Geographical distribution of dioecy and its ecological correlates based on fine-scaled species distribution data from a subtropical island

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Abstract
Dioecy is a rather rare sexual expression system guarantees outcrossing to avoid the deleterious effects of inbreeding. The incidence of dioecy varied among local floras and suggested inclining to tropical and oceanic environments, but its eco-correlates received little research attention. In this article, we explored geographical patterns and variations in sexual expression systems of angiosperms in mountainous environments of Taiwan, a subtropical island in East Asia. A comprehensive geo-database of vegetation inventories and herbarium specimens were used to identify eco-correlates causing variations in the horizontal geographical extent and along a large elevational gradient of more than 3,500 m. We found the average incidence of dioecy in the flora of Taiwan to be 8.2%, but it exhibits geographical variations from islets in the Taiwan Strait to the Pacific Ocean. Detailed studies on the main island of Taiwan revealed that the incidence of dioecy varied among land cover types and elevational zones. An apparent two-step decreasing pattern of dioecy percentages with elevation was found, with the highest proportion in the lowlands (0–600 m; 23.96%), followed by middle elevations (600–2,700 m; 20.87%) and subalpine regions (2,700–3,900 m; with a range of 11.38–0%). We found that spatial variations of dioecy were associated with eco-correlates of land cover, elevation, woodiness, species richness, and mean annual temperature. Results of this study partially support Bawa’s hypothesis of a higher incidence of dioecy on oceanic islands, and is consistent with Baker and Cox’s observations of richer dioecious species on high-mountain islands in the tropics and subtropics.

Keywords
dioecy, elevational gradient, sexual expression system, subtropics, Taiwan

1 | INTRODUCTION

Dioecy is a rather rare breeding system in plants that guarantees outcrossing to avoid the deleterious effects of inbreeding. The global incidence of dioecy among angiosperms is estimated to be 6% (Renner & Ricklefs, 1995), and its presence can vary among local floras. Some researchers found higher proportions of dioecious species in tropical floras (22.0–40.0% by Bawa & Opler, 1975; 30.6% in Venezuela by Sobrevila & Arroyo, 1982) than in temperate floras such as the British Isles, North Carolina, southern California, and South Australia (less than 4.0% by Bawa, 1980).
In addition, oceanic islands were suggested as being hotspots of dioecy (Baker & Cox, 1984; Bawa, 1982). For example, Hawaii (27.7% by Bawa, 1982; 14.7% by Sakai, Wagner, Ferguson, & Herbst, 1995), New Zealand (12.0–13.0% by Godley, 1979), Tonga (16.0% by Yuncker, 1959, in Baker & Cox, 1984), and Samoa (17.0% by Setchell, 1924, in Baker & Cox, 1984) are the most dioecy-rich islands in the world. Baker and Cox (1984) reported that the maximum elevation plays an important role in the percentage of dioecy on islands. However, variations in the incidences of dioecy among elevation, vegetation types, and possible ecological correlates have received little research attention. During the past few decades, several studies focused on the relationship between dioecy and elevation. There is evidence that the percentage of dioecious species increases with increasing elevation (Arroyo & Squeo, 1990), or dioecy and elevation exhibit a unimodal relationship that peaks in middle elevations (Vamosi & Queenborough, 2010). It is known that dioecy is also correlated with several life-form attributes such as woodiness (Bawa, 1980; Bullock, 1985; Sakai et al., 1995; Webb, Llloyd, & Delph, 1999); small, inconspicuous, or greenish flowers (Bawa, 1980; Fox, 1985); fleshy fruits (Bawa, 1980; Givnish, 1980; Webb et al., 1999); unspecialized pollinators (Baker & Cox, 1984; Bawa & Opler, 1975); and a young successional stage (Réjou-Méchain & Cheptou, 2015).

Taiwan is a continental island on the western edge of the Pacific Ocean; it is located approximately 200 km east of the Asian mainland and 360 km north of Luzon Island, the Philippines (Hsieh & Shen, 1994). More than 73% of the land is occupied by hills and mountains, and the Central Mountain Range reaches nearly 4,000 m above sea level. The main landmass of Taiwan was formed as an island during the Miocene epoch, but is generally believed to have been connected to the Asian mainland during the four glacial periods of the late Quaternary, with the final connection occurring at the end of the last glacial period approximately 10,000 years ago (Shen, 1994). The dynamic environment of the island creates diverse topography and habitats harboring more than 4,200 vascular plant species (with approximately 3,500 species being angiosperms), of which 1,052 (22.9%) are endemic to Taiwan. A total of 60.7% of the island is covered by forests, in which 79% is natural (https://www.forest.gov.tw/EN/0002664) and shows a clear vertical zonation caused by elevational variations in climate conditions (Su, 1984). Hills below 500 m are considered subtropical to tropical environments and are occupied by *Ficus-Machilus* forests. Areas at 500–1,500 m, corresponding to the subtropical climate zone, are occupied by broadleaf evergreen forests and are mainly dominated by species of the Lauraceae and Fagaceae. Mountains at 1,500–2,500 m are considered the cool temperate vegetation zone, usually dominated by *Quercus* species. Forests ranging 2,500–3,500 m are comparable to the cold temperate zone and are dominated by coniferous species such as *Tsuga, Picea*, and *Abies*. Areas above 3,500 m are considered subarctic environments that approach the timber line of Taiwan (Hsieh, Shen, & Yang, 1994).

