and germination of *E. cyclocarpum* seed, and that hydrochory (dissemination by water) is suggested as the preferred dispersal strategy. In the case of cycad seeds, their toxicity and knowing that almost all with viable embryos sink in water, hydrochory (except in known cases of a few *Cycas* species, such as *C. litoralis*, *C. micronesica*, and *C. rumphii*) is ruled out in most cases, and dispersal by animals

has been reported as actually being observed in many cycads in Africa, Southeast Asia, and Australia, but very little information has been given for American cycads (Jones, 2002).

There are anecdotal reports of human consumption of cycad seeds in the aboriginal region of eastern Panama (Taylor, 2012), and there is a first report of the pre-Columbian use of *Zamia* starch grains on cutting utensils in an unknown aboriginal group in western Panama during preceramic times (Dickau, 2007). But in none of these cases is there irrefutable evidence of human beings as actual dispersers of the species. At present, the aboriginal groups that make use of these plants usually take the parts needed from the wild. In eastern Panama, however, we have seen a few plants that have been sown around the Embera village, but still near the original natural population of *Z. ipetiensis*.

## 6. “Island” biogeography & isthmian cycads

As mentioned above, the immigration of cycads from North and South America into the newly forming isthmus and subsequent speciation events—which have occurred from late Pliocene to recent geologic time—account for most of the cycad species on the isthmus based on congruence of observed patterns of phylogenetic relationships combined with the current geographical distribution of species (Caputo et al., 2004). Conversely, the plicate-leaved zamias of northwestern Panama—specifically those in the Bocas del Toro region—may have originated on an ecological time scale, and the current distribution of this unique assemblage may best be explained by a modification of the “dynamic habitat” hypothesis of Gregory and Chemnick (2004), which states that *Dioon* populations in Mexico migrated up and down in elevation, and north and south, in response to warming and cooling climatic cycles corresponding to glaciation events (see Taylor et al., 2008).

### 6.1 The plicate-leaved zamias & their distributions

The plicate-leaved zamias are distributed from western Central America into northern South America. There is evidence that leaflet “plication” evolved independently within the genus, and that the South American plicate-leaved taxa (e.g., *Zamia roezlii* and *Z. wallisii*) are phylogenetically unrelated to those in Central America (Caputo et al., 2004). The Central American representatives are largely restricted to the Atlantic slope of the continental divide and include *Z. dressleri*, *Z. hamannii*, *Z. imperialis*, *Z. nesophila*, *Z. neurophyllidia*, and *Z. skinneri* in Panama (the latter two may also occur in coastal southeastern and south-central Costa Rica, respectively), as well as one or more undescribed species in Costa Rica and southern Nicaragua. All of the named species, except *Z. dressleri*, occur in the Bocas del Toro region, with at least three of these species—*Z. hamannii*, *Z. imperialis*, and *Z. nesophila*—being Panamanian endemics (Taylor et al., 2008).

### 6.2 Evolutionary hypothesis

The Bocas del Toro region of northwestern Panama was a site of intense volcanic activity from about 20 mya to less than 2.8 mya when the final closure of the isthmus took place (Coates et al., 2005; Fig. 11). During this period, there was ample time for the immigration of plant and animal species from the northern and southern continents into the isthmus. Sea level rise and continental submergence over the past few thousand years have created numerous islands and peninsulas in the Bocas del Toro region (Anderson & Handley, 2002)

and have resulted in marked morphological differentiation in insular mammals (Anderson & Handley, 2001; 2002) and plants (Taylor et al., 2008) compared to their mainland counterparts. Surprisingly, the processes that have led to this striking level of divergence may have occurred in as little as 5,000-10,000 years, according to recent estimates of the ages of the islands in this region (Anderson & Handley, 2002).

Taylor et al. (2008) hypothesized an explanation for the biogeographical and evolutionary patterns of the plicate-leaved zamias of northwestern Panama in their “dynamic habitat” hypothesis, which is similar to that proposed by Gregory and Chemnick (2004) for the Mexican species of *Dioon*. In Mexico, movement to higher elevations during inter-glacial periods resulted in colonization of new river valleys by *Dioon*, followed by secondary isolation within and between river drainages and subsequent rapid vicariance of the majority of extant species. During ice age phases, however, populations are forced downslope and southward, possibly resulting in genetic remixing. These processes have, then, been repeated numerous times over the past two million years (Gregory & Chemnick, 2004).

