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RESEARCH PAPER

Sexual systems in gymnosperms: A review

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Abstract

The aim of this study was to update figures for the presence of dioecy among the gymnosperms and investigate its correlation with climate, growth form, pollination and seed dispersal syndromes, and risk of extinction. Dioecy was found in almost 65% of contemporary gymnosperm species, a higher percentage than previous estimates. It dominates in 8 of the 12 families. As in angiosperms, dioecious gymnosperms are particularly common in climbers and are more commonly found in tropical climates. Analysis of the degree of threat using IUCN red list categories showed that the proportion of threatened species is higher in dioecious than in monoecious species only in temperate climate. The high sensitivity of dioecious species to environmental changes associated with human activity in temperate climate may explain this phenomenon. The monophyly of extant gymnosperms and the relatively small number of species (about 1000) create the possibility of treating them as a model group in investigating the evolution of sexual systems.

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Introduction

Dioecy is relatively rare in plants. Hermaphroditic species dominate among angiosperms and dioecious species account for around 6% of plants (Renner & Ricklefs, 1995; Weiblen et al. 2000; Renner, 2014). Despite its rarity, dioecy does have its advantages. The most emphasized advantage of dioecy is the complete exclusion of the risk of self-pollination (Darwin, 1876; Charlesworth & Charlesworth, 1978). A second advantage is the optimization of resource allocation to both male and female functions. This is one of the explanations why

fleshy, presumably expensive, fruits are more common in dioecious species (Maynard-Smith, 1978; Charnov, 1982; Renner & Ricklefs, 1995).

Nevertheless, it is often emphasized that dioecy is not an optimal sexual system in sedentary organisms. Indeed, hermaphroditism is considered to be the best strategy for optimizing fitness where cross-pollination opportunities are limited since automatic or pollinator-assisted self-pollination is sometimes possible if no other partner is near (Charnov, 1982). A second disadvantage of dioecy is that the number of individuals producing seed is half that of hermaphrodites because seeds are carried only by females. This results in dioecious species having reduced seed dispersal, the so-called seed-shadow handicap (Heilbut, Ilves, & Otto, 2001). Moreover, although female organisms can optimise resource

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allocation, they often expend greater reproductive effort over a longer period of time compared to males (Vessella, Salis, Scirè, Piovesan, & Schirone, 2015; Garbarino, Weisberg, Bagnara, & Urbinati, 2015; Matsushita, Takao, & Makita, 2016; Zarek, 2016). It is also known that sexes differ in their response to stress (Juvany & Munné-Bosch, 2015; Ariel & Alejandro, 2016), and sexes can also have varying environmental requirements and occupy slightly different niches, potentially leading to spatial sex segregation (Cox, 1981; Bierzychudek & Eckhart, 1988).

Due to these disadvantages, a hypothesis has emerged that dioecy is evolutionarily less advantageous than hermaphroditism, that is, sporophytes with bisexual strobili or flowers (Westergaard, 1958). Supporting this, it has been shown that within the angiosperms, clades that consist of dioecious plants contain fewer species than their sister clades; this suggested that dioecious species were more prone to extinction and that dioecy was an evolutionary ‘dead end’ (Heilbuth, 2000). Nevertheless, species diversification rates have been shown to be as high in dioecious as in hermaphrodite lineages (Käfer et al., 2014; Käfer & Mousset, 2014; Sabath et al., 2016). Thus, the primary cause of the lower number of dioecious species in sister clades could be the frequent reversion to hermaphroditism (Käfer, Marais, & Pannell, 2017; Goldberg et al., 2017), in agreement with reports arguing that such reversions are not infrequent in angiosperms (Barrett, 2013; Renner, 2014).