A tropical climate (Baker, 1959; Baker & Cox, 1984; Bawa & Opler, 1975) and island habitats (Baker & Cox, 1984; Sakai et al., 1995) have long been speculated to be correlated with the presence of dioecy. Taiwan contains plant species that migrated from temperate Asia via a land bridge during the last glacial maximum (LGM); however, this island also harbors abundant tropical species conveyed by ocean currents and animals. Because of the transition between temperate- and tropical-originating floras and the obvious elevational climatic variations that exist in Taiwan, we can reasonably assume that sexual expression systems should gradually vary along geographical and elevational gradients. In our previous study, we documented the incidence of dioecy in Taiwan using species lists and taxonomic revisions from the second edition of the *Flora of Taiwan* (Huang and Editorial Committee of the Flora of Taiwan, 1993, 1996, 1998, 2000, 2003). We found that the overall percentage of dioecious species was approximately 8%, but the percentage varied among different forests and climatic zones in selected plots. We also found that dioecy probably tended to decrease with elevation (Tseng, Hsieh, & Hu, 2008) based on data from seven selected forest plots at different elevations. However, descriptive data of the flora were only preliminary in that research on breeding systems; further detailed and advanced studies are required to elucidate correlations between dioecy and ecological factors. In this study, we applied a geographic information system (GIS) to accurately integrate geo-referenced data from extensive plot-based vegetation surveys and herbarium specimen collections with ecological factors for each species occurrence. Our main objectives were to: (a) determine the incidences of dioecy and other sexual system for more than 3,500 angiosperms based on data of newly updated vegetation surveys and herbarium specimens; and (b) explore changes in dioecy percentages along geographical and elevational gradients and their possible ecological correlates.

## 2 METHODS

### 2.1 Data source

We collected distribution data of angiosperms, including 379,962 specimen records from four main herbaria (TAI, TAIF, HAST, and TNM) and 991,455 occurrences from two national biological resource inventory projects in Taiwan (Figure S1). Specimen metadata from the herbaria included...
the following content: scientific name, collection date, locality, collectors and field number, and identifiers. Specimens with collection locality descriptions but without geographical coordinates were assigned coordinates by consulting place name databases and archival and online maps. The two national biological resource inventory projects were the National Vegetation Mapping implemented in 2003–2008 and the Survey of Invasive Alien Plants implemented in 2009–2012. In the National Vegetation Mapping project, 3,564 plots (400 m² in size) were established and surveyed in national forest districts throughout Taiwan. In the Survey of Invasive Alien Plants project, another 3,566 plots (125 m²) were established at low elevations and on the plains. In accordance with criteria set forth by the vegetation survey team, each plot was categorized into one of eight land cover types: bamboo forest (BAM), cropland (CL), grassland (GL), natural forest (NF), plantation (PL), roadside (RS), shrub land (SL), and *Yushania* grassland (YUS). For each plot, the following parameters were measured: geographical coordinates, abiotic environmental factors (elevation, slope, and aspect), and biotic factors (species, diameter at breast height for woody plants, and coverage of herbaceous plants and seedlings). Ultimately, 1,364,490 occurrence records were compiled into our GIS database, including 187 families, 1,216 genera, and 3,537 angiosperm taxa.

### 2.2 Estimates of climatic variables for field survey plots

Because of difficulties in measuring climatic variables in each plot, we utilized *clim.regression*, a climate downscaling program based on algorithms of bilinear interpolation and dynamic elevation adjustment (Lin et al., 2018; Wang, Hamann, Spittlehouse, & Carlos, 2016; Wang, Wang, Innes, Seely, & Chen, 2017), to downscale the 5-km-gridded climate data produced by the Taiwan Climate Change Projection and Information Platform into a scale-free surface, rendering it more suitable and accurate for ecological research. Based on the coordinates and elevation of each plot, five climatic variable estimates,
namely the mean annual temperature (MAT), mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), temperature difference between the MWMT and MCMT (TD), and mean annual precipitation (MAP), were obtained.

### 2.3 Identification of sexual systems

Tseng et al. (2008) documented sexual expression systems of the flora of Taiwan, including 181 families, 1,120 genera, and 3,052 native species. Following Tseng et al.’s report, plant sexual systems were divided into four categories in this study: monoecious, dioecious, hermaphroditic, and “polygamous and others.” Species described as “monoecious or dioecious” in the *Flora of Taiwan* were considered monoecious because dioecious records sometimes reflect the dichogamous expression of unisexual flowers. Species listed as “dioecious or rarely monoecious” or “functionally dioecious” were considered to be dioecious. Species were recorded as hermaphroditic if they had bisexual flowers. Species recognized as “polygamous and others” included andromonoecious, gynomonoecious, androdioecious, polygamo-dioecious, polygamous-monocoeious, dioecious or hermaphroditic, dioecious or polygamous, monoecious or polygamous, dioecious or hermaphroditic or polygamous, dioecious or monoecious or polygamous, and species without detailed sexual system information. In Tseng et al.’s study, species with more than one variety, subspecies, or forma were considered one record to reduce double counts at the infraspecific level. However, ecological niches and geographical distributions may differ among varieties and subspecies; to reveal spatial and ecological identities of sexual expression systems, we narrowed our data down to the infraspecific level based on definitions provided in previous research and descriptions provided in the *Flora of Taiwan*. Finally, sexual expression systems of 3,537 taxa of angiosperms belonging to 187 families and 1,216 genera were documented in this study.

