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A Review of Current Knowledge of Zamiaceae, With Emphasis on *Zamia* From South America

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Abstract

Zamiaceae, a family of the ancient order Cycadales, is distributed throughout the tropical and subtropical regions of both the Old and New Worlds. Here, we present a systematic review of Zamiaceae with emphasis on *Zamia* species from South America. We aim to (a) establish the current knowledge, (b) identify research gaps, and (c) indicate directions for future studies, discussing ecology and conservation of South America species. The search recovered 508 papers, further classified into 11 research topics: taxonomy and systematics, morphology, biochemistry, genetics, phylogeography, population ecology, reproductive biology, ecological interactions, plant propagation, conservation, and reviews. The number of publications doubled in the 21st century, mostly focusing on genetics ($n = 60$), taxonomy and systematics ($n = 52$), morphology ($n = 36$), ecological interactions ($n = 30$), and an increasing interest in population ecology ($n = 29$) and conservation ($n = 32$). Studies are concentrated in North and Central America (54% of all studies) with just 6% (29) addressing South America species of *Zamia*. Overall, studies point out the key role of pollinators in promoting gene flow through pollen dispersal among populations of Zamiaceae. Therefore, investigate natural history, ecology, reproductive biology, genetic, and phylogeography, especially for South America species, are needed. Moreover, the implementation of in situ and ex situ collections and germplasm banks linked to botanical gardens are essential for the conservation and reestablishment of local populations of critically endangered *Zamia* species in South America. Concomitantly, we suggest studies modeling the distribution of *Zamia* species in future climate change scenarios.

Keywords

reproductive system, ecological interactions, cycad conservation, seed dispersal, phylogeography

Introduction

The family Zamiaceae, together with Cycadaceae and Stangeriaceae, form a monophyletic group belonging to the order Cycadales, an ancient lineage of vascular plants (Donaldson, Dehgan, Vovides, & Tang, 2003; Grobbelaar, 2002; Norstog & Nicholls, 1997; Walters, Osborne, & Decker, 2004). Even though Cycadales occupies a key phylogenetic position among current terrestrial plants, exhibiting characteristics that transition between seedless vascular plants and more derived seed plants, ecological and reproductive aspects of Zamiaceae species are still underexplored (Krieg, Watkins, Chambers, & Husby, 2017), especially in the genus *Zamia* from South America. Understanding of *Zamia* evolution, including the evolution of reproductive strategies and mutualistic interactions (Tang, Xu, et al., 2018; Vovides, 2000), are fundamental for their conservation.

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Zamiaceae is composed of seven genera and 235 species, according to the cladistic analysis of Stevenson (1990) and formal classification of Stevenson (1992): *Ceratozamia* Brongniart (31), *Dioon* Lindley (16), *Encephalartos* Lehmann (65), *Lepidozamia* Regel (2), *Macrozamia* Miquel (41), *Microcycas* (Miq.) A. DC. (1), and *Zamia* L. (80) (Calonje, Stevenson, & Osborne, 2019), which are distributed throughout Africa, the Americas, Australia, and the Greater Antilles (Donaldson et al., 2003; Stevenson, 2004a; Taylor, Haynes, Stevenson, Holzman, & Mendieta, 2012; Walters et al., 2004). In the Americas, Zamiaceae species occur from sea level to an altitude of 2,500 m, in well-drained calcareous soils and different types of habitat, such as tropical forests, savannas, dunes, swamps, and deserts (Lopez-Gallego, 2015; Stevenson, 2004a; Whitelock, 2002). The greatest species diversity is found in the genera *Ceratozamia*, *Dioon*, and *Zamia*, all endemic to the New World (Lopez-Gallego, 2015; Stevenson et al., 2003; Stevenson, 2004a; Taylor et al., 2012; Walters et al., 2004). From those, *Zamia* is considered the most diverse genus of the extant cycads in terms of ecology and morphology (Calonje, Stevenson, et al., 2019; Norstog & Nicholls, 1997). Many *Zamia* populations suffer from habitat loss and often occur in disjunct, small populations (Calonje, Meerow, et al., 2019; Mankga & Yessoufou, 2017; Stevenson, 1993; Walters et al., 2004).

Information regarding *Zamia* populations (structure, dynamics, interactions, etc.) is scarce and one of the explanations is the difficult access to populations, given their remote distribution, hindering research and species conservation actions, even though many are endangered and occur outside protected areas (Calonje, Stevenson, et al., 2019; Donaldson, 2003; Lopez-Gallego, 2015; Mankga & Yessoufou, 2017; Stevenson et al., 2003). Most of the areas where *Zamia* species occur in South America are also considered biodiversity hot spots (Stevenson et al., 2003). In this revision, we aimed to gather information regarding the Zamiaceae family based on a systematic survey of studies from different databases. We focused mainly on the ecology and reproductive biology of *Zamia*, especially the species from South America. We aim to (a) establish the current knowledge, (b) identify research gaps, and (c) indicate directions for future studies, emphasizing the ecology and conservation of the understudied South America species of *Zamia*, within the framework of the literature review of Zamiaceae.

Review Method

We searched through the databases of Web of Science and Google Scholar using the term *Zamia** to compile studies on Zamiaceae and *Zamia* up to June 2018. We also searched The Cycad Society, The World List of Cycads, and the International Union for Conservation of Nature using the same term. Indexed publications (DOI, ISSN, and ISBN) as well as those relevant classical papers and monographs not indexed (listed in Files in Data Supplement—FDS) were included in this review. Unpublished data were only included if from the authors of this review. After compilation, we conducted a systematic classification of the studies, summarizing the most important themes pointed out in each paper reviewed, resulting in 11 research topics: taxonomy and systematics, morphology, biochemical (biochemical composition), genetics, phylogeography, population ecology, reproductive biology, ecological interactions (mutualism and antagonism), plant propagation, conservation, and reviews. After classification, for each study, we extracted the following information: year of publication, geographic region (main region or local distribution area), species under study, and if applicable, the interaction type (mutualism/antagonism/other), and interacting agent (name of the interacting species). All studies surveyed and additional information can be found in FDS.

Considering the small number of publications in South America (FDS) and in order to show the current distribution of *Zamia* in this region throughout different vegetation types, according to the classification of Olson et al. (2001), we created a distribution map of *Zamia* species using the data available at the Global Biodiversity Information Facility (2019), SpeciesLink (2018), and publications presenting geographic coordinates or indications of localities of the species (Segalla & Calonje, 2019). Olson's classification was extracted from http://www.worldwildlife.org/publications/ terrestrial-ecoregions-of-the-world) and the manipulation of geospatial data was done using QGIS (http//qgis.osgeo.org). To identify the knowledge gaps and guide future efforts, we also compiled information of *Zamia* species of South America, including their conservation status according to the International Union for Conservation of Nature (IUCN; Calonje, Stevenson, et al., 2019 in World List of Cycads—http://www.cycadlist.org, 2013–2019, and Red List of Threatened Species—IUCN 2010–2019 in https://www.iucnredlist.org), and possible causes for population decline.

