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Ecology and Ecophysiology of Ferns and Lycophytes in a Changing Climate: A Special Issue of the American Fern Journal

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The last decade has seen an unprecedented increase in fern and lycophyte research, especially in the fields of floristics (with the completion of large floras such as for Brazil (Flora e Funga do Brazil, 2022), and China (Zheng-yi, Raven, and DeYuan, 2013)); species checklists (such as for Colombia (Bernal *et al.*, 2019) or the World (Hassler, 2022)); genomics (with now six complete genomes (Banks *et al.*, 2011; Li *et al.*, 2018; Huang *et al.*, 2022; Fang *et al.*, 2022; Marchant *et al.*, 2022), a topic covered in a recent special issue of the American Fern Journal (Wolf and Barker, 2019)); an updated classification system (PPG I, 2016); a molecular phylogeny incorporating over 4000 taxa (Testo and Sundue, 2016); and now an open fern tree of life that can be continuously updated (Nitta *et al.*, 2022). Two recent textbooks specializing in ferns cover a wide array of topics, with a central focus on progress in biotechnology (Fernández, 2018; Marimuthu *et al.*, 2022).

Although the number of studies focusing on the ecology and ecophysiology of ferns are equally on the rise (Mehltreter, Walker, and Sharpe, 2010), the smaller community of researchers working in these areas means our progress may appear slower than that of the taxonomic and molecular-driven disciplines of fern research. The importance of this work though cannot be understated. The existential threats of habitat loss and contamination, in combination with global climate change, provide a desperate urgency for field and laboratory studies that measure, understand, and predict the responses of ferns and lycophytes to the threats of the Anthropocene, and promote actions for their protection and conservation. The rapid progress in other scientific disciplines provides welcome support in accelerating ecological and ecophysiological fern research. Online floras and open-access publications accelerate species identification and increase access to scientific literature independently of paywalls and academic libraries. Ever more portable, smaller, and faster devices to perform environmental and ecophysiological measurements with increased ease, are enhancing our opportunities to monitor more traits in the field, transfer data over a network, and allow for live access to data (*e.g.,* Internet of Things), while shared analytical open-resource tools such as R (R Core Team, 2018) promote the publication of protocols. We live in a time of enormous scientific progress and innovation, but also in a time of immense ecological challenges that require increasingly sophisticated approaches to collecting ecological and ecophysiological data.

What are the main ecological currents and limitations of fern research? Many studies investigate the impact of anthropogenic disturbance and land use change on fern diversity, their capacity to accumulate heavy metals for phytoremediation, the traits that make some fern species invasive, and their phytochemical composition in search of possible medicinal compounds. Most studies are limited to a few species of agricultural, industrial, medicinal, ecological, or molecular interest such as *Azolla filiculoides*, *Equisetum arvense*, *Huperzia serrata*, *Pteridium aquilinum*, *Pteris vittata*, and *Selaginella moellendorffii*. In contrast, basic research into spore dispersal mechanisms, soil preferences of ferns, gametophyte physiology and reproduction, fern mycorrhizae, fern-animal interactions, desiccation, and heat tolerance are required to improve our understanding of the differences in the ecological requirements of ferns. Furthermore, sampling a wider array of the over 12,000 species of extant ferns and lycophytes at wider spatial and temporal scales is essential for future studies, achievable by increased collaboration and automation.

Within the last decade, ferns have been used as model plants for southern temperate forests (Brock *et al.,* 2016), and as indicators of disturbance and edge effects (Silva, Mehltreter, and Schmitt*,* 2018). Invasive fern species have been investigated to understand their distribution patterns, the reasons for their invasiveness, and methods to control them (Jones *et al.*, 2018). On the other hand, rare fern species have been studied to answer questions about the possible causes of rarity and to improve conservation management (Tájek, Bucharová, and Müzbergová*,* 2011; Cicuzza, 2021). We are now aware that ferns are also a far more palatable and common food source for animals than previously thought and may contain a diverse microbiome (Masocha *et al.*, 2022). Recent reviews document over 800 insects feeding on ferns (Fuentes-Jacques *et al.*, 2022) and 93 host species of gall-forming fern insects (Santos *et al.,* 2019). Against these herbivore attacks, ferns possess a syndrome of defenses (Farias *et al.*, 2020), including sometimes even ant-attracting nectaries found in 101 fern species (Mehltreter, Tenhaken, and Jansen, 2022). We have also improved our understanding of the methods of fern spore dispersal, which is diverse and dependent on spore mass and density (Gómez-Noguez *et al.*, 2022), with an increasing number of studies showing that spores might be successfully dispersed by birds (Hervías-Parejo *et al.*, 2019) and bats (Sugita *et al.*, 2013), and are often viable after passing the guts of other herbivores (Boch *et al.,* 2016), a fact that could profoundly alter our historic idea that ferns are exclusively wind-dispersed species.