### 2.4 Data analysis

Taiwan is located on the southeastern edge of Eurasia Plate and is surrounded by islets that originated from different geological events. The Taiwanese flora also displays a transition from the Eastern Asiatic Region to the Malesian Region due to its geographical and historical context (Takhtajan, 1986). To express geographical patterns of sexual systems, georeferenced specimens, and inventory data were used to calculate the relative representation of sexual expression systems (dioecious, monoecious, hermaphroditic, and “polygamous and others”) among Taiwan and its associated islets (Figure 1).

In order to exclude imprecise ecological factors from ambiguous localities of specimen metadata, we extracted data from two national biological resource inventory projects which contained accurate GPS coordinates and plot parameters to conduct further analyses (Figure S1b). An analysis of

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**Table 1** Number of taxa and proportions of sexual expression systems of angiosperms in the flora of Taiwan and associated islands

| Region               | Area (km²) | Number of angiosperms | Sexual system       |
|----------------------|------------|-----------------------|---------------------|
|                      |            |                       | Dioecy | Monoecy | Hermaphrodite | Polygamy and others |
| Kueishan Island (KI) | 2.84       | 372                   | 50     | 37      | 247          | 38                  |
|                      |            |                       | 13.44% | 9.95%   | 66.40%       | 10.22%              |
| Orchid Island (OI)   | 48.39      | 957                   | 108    | 115     | 649          | 85                  |
|                      |            |                       | 11.29% | 12.02%  | 67.82%       | 8.88%               |
| Green Island (GI)    | 15.09      | 529                   | 56     | 61      | 359          | 53                  |
|                      |            |                       | 10.59% | 11.53%  | 67.86%       | 10.02%              |
| Taiwan (TW)          | 35,582.62  | 3,484                 | 281    | 371     | 2,548        | 284                 |
|                      |            |                       | 8.07%  | 10.65%  | 73.13%       | 8.15%               |
| Hsiao Lyukyu (HL)    | 6.80       | 360                   | 24     | 41      | 257          | 38                  |
|                      |            |                       | 6.67%  | 11.39%  | 71.39%       | 10.56%              |
| Penghu (PH)          | 126.86     | 303                   | 13     | 33      | 226          | 31                  |
|                      |            |                       | 4.29%  | 10.89%  | 74.59%       | 10.23%              |
| Cotton Islet (CI)    | 0.12       | 158                   | 6      | 8       | 119          | 25                  |
|                      |            |                       | 3.80%  | 5.06%   | 75.32%       | 15.82%              |
| Total                | 35,782.72  | 3,537                 | 290    | 379     | 2,582        | 286                 |
|                      |            |                       | 8.20%  | 10.72%  | 73.00%       | 8.09%               |
variance (ANOVA) and Tukey's honest significant difference (HSD) post-hoc test were used to examine differences in the percentage of dioecy among land cover types and elevational zones. A linear regression was conducted to explore relationships between dioecy and elevation. However, in order to verify the difference among land cover types, the regression analysis was carried out for each land cover type separately. To assess the detailed elevational patterns of dioecy of natural vegetation, plots of the four natural land cover types (NF, SL, GL, and YUS) were extracted and categorized into 13 elevational groups of 300-m contour intervals for local polynomial regression function (LOESS) analysis to reveal the overall variation in dioecy with the change in elevation.

Dioecy is unevenly distributed among regions, life forms, and families of angiosperms (Bawa, 1980). Many biotic and abiotic correlates of dioecy have been recognized, such as woody communities (Bawa, 1980), tropical floras on islands (Baker & Cox, 1984; Bawa, 1980; Bawa, 1982), species richness, phylogenetic diversity (Vamosi & Queenborough, 2010), and mesic habitats in lowlands and lowland-montane regions (Sakai et al., 1995). Most of the factors are highly entangled, and correlations cannot be easily separated, especially when using vegetation data from field surveys. For this reason, a principal component analysis (PCA) was conducted to explore possible variables related to sexual expression systems. Proportion of sexual expression systems of each surveyed plot was used as input data and first analyzed by the PCA, and then groups of biotic variables (number of species; the rate of endemic species; proportion of tree, shrub, herbaceous, and climber species; proportion of native, naturalized, and cultivated species of each plot) and abiotic variables (elevation, slope, and aspect from field measurement and MAT, MAP, and TD from the output of clim. regression) were added separately as passive variables and projected on the ordination plot. All data processing and analyses were performed with the ESRI ArcGIS 10.5 and R 3.3.1 software (R Core Team, 2016).

3 | RESULTS

3.1 | Distribution patterns of sexual systems in Taiwan and its associated islands

According to our compiled database based on specimens and inventory surveys, 290 (8.20%), 379 (10.72%), 2,582 (73.00%), and 246 (6.96%) of 3,537 taxa were dioecious, monoecious, hermaphroditic, and “polygamous and others”, respectively. The remnant 40 taxa (1.12%) are lack of sexual expression information.