The Knowledge of Zamiaceae Over Time, Research Topic, Species, and Continents

We reviewed 508 studies that addressed Zamiaceae according to our review criteria (FDS). The first study dates from 1897 (Webber, 1897), describing the pollen tube dynamics of *Zamia integrifolia* L.f. (Webber, 1897). This study was followed by sparse publications until the 1980s, totaling 34 papers, mostly related to the morphology ($n = 12$), propagation ($n = 5$) and biochemistry

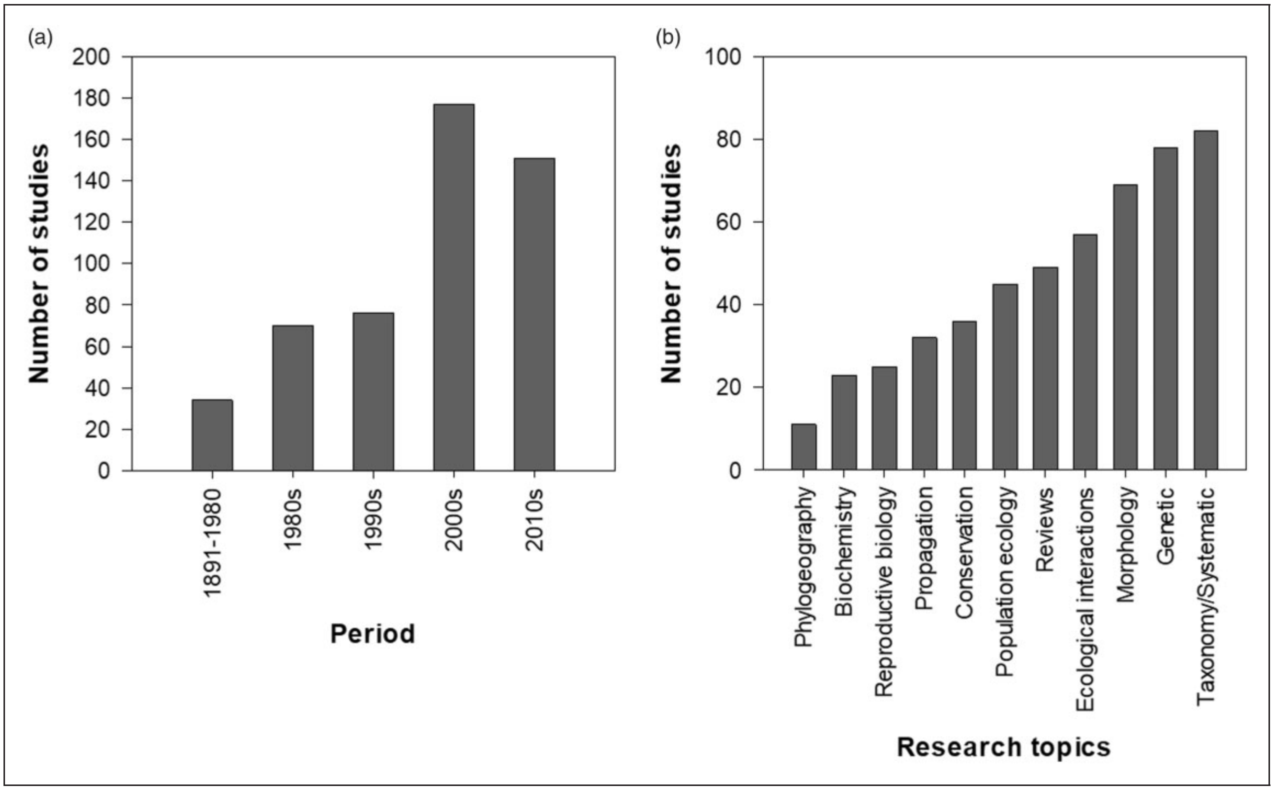

Figure 1. Summary of Zamiaceae review. (a) Number of publications reviewed per decade, between 1871 and June 2018. (b) Number of publications surveyed according to research topics defined in the review: taxonomy and systematics, morphology, biochemical composition, genetics, phylogeography, population ecology, reproductive biology, ecological interactions, plant propagation, conservation, and reviews.

($n = 4$) of Zamiaceae. We grouped the studies in five periods, considering the first as 1891 to 1980 (Figure 1(a)). From the 1980s, research on Zamiaceae showed a significant increase ($n = 70$) mainly focusing on taxonomy and systematics ($n = 15$), ecological interactions ($n = 12$), and a similar number of studies in morphology ($n = 13$). From the period 1991 to 2000 ($n = 76$), researchers kept their interest in taxonomy and systematics ($n = 12$) and ecological interactions ($n = 12$), but now also branched into genetics ($n = 11$), with biochemistry, morphology, population ecology, and propagation with similar numbers of publications (six to nine studies). The number of publications doubled after the 21st century ($n = 328$), with research focusing on genetics ($n = 60$), taxonomy and systematics ($n = 52$), reviews ($n = 41$), morphology ($n = 36$), ecological interactions ($n = 30$), and a surprisingly increasing interest in population ecology ($n = 29$) and conservation ($n = 32$) (Figure 1(a) and (b)).

Our review revealed that over the decades, the following research topics predominated, with more than 30 publications on each: ecological interactions ($n = 57$), reviews ($n = 49$), population ecology ($n = 45$), conservation ($n = 36$), and propagation ($n = 32$) (Figure 1(b), FDS). Taxonomy and systematics, genetics, and morphology research topics had over 60 publications each, indicating that most studies on Zamiaceae have a more descriptive/comparative aspect. Less studied research topics were reproductive biology ($n = 25$), biochemistry ($n = 23$), and phylogeography ($n = 11$). Currently, a multidisciplinary focus combining morphological, anatomical, and molecular data have been used to approach questions related to the speciation processes, also considering climatic conditions and species biogeography, as described for the genera *Ceratozamia* (Vovides, Stevenson, Pérez-Farrera, López, & Avendaño, 2016) and *Dioon* (Vovides et al., 2018).

The large number of reviews and studies focusing on taxonomy and systematics, morphology, and genetics can be linked to the existence of research centers that contain large herbaria with important cycad collections, such as the South African National Botanical Institute (South Africa), the Montgomery Botanical Center in Miami (USA), and Nong Nooch Tropical Garden (Thailand) (Walters, 2003). However, additional taxonomic work is required to resolve taxonomic issues of species from Brazil, Venezuela, and Colombia (Calonje, Meerow, et al., 2019). The gradual increase in studies focusing on population ecology and conservation is

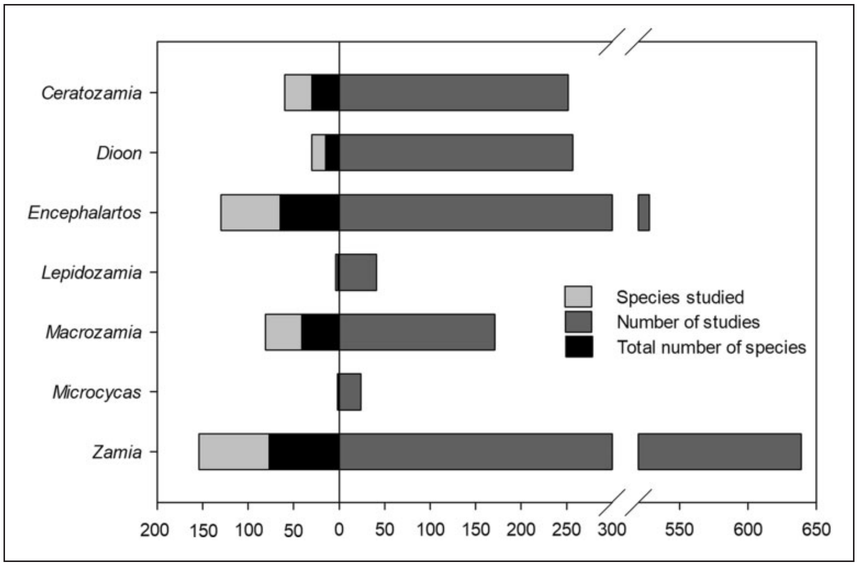

Figure 2. Number of species per genus (black bar), number of species studied (light gray), and of studies per species (dark gray) in the Zamiaceae family.

most likely driven by the growing destruction of suitable habitat for cycad populations around the world, a noticeable factor since the beginning of the 21st century. Finally, the reduced number of studies addressing reproductive biology, biochemistry, and phylogeography could be explained by the fact that these research topics are more expensive both in time and resources, requiring extensive fieldwork or expensive technological analyses not always accessible, especially until recently in the New World.

Considering the diversity of species, the most studied genera of Zamiaceae are *Zamia*, *Encephalartos*, *Ceratozamia*, *Dioon*, and *Macrozamia* (Figure 2). Most of the studies focus on morphology and genetics (FDS). Despite the number of studies, information is still scarce, especially for *Zamia* and *Encephalartos* (FDS). In addition, *Microcycas* and *Lepidozamia* have few species and, thus, studies surveyed (Figure 2, FDS). Most of the Zamiaceae studies are concentrated in the North American continent ($n = 273$), corresponding to 54% of all studies found in our survey, followed by Africa ($n = 73$; 14%), Australia ($n = 54$; 11%), South America ($n = 31$; 6%), Europe ($n = 23$; 5%), and Asia ($n = 14$; 3%). The remaining 7% ($n = 40$) correspond to reviews. Studies identified as being from North America and Europe are classified as such due to the affiliation of the main authors. It is interesting to note that, although the species do not naturally occur in these areas, a considerable part of the studies have been done by researchers from these regions.