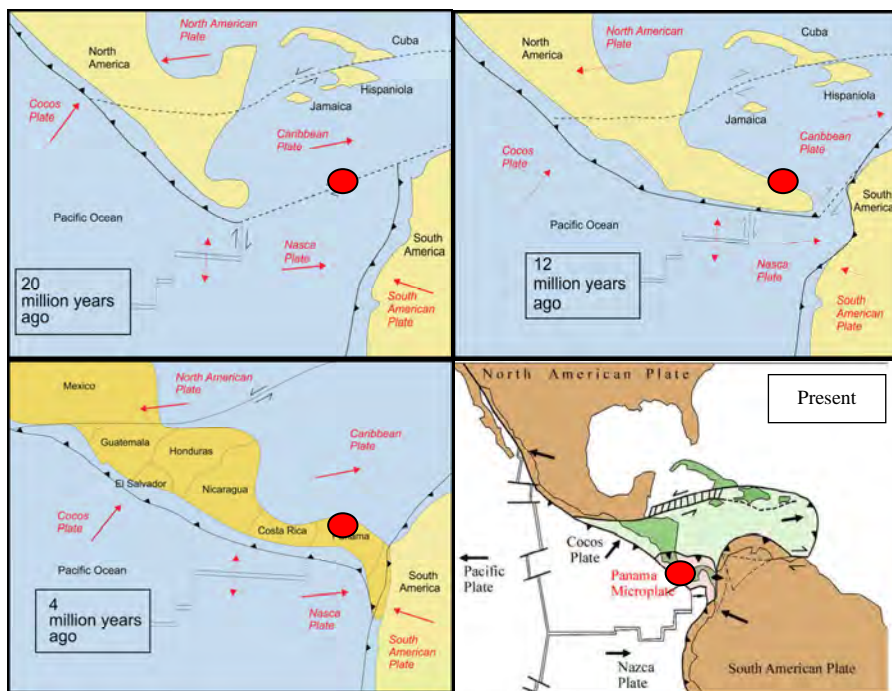


Fig. 11. Timeline of formation of the Isthmus of Panama. Maps kindly donated by Dr. Anthony Coates of the Smithsonian Tropical Research Institute (STRI) in Panama City. (The red dot indicates the approximate location of the Bocas del Toro region of Panama.)

The primary difference between Gregory and Chemnick’s (2004) hypothesis and that proposed by Taylor et al. (2008) for the plicate-leaved zamias of Bocas del Toro is that, rather than (or in addition to) temperature fluctuations being the primary driving factor, the current distribution of taxa is primarily due to the periodic rise and fall of sea levels that accompanied the dramatic

Pleistocene changes in climate. Higher sea levels during warmer inter-glacial periods created geographical barriers that isolated cycad populations and allowed them to evolve independently, whereas lowered sea levels during the periodic ice ages allowed for renewed genetic interchange and introgression as populations merged back together into newly exposed land areas. This sea-level change cycle has been repeated several times, following each ice age, resulting in relatively brief but intense periods of isolation.

Following this logic, isolation onto separate islands combined with unique environmental pressures associated with an insular existence likely contributed to allopatric speciation of *Zamia hamannii* and *Z. nesophila* from their mainland counterparts, possibly over just the past 5,000-10,000 years. Similar evolutionary processes likely played a role in the vicariance of *Z. imperialis* and *Z. neurophyllidia*, except that instead of being restricted to different islands, the propensity of these latter species to grow inland away from the coast was likely an important factor in maintaining their isolation from populations nearer the coast, thus allowing for their independent evolutionary pathways (Taylor et al., 2008). Because the isolation processes have occurred several times in the past million years, genetic evidence will be needed to distinguish the most recent event from previous sea-level increases.

As Taylor et al. (2008) suggested, *Zamia skinneri* is unique within this species complex with regard to its biogeographical and evolutionary patterns because it is widespread throughout coastal mainland Bocas del Toro Province (and possibly into southeastern Costa Rica) and because it exhibits surprisingly high levels of phenotypic variation within and among populations, thereby suggesting that the entire coastal region of northwestern Panama represents a zone of repeated, episodic convergence/hybridization events resulting from regular cycles of rising and falling sea levels. If so, this area represents an extremely important genetic refuge for the plicate-leaved zamias of northwestern Panama.