The percentage of dioecy considerably varied among Taiwan proper and its associated islets. The dioecy percentage of the main island of Taiwan was 8.07%. Richer assemblages of dioecious species were discovered on three volcanic islands of Kueishan Island (KI), Orchid Island (OI), and Green Island (GI), representing 13.4, 11.3, and 10.6% of the overall proportions, respectively. All three of these islets which were richer in dioecious species are located off the east coast of Taiwan and are isolated by ocean waters deeper than 200 m. Other islets located to the west in the Taiwan Strait, with sea depths shallower than 200 m, exhibited lower proportions of dioecy, ranging 3.8–6.7% (Figure 1 and Table 1).

In addition to the increasing incidence of dioecy through a west-to-east gradient from the Taiwan Strait to the Pacific Ocean, distributions of sexual expression systems were also highly variable among local habitats of Taiwan. Field data from 5,857 plots belonging to eight land cover types were used to evaluate the incidences of dioecy within different environmental surroundings. The average incidence of dioecy in Taiwan was 8.20%, however, results of the ANOVA indicated that it was significantly inconsistent among land cover types (Table 2a, F = 1.097, p < .001). The result of Tukey’s HSD test further grouped land cover types into three categories based on their dioecy proportion. Natural forests (NF) were the most dioecy-rich community with an average incidence of 20.81%. Dioecious species were also common in woody-

### Table 2

ANOVA (a) and Tukey’s HSD test (b) for dioecy percentage among different land cover types

| Land cover type          | No. of plots | Average dioecy (%) | SD (%) | Tukey’s HSD test (conf. level = 0.95) |
|--------------------------|--------------|--------------------|--------|-------------------------------------|
| Natural forests (NF)     | 3,240        | 20.81              | 7.81   | d                                   |
| Plantations (PL)         | 323          | 17.28              | 9.30   | c                                   |
| Bamboo forests (BAM)     | 150          | 17.01              | 8.82   | c                                   |
| Shrub lands (SL)         | 53           | 15.41              | 15.51  | c                                   |
| Roadside (RS)            | 1,131        | 4.26               | 4.56   | b                                   |
| Grasslands (GL)          | 75           | 4.30               | 7.26   | ab                                  |
| Yushania grasslands (YUS)| 79           | 2.16               | 5.72   | ab                                  |
| Croplands (CL)           | 806          | 2.56               | 4.21   | a                                   |

*Note: a, b, c, or d is group divided by Tukey's HSD test. The means in the same group are not different significantly by the test. Abbreviations: df, degrees of freedom; HSD, honest significant difference; MS, mean squares; SD, standard deviation; SS, sum-of-squares.*
dominant communities, including plantations (PL), bamboo forests (BAM), and shrub lands (SL), with proportions ranging 15.41–17.28%, which were relatively lower compared to natural forests. The lowest incidences of dioecy were found in disturbed, early successional, and non-woody vegetation, such as roadsides (RS), grasslands (GL), Yushania grasslands (YUS), and croplands (CL), with proportions ranging 2.56–4.26% (Table 2b). The mapped distribution of sexual expression systems also exhibited high spatial heterogeneity. Hotspots of dioecy usually occurred in mountainous areas, whereas the western plains and islets in the Taiwan Strait were mostly dioecious-poor and dominated by polygamous and hermaphroditic species (Figure S2).

3.2 Elevational patterns of dioecy and their ecological correlates

Results of the linear regression analysis revealed that the dioecy percentage significantly decreased with increasing elevation \((m < 0, p < .001)\) for each of the four natural land cover types of natural forests (NF), shrub lands (SL), grasslands (GL), and Yushania grasslands (YUS). Contrary results were obtained for anthropogenic vegetation and...
human-exploited areas. The incidence of dioecy for both bamboo forests (mostly planted on the main island of Taiwan) and croplands (CL) exhibited an increasing trend with elevation ($m > 0, p < .001$), but no consistent trend was observed for the dioecy proportion of plantation forests (PL) or roadside (RS) habitats with elevation (Figure 2). Several authors mentioned that the percentage of outbreeding or dioecious species in natural forests displayed a decreasing (Jacquemyn, Micheneau, Roberts, & Pailler, 2005; Tseng et al., 2008) or unimodal relationship (Vamosi & Queenborough, 2010) with elevation. Our data supported the declining incidence of dioecy with elevation; however, this pattern was only found for natural vegetation types and not for anthropogenic or disturbed habitats.

Results of Tukey's HSD test (Table 3) indicated that plots sampled from natural vegetation below 600 m had a significantly higher dioecy percentage, with a mean value of 23.96%. No statistically significant difference was detected among the groups in middle elevations (at 600–2,400 m, with a mean value of 21.14%), which represented a slightly decreased incidence of dioecy than that at low elevations. The dioecy percentage significantly declined in elevational groups above 2,400 m, and no dioecious species were found in any subalpine plots (at $\geq 3,600$ m). The LOESS regression demonstrated that the relationship between dioecy and elevation in natural habitats could be split into two segments with a breakpoint at approximately 2,200 m (Figure 3). The segment below 2,200 m showed a moderate decreasing trend for the dioecy proportion, whereas it became distinctly steeper above the breakpoint. In high-elevation plots above 2,500 m, zero values of dioecy were common, especially for Yushania grasslands (YUS) and grasslands (GL).