Regarding the species from the New World, the vast majority of studies have been conducted in North and Central America (FDS). Mexico, the country with most studies on Zamiaceae, holds the greatest diversity of cycads in the Neotropics with a high percentage of endemic species (Lopez-Gallego, 2015; Nicolalde-Morejón et al., 2014; Vovides et al., 2003). Of the 62 cycad species found in Mexico, 58 are endemic (Calonje, Stevenson, et al., 2019), of which *Zamia furfuracea* L.f., *Dioon edule* Lindl., and *Ceratozamia mexicana* Brongn. are the most studied ones (Nicolalde-Morejón et al., 2014). Mexico is also an exception regarding action plans for conservation. The country has developed local conservation actions based on national collections, botanical gardens, investing in sustainable use of cycad species by means of educational programs (Donaldson, 2003; Lázaro-Zermeño, González-Espinosa, Mendoza, & Martínez-Ramos, 2011; Pérez-Farrera, Quintana-Ascencio, Salvatierra, & Vovides, 2000; Pérez-Farrera & Vovides, 2006; Vovides, Iglesias, Luna, & Balcázar, 2013; Vite, Pulido & Vázquez, 2013). Following this example, Australia and South Africa have also increased the number of cycad related studies (FDS). Such studies and efforts are needed in South America. However, due to the numerous political borders across the geographical distribution of cycads in the Americas, research efforts have evolved slowly (Terry et al., 2012).

Within Zamiaceae, *Zamia* is the genus with the greatest number of species (80), of which 30 are found throughout South America (Figure 3). Despite the fact that many species have been well studied, others still require basic research (Table 1). The rate of habitat loss has increased faster than species distribution data is updated, giving the wrong impression that populations are stable when in fact numbers are declining fast and they are endangered. In addition, the disjunct nature of populations makes it difficult to assess their dynamics or

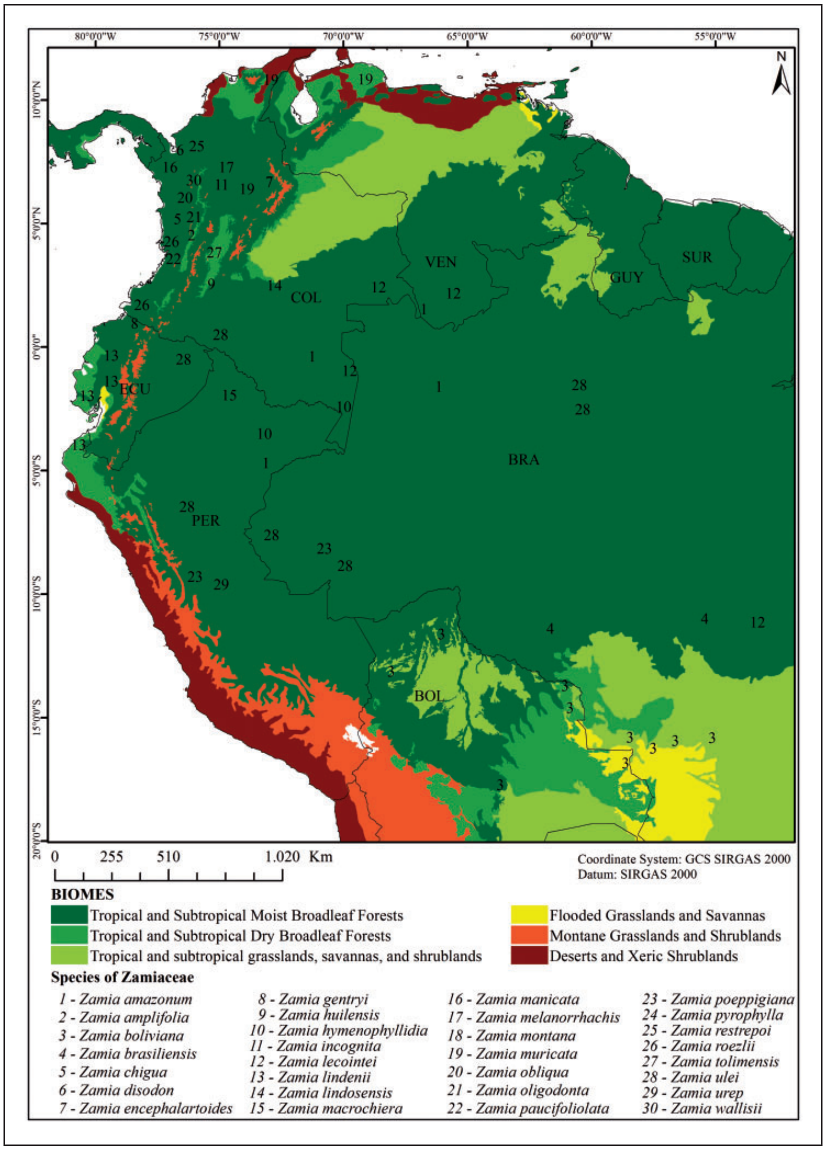

Figure 3. Geographical distribution of the 30 Zamiaceae species of South America considering the different vegetation types where they occur.

stability under different scenarios without extensive fieldwork. This is a critical limitation in South America (Donaldson et al., 2003; Stevenson, 1993). The 30 species of *Zamia* occurring in South America are distributed between Brazil, Colombia, Ecuador, Peru, and Venezuela (Calonje, Stevenson, et al., 2019). Colombia has 21 species of *Zamia* with populations in all biogeographical regions (Lopez-Gallego, 2015). About 62% of these species them considered endemic to South America and are distributed in the floristic elements of Chocó, montane, Río Magdalena Valley, and Amazonian Basin (Lopez-Gallego, 2015; Stevenson, 2004b). Brazil and Bolivia have species inhabiting the ecosystems of the Amazon Basin, Cerrado (Savanna), and the transition areas between the two (Segalla & Calonje, 2019). For species shaing similar regions but crossing geographical borders, research efforts and joint conservation plans should be established between countries.

Reproductive Biology and Ecological Interactions on Zamiaceae

Most of the studies focusing on ecological interactions involve *Ceratozamia*, *Dioon*, and *Zamia*. Thus, we focused on these genera. Basic aspects of the morphology of reproductive structures, common to all cycads, were previously revised somewhere else (Stevenson, 1993; Stevenson, 2004a; Terry et al., 2012).

Table 1. General Overview of Possible Studies With the Genus *Zamia* From South America: Conservation Status of Species, Potential Causes of Population Decline, and Topics for Future Studies.

Zamiaceae Taxa	Conservation status	Causes of population decline	Suggested topics for future studies: Natural history and phenology 1	Population dynamics 2	Reproductive biology 3	Ecological interaction 4	Habitat characteristics 5	Populations reestablishment translocations 6	Ex situ collections/ Germplasm bank 7	Phylogeography 8	Ethnobotany/ Ecotourism 9	Intercountry conservation actions 10	Source
Zamia amazonum D.W. Stev.	Near threatened/ Vulnerable	Loss of habitat	X	X	X	X	X	X	X	X	X	X	1, 9
Zamia amplifolia W. Bull ex Mast.	Critically endangered	Small area of occupation	X	X				X	X		X		1, 9
Zamia boliviana (Brongn.) A.DC.	Near threatened/ Vulnerable	Fragmented population		X			X		X	X	X	X	1, 2, 9
Zamia brasiliensis Calonje & Segalla	Endangered	Small area of occupation	X	X	X	X		X	X	X	X	X	13
Zamia chigua Seem.	Near threatened/ Vulnerable	Loss of habitat/ Other causes		X									1, 7, 9
Zamia disodon D.W. Stev. & Sabato	critically Endangered	Small area of occupation					X	X		X			1, 9
Zamia encephalartoides D.W. Stev.	Vulnerable/ Endangered	Small area of occupation	X	X				X	X		X		1, 9
Zamia gentryi Dodson	Critically endangered	Small area of occupation/ Loss of habitat	X	X			X	X		X			1, 9
Zamia huilensis Calonje, Esquivel, & Stev	Critically endangered	Small area of occupation/ Loss of habitat/ Illegal trade		X		X			X		X		1, 6
Zamia hymenophyllidia D.W. Stev.	Critically endangered	Small area of occupation/ Fragmented population	X	X	X	X		X	X				1, 9
Zamia incognita A. Lindstr. & Idárraga	Vulnerable	Loss of habitat/ Petroleum and Ore exploration		X						X			1, 7, 8, 9
Zamia lecointei Ducke	Near threatened/ Vulnerable	Loss of habitat	X	X						X			1, 9
Zamia lindenii Regel ex André	Deficient data	Loss of habitat	X	X	X	X							3, 9
Zamia macrochiera D.W. Stev.	Critically endangered	Loss of habitat	X	X	X	X		X			X		1, 9
Zamia lindosensis D.W. Stev., D. Cárdenas & N. Castaño	Endangered	Loss of habitat/ Agricultural expansion		X	X	X		X	X	X			1, 9,10
Zamia manicata Linden ex Regel	Near threatened/ Vulnerable	Current land use and occupation	X	X		X							1, 9
Zamia melanorrhachis D.W. Stev.	Endangered	Loss of habitat/Small area of occupation	X	X		X			X				1, 9

