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SPECIAL FEATURE PREFACE

Current topics on cycad biology: Deciphering the Rosetta Stone of plant evolution

Preface of Special Feature "Current topics on cycad biology: Deciphering the Rosetta Stone of plant evolution." Part II: Perspectives from natural history

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[Correction added on 27 November 2025, after first online publication: The copyright line was changed.]

The cycads (Cycadales) and the ginkgoes (Ginkgoales) are two of the most ancient lineages of seed plants (Linkies et al., 2010), with origins dating back approximately 330 million years (Coiro & Seyfullah, 2024). Today, both groups have living representatives that are often referred to as "living fossils" due to their morphological and anatomical similarities to their fossil ancestors. However, while a single extant species, *Ginkgo biloba*, now represents the Ginkgoales, there are currently 380 species of living cycads worldwide (Deloso et al., 2025). This high diversity suggests that cycads have not only persisted through deep evolutionary time but have also successfully adapted and diversified across a wide range of Cenozoic land environments.

While their label of "living fossils" has been questioned in light of the latest research (Coiro & Seyfullah, 2024), it is certain that cycads have preserved many of their ancestral features, serving as a key to understanding the functional and developmental processes behind the origin of seed plants. Because of this, biologist Knut Norstog (1921–2003) sometimes used the "Rosetta Stone analogy" when referring to cycads (Stevenson, 2004). The Rosetta Stone is a monolith excavated by Europeans in 1799 that contains the same text written in three different scripts: Ancient Greek, Demotic, and Egyptian hieroglyphs—the last of which was undeciphered by modern civilizations until the 19th century. The Rosetta Stone connects ancient and modern civilizations because it acted as a "translation key" to decode hieroglyphs, with the Greek text providing a known reference. Similarly, today's cycad species act as a kind of time capsule, offering insights into the ancient past of seed plants; understanding cycad biology helps us decode how seed plants originated and why they thrived across continents.

As we saw in the first part of this Special Issue of *Plant Species Biology* focused on the conservation of the biological and cultural heritage of cycads (https://esj-journals.onlinelibrary.wiley.com/toc/14421984/2025/40/4) and the Virtual Issue that compiles cycad articles published in *Plant Species Biology* and *Ecological Research* (https://esj-journals.onlinelibrary.wiley.com/doi/toc/10.1111/(ISSN)1442-1984.cycad-biology), the appreciation for cycads is strongly motivated by those ancient characteristics that make them unique among the seed plants. While conserving them will help preserve their evolutionary significance, studying their natural history can advance our understanding of the many strategies seed

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plants used to become the dominant vegetation worldwide. This second part of the Special Feature includes studies from a broad range of fields related to the natural history of cycads. I would like to briefly introduce them as an invitation to read these valuable contributions.

The first article by Medina-Villarreal et al. (2025) addresses species delimitation within the *Ceratozamia mexicana* species complex, a group within *Ceratozamia* from Mexico. *Ceratozamia* is a genus that is challenging to study taxonomically because species that are geographically or genetically close often exhibit significant overlap in their morphological traits, making clear identification difficult in many cases. Since morphology alone can sometimes be insufficient to make a distinction among taxa, integrative approaches that include genetic or habitat characterizations are helpful. In this study, the authors used multiple analyses to determine species boundaries within the *Ceratozamia mexicana* species complex. They identified seven lineages that should be recognized as species, one of which has yet to be formally described. This research exemplifies the myriad methodologies that are sometimes necessary to detect the discontinuities in the tree of life that we arbitrarily use to assign labels of "species" to different lineages.

In the second article, Contreras-Negrete et al. (2025) make a first characterization of the bacterial community living inside the leaflet tissue of six species of the cycad genus *Dioon*. The relevance of this study is that, while most studies on the microbiota of cycads have been focused on the communities living inside their roots (well-known reservoirs of cyanobacteria and other prokaryotic groups), a few studies have been concerned about those communities inside the leaflet tissues, belonging to organs that are directly exposed to harsher environments than their subterranean counterparts. By employing the 16S ribosomal RNA gene as a molecular marker, the prokaryotic diversity was identified in 10 individuals of three *Dioon* sister pairs. Despite the low number of plants examined, some interesting patterns were identified; most importantly, a pattern suggesting that for each sister pair, the species living in xeric environments tend to have a higher diversity of endophytic prokaryotes. This opens a new testable hypothesis that should be explored in further research.