Results of the PCA showed that the first two principal components (axes) together accounted for 80.65% of the total variance in the sexual expression dataset. The first component was primarily related in one extreme (negative values) with high proportions of dioecious and monoecious species, and at the opposite extreme (positive values) with high proportions of hermaphroditic species (Figure 4). The second component represented a sharp contrast between polygamous species and those with other sexual expressions. Plots near the top tended to have a high proportion of polygamy, and this was strongly independent of the occurrence of dioecious and hermaphroditic species along the first component. Biotic variables of each plot, including the proportions of life forms (trees, climbers, shrubs, and herbs), proportions of origins (native, naturalized, and cultivated), species richness, and the rate of endemic species were orthogonally projected onto the first two principal components (Figure 4a). This illustrated that dioecy was significantly related to tree- and climber-dominant, and species-rich communities; in contrast, hermaphrodites were more common in herbaceous-dominant
communities, and they also demonstrated a positive relationship with the rate of endemism. Polygamous species was usually found in habitats rich in naturalized and cultivated species. Figure 4b displays the orthogonal projection of abiotic factors. Only two variables, MAT and elevation, were correlated with the composition of sexual expression systems, especially for the presence of dioecious and hermaphroditic species. This result revealed that dioecious species may prefer low-elevation regions with a warm climate, while hermaphroditic species exhibited higher dominance in subalpine areas with lower annual temperatures. The remaining abiotic factors (TD, MAP, slope, and aspect) seemed to have little effect on the distributions of sexual expression systems.

4 | DISCUSSION

4.1 | The horizontal distribution of dioecy—From continental to oceanic

The continental and oceanic distributions of dioecism and its latitudinal pattern have long been the subject of biogeographical research. Most studies relied on regional floristic checklists (Baker & Cox, 1984; Sakai et al., 1995; Tseng et al., 2008), but analyses examining dioecy and its geographical patterns based on complete and detailed inventory data are lacking. A review (Sakai & Weller, 1999) of geographic patterns of dioecism noted that dioecy is mainly related to island habitats (Baker, 1967; Baker & Cox, 1984; Bawa, 1980; Sakai et al., 1995) and tropical climates (Bawa, 1980; Givnish, 1980). Baker and Cox (1984) reported a strong correlation between the level of dioecy on islands and proximity to the equator as well as the maximum elevation of the island. Based on these perspectives, the level of dioecism in Taiwan should be higher than those of continents and should display a transitional characteristic between continental and oceanic floras due to its historical and geographical contexts. Our study documented that the average incidence of dioecy is 8.07% for the main island of Taiwan, and also discovered high dioecy percentages for three volcanic islets off eastern Taiwan (KI, OI, and GI, ranging 10.6–13.4%), which were isolated by deep ocean waters since their formation. Dioecy-poor floras were observed in islets west of Taiwan in the Taiwan Strait (CI, PH, and HL, ranging 3.80–6.67%), which were connected to the Asian mainland and Taiwan by the continental shelf during the LGM. The increasing trend of dioecy along islets from the Taiwan Strait toward the Pacific Ocean, which corresponds to the transition between continental and oceanic geographical contexts, might be a phenomenon supporting Bawa’s hypothesis (Bawa, 1980, 1982), which refers to a higher proportion of dioecy for tropical and oceanic insular floras.

In addition to the geographical reasons we stated, habitat type could be another factor affecting the composition of sexual systems of local floras. Sakai et al. (1995) explored the biogeographical and ecological correlates of dioecy in Hawaii. They found that dioecious species were rich in lowland and lowland-montane habitats but poor in coastal, coastal-lowland, and montane-subalpine habitats. In addition, tropical and subtropical forests are often reported to have higher incidences of dioecy than the regional average, such as subtropical evergreen broadleaf forests of Yunnan, China (24%, woody angiosperms only; Chen & Li, 2008a), azonal tropical forests in Yunnan (25.1%; Chen & Li, 2008b), tropical montane forests of Costa Rica (30.5%; Vamosi & Queenborough, 2010), and Neotropical forests in the Volta Velha Reserve, Brazil (28%; Vamosi, 2006). In Taiwan, Tseng et al. (2008) first reported the average proportion of dioecy to be 7.9%; however, they also identified higher dioecy percentages (11.9–23.9%) for seven selected forest sites. In this study, data from numerous field plots were utilized to confirm the high proportions of dioecy in woody communities, and a range of 15.41–20.81% was found (SL, BAM, PL, and NF in Table 2b). In contrast, we also proved that non-woody
communities (CL, YUS, GL, and RS) are poorer in dioecy than the average of the total flora. This result implies that regional incidences of sexual expression systems might not serve as the only indicator in breeding system studies, and varieties among habitats and local floras (e.g., montane broadleaf forests and subalpine coniferous forests) also need to be considered.

4.2 | The elevational distribution of dioecy—From lowlands to the subalpine zone

Variations in dioecy with changes in elevation are the other issue with which researchers are concerned but which have received comparatively little attention. Vamosi and Queenborough (2010) used inventory data from 15 permanent 1-ha plots, that ranged from 30 to 2,600 m, to explore relationships between the proportion of dioecy and elevation in tropical montane forests of Costa Rica. That study reported a unimodal relationship with a peak at 750 m, and a positive association with species richness. They suggested that the coincident decline in pollinator abundances with elevation may be one of the reasons, but could not provide further evidence in support of the underlying hypothesis. Another relevant study was an investigation of the change in orchid breeding systems with elevation on Réunion Island by Jacquemyn et al. (2005). Relatively high proportions of animal-pollinated orchids were found in low- to mid-elevation zones (below the sector of 1,601–2,000 m), whereas a reverse trend was observed at higher elevations (>2,000 m) with almost no outcrossing orchid species observed. They proffered two explanations for the observed patterns of elevational variation in the orchid breeding systems: a decline of pollinators, mainly dominated by long-tongued moths and flies, with elevation; and harsher more-disturbed habitats above 2,000 m where pollinator activities may have been more unpredictable than those in stable forest environments at low- to mid-elevation regions.