(continued)

Table 1. Continued.

Zamiaceae Taxa	Conservation status	Causes of population decline	Suggested topics for future studies: Natural history and phenology 1	Population dynamics 2	Reproductive biology 3	Ecological interaction 4	Habitat characteristics 5	Populations reestablishment translocations 6	Ex situ collections/ Germplasm bank 7	Phylogeography 8	Ethnobotany/ Ecotourism 9	Intercountry conservation actions 10	Source
Zamia montana A. Braun	Critically endangered	Small area of occupation/ Loss of habitat	X	X		X		X	X				1, 9
Zamia muricata Willd.	Near threatened/ Vulnerable	Fragmented population/ Current land use and occupation	X	X	X		X			X			1, 7, 9
Zamia obliqua A. Braun	Near threatened/ Vulnerable	Loss of habitat	X	X	X								1, 7, 9
Zamia oligodonta E. Calderón & D.W. Stev.	Endangered	Loss of habitat/ Illegal trade		X	X	X		X	X				1, 12
Zamia paucifoliolata Calonje	Endangered	Loss of habitat/Small area of occupation	X	X	X	X		X	X				1, 9,11
Zamia poeppigiana Mart. & Eichler	Near threatened	Loss of habitat	X	X	X	X							1, 9
Zamia pyrophylla Calonje, D.W. Stev. & A. Lindstr.	Critically endangered	Loss of habitat/Current land use and occupation	X	X	X			X	X				4, 9
Zamia restrepoi (D.W. Stev.) A. Lindstr.	Critically endangered	Loss of habitat/Small area of occupation		X				X	X				1, 7 , 9
Zamia roezlii Linden	Vulnerable	Current land use and occupation		X	X			X	X		X		1, 7
Zamia tolimensis Calonje, H.E. Esquivel & D. W. Stev.	Critically endangered	Fragmented population/ Current land use and occupation	X	X	X			X	X				5, 6, 7, 9
Zamia ulei Dammer	Near threatened	Ore exploration/Loss of habitat	X	X	X	X							1, 7, 9
Zamia urep B. Walln.	Critically endangered	Deficient data	X	X	X	X		X			X	X	1, 9
Zamia wallisii A. Braun	Critically endangered	Loss of habitat/Small area of occupation/ Illegal trade	X	X	X			X					1, 7, 9

Source: (1) International Union for Conservation of Nature (IUCN) 2013–2019, (2) Skelley & Segalla (2019), (3) Lindström (2010), (4) Calonje et al. (2010), (5) Calonje, Kay, and Griffith (2011), (6) Calonje, Esquivel, Morales, Mora-Lizcano, and Stevenson (2012), (7) Lopez-Gallego (2015), (8) Valencia-Montoya, Tuberquia, Guzmán, and Cardona-Duque (2017), (9) Calonje et al. (2019), (10) Stevenson et al. (2018), (11) Calonje et al. (2018), (12) Calderón-Sáenz and Stevenson (2003), and (13) Segalla and Calonje (2019).

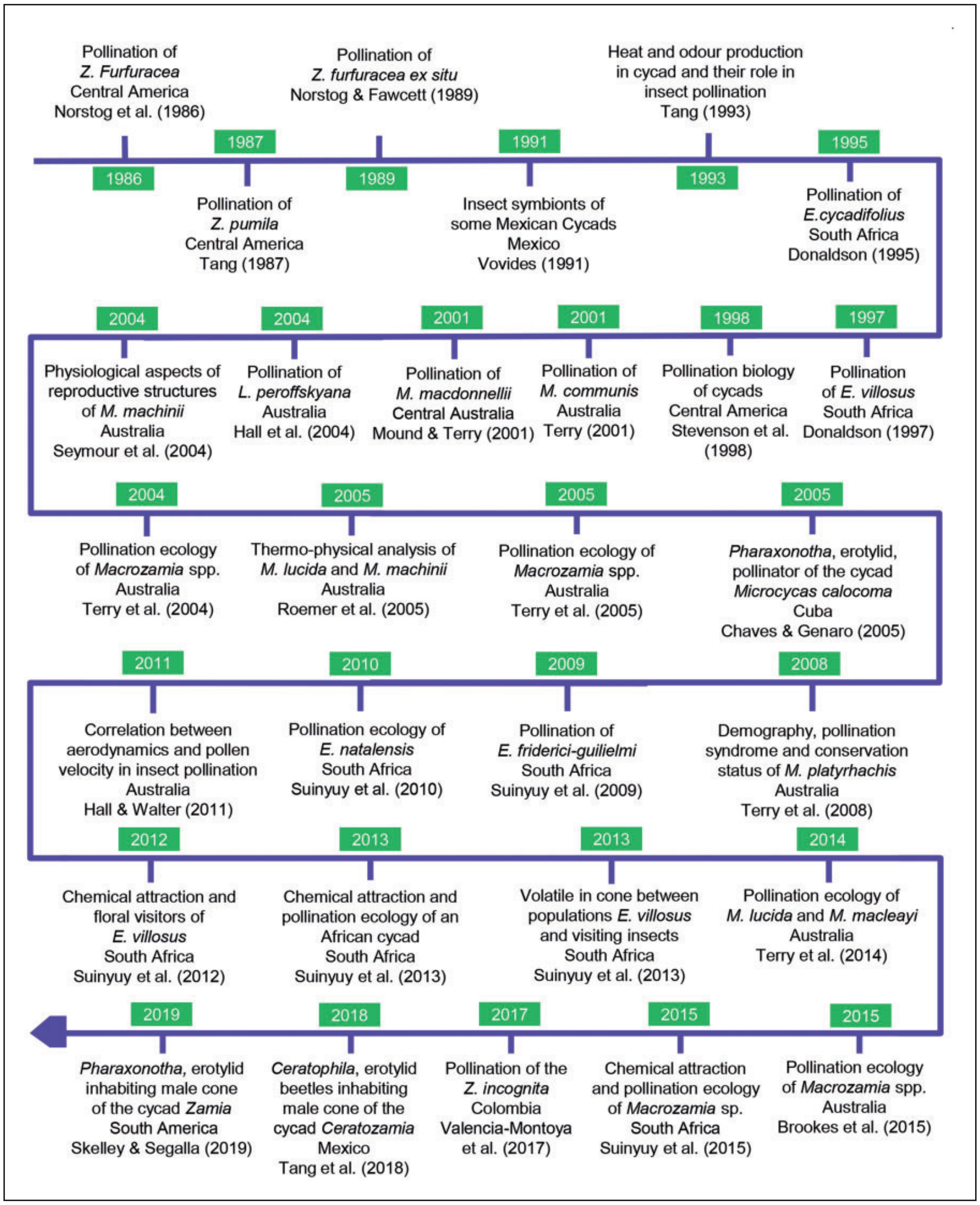

Figure 4. Timeline of main studies considering the reproductive biology of Zamiaceae.

