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The pattern of dioecy in terrestrial, temperate plant succession

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ABSTRACT

Hypothesis: Inbreeding avoidance theory suggests that dioecious plant species (those with separate-sexed individuals) should have high fitness because they result from obligate outcrossing. Thus, these species should be more competitive than those that engage in some form of inbreeding. Competitive ability increases with successional stage in many successional series studies. Accordingly, we expect dioecious species to be disproportionately represented in late successional stages.

Data: Species presence/absence and importance (number of individuals) taken from eight studies of open land and forest succession in North America.

Analysis methods: *Presence/absence*: We assessed the proportion of dioecious species at each successional stage. We then compared these proportions to a random model. *Importance*: We compared the importance of dioecious species at each successional stage. We then tested these importance values against a random model.

Conclusions: *Presence/absence*: Dioecious species were not more prevalent in late successional stages. There was no significant increase in dioecious species and in most cases the number of dioecious species declined with successional stage, although this trend was not significant. *Importance*: Dioecious species were significantly less important in late successional stages compared with early or mid successional stages. Finally, dioecious species were rarely present in climax communities.

Keywords: dioecy, dispersal, inbreeding avoidance, plant mating systems, succession.

INTRODUCTION

Dioecious plants have separate-sexed individuals whereas over 90% of all angiosperm species combine male and female parts in a single individual (Renner and Ricklefs, 1995, and references cited therein). Yet dioecious plants are disproportionately common among woody plants, wind-pollinated (or generalist-pollinator) plants, and plants with animal-dispersed fruits/seeds (Freeman *et al.*, 1980; Thomson and Brunet, 1990; Renner and Ricklefs, 1995; Vamosi *et al.*, 2003). Moreover, dioecy

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has evolved numerous times in many independent lines (Renner and Ricklefs, 1995) with many different mechanisms underlying the development of unisexual flowers (Diggle *et al.*, 2011).

The population biology of dioecious species has been well studied, especially population sex ratios (Sinclair *et al.*, 2012; Field *et al.*, 2013). In some dioecious species, there is a spatial separation of the sexes (Freeman *et al.*, 1976, 1997; Bierzychudek and Eckhart, 1988; Eppley, 2005) and such species often exhibit sexual lability (Freeman *et al.*, 1980, 1997; Korpelainen, 1998; Ainsworth, 2000). Although species displaying dioecy are found in many ecosystems, dioecy is particularly common in tropical rainforests and deserts (Bawa and Opler, 1975; Freeman *et al.*, 1980; Renner and Ricklefs, 1995). In deserts, half or more of the individuals in the community often belong to dioecious species (Freeman *et al.*, 1980). Curiously, patterns of dioecy through succession have not been studied, yet this aspect of biology is important because it might provide an ecological context in which to understand dioecy.

There are two views regarding the forces responsible for the evolution of dioecy. Charlesworth and Charlesworth (1978), Lloyd (1979), and others argue that inbreeding avoidance (high self-fertilization coupled with high inbreeding depression) is the major driving force. Others (Darwin, 1877; Freeman *et al.*, 1997) argue that sexual specialization (increased dispersal ability, flower location and timing, plant architecture) has played the prominent role. Compensation (an increased production of the retained sexual function) has also long been considered an important step in facilitating the evolution of dioecy (Charlesworth and Charlesworth, 1978). These views need not be mutually exclusive. Recently, Sinclair *et al.* (2013) examined the effect of inbreeding, specialization, and compensation in the evolution of dioecy. They found that although it is theoretically possible for dioecy to evolve solely as a result of inbreeding avoidance, in practice it is difficult due to extreme ecological constraints. Therefore, it should happen infrequently. Specialization pressures allow males to invade a population readily, while inbreeding combined with specialization facilitates the invasion of females.