Our study discovered high dioecy proportions in low- and mid-elevation areas in Taiwan, which exhibited a declining and two-step linear pattern toward the subalpine zone with a distinct transition at elevations of 2,200–2,400 m. Results of the PCA also demonstrated clear associations of dioecy with elevation, warm temperatures, and woodiness. However, the two variables, MAT and elevation, are highly negative correlated because of the effect of lapse rate. Due to the multicollinearity problem between temperature and elevation, even though the patterns we revealed are closer to Jacquemyn’s observations on Réunion, however, the causal effects of decreasing dioecy or out-crossings along elevational and temperature gradients are still obscure and could not precisely be explained by the present approach. The estimation of causal relationships by detailed field sampling and statistical modeling would be an issue worthy for further studies.

This article demonstrated that tropical and subtropical zones of Taiwan were the most dioecy-rich regions, with proportions of 20–24%, values which are concordant with those found in azonal tropical forests (25.1%; Chen & Li, 2008a) and subtropical evergreen broadleaf forests.

![Biplots of the principal component analysis (PCA) showing relationships between sexual expression systems and (a) biotic and (b) abiotic correlates. The variables are indicated by vectors pointing in the direction of maximum variation. Long vectors indicate strong trends, and the angle between pairs of vectors approximates the correlation between the respective variables. Each vector points in the direction of increase for a given variable, and its length indicates the relative importance of that variable in the dataset.](image)
(24%, woody angiosperms only; Chen & Li, 2008b) of southwestern China at a similar latitude. Lowland forests in Taiwan are mainly dominated by Ficus (37 species in total, 27 of which are dioecious), and commonly contain dioecious-rich genera such as Smilax (19/19 of which are dioecious), Diospyros (10/10 of which are dioecious), and Mallotus (5/6 of which are dioecious). This may be the main reason supporting the highest incidences of dioecy in tropical and subtropical zones of Taiwan. However, the temperate vegetation of Taiwan displays dioecy proportions of 19.29–21.26%, which are completely incongruent with those in other temperate continental areas such as Ohio (11.0%; Braun, 1950 in Bawa & Opler, 1975), California (3.5%; Freeman, Harper, & Ostler, 1980), and the British Isles (4.3%; Kay & Stevens, 1986). We speculated that floras composed of plants with high phylogenetic affinities might, at least, partially explained the high levels of dioecy in subtropical and warm-temperate montane forests. For example, subtropical and warm-temperate montane forests in Taiwan commonly contain widespread genera such as Ilex (all 24 species of which are dioecious), Dioscorea (14/16 of which are dioecious), Litsea (14/14 of which are dioecious), Eurya (12/12 of which are dioecious), Neolitsea (12/12 of which are dioecious), Lindera (7/7 of which are dioecious), and Elatostema (6/15 of which are dioecious), which contribute to and support the high incidences of dioecy.

In this study, the average incidence of dioecy in coniferous and subalpine zones in Taiwan was 4.34%, which approximates those in subarctic and arctic territories such as Alaska (5.8 and 3.9%; Fox, 1985) and Iceland (3.0%; Baker & Cox, 1984). The dramatic decrease in dioecy at elevations above 2,400 m coincided with the lower bound of coniferous forests in Taiwan. We speculated that the decrease in dioecious species could be associated with the transition from broadleaf forests to coniferous forests as well as the simplified floristic compositions found at higher elevations.

Pollination by small generalist insects is one of the most important characteristics of dioecy (Bawa, 1980; Bawa & Opler, 1975; Sobrevila & Arroyo, 1982). Some studies reviewed the richness of terrestrial insect species along elevational gradients (Hodkinson, 2005). Most such studies, which were conducted at 0–2,000 m, revealed a decreasing pattern of insect richness with elevation (Hanski, 1983, in Indonesia; Wolda, 1987, in Panama; McCoy, 1990, in the southeastern United States; Perillo, Neves, Antonini, & Martins, 2017, in tropical Brazil), or discovered a pattern that peaks at mid-elevations (Gagne, 1979, in Hawaii; McCoy, 1990, in the southeastern United States; Lefebvre, Villetmant, Fontaine, & Daugeron, 2018, in the southern Alps, France). Insects are the main pollinators of flowering plants in general, regardless of whether they are generalists or specialists (Jacquemyn et al., 2005), thus it is reasonable to suspect that our finding on the decline in dioecy may be partially correlated with the change of insect pollinators along the elevational gradient. Nevertheless, pollinators in Taiwan have been insufficiently surveyed to support our assumptions, more investigations on the relationship between plant sexual expressions and pollinators would be a future subject.

Overall, natural vegetation in the low- to mid-elevation regions of Taiwan showed higher proportions of dioecious species than the average global proportion, and demonstrated a decreasing trend toward the subalpine zone. This might be associated with the island context, and responses to a warm climate, woody floras, and the richness of insect pollinators on an elevational gradient. Although the intact species distribution database that we used in this article was helpful in studying geo-patterns of breeding systems, better knowledge and investigations of patterns of pollinator richness, phylogenetic affinities of components of the local floras, and further ecological studies are required to verify the causalities.