Mutualistic Interactions: Plant-Pollinators

The pollination of different species of Zamiaceae seems to be mediated by host-specific insects, typically Coleoptera and Thysanoptera (Franz & Skelley, 2008; Tang, Skelley, & Pérez-Farrera, 2018; Terry et al., 2004; Terry, Forster, Moore, Roemer, & Machin, 2008; Valencia-Montoya et al., 2017). We prepared a timeline of the main studies addressing the pollination biology of Zamiaceae species (Figure 4). Historically, the pollination of Zamiaceae was attributed exclusively to anemophily. As with other gymnosperms, wind was considered the only facilitating agent of pollination (Terry, Roe, Tang, & Marler, 2009). This idea was refuted only in the 1980s with the classic experimental studies of Norstog, Stevenson, and Niklas (1986); Tang (1987); Norstog and Fawcett (1989); Vovides (1991); and Tang (1993) confirming that beetles of the genera *Pharaxonotha* (Curculionoidea: Erotylidae) and *Rhopalotria* (Curculionoidea: Belidae) are the pollinators of different species of *Zamia*. Such studies stimulated further experimental research, corroborating insect pollination in *Zamia* species. In fact, research on pollination published after these first studies frequently report beetles as pollinators of Zamiaceae, as well as of basal angiosperms (Ollerton, 2017), suggesting an evolutionary process between cycads and beetles acting as pollinators (Walters et al., 2004).

Pharaxonotha has been commonly described as a mutualistic agent of *Zamia* and has also been found in strobili of species from other genera, such as *Ceratozamia*, *Dioon*, and *Microcycas* (Chaves & Genaro, 2005; Franz & Skelley, 2008). Recently, a new species of *Pharaxonotha* Reitter (Coleoptera: Erotylidae) was found inhabiting the male strobilus of *Zamia boliviana* (Brongn.) A.DC. from central South America (Skelley & Segalla, 2019), and a new species of the genus *Ceratophila* Tang, Skelley, and Pérez-Farrera (Erotylidae: Pharaxonothinae) was described inhabiting male strobili of *Ceratozamia* in Mexico (Tang, Xu, et al., 2018). Surveys of Coleoptera inhabiting the strobilus of other cycad genera in the New World, including *Dioon*, *Microcycas*, and *Zamia*, indicate that *Ceratophila* is restricted to *Ceratozamia*, the only known host of these beetles (Tang, Xu, et al., 2018). The existence and nature of insect interactions with cycads species of South America, especially as it relates to ecology and reproductive biology, still need ample effort of investigation.

Molecular and morphological phylogenetic analyses of beetles present in cycads from the New World suggest that pollinator type may impact the population genetic structure of their host species (Tang, Skelley, et al., 2018). The new findings indicate that this is a fruitful avenue of research (Tang, Skelley, et al., 2018), applicable mainly to the conservation of South American cycads. In tropical regions, the size and lifespan of the strobilus is short, limiting the attractiveness of visitors that have long reproductive periods and acts as a barrier to the colonization of certain species (Terry et al., 2012). Strategically, this characteristic promotes greater activity in the beetles to move from one plant to another, favoring pollen dispersion over longer distances (Terry et al., 2012). This hypothesis remains to be tested for South American cycads.

Mutualistic Interactions: Seed Dispersers and Consumers

Seed dispersal by animals is a facultative mutual relationship relevant to the gene flow and maintenance of plant species. Birds, rodents, and probably many other animals disperse cycad seeds by ingesting the sarcotesta and dropping the stony layer and its contents away from the mother plant (Hill & Osborne, 2001; Taylor & Holzman, 2012), but these events need to be better studied in Zamiaceae species (Lopez-Gallego, 2015). Seed dispersal maintains the local genetic structure of species even more than pollen dispersal (Dow & Ashley, 1996; Dyer, 2007; Ortego, Bonal, & Muñoz, 2010). Although pollen dispersal may promote high diversity at a global scale, seed dispersal acts locally, determining the structure of populations (Cabrera-Toledo, González-Astorga, & Flores-Vázquez, 2012). Table 2 summarizes the studies addressing seed dispersal agents in Zamiaceae species and shows that in general, seed dispersal mechanisms need to be investigated for most species.

The relationship between dispersal and recruitment is still poorly understood for most Zamiaceae species. Gregory and Chemnick (2004) observed that in *Dioon* species most seeds germinating near the mother plant do not survive. According to these authors, seedling survival is determined by seed storage period and depth of burial, as seeds that are buried deeper in the soil are more likely to avoid predation and germinate successfully. Recruitment of seeds next to the mother plant also suggests that seed dispersal by animals is not as effective (Pérez-Farrera et al., 2000). For example, *Ceratozamia matudae* Lundell interacts very little with predators and dispersers due to the large size of its seeds (2–3 cm in diameter) and due to its high concentration of neurotoxins (Pérez-Farrera et al., 2000). The *C. matudae* plants are usually found in areas with steep topography (Pérez-Farrera et al., 2000) and gravity might be responsible for the limited local seed dispersal (Jones, 1993). Potential differences in pollen or seed dispersal distances between native- and degraded-forest habitats as in *Zamia fairchildiana* L.D. Gómez populations are difficult to evaluate, given the limited knowledge of its pollination and dispersal biology (Lopez-Gallego & O'Neil, 2010). Other relationships with species of *Zamia*, such as opportunistic associations with ants as removal agent of fresh sarcotesta (Lázaro-Zermeño et al., 2011), are also important as maintainers of ecological services, but are poorly understood. The dispersal of seeds and other aspects of the natural history of *Zamia* species, as well as others around the world, require further research (Lopez-Gallego, 2015).

Antagonist Interactions: Herbivores and Seed Predators

Zamia species, like many other plant species, produce a variety of secondary toxic substances (allelochemicals) to defend themselves against antagonists, mainly herbivores. Dimeric flavones, the nitrogen-containing methylazoglucosides cycasin, macrozamin, and several neocycasins are among the most important allelochemicals, and palatable to only a few animal species (Brenner, Stevenson, & Twigg, 2003; Prado, 2011; Schneider, Wink, Sporer, & Lounibos, 2002). Table 3 summarizes the studies addressing antagonist interactions, such as herbivory and predation, in Zamiaceae from the New World. In general, studies indicate that there is a high dependence by animals on the host plant (Table 3). Nonetheless, the mechanisms involved in the

Table 2. Compilation of Studies on Seed Dispersal and Predation on Different Species of the Zamiaceae Family.

Taxa de Zamiaceae	Seed dispersers and predators	Geographical region/Country	Source
Ceratozamia matudae Lundell	*Peromyscus mexicanus* (Saussure, 1860); *Pecari tajacu* Linnaeus, 1758	Mexico	Pérez-Farrera et al. (2000)
Ceratozamia mirandae Vovides, Pérez-Farr. & Iglesias	Peccaries (Tayassuidae)	Mexico	Pérez-Farrera et al. (2006)
Dioon edule Lindl.	*P. mexicanus*	Mexico	Vovides et al. (2003)
Dioon merolae De Luca, Sabato & Vázq.Torres	*P. mexicanus*	Mexico	Lázaro-Zermeño, González-Espinosa, Mendoza, and Martínez-Ramos (2011)
Dioon spinulosum Dyer ex Eichler	Birds, coatis, and rodents	Mexico	Chemnick (2013)
Encephalartos barteri subsp. *barteri*	Big mammals and large flying birds	Benin/Africa	Ekué et al. (2008)
Macrozamia lucida L.A.S. Johnson	*Trichosurus Vulpecula*, *Rattus fuscipes*	Queensland, Australia	Snow and Walter (2007)
Macrozamia miquelii (F. Muell.) A.DC.	*Trichosurus vulpecula*	Queensland, Australia	Hall and Walter (2013)
Macrozamia riedlei (Gaudich.) C.A. Gardner	Birds, parrots, and marsupials	Western Australia	Burbidge and Whelan (1982)
Zamia amblyphyllidia D.W. Stev.	Small and medium mammals	Puerto Rico	Negron-Ortiz and Breckon (1989)
Zamia fairchildiana L.D. Gómez	*Saltator* spp. (Cardinalidae), *Ramphocelus passerinii* Bonaparte, 1831	Costa Rica	Gómez (1993)
Zamia lindenii Regel ex André	*Dasyprocta punctata* Gray, 1842	Equador	Lindström (2010)
Zamia pumila L.	Mockingbird (Mimidae)	Florida/USA	Eckenwalder (1980)

Note. Interaction species, geographical region of study and references are provided.

interaction between the antagonist agents and the chemical substances are not fully understood (Prado, 2014).