Early successional species are often short-lived, often self-compatible, and often herbaceous with high dispersal abilities and low genetic flexibility (Baker, 1955; Levin, 1975; Bazazz, 1979). Late successional species are conversely described as long-lived, highly competitive, genetically flexible, and likely to exhibit outcrossing (Baker, 1955; Levin, 1975; Bazazz, 1979). Coupled with our knowledge that dioecious species are obligate outcrossers and most common among plants with a woody life form (Renner and Ricklefs, 1995) and, in conjunction with the theory that dioecious species are good competitors due to genetic variability that comes with outcrossing (Charlesworth and Charlesworth, 1987), we can expect dioecious species to predominate in late successional stages. If, on the other hand, dioecious species are more common in early successional stages, perhaps dispersal ability and colonizing characteristics are the more important traits in the evolution of dioecy.

We examined the incidence of dioecy in eight successional series. Specifically, we examined the classic successional series at Glacier Bay, Alaska (Cooper, 1923), Olson's (1958) Lake Michigan sand dune succession, Oosting's (1942) classic study of secondary succession in the Piedemont of South Carolina (an old field study and a pine forest study), Antos and Habeck's (1981) Forbes Forest study, Schoonmaker and McKee's (1988) Oregon Cascades study, and Lichter's (1998) sand dune study. Because some of these studies report only lists of species, we also examined the successional series reported in pine forests in Mexico (Gonzalez-Espinosa *et al.*, 1991) because that study reports the importance of the species in addition to a list of species, and also the order of colonization for woody species. Bazzaz's (1968) classic study of field succession was excluded because there were no recorded dioecious herbs: all the

dioecious species observed were trees and the 40 years of records was insufficient to examine the full extent of forest succession. Note that the time frame for a successional study depends on the system. For instance, Oosting's old field study lasted 3 years; Oosting's forest study covers 75 years; and Olson's sand dune study spans 10,000 years. Each study is relevant in the context of its system; an old field will often succeed to shrubland and then to forest in the course of a few years, while a forest may persist for several hundred years (barring disturbance), and some of Olson's sand dune sites remain sand dunes to this day.

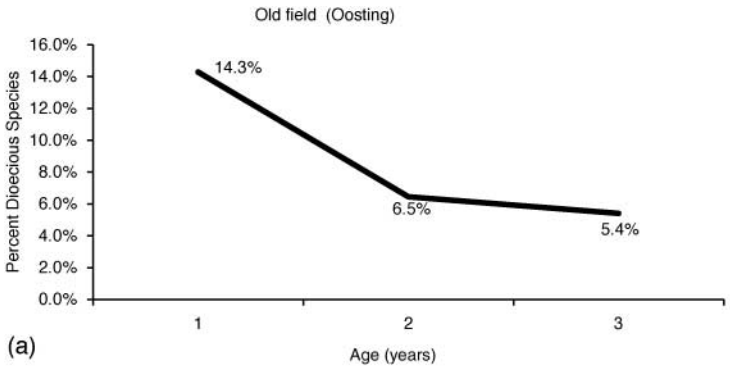
METHODS

For each study, we examined the list of species corresponding to each successional stage and used published reports, principally the *Manual of Vascular Plants of Northeastern United States and Adjacent Canada* (Gleason and Cronquist, 1998), to ascertain whether a species had perfect flowers, was monoecious, dioecious, or polygynous. We then computed the percentage of dioecious species by stage, and, where possible, the percentage of individuals that were dioecious or the importance of the dioecious species.