The plicate-leaved zamias of Bocas del Toro are members of a convoluted, actively evolving species complex that has undergone numerous cycles of geographic isolation and admixture/introgression during inter-glacial periods and ice ages, respectively (Schutzman, 2004; Taylor et al., 2008). The coastal mainland region, which is home to *Zamia skinneri*, represents the center of diversity of this complex, and *Z. hamannii*, *Z. imperialis*, *Z. nesophila*, and *Z. neurophyllidia* are incipient species that have evolved allopatrically on the periphery as a result of geographic isolation (in the case of *Z. hamanni* and *Z. nesophila*) and/or other as yet unknown abiotic and/or biotic factors (in the case of *Z. imperialis* and *Z. neurophyllidia*) perhaps during the current inter-glacial period (Taylor et al., 2012). As such, the 'Skinneri Complex' represents another example (in addition to the Mexican species of *Dioon*) of rapid evolution in this ancient plant group, effectively countering the assumption of gradual divergence of taxa over evolutionary time that is often ascribed to such long-living organisms.

## 7. Phylogeny of isthmian cycads

All of the described species of isthmian cycads have acquired species status by the usual method of Adansonian discrimination, based on overall similarity of morphologic characteristics considered important. However, newer methods in phylogenetics that combine morphology and molecular data are opening new avenues for understanding speciation in cycads. Morphological and morphometric character sets in cycad identification and systematics should be used with caution, however, because under *ex situ* conditions (gardens, homes, landscapes), modification of those characters can cause confusion if not

taken into account and clarified. Conversely, data from morphology and morphometrics, combined with a molecular approach and analyzed using cladistic methods, can define monophyletic groups (clades) of taxa (Schuh and Brower, 2009; Wiley and Lieberman, 2011).

Within the Zamiaceae, *Zamia* Linnaeus, with 71 currently recognized species (Osborne et al., 2012) distributed from southeastern USA through Central America and the Caribbean to Brazil, is the least-studied genus in terms of phylogenetics. However, there are two previous studies on the phylogeny of *Zamia* (Caputo et al., 1996; 2004), with the latter using a data matrix that combined molecular data with morphological data. Caputo et al. (2004) demonstrated that *Zamia* is divided into four major clades, which are also supported by geography (Fig. 12). The backbone of the consensus tree was composed of various species found in Mega-Mexico (see Nicolade-Morejon et al. [2009] for a thorough discussion of *Zamia* in Mega-Mexico) and is herein referred to as the Mega-Mexico Grade (Fig. 12). While the pattern of phylogenetic relationships uncovered by Caputo et al. (2004) was broadly congruent with geographical distribution, it was not so with morphological resemblance within the genus. An example of the latter is the independent evolution of leaflet “plication” within the genus, as mentioned above and discussed again below.

The current phylogenetic research on *Zamia* has expanded the sampling of species by 30%, from 23 species in the Caputo et al. (2004) paper to 36 species in this paper. All data were obtained and analyzed exactly as in Caputo et al. (2004), and the results produced one fully resolved tree whose topology has remained the same as the consensus tree of Caputo et al. (2004), including the nesting of *Chigua* within *Zamia* (Fig. 12). Not too surprisingly, Lindström (2009) recently synonymized *Chigua* with *Zamia*. The phylogenetic and biogeographic implications of this expanded study led to some surprising conclusions as summarized below.

The results of this investigation offer new insights into the phylogeny of *Zamia* and provide fertile ground for further testing the addition of new species. One of the most surprising results is the relationship of the Panamanian endemic *Z. ipetiensis* in the Panama Clade with the Colombian endemic *Z. wallisii* in the South American Clade. These two species show little or no resemblance to each other, other than belonging to the same genus. However, given that *Z. manicata* is found only in Colombia and the Darién region of Panama—and as such represents a South American element in Colombia—the same may well be true for *Z. ipetiensis*, which, along with *Z. cunaria*, may represent a relic. This issue should be more rigorously tested by inclusion of the latter in future studies.

Within the Panama Clade (the “*pseudoparasitica* clade” of Caputo et al. [2004]), there is a subclade of plicate-leaved zamias, consisting of *Z. dressleri*, *Z. neurophyllidia*, and *Z. skinneri*, with *Z. obliqua* (without plicate leaflets) nested inside. Interestingly, *Z. obliqua* was taken by Caputo et al. (2004) to be an exception in their inclusive clade of Central American taxa because its distribution was then thought to be extreme eastern Panama to the southern Chocó of Colombia; however, the known range of this species actually extends to at least west-central Panama. As mentioned previously, the presence of plicate leaflets has clearly evolved at least twice within *Zamia*, and the relationship of plicate leaflets to habitat and other factors is enigmatic, as is the apparent loss of leaflet plication in *Z. obliqua*.