Antagonist interactions with Lepidoptera and Coleoptera have been observed for many Zamiaceae species. For example, butterflies of the genus *Eumaeus* (Lepidoptera: Lycaenidae) are obligate cyclic herbivores that consume both vegetative and reproductive parts of many Neotropical Zamiaceae (Figure 5(a)–(c)), while beetles (Coleoptera: Chrysomelidae and Aulacoscelinae) act as predators (Cascante-Marín & Araya, 2012; Castillo-Guevara & Rico-Gray, 2002; Contreras-Medina et al., 2003; Koi & Daniels, 2015; Pérez-Farrera & Vovides, 2004; Prado et al., 2011; Ruiz-García et al., 2015; Taylor et al., 2008). Those studies are limited, however, and only provide brief descriptions of the observed interactions.

The different adaptations needed to overcome the toxicity of cycads are not restricted only to herbivory or predation but also to the possible gains by the insect using the plant's secondary metabolites (Prado, 2011). The aposematic traits of *Eumaeus* larvae which feed on *Zamia* species, suggest a long evolutionary association where insects are tolerant to the plant's defenses while exploring the resources free from competition (Castillo-Guevara & Rico-Gray, 2002; Schoonhoven, van Loon, & Dicke, 2005). Prado, Rubio-Mendez, Yañez-Espinosa, and Bede (2016) recommend studies on the life cycles of both plants and herbivores to evaluate preference, performance, and levels of damage throughout different ontogenetic stages between male and female individuals.

Biogeographic Studies as a Conservation Strategy for Zamia Species

Variability is a basic requirement for plant survival and adaptive evolution. Populations that are genetically related have higher degrees of endogamy, which brings negative consequences for future generations (Linhart, 2014). Gene transfer between populations is even more important given the decline of pollinator populations, increase in habitat loss and fragmentation, and shifts in species distribution due to climate change (Gutiérrez-Ortega, Yamamoto, et al., 2018b; Liu, Compton, Peng, Zhang, & Chen, 2015). Indeed, several studies have detected low genetic diversity and high levels of inbreeding in Zamiaceae, particularly in the Australian species of *Macrozamia* (Sharma, Jones, Forster, & Young, 1998; Sharma et al., 1999, 2004). Studies of genetic variation and structure in cycad populations have given variable results, mainly in Asian *Cycas* species (reviewed by Liu et al., 2015), which

Table 3. Compilation of Studies (1870–2019) Regarding Antagonistic Interactions Involving Zamiaceae Species From the New World.

Agent	Zamiaceae		Behavior of the agent	Geographical region	Source
	Genus	Taxa			
Aulacoscelis appendiculata (Cox & Windsor, 1999), (Coleoptera: Chrysomelidae)	*Zamia*	*Zamia elegantissima* Schutzman, Vovides & R.S. Adams	Predation	Panama	Prado, Ledezma, Cubilla-Rios, Bede, and Windsor (2011)
Aulacaspis yasumatsui (Hemiptera: Sternorrhyncha: Diaspididae)	*Dioon*	*Dioon califanoi* De Luca & Sabato	Parasitism	Mexico	Howard et al. (1999)
		Dioon edule Lindl.	Parasitism	Mexico	Howard et al. (1999)
		Dioon merolae De Luca, Sabato & Vázq.Torres	Parasitism	Mexico	Howard et al. (1999)
		Dioon spinulosum Dyer ex Eichler	Parasitism	Mexico	Howard et al. (1999)
		Dioon tomasellii De Luca, Sabato & Vázq.Torres	Parasitism	Mexico	Howard et al. (1999)
		Dioon rzedowskii De Luca De Luca, A. Moretti, A. Moretti, Sabato, Sabato & Vázq.Torres & Vázq.T	Parasitism	Mexico	Howard et al. (1999)
	Microcycas	*Microcycas calocoma* (Miq.) A.DC.	Parasitism	Cuba	Howard et al. (1999)
Aulacoscelis vogti (Monrós, 1959), (Coleoptera: Orsodacnidae)	*Dioon*	*Dioon edule* Lindl.	Predation	Mexico	Prado et al. (2011)
Eumaeus atala (Poey, 1832), (Lepidoptera: Lycaenidae)	*Zamia*	*Zamia integrifolia* L.f.	Herbivory	Florida	Schneider et al. (2002)
Eumaeus childrenae (G. Gray, 1832), (Lepidoptera: Lycaenidae)	*Zamia*	*Zamia fischeri* Miq.	Herbivory	Mexico	Contreras-Medina, Ruiz-Jiménez, and Vega (2003)
		Zamia cremnophila Vovides, Schutzman, & Dehgan	Herbivory	Mexico	Jiménez-Pérez et al. (2017)
	Ceratozamia	*Ceratozamia matudae* Lundell	Herbivory	Mexico	Pérez-Farrera and Vovides (2004)
E. childrenae	*Dioon*	*Dioon merolae* De Luca, Sabato & Vázq.Torres	Herbivory	Mexico	Lázaro-Zermeño et al. (2011)
Eumaeus godartii (Boisduval, 1870), Lepidoptera: Lycaenidae)	*Zamia*	*Zamia fairchildiana* L. D. Gómez	Herbivory	Costa Rica	Lopez-Gallego (2007)
		Zamia skinneri Warsz. ex A. Dietr.	Herbivory	Panama	Taylor, Haynes, and Holzman (2008)
		Zamia acuminata Oerst. ex Dyer	Herbivory	Costa Rica	Cascante-Marín and Araya (2012)
		Zamia stevensonii A.S. Taylor & Holzman	Herbivory	Panama	Taylor and Holzman (2012); Prado et al. (2014)
		Zamia incognita A. Lindstr. & Idárraga	Herbivory	Colombia	Lopez-Gallego (2015); Valencia-Montoya et al. (2017)
Eumaeus minyas (Hübner, 1809), (Lepidoptera: Lycaenidae)	*Zamia*	*Zamia neurophyllidia* D.W. Stev.	Herbivory	Costa Rica	Clark et al. (1992)
		Zamia loddigesii Miq.	Herbivory	Mexico	Castillo-Guevara and Rico-Gray (2002)
		Zamia encephalartoides D.W. Stev.	Herbivory	Colombia	González (2004)
		Zamia boliviana (Brongn.) A.DC.	Herbivory	Brazil	Segalla and Morellato (2019)

(continued)

Table 3. Continued.

Agent	Zamiaceae		Behavior of the agent	Geographical region	Source
	Genus	Taxa			
Eumaeus toxea (Godart, 1824) (Lepidoptera: Lycaenidae)	*Zamia*	*Zamia poeppigiana* Mart. & Eichler	Herbivory	Mexico	Ruiz-García, Méndez-Pérez, Velasco-García, Sánchez-de la Vega, and Rivera-Nava (2015)
Eumaeus sp.	*Zamia*	*Zamia lindenii* Regel ex André	Herbivory	Equador	Lindström (2010)
Eumaeus sp.	*Zamia*	*Zamia pyrophylla* Calonje, D. W. Stev. & A. Lindstr.	Herbivory	Colombia	Calonje et al. (2010)
Eumaeus sp.	*Zamia*	*Zamia huilensis* Calonje, H.E. Esquivel & D.W. Stev.	Herbivory	Colombia	Calonje et al. (2012)
Eumaeus sp.		*Zamia nana* A. Lindstr., Calonje, D.W. Stev. & A. S. Taylor	Herbivory	Panama	Lindström et al. (2013)
Eumaeus sp.	*Ceratozamia*	*Ceratozamia subroseophylla* Mart.-Domínguez & Nic.-Mor.	Herbivory	Mexico	Martínez-Domínguez et al. (2016)
Janbechynea elongata (Coleoptera: Polyphaga: Orsodacnidae)	*Ceratozamia*	*Ceratozamia huastecorum* Avendaño, Vovides & Cast.-Campos	Herbivory	Mexico	Reyes-Ortiz et al. (2016)
Janbechynea paradoxa (Monrós, 1953), (Coleoptera: Chrysomelidae)	*Zamia*	*Zamia boliviana* (Brongn.) A.DC.	Predation	Bolivia	Prado et al. (2011)
Seirarctia echo (J. E. Smith, 1797), (Lepidoptera: Erebidae)		*Zamia pumila* L.	Herbivory	EUA	Negrón-Ortiz and Gorchov (2000)

Note. The interacting agents (plant–animal species), behavior, geographical region of the study, and references are shown.

may be related to its occurrence on islands (Keppel, Lee, & Hodgskiss, 2002) and in naturally fragmented landscapes as this may facilitate pollen and seed movement in some species but not in others (Xiao, Ge, Gong, Hao, & Zheng, 2004; Xiao et al., 2005).