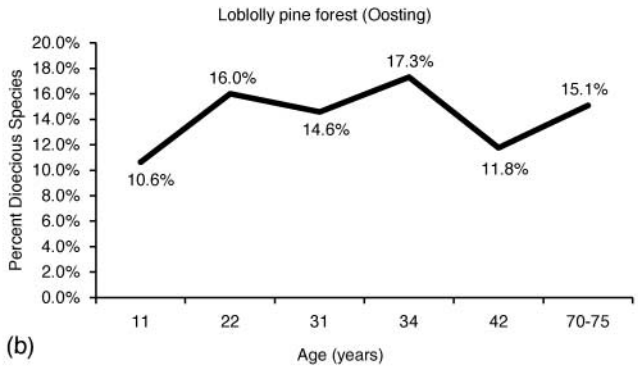
Our analysis had to adjust to the fact that primary authors recorded different characteristics in their original study. Oosting (1942) recorded the density and frequency of each species in each stage. In this case, to indicate importance, we calculated the product of density and frequency, before averaging it by the number of fields used by Oosting for that stage. Gonzalez-Espinosa *et al.* (1991) used species importance and divided each successional stage into life form categories (shrubs, understory trees, canopy). We summed the importance values of each species within each successional stage and then examined the percentage of importance of the dioecious species. Cooper (1923) recorded species names only and so for the Glacier Bay, Alaska study we were able to report only the percentage of dioecious species versus successional stage. Olson (1958) divided the successional series into pioneer, several seral stages, and climax. He recorded the duration of species; thus, for example, some were found in the pioneer stage until seral stage 2. We followed his lead and reported the percentage of dioecious species found in each stage. Antos and Habeck (1981) recorded both the frequency and percent cover of each species in mature and immature forests. For this study, we used the product of cover and frequency as the measure of importance.

Schoonmaker and McKee's (1988) Oregon cascade study and Lichter's (1998) sand dune study both used cover-class information recorded as decimals, not counts, which prevented us from analysing importance in both these cases. However, we did analyse the percentage of dioecious species versus successional stage. To visualize trends, we include graphs depicting this relationship even though we did not subject these data to statistical analysis.

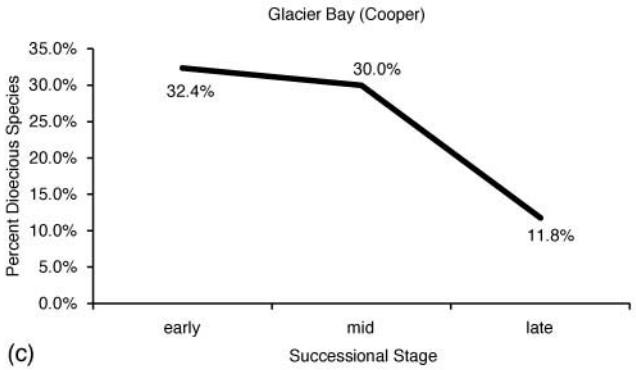
We also consider patterns as a result of phylogenetic correlation. However, in all studies, the number of species equals or just barely exceeds the number of genera (Table 3), with more than two species of the same genus occurring a total of three times in two studies (*Salix* in Cooper's early Glacier Bay study, and *Salix* and *Juniperus* in Lichter's sand dune study). We are therefore confident that the patterns seen are not a result of phylogenetic similarity. Furthermore, because in all cases the object of the original study was to catalogue a given community completely and over a period of time, we can accept with a high degree of certainty any patterns published by the primary authors. We analysed the data with Fisher's exact test and chi-square.


Old field (Oosting)
Percent Dioecious Species
16.0%
14.0%
12.0%
10.0%
8.0%
6.0%
4.0%
2.0%
0.0%
14.3%
6.5%
5.4%
1
2
3
Age (years)

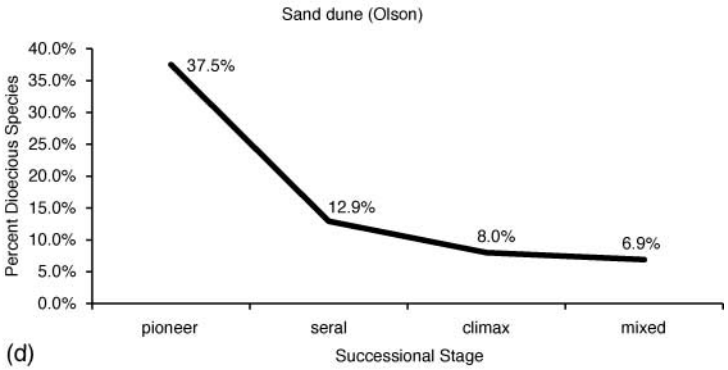
(a)


Loblolly pine forest (Oosting)
Percent Dioecious Species
20.0%
18.0%
16.0%
14.0%
12.0%
10.0%
8.0%
6.0%
4.0%
2.0%
0.0%
10.6%
16.0%
14.6%
17.3%
11.8%
15.1%
11
22
31
34
42
70-75
Age (years)