The distribution of *Zamia obliqua* also warrants further field work, with more samples taken across its range included in phylogenetic studies. *Zamia obliqua* has a disjunct distribution from central Panama to the Darién and adjacent Chóco of Colombia and then to Cabo Corrientes, Colombia. At issue here is whether or not *Z. obliqua* represents a disjunct

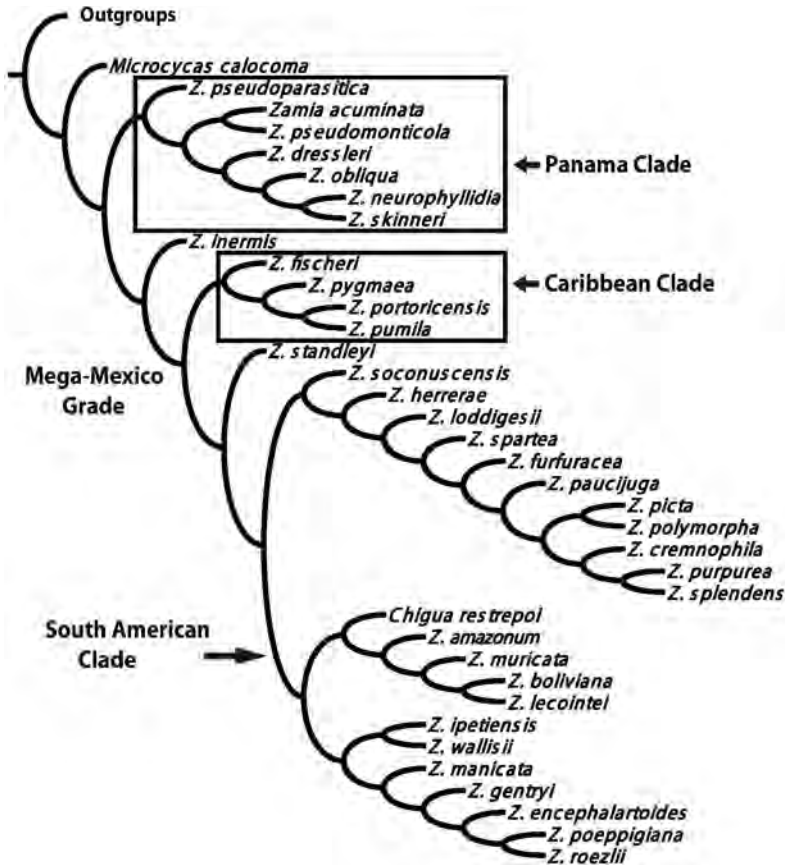


Fig. 12. Resolved tree of the genus *Zamia* using molecular and morphological data (Caputo et al., 2004; current paper): 1. Caribbean Clade, with the Mexican *Z. fischeri* as its sister species; 2. South American Clade; 3. Panama Clade; and 4. Mega-Mexico grade.

distribution of a single species or the existence of more than one related species. Regardless if it is one species or a clade of sister species, it appears that *Z. obliqua* is a Panamanian taxon that also occurs in Colombia. If, however, *Z. obliqua* represents two species in different clades (i.e., one in the Panama Clade and one in the South America Clade), then the common morphology of plants in the various disjunct localities must have evolved independently in response to similar environmental pressures.

Another interesting disjunct distributional pattern is that of *Zamia chigua* and *Z. lindleyi*. These two species are currently recognized as distinct taxa (Osborne et al., 2012) but have been considered conspecific in previous treatments of *Zamia* for Panama (Stevenson, 1993) and for Colombia (Stevenson, 2001). However, recent work has shown that these do, indeed, represent two distinct species based on morphological features of leaves, cones, and spines (Calonje et al., 2011). These two entities are strikingly disjunct, with *Z. chigua* known only from the Cabo Corrientes area of the Chóco region of Colombia, and *Z. lindleyi* known only from a small area of Chiriquí Province in northwestern Panama. Given that these two

species are obviously very similar morphologically, the question arises whether they are sister species or are each related to species in other clades. Regardless, the ecology and biology of these organisms must be better known to understand why they are so widely disjunct but yet currently so restricted in range.