In general, cycads evolved under limiting local conditions and many populations are critically small, as described by Silva, Donaldson, Reeves, and Hedderson (2012) for *Encephalartos latifrons* (Lehmann). The high levels of genetic diversity within *E. latifrons*, despite the weak genetic structure, suggest that remaining subpopulations are remnants of the original panmictic population with high levels of gene flow (Silva et al., 2012). Such patterns may be extended to other cycad species that had originally small species distribution (Silva et al., 2012). Indeed, genetic studies may clarify many demographic questions in Zamiaceae by explaining the relative role of pollen and seed dispersal in keeping the genetic integrity and cohesion of *Zamia* populations, and how such species cope with demographic oscillations such as founder effects, bottlenecks, and genetic drift. Investigating these subjects inform decision makers about which populations are likely to be most important for conservation initiatives, and which management procedures are most appropriate for keeping its evolutionary potential (Frankham, 2010; González-Astorga, Vovides, Cruz-Angon, Octavio-Aguilar, & Iglesias, 2005; González-Astorga, Vovides, Ferrer, & Iglesias, 2003; Cabrera-Toledo et al., 2010). Genetic techniques are important conservation tools when associated with other biological, ecological, and biogeographical information (Miyaki & Alves, 2006). Recently, the number of phylogenetic analyses with Zamiaceae has increased (Gutiérrez-Ortega, Kajita, & Molina-Freaner, 2014; Gutiérrez-Ortega, Jimenez-Cedillo, et al., 2018a; Gutiérrez-Ortega, Yamamoto, et al., 2018b), offering an unprecedented amount of molecular data. Such phylogenetic inferences will deepen our understanding about the evolution of niche conservatism, morphological traits associated with specific reproductive strategies, and speciation rates, as observed in other plant groups (Cardoso-Gustavson et al., 2018; Vasconcelos et al., 2019). Since cycads represent an old lineage of seed plants, new evidence on diversification mechanisms obtained by using multiple approaches would provide a solid framework for the comprehension of plant evolution and speciation pathways and also contribute to the conservation of this

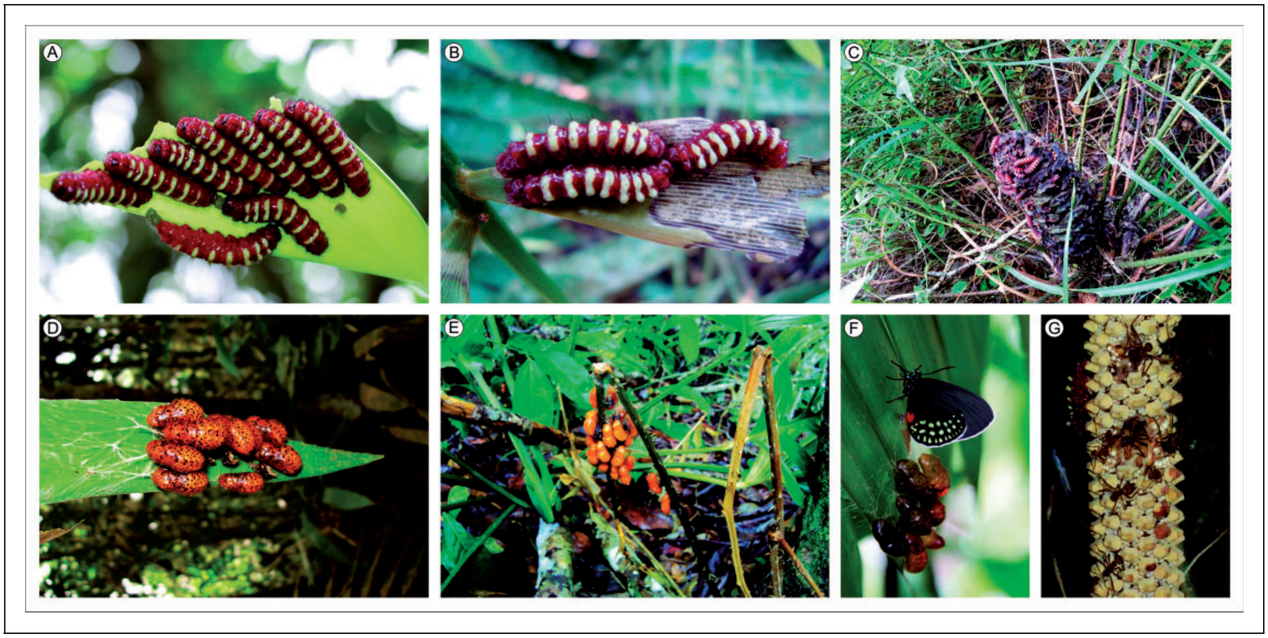

Figure 5. Ecological interactions with Zamiaceae: (a) Larvae of *Eumaeus* sp. in *Z. huilensis*; (b) Larvae of *Eumaeus* sp. in *Z. incognita*; (c) Larvae of *Eumaeus* sp. in *C. mirandae*; (d) Pupae of *Eumaeus* sp. in *Z. incognita*; (e) Pupae of *Eumaeus* sp. in *Z. manicata*; (f) *Eumaeus* sp. adult in *Z. encephalartoides*; and (g) *Atta* sp. (Formicidae), larvae of *Eumaeus* sp. and *Pharaxonotha* sp. in pollen strobili of *Z. incognita*. Photo credits: (a) and (f)—Machael Calonje; (b), (d), and (g)—Arturo Aristizabal; (c)—Chip Jones; and (e)—Cristina Lopez-Gallego. Source: Calonje, Stevenson, et al. (2019). License: CC BY-NC-SA 4.0.

charismatic but threatened plant group (Gutiérrez-Ortega, Yamamoto, et al., 2018b).

Challenges and Perspectives, With Emphasis on *Zamia* From South America

Not only *Zamia* species tend to be rare in their habitats (low abundance and restricted geographic distribution) compared with other species of tropical plants (Lopez-Gallego, 2015), but they are also mainly endemic, with populations growing mostly in remote areas with restricted access (Calonje, Meerow, et al., 2019; Stevenson, 1993). Although most of these distribution areas are considered biodiversity hot spots, many populations of *Zamia* occur outside protected areas (Donaldson, 2003; Mankga & Yessoufou, 2017; Skelley & Segalla, 2019). Shifts in land use, overexploitation of plant populations as ornamentals, reduction or loss of pollinators, and other interactors due to insecticides and herbicides are some of the threats faced by populations (González, 2004; Lopez-Gallego, 2015; Taylor et al., 2012). To preserve the multiple aspects of biodiversity hot spots, a biogeographic approach, associated with the current state of species conservation, population dynamics, and ecology (Lopez-Gallego, 2015; Mankga & Yessoufou, 2017) is necessary. However, implementation of such studies still represents a challenge for South American cycads (Schutzman, 2004).