(b)


Glacier Bay (Cooper)
Percent Dioecious Species
35.0%
30.0%
25.0%
20.0%
15.0%
10.0%
5.0%
0.0%
32.4%
30.0%
11.8%
early
mid
late
Successional Stage

(c)


Sand dune (Olson)
Percent Dioecious Species
40.0%
35.0%
30.0%
25.0%
20.0%
15.0%
10.0%
5.0%
0.0%
37.5%
12.9%
8.0%
6.9%
pioneer
seral
climax
mixed
Successional Stage

(d)

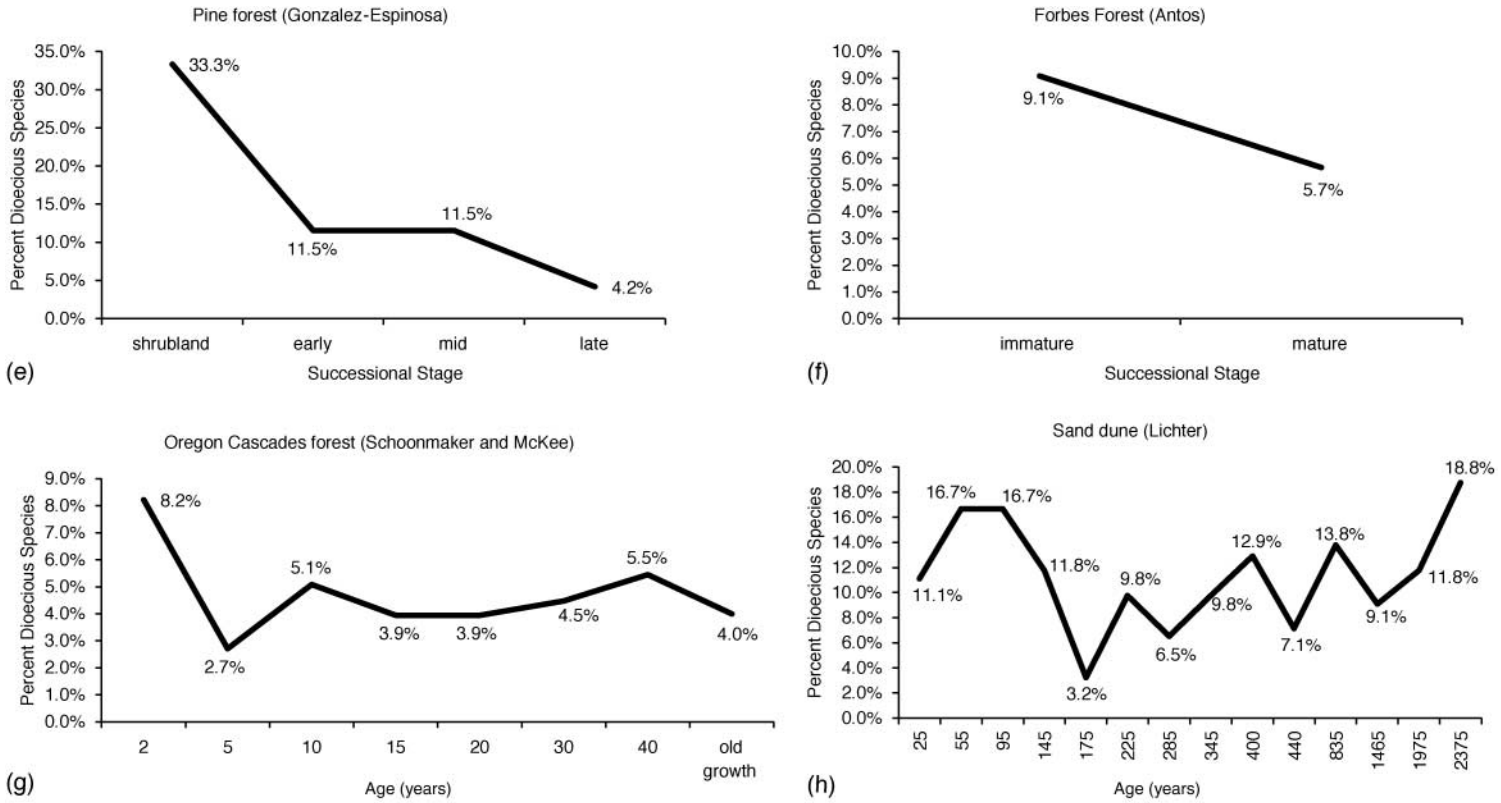


Fig. 1. Percent of species present that are dioecious at various successional stages: (a) Oosting's old field study; (b) Oosting's loblolly forest study; (c) Cooper's Glacier Bay study; (d) Olson's sand dune study; (e) Gonzalez-Espinosa's pine forest study; (f) Antos and Habeck's Forbes Forest study; (g) Schoonmaker and McKee's Oregon Cascades study; and (h) Lichter's sand dune study

RESULTS

Dioecious species consistently represent a higher proportion of the flora in the pioneer and seral stages than in the climax stage (six of the eight studies; Fig. 1). But in no case was the difference significant (Table 1).

The importance (calculated using frequency and/or cover) of dioecious individuals in the community does significantly differ from random (Table 2). Peaks are present in early to mid succession (Figs. 2–4). We performed no statistical tests on importance based on cover, but the percentages of cover represented by dioecious individuals are shown in Figs. 5 and 6. Schoonmaker and McKee's (1988) study in the Cascades displays a curious alternation between increasing and decreasing coverage, although the overall trend is one of increase (Fig. 5). Finally, dioecious coverage in Lichter's (1998) sand dune study peaks in early to mid succession, although there is a second, smaller peak followed by a rapid decline late in the successional series (Fig. 6).

DISCUSSION