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AUTHOR CONTRIBUTIONS

J.H. conceived the idea; H.L. carried out analyses and led the writing; Y.T. and C.H. contributed data; all authors commented on the manuscript.

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REFERENCES

Arroyo, M. T. K., & Squeo, F. A. (1990). Relationship between plant breeding systems and pollination. In S. Kawana (Ed.), Biological approaches and evolutionary trends in plants (pp. 205–227). London: Academic Press.
Baker, H. G. (1959). Reproductive methods as factors in speciation of flowering plants. *Cold Spring Harbor Symposia on Quantitative Biology*, 24, 177–191.

Baker, H. G. (1967). Support for Baker's law—As a rule. *Evolution*, 21, 853–856. https://doi.org/10.2307/2406780

Baker, H. G., & Cox, P. A. (1984). Further thoughts on dioecism and islands. *Annals of the Missouri Botanical Garden*, 71, 244–253. https://doi.org/10.2307/2399068

Bawa, K. S. (1980). Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics*, 11, 15–39. https://doi.org/10.1146/annurev.es.11.110180.000311

Bawa, K. S. (1982). Outcrossing and the incidence of dioecism in island florbas. *The American Naturalist*, 119, 866–871.

Bawa, K. S., & Opler, P. A. (1975). Dioecy in tropical forest trees. *Evolution*, 29, 167–179. https://doi.org/10.2307/2407150

Bullock, S. H. (1985). Breeding systems in the flora of a tropical deciduous forest in Mexico. *Biotropica*, 17, 287–301. https://doi.org/10.2307/2388591

Chen, X.-S., & Li, Q.-J. (2008a). Patterns of plant sexual systems in subtropical evergreen broad-leaved forests in Ailao Mountains, SW China. *Journal of Plant Ecology*, 1, 179–185. https://doi.org/10.1093/jpe/rtn019

Chen, X.-S., & Li, Q.-J. (2008b). Sexual systems and ecological correlates in an azonal tropical forest, SW China. *Biotropica*, 40, 160–167. https://doi.org/10.1111/j.1744-7299.2007.00364.x

Freeman, D. C., Harper, K. T., & Ostler, W. K. (1980). Ecology of plant dioecy in the intermountain region of western North America and California. *Oecologia*, 44, 410–417. https://doi.org/10.1007/BF00545246

Fox, J. F. (1985). Incidence of dioecy in relation to growth form, pollination and dispersal. *Oecologia*, 67, 244–249. https://doi.org/10.1007/BF00384293

Gagne, W. C. (1979). Canopy-associated arthropods in Acacia koa and Metrosideros tree communities along an altitudinal transect on Hawaii Island. *Pacific Insects*, 21, 56–82.

Givnish, T. J. (1980). Ecological constraints on the evolution of breeding systems in seed plants: Dioecy and dispersal in gymnosperms. *Evolution*, 34, 959–972. https://doi.org/10.2307/2408001

Godley, E. J. (1979). Flower biology in New Zealand. *New Zealand Journal of Botany*, 17, 441–466. https://doi.org/10.1080/00288329.1979.10432564

Hanski, I. (1983). Distributional ecology and abundance of dung and carrion feeding beetles Scarabaeidae in tropical rain forests in Sarawak, Malaysia. *Acta Zoologica Fennica*, 167, 1–45.

Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biological Reviews*, 80, 489–513. https://doi.org/10.1111/j.1469-7265.2006.006767

Hsieh, C.-F., & Shen, C.-F. (1994). Introduction to the flora of Taiwan, 1: Geography, geology, climate, and soils. In T. C. Huang & Editorial Committee of the Flora of Taiwan (Eds.), *Flora of Taiwan* (2nd ed., pp. 1–3). Taipei: Editorial Committee of the Flora of Taiwan.

Hsieh, C.-F., Shen, C.-F., & Yang, K.-C. (1994). Introduction to the flora of Taiwan, 3: Floristics, phytogeography, and vegetation. In T. C. Huang & Editorial Committee of the Flora of Taiwan (Eds.), *Flora of Taiwan* (2nd ed., pp. 7–16). Taipei: Editorial Committee of the Flora of Taiwan.

Huang, T. C., & Editorial Committee of the Flora of Taiwan (Eds.). (1993). *Flora of Taiwan* (Vol. 3, 2nd ed.). Taipei, Taiwan: Editorial Committee of the Flora of Taiwan.

Huang, T. C., & Editorial Committee of the Flora of Taiwan (Eds.). (1996). *Flora of Taiwan* (Vol. 2, 2nd ed.). Taipei, Taiwan: Editorial Committee of the Flora of Taiwan.

Huang, T. C., & Editorial Committee of the Flora of Taiwan (Eds.). (1998). *Flora of Taiwan* (Vol. 4, 2nd ed.). Taipei, Taiwan: Editorial Committee of the Flora of Taiwan.

Huang, T. C., & Editorial Committee of the Flora of Taiwan (Eds.). (2000). *Flora of Taiwan* (Vol. 5, 2nd ed.). Taipei, Taiwan: Editorial Committee of the Flora of Taiwan.

Huang, T. C., & Editorial Committee of the Flora of Taiwan (Eds.). (2003). *Flora of Taiwan* (Vol. 6, 2nd ed.). Taipei, Taiwan: Editorial Committee of the Flora of Taiwan.