Some striking aspects concerning the distribution of *Zamia* in Central America, excluding Mega-Mexico, is the high endemism and morphological diversity in western Panama and adjoining Costa Rica. The Panama Clade contains one of the smallest *Zamia* species known (*Z. acuminata*), the only epiphytic cycad (*Z. pseudoparasitica*), and the majority of the largest trunking species in the genus (*Z. hamannii*, *Z. nesophila*, *Z. obliqua*, and *Z. skinneri*). Habitats also vary greatly, ranging from high-level cloud forest to sea-level island beaches. The recent elucidation of the variability within the previously described *Z. neurophyllidia* and *Z. skinneri* resulted in the recognition of three new distinct species, *Z. hamannii*, *Z. imperialis*, and *Z. nesophila*, all of which are plicate-leaved (Taylor et al., 2008). These discoveries await detailed phylogenetic and ecological analyses, but clearly show adaptations to varied conditions. In contrast to the other plicate-leaved species in Panama that occur primarily in montane forests, *Z. nesophila* and *Z. hamannii* are island-dwellers that are exposed to, and often inundated by, seawater. Interestingly, *Z. roezlii*, which is endemic to the Buenaventura area of the Chóco, Colombia, also has plicate leaves and can live in mangrove swamps.

Finally, it should be noted that *Zamia acuminata* needs to be better defined, because the originally described species grows along the San Juan River in Nicaragua, and is reportedly morphologically dissimilar to the plants bearing the same (misapplied) name in Panama (Schutzman, 2004; Lindström, pers. comm.).

## 8. Conservation efforts & isthmian cycads

Cycads in Panama face an ongoing condition of destruction and illegal extraction in almost all natural populations visited. Populations near newly opened highways are readily disposed of, either because the people working nearby do not know the academic or commercial value of the plants or because they become readily available to poachers. On many occasions a few colleagues have addressed the issue, and an international conference on cycad biology took place in Panama City in 2008, in which all delegates signed a public petition for the government of Panama through the auspices of the University of Panama to take under its responsibilities the extension of cycad biology works and conservation and to make the public aware of the problem at issue. However, outside the support of the university for the senior author's basic research on isthmian cycad biology and conservation as a full time research faculty, including minimal support for a fledging *ex situ* cycad garden, very little has been done to insure the health of cycad populations throughout the isthmus. Furthermore, basic funding for cycad research is lacking.

### 8.1 Conservation status of natural forests & cycad survival

The Isthmus of Panama has a natural forest surface of approximately 3 million ha (44% of the land surface), although conditions of climate and soil are adequate for almost all the available land surface to be forested. The loss of forest surface is associated with anthropogenic activities occurring at different times, and deforestation of natural vegetation is a threat to the survival of isthmian cycads because they are almost all understory species. The history of the isthmus shows that deforestation began with the first human settlements, approximately 7 kya (Cooke,

2003). Since then, destruction of the forests has been continual, with periods of lesser activities. More recently, although the rate of deforestation has been reduced, there is still pressure to use forest land for different types of human activities, such as the establishment of human centers and for the production of foodstuffs. To face this threat of losing natural forests and their biodiversity, a National System of Protected Areas (SINAP for the Spanish acronym for Sistema Nacional de Áreas Protegidas) has been established, which covers 36% of the land mass of the isthmus. Although there are efforts to preserve forests, the habitat of cycads, there are still natural populations of cycads outside of protected areas. In certain cases, forests outside protected areas still have large populations of cycads, such as *Zamia pseudoparasitica*, which survives primarily on very high branches of trees in Veraguas, Coclé, and Colón provinces of north-central Panama. Because of this, it is vital to conduct research that points to forests with extant cycad populations for these forests to be included in SINAP.

## 8.2 Local conservation initiatives

The best approach for cycad conservation in Panama is to meet with local people and to form a team, with communication between researchers and locals at fixed intervals. Donating cell phones, in certain areas, and even small digital cameras, can help volunteers locate and relay situations in the field to a center with better infrastructure. At all times, Panamanian National Environmental Authority (ANAM) personnel should be kept abreast of what is being done. Thousands of plants and many populations have been destroyed for road building, creation of pastures for cattle grazing, or just because the plants had no immediate use for the community. ANAM states that there is no money to save cycads. This being the case, the job is left to academic institutions and the private sector. As a result, all of the Panamanian species should have at least the following Red List category rating: Critically Endangered (CR B1, I, iii-v) (IUCN, 2001). Land owners in most provinces with cycads have been approached, and the discussion of conservation has been positive. However, the problem remains quite unsettled (see also Taylor et al., 2007). In fact, many populations that were quite healthy and with sizeable numbers of individuals, are now down to few and scattered plants, and even places in which the owners had given hope of conservation have not been left unscathed, basically because new roads have been opened during the intervening years and new settlements have been made. Populations in northwestern Panama along river embankments are at the moment safe because of the difficulty of getting to those places and the very aggressive attitude of aboriginals in their homelands to defend their environment. Alas, even here, at present, there is danger of deforestation due to the construction of dams and the human use of the surrounding land in which the cycad populations survive.