Cross-pollination, mandatory in dioecious species (Canuto, Alves-Ferreira, & Côrtes, 2014), benefits plant populations in many ways, mainly by increasing genetic diversity (Nybom, Weising, & Rotter, 2014). However, *Zamia* populations may be negatively affected considering their dioecious reproductive system, suffering both biotic (presence of pollinators and dispersers) and abiotic pressures (related to habitat loss and fragmentation), which may prevent gene flow between populations (Barrett, 2010; Donaldson, 2003; Laidlaw & Forster, 2012; Liu et al., 2015). Generally, *Zamia* species that are critically threatened (Table 1), with less than 250 adult individuals, are found in small isolated fragments (Stevenson, Vovides, & Chemnick, 2003). This is particularly problematic because (a) all species are dioecious, (b) isolated plants rarely reproduce, and (c) pollination depend on specialized vectors, with reproductive success determining plant populations persistence, increasing the chances of extinction when in reproductive disadvantage (Donaldson et al., 2003; Mora, Yáñez-Espinosa, Flores, & Nava-Zárate, 2013; Stevenson et al., 2003). Studies suggest that environmental differences as a result of anthropogenic disturbance in forest habitats of *Z. fairchildiana* can significantly affect the life history of subpopulations, particularly their growth rate and allocation to fecundity, and the availability of mates for a female in a given reproductive season (Lopez-Gallego & O'Neil, 2010). Calonje et al. (2011) emphasize the importance of understanding the reproductive biology of cycads and propagation techniques, storage and viability of pollen, manual pollination, seed storage, and germination, in order to increase the availability of these rare plants and reduce the demand for wild-collected plants in areas where they are economically and culturally relevant.

Despite the current political and environmental scenarios of many countries where *Zamia* species occur in South America, conservation actions and strategies must be integrated into a larger action plan across borders, involving the countries and subregions to facilitate better outcomes for conservation, not only of their cycads, but also the Neotropical flora and interactions associated with them. Except for Colombia, which has recently developed a plan of action for the conservation of cycads, the remaining species of *Zamia* in South American countries lack conservation plans in their territories. Countries such as Colombia and Brazil suffer from constant agrarian and economic conflicts, causing irreversible modifications of habitats of many species of cycads (Lopez-Gallego, 2015; Segalla & Calonje, 2019; Skelley & Segalla, 2019). Initiatives such as the National Program of Cycads of Mexico are recommended in South America. This project proposes priorities such as ex situ and in situ conservation, sustainable management, ethnobotanical education, and law enforcement for conservation of the Zamiaceae species. A special subcommittee has been established and the cycads have been listed, among other threatened flora and fauna, as a national conservation priority (Lillo et al., 2000). These policies and actions are very important for small endemic populations and can help in the establishment of sanctuaries or protected areas with a high number of adult individuals and less disturbed habitats (González-Astorga et al., 2005). Cycad Specialists in the New World, especially in South America, have the challenge of implementing conservation actions to protect the species of cycads in a scenario marked by a large geographical extension of their territories (Calonje, Meerow, et al., 2019), sociocultural and economical conflicts, difficulties in accessing remote populations, associated with a lack of government incentives and funding for research. More efforts should be made to preserve South American populations and equally their interactions with other organisms (Lopez-Gallego, 2015; Walters et al., 2004; Mankga & Yessoufou, 2017).

Concluding Remarks

This review has shown that the number of studies involving species in the family Zamiaceae has increased over the decades, especially within the genera *Encephalartos* (Africa), *Lepidozamia* and *Macrozamia* (Australia), *Dioon* (Honduras and Mexico), and *Zamia* (Isthmus region, Central and South America). However, despite the importance of these species to biodiversity and the maintenance of ecological interactions (Franz & Skelley, 2008; Segalla & Calonje, 2019; Skelley & Segalla, 2019; Tang, Xu, et al., 2018; Valencia-Montoya et al., 2017), their intrinsic value to science and society and the continuing decline of especially Lepidoptera, Hymenoptera, and Coleoptera species (Sánchez-Bayo & Wyckhuys, 2019), we lack the basic knowledge for many cycad species, especially when considering the genus *Zamia* in South America. As an attempt to direct future research with *Zamia* species on the South American continent, we list the topics that we consider most important, in order to contribute not only to the acquisition of basic information, but also to applied fields such as restoration and conservation of cycads in this region.

1. Species distribution—records from floristic studies, mapping the current distribution of species, and modeling species occurrence taking into consideration environmental and anthropic factors, current climate data and future scenarios. These models can be useful to understand how environmental conditions influence the occurrence and abundance of *Zamia* species and may predict and indicate environmental suitability for conservation actions. Support and recommendations for studies of this nature are found at: Rodríguez, Brotons, Bustamante, and Seoane (2007); Pearson (2007); Feeley and Silman (2010); Guisan et al. (2013); Velazco, Galvão, Villalobos, and Marco Júnior (2017); and Gomes et al. (2018). Other studies applied for cycads conservation plans are found at: Lillo et al. (2000); Vovides, Pérez-Farrera, and Iglesias (2010); Lopez-Gallego, Calonje, and Idárraga-Piedrahíta (2011); Lopez-Gallego (2015); and Mistry, Schmidt, Eloy, and Bilbao (2018) Vite, Pulido & Vázquez (2013).
2. Population monitoring—to better understand population dynamics, including the potential short- and long-term effects of habitat modifications on the life history and spatial distribution, genetic variation, sex ratio, phenology, and the relationship with abiotic factors. The studies with *Macrozamia riedlei* (Gaudich.) C.A. Gardner (Ornduff, 1985, 1991); *Zamia skinneri* Warsz. ex A. Dietr. (Clark & Clark, 1987); *Encephalartos transvenosus* Stapf & Burtt Davy (Grobbelaar, Meyer, & Burchmore, 1989); *Ceratozamia matudai* (Pérez-Farrera & Vovides, 2004); *C. mirandae* Vovides, Pérez-Farr. & Iglesias (Pérez-Farrera et al., 2006); *Macrozamia macdonnellii* (F.Muell. ex miq.) A.DC, Preece, Duguid, and Albrecht (2007); *Z. fairchildiana* (LopezGallego & O'Neil, 2010, 2014); *Z. fairchildiana* (Lopez-Gallego, 2013); *Dioon edule* (Mora et al., 2013); *Z. furfuracea* (Octavio-Aguilar, Iglesias-Andreu,

Cáceres-González, & Galván-Hernández, 2017); and with *Z. portoricensis* Urb. (Lazcano-Lara & Ackerman, 2018) are good models to follow for future studies related to these topics and offer useful insights for conservation strategies.

3. Reproductive ecology—detailed studies of pollination mechanisms, maturation of reproductive structures, seed germination ecology, seedling recruitment, and the relationship between strobilus temperature and attractiveness to pollinators. Studies involving cone odor, thermogenesis, and cycad pollinators as for *Encephalartos* (Suinyuy, Donaldson, & Johnson, 2013a, 2013b, 2015) and *Macrozamia* of the Old World (Terry et al., 2004; Terry, Roemer, Walter, & Booth, 2014; Terry, Roemer, Booth, Moore, & Walter, 2016) and *Zamia* of the New World (Valencia-Montoya et al., 2017) are recommended for cycads of South America. Further studies on chemical signal perception and cognition of the beetle pollinators, together with efforts to resolve the detailed phylogeny of cycads and their associated pollinators, will improve our understanding of cycad-insect mutualism (Suinyuy et al., 2015).
4. Investigation of ecological interactions of different species, including the levels of specialization of each interacting organism, as well as the impact on the fitness of individuals, with consequences for future generations. Conservation plans need to ensure the continued existence of key interactions with root symbionts, pollinators, and dispersal agents, but it is equally important to conserve cycads because they have a key function in the life histories of other organisms (Walters et al., 2004). Once these processes are uncovered, resulting data will probably have a significant impact on *taxa* conservation.
5. The use of genetic markers to estimate levels of gene exchange based on pollen and seed dispersal in order to access the role of pollinators and frugivores in keeping genetic diversity; detecting demographic processes such as founder events and bottlenecks, and estimate the importance of evolutionary forces such as drift, gene flow, and selection in shaping the current patterns of genetic structure and diversity observed in natural populations, as recommend by Gutiérrez-Ortega, Jimenez-Cedillo, et al. (2018a) and Gutiérrez-Ortega, Yamamoto, et al., (2018b).
6. The establishment of ex situ collections and monitoring of species reproduction and germination/propagation after disturbances, both natural and human induced, as indicated by Vovides et al. (2010); Calonje et al. (2011); Vovides et al. (2013); Griffith et al. (2015); and Griffith et al. (2017) for *Zamia* species. The implementation of in situ and ex situ collections and germplasm banks linked to botanical gardens are useful to promote the value of tropical cycads and may stimulate scientific and educational research aimed at the conservation of the group.

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Supplemental material

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