Dioecy in angiosperms has evolved repeatedly, either from monoecy or from gynodioecy (Charlesworth & Charlesworth, 1978; Renner & Won, 2001; Barrett, 2002). There is also the possibility of the reverse phenomenon, that monoecy can evolve from dioecy, as exemplified in the *Momordica* genus, where it has possibly happened seven times (Schaefer & Renner, 2010). In gymnosperms, dioecy has repeatedly evolved from monoecy, for example, 10–13 times just within the Pinopsida (Leslie, Beaulieu, Crane, & Donoghue, 2013). Gymnosperms do not have gynodioecy nor any of the many other sexual systems from which dioecy can and has evolved in angiosperms. Differences in the genetic mechanisms of sex determination in both angiosperms and gymnosperms suggest that there are multiple pathways of the evolution of dioecy. Sex chromosomes are known in only about 40 species of plants, mainly in angiosperms (Ming, Bendahmane, & Renner, 2011), however, heterochromosomes in gymnosperms have been found in *Ginkgo biloba* L., where a ZW/ZZ system is present, whereas *Cycas revoluta* Thunb. is characterized by a XX/XY system. Species of *Podocarpus*, such as *P. macrophyllus* (Thunb.) Sweet, *P. longifoliolatus* Pilg. and *P. elatus* Seem. ex Parl., also present a unique if unspecified system of sex determination (Hizume, Shiraishi, & Tanaka, 1988; Ming et al., 2011); *P. macrophyllus* females have four sex chromosomes ($X_1X_1X_2X_2$) while males have three (X_1X_2Y). On top of any genetic determination, many dioecious species can change sex under the influence of environmental factors.

More research on reproductive syndromes has been carried out on angiosperms than on gymnosperms. It has been shown that dioecy in angiosperms is found more frequently among trees, lianas or shrubs than among herbaceous species (Renner & Ricklefs, 1995; Vamosi, Mazer, & Cornejo, 2008). Dioecy is also more common in tropical climates and islands than in moderate or cold conditions (Bawa, 1980; Baker & Cox, 1984; Vamosi & Vamosi, 2004). Additionally, pollination in dioecious species is frequently by wind rather than insects whereas seed dispersal is by animals rather than wind (Bawa, 1980; Thomson & Brunet, 1990; Charlesworth, 1993; Vamosi, Otto, & Barrett, 2003; Schlessman, Vary, Munzinger, & Lowry, 2014). Accordingly, Givnish (1980) concluded that wind-pollinated and animal-dispersed gymnosperms are usually dioecious, and wind-dispersed gymnosperms are usually monoecious. However, the classification of gymnosperms has recently changed dramatically and there is a need for a review of sexual systems in gymnosperms in the light of the new groupings to see if these generalisations still hold true.

The proportion of gymnosperm species assumed to be dioecious has varied. Thus, Givnish (1980) scored 420 (52%) of 804 gymnosperm species as dioecious. Owens, Hardev, and Eckenwalder (1990) reported that 25% of 680 species were entirely dioecious and another 11% sometimes dioecious, sometimes monoecious. Ming et al. (2011) calculated that 36% of 1010 gymnosperms are dioecious, including all Ginkgoaceae, Cycadaceae and Gnetaceae, and Kumar, Kumari, and Sharma (2014) reported that 36% of 1021 species are dioecious. Here we review the current knowledge about the occurrence of dioecy in gymnosperms and determine whether dioecy is related to climate, growth form, pollination system, strobilus type.

Materials and methods

Data on dioecy were compiled for 1033 species across all gymnosperm families from available literature (Farjon, 2010; Osborne, Calonje, Hill, Stanberg, & Stevenson, 2012; Ickert-Bond & Renner 2016) and databases such as The International Plant Names Index, The Plant List, World Checklist of Selected Plant Families and The Gymnosperm Database. In addition to sexual dimorphism, data were compiled on the climate in which a particular species is present, method of pollination, seed dispersal mechanism (animal or wind), growth form (Raunkiaer, 1934; De Langhe, Delvosalle, Duvigneaud, Lambinon, & Van den Berghen, 1983), and the degree and threat of extinction according to the red list of International Union for Conservation of Nature (IUCN). Statistical analysis was carried out using JMP software (SAS Institute).

Results

In total, 667 of the 1033 (64.6%) species currently accepted (see Appendix A in Supplementary material; Table 1) are

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