## 9. Conclusion

Cycads arrived from both South and North America into the Isthmus of Panama, and new species evolved there, the original progenitors having existed globally for over 300 million years and predating the breakup of Pangaea. Today's extant cycads occupy mainly tropical and subtropical regions of the world. Panama supports at least 17 species, making the isthmus a cycad biodiversity hotspot because there are more representatives per unit land mass than in any other region of the neotropics.

Endemism has been the rule, with most cycads in the Isthmus of Panama forming relatively small, endemic populations, and with most populations numbering only a few hundred individuals. Morphological diversity is rampant within the Panamanian cycad flora—from



those with underground stems to those with huge trunks and a wide range of other divergent characters, such as cone morphology and morphometrics, and leaf type and number. We still cannot answer the question of why cycads have survived so long with relatively similar vegetative and reproductive structures of millions of years ago, but it could be linked to their individual longevity, production of toxic substances, and absence of herbivores as a result of those substances. Cycad survival is challenged by human alteration of habitat, including clearing of forests and converting “cycad land” to roads, development, and cattle ranching, as well as illegal removal of plants for black market sale, which is taking many rare species to the brink of extinction.

We describe cycad distribution and evolution in relation to the origin of the Isthmus of Panama and the Great American Biodiversity Interchange, which was completed beginning about 3 mya (although there were temporary closings and openings of the seaway for millions of years before definite closure), and during which period cycads likely made their way from both the north and the south towards the isthmus. We also summarize our hypothesis for the current biogeography and ongoing evolution of the plicate-leaved ‘Skinneri Complex’ in northwestern and north-central Panama.

A complete phylogeny is still lacking for the genus *Zamia*, but what is known provides insight and testable hypotheses into how the genetic makeup of this genus relates to geologic changes and the present-day geographic distribution of the member species. Future work with more species examined and using other genome sets and/or molecular markers will provide a better understanding of this problem, and more species surveys and descriptions are needed to address the question of synonymy of many entities, with *Z. cunaria* vs. *Z. ipetiensis* and *Z. acuminata* in Panama vs. *Z. acuminata* from Central America being noteworthy examples. More work is also needed in the ‘Skinneri Complex’, and the arduous work already conducted (Taylor et al., 2008) should be addressed when speaking of *Z. skinneri* in a general way.

The study of cycad pollination biology in Panama is under way, and the genera (or similar/related genera) of some insect pollinators have been determined. This ongoing work includes a phylogeny of the pollinators as well as descriptions of putative new species. Also, new work will soon begin on heat production in *Zamia* cones and the volatile emissions that are associated with pollinator activity.

Last but not least, we address the problem of disappearing forests and the clearing of natural populations of *Zamia* on the isthmus. A great fear is that populations not yet studied will disappear in the immediate future, due to the clearing of land for human use and the inability of the understaffed and inadequate organization of the Natural Environmental Authority of Panama. In this respect, just trying to save what is left of these populations is a great challenge.

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Dr. Larry Stevens is the Curator of Ecology and Conservation at the Museum of Northern Arizona in Flagstaff. He is an evolutionary ecologist and a leading authority on the biology of the Grand Canyon region. He formerly served as the Park Ecologist for Grand Canyon National Park, and in addition to his curatorial post he presently also serves as Senior Ecologist for Grand Canyon Wildlands Council, Inc., a non-governmental conservation organization. Stevens has worked on a wide array of scientific topics over his career, including biogeography, regulated river ecology, endangered species biology, and most recently the ecology and stewardship of springs. He has authored or coauthored several books and numerous scientific and popular articles on topics, recently ranging from robberfly taxonomy, waterbug biogeography, peregrine falcon foraging behavior, river and dam management, springs ecosystem ecology, and whitewater river running. His primary scientific interests focus on assemblage responses to landscape development and environmental change over time.

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