The last decade of fern and lycophyte ecophysiology has completely transformed our functional understanding of this group of plants, particularly with regard to adaptations that enhance survival during periods of water deficit. While traditionally viewed as ecologically constrained by a reproductive need for liquid water, discoveries of widespread gametophyte desiccation-tolerance place an increasing emphasis on the ecological importance of the sporophyte physiology of ferns and lycophytes (Pittermann, Brodersen, and Watkins, 2013). Recent work suggests that adaptations enabling fern and lycophyte survival in non-mesic environments converge on variation in xylem function (Suissa and Friedman, 2021; Cardoso *et al.*, 2020; Holmlund *et al.*, 2020). This stands in contrast to stomatal regulation during water deficit, which is near-universally under simple passive control in ferns and lycophytes, a mode of action that differs considerably from the derived hormonal and metabolically regulated stomata during drought in seed plants (McAdam and Sussmilch, 2021). To survive seasonally dry and ever-wet environments some fern and lycophyte species have evolved a highly embolism-resistant xylem that is as resistant as the xylem of many drought-tolerant seed plants (Pittermann, Baer, and Sang, 2021). The ability of some species to recover complete physiological function after extreme desiccation or retain photosynthetic function through freeze-thaw cycles during winter may have been the catalyst for evolutionary radiations into deserts and environments with a freezing winter, respectively (Fernández-Marín *et al.,* 2021).

Studies are also capitalizing on the considerable diversity in form and function across ferns and lycophytes as a model system for answering important questions about plant function. Recent work has started to utilize this considerable diversity to test important questions ranging from the functional role of highly diverse stelar arrangements to the nature and evolution of stomatal control and photosynthetic capacity, through to xylem function (Suissa and Friedman, 2021).

In this special issue, we present a collection of articles that span the breadth of cutting-edge ecological and ecophysiological work on ferns and lycophytes, including original data and reviews.

Castrejón-Varela *et al.* (2022) review the biochemical compounds of ferns with possible defensive functions against herbivores. Excellent former reviews were mainly interested in the presence of the large array of chemical compounds, their structure, and metabolic pathways (*e.g.*, Vetter, 2018), but often left out their ecological functions, an omission now addressed.

Sharpe (2022) studies the impact of hurricanes on Puerto Rican fern communities. Because most research on the disturbance ecology of ferns are short-term studies on small scales, this contribution fills an often-neglected gap: the effect of recurring climatic factors happening at larger time scales.

Castrejón-Alfaro *et al.* (2022) provide the first phenological study on ferns from seasonally dry forests of Mexico. This work demonstrates that xerophytic fern species are phenologically well-adapted to the local environment, having evolved leaf deciduousness or desiccation-tolerance to survive the dry seasons and a preference for low canopy cover to reach fertility.

Kessler and Kluge (2022) investigate the possible effect of climate change on altitudinal distribution patterns and predict a future upward displacement of mountain ferns in search of colder climates. If their predictions are correct, the geographic distribution range of mountain ferns will shrink as the land surface area decreases with altitude, and the cold-adapted species at the highest elevations may face extinction.

Two papers investigate stomatal control in the ecologically and morphologically unique, semi-aquatic Marsileaceae. Aros-Mualin *et al.* (2022) discuss research on the nature of a unique circadian regulation of stomata in this family. The circadian responses of stomata from the four studied species differ considerably and play an important role in the differential regulation of water use during the day.

Westbrook and McAdam (2022) also consider stomatal function across the Marsileaceae, finding that the aquatic environment has facilitated considerable evolutionary innovations in stomatal function within this family, including the loss of a stomatal response to light in *Pilularia*. In addition, a new perspective on the evolutionary origins of the filiform leaves in *Pilularia* is proposed, one which suggests that these leaves are simply stipes without a lamina.

Suissa *et al.* (2022) provide a comprehensive review of recent advances to our understanding of xylem function in ferns and lycophytes. They conclude that xylem function is highly diverse across species, and that many terrestrial fern species have evolved hydraulic segmentation between the leaf and rhizome.

Watts and Watkins (2022) investigate the future distribution of the fern and lycophyte flora of New Zealand. The future ranges of most species are forecast to move upslope or further south, with more than half of all species predicted to have a greatly reduced suitable habitat 50 years from now, particularly the enigmatic tree ferns.

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