One of the most notable features that defines cycads is dioecy: the condition in which male and female sexes are found in separate individuals. Dioecy is rare in vascular plants overall but present in all cycad species. This brings important evolutionary and demographic implications that are discussed and reviewed by Iglesias Andreu et al. (2025). The authors identified that sex determination in cycads has been studied based on methods in karyology, morphology, anatomy, biochemistry, and genetics, while other perspectives that have arisen in discussion include ecophysiology or epigenetics. The difficulty of identifying the sex of individuals in the wild and ex situ collections poses a challenge to conservation actions, a persisting concern for threatened species, as exemplified by the authors for Mexican cycads in the genera *Dioon*, *Ceratozamia*, and *Zamia*.

Pulido-Silva et al. (2005) documented the spatial distribution patterns in five populations of *Ceratozamia fuscoviridis*, an endangered and endemic cycad from Mexico. The authors showed that, as in many other cycad populations, the individuals of this species tend to form small aggregates, likely because of the limited seed dispersal abilities typical of cycads. This aggregation was measured across different age groups (i.e., seedlings, infants, juveniles, adults) in various distance categories. The results indicated that, although seedlings are commonly found mixed with other age classes, in two populations, young plants tend to be separated from adults, suggesting possible intrapopulation competition. This is the first report of potential intraspecific spatial competition in cycads.

Two contributions in this issue focus on the species *Zamia manicata* from Colombia. First, Taborda-López et al. (2025) present a literature review on plant–animal interactions involving cycad seeds. Among 71 reviewed studies, only six provided systematic measurements of seed dispersal, making evident the limited understanding of biotic dispersal mechanisms in cycads. Through field observations and seed marking, the authors found that ~6% of seeds were dispersed at least 10 meters from the mother plant, suggesting that gravity itself might not explain seed dispersal. Camera trap footage revealed interactions between *Z. manicata* seeds and a medium-sized bird, *Baryphthengus martii*, which was observed feeding on the seeds, indicating it could act as a seed disperser.

In a separate study, Lopez-Gallego (2025) compared the demography of three *Z. manicata* populations located in different zones of a forest fragmented by anthropogenic activity: an interior (low-degraded), an edge (high-degraded), and an intermediate zone. Significant differences were found across several demographic parameters. Contrary to expectations, the edge population exhibited higher population growth rates, faster individual plant growth, and overall greater stability compared to the other two populations. The author suggests that increased light availability due to a more open canopy at the forest edge may benefit this population, though long-term monitoring will be essential to fully understand the ecological dynamics behind these patterns.

The final two articles offer historical perspectives that are essential for informing cycad conservation efforts. First, Deloso et al. (2025) present a comprehensive review

of the Missouri Botanical Garden's long-standing role as a repository for cycad education, research, and conservation. Since 1879, this plant collection has supported numerous cycad researchers from the United States and abroad. Its value has grown especially in recent decades, particularly with the progress of genetic approaches that have advanced our understanding of cycad development, taxonomy, and evolutionary history. The authors emphasize the importance of ex-situ conservation in light of recent threats, such as the cycad aulacaspis scale (CAS) invasion affecting Japan and other parts of Asia. Besides, Brooke et al. (2025) review the challenges faced in ex-situ conservation efforts for *Cycas micronesica* in Guam. Despite having a clearly defined conservation plan from the onset of the CAS invasion in 2005, changes in management personnel, and particularly the exclusion of the resident crew responsible for plant care, may have contributed to the failure to protect these plants from infestation. This case provides valuable lessons that can inform the design and implementation of future conservation initiatives.

I hope this second part of the Special Feature provides a broader perspective on current topics in cycad biology. As highlighted throughout, cycads are valued for a range of unique attributes, including their rarity and ancestral traits of uncertain origin: features that contribute to their appeal. The studies presented here offer a glimpse into ongoing research, primarily focusing on four genera: *Cycas*, *Dioon*, *Zamia*, and *Ceratozamia*. However, the remaining six genera are also of significant interest: *Stangeria*, *Microcycas*, *Bowenia*, and *Lepidozamia* are genera with only one or two extant species, and their biology would tell us more about their rare evolutionary pathways. *Encephalartos* (71 species) and *Macrozamia* (41 species) are diverse genera geographically restricted to Africa and Australia, respectively, and the factors involved in their diversification would tell us more about how cycads could adapt to wide ranges of environments within those regions. We can expect future research on them to appear in *Plant Species Biology* or other journals. While this issue has centered on cycads, many other fascinating plant groups remain to be explored, each offering insight into the origins of the biodiversity that surrounds us.

CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

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