Jacquemyn, H., Micheneau, C., Roberts, D. L., & Paillier, T. (2005). Elevational gradients of species diversity, breeding system and floral traits of orchid species on Réunion Island. *Journal of Biogeography*, 32, 1751–1761. https://doi.org/10.1111/j.1365-2699.2005.01307.x

Kay, Q. O. N., & Stevens, D. P. (1986). The frequency, distribution and reproductive biology of dioecious species in the native flora of Britain and Ireland. *Botanical Journal of the Linnean Society*, 92, 39–64. https://doi.org/10.1111/j.1095-8339.1986.tb01426.x

Lefebvre, V., Vilmant, C., Fontaine, C., & Daugeron, C. (2018). Altitudinal, temporal and trophic partitioning of flower-visitors in alpine communities. *Scientific Reports*, 8, 4706. https://doi.org/10.1038/s41598-018-23210-y

Lin, H.-Y., Hu, J.-M., Chen, T.-Y., Hsieh, C.-F., Wang, G., & Wang, T. (2018). A dynamic downscaling approach to generate scale-free regional climate data in Taiwan. *Tawania*, 63, 251–266. https://doi.org/10.6165/taw.2018.63.251

McCoy, E. D. (1990). The distribution of insects along elevational gradients. *Oikos*, 58, 313–322. https://doi.org/10.2307/3545222

Perillo, L. N., Neves, F. S., Antonini, Y., & Martins, R. P. (2017). Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient. *PLoS ONE*, 12(7), e0182054. https://doi.org/10.1371/journal.pone.0182054

Core Team, R. (2016). *R: A language and environment for statistical computing*. R foundation for statistical computing. Vienna: Austria https://www.R-project.org/.

Réjou-Méchain, M., & Cheptou, P.-O. (2015). High incidence of dioecy in young successional tropical forests. *Journal of Ecology*, 103, 725–732. https://doi.org/10.1111/1365-2699.12393

Renner, S. S., & Ricklefs, R. E. (1995). Dioecy and its correlates in the flowering plants. *American Journal of Botany*, 82, 596–606. https://doi.org/10.2307/2445418

Sakai, A. K., Wagner, W. L., Ferguson, D. M., & Herbst, D. R. (1995). Biogeographical and ecological correlates of dioecy in the Hawaiian flora. *Ecology*, 76, 2530–2543. https://doi.org/10.2307/2265826

Sakai, A. K., & Weller, S. G. (1999). Gender and sexual dimorphism in flowering plants: A review of terminology, biogeographic patterns, ecological correlates, and phylogenetic approaches. In M. A. Geber, T. E. Dawson, & L. F. Delph (Eds.), (pp. 1–31). Berlin: Gender and sexual dimorphism in flowering plants, Springer. https://doi.org/10.1007/978-3-662-03908-3_1

Shen, C.-F. (1994). Introduction to the flora of Taiwan, 2: Geotectonic evolution, paleogeography, and the origin of the flora. In T. C. Huang & Editorial Committee of the Flora of Taiwan (Eds.), *Flora of Taiwan* (2nd ed., pp. 3–7). Taipei: Editorial Committee of the Flora of Taiwan.
Sobrevila, C., & Arroyo, M. T. K. (1982). Breeding systems in a tropical montane cloud forest in Venezuela. *Biotropica, 10*, 221–230. https://doi.org/10.1007/BF02409895

Su, H.-J. (1984). Studies on the climate and vegetation types of the natural forests in Taiwan (II). Altitudinal vegetation zones in relation to temperature gradient. *Quarterly Journal of Chinese Forestry, 17*(4), 57–73.

Takhtajan, A. (1986). *Floristic regions of the world*. Berkeley: University of California Press. [translated by T. J. Crovello & A. Cronquist].

Tseng, Y.-H., Hsieh, C.-F., & Hu, J.-M. (2008). Incidences and ecological correlates of dioecious angiosperms in Taiwan and its outlying Orchid Island. *Botanical Studies, 49*, 261–276.

Vamosi, S. M. (2006). A reconsideration of the reproductive biology of the Atlantic forest in the Volta Velha reserve. *Biodiversity & Conservation, 15*, 1417–1424. https://doi.org/10.1007/s10531-005-0308-4

Vamosi, S. M., & Queenborough, S. A. (2010). Breeding systems and phylogenetic diversity of seed plants along a large-scale elevational gradient. *Journal of Biogeography, 37*, 465–476. https://doi.org/10.1111/j.1365-2699.2009.02214.x

Wang, T., Hamann, A., Spittlehouse, D., & Carlos, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE, 11*(6), e0156720. https://doi.org/10.1371/journal.pone.0156720

Wang, T., Wang, G., Innes, J. L., Seely, B., & Chen, B. (2017). ClimateAP: An application for dynamic local downscaling of historical and future climate data in Asia Pacific. *Frontiers of Agricultural Science and Engineering, 4*, 448–458. https://doi.org/10.15302/J-FASE-2017172

Webb, C. J., Lloyd, D. G., & Delph, L. F. (1999). Gender dimorphism in indigenous New Zealand seed plants. *New Zealand Journal of Botany, 37*, 119–130. https://doi.org/10.1080/0028825X.1999.9512618

Wolda, H. (1987). Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society, 30*, 313–323. https://doi.org/10.1111/j.1095-8312.1987.tb00305.x

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