In theory, dioecious species should pay a heavy price by being unisexual. Some have argued that each individual of a dioecious species has lost half its potential fitness in return for the certainty that its offspring will be the result of outcrossing (Charlesworth and Charlesworth, 1978; Lloyd, 1979). These authors view the reward as obligate outcrossing, which reduces inbreeding depression and results in offspring with higher fitness (Charlesworth and Charlesworth, 1987).

Table 1. Statistics and *P*-values obtained for each study using Fisher's exact test

Study	Figure	Test used	Statistic	d.f.	*P*-value
Old field	1a	Fisher's exact	2.355	2	0.308
Loblolly forest	1b	Fisher's exact	1.695	5	0.89
Glacier Bay	1c	Fisher's exact	2.217	2	0.33
Olson's sand dune	1d	Fisher's exact	7.709	3	0.052
Pine forest	1e	Fisher's exact	5.371	3	0.147
Forbes Forest	1f	Fisher's exact	0.463	1	0.496
Oregon Cascades	1g	Fisher's exact	3.011	7	0.884
Lichter's sand dune	1h	Fisher's exact	6.183	13	0.939

Table 2. Statistics and *P*-values obtained for the studies that included individual frequency data

Study	Figure	Test used	Statistic	d.f.	*P*-value
Old field (individuals)	2a	Chi-square	869.08	2	$\ll 0.01$
Loblolly forest (individuals)	2b	Chi-square	341.14	5	<0.02
Pine forest (individuals)	3	Chi-square	50.5	3	<0.03
Forbes Forest (individuals)	4	Chi-square	129.38	1	$\ll 0.01$
Oregon Cascades (cover)	5	N.A.			
Lichter's sand dune (cover)	6	N.A.			

Note: Cover data could not be used due to the nature of the data collection.

Table 3. Breakdown of the total number of species and genera as well as the number of dioecious species and genera for each successional phase in each study

Study	No. of species	No. of genera	No. of dioecious species	No. of dioecious genera
Old field				
Year 1	35	30	5	3
Year 2	62	45	4	4
Year 3	37	32	2	2
Loblolly forest				
Year 11	47	44	5	5
Year 22	50	42	8	7
Year 31	48	40	7	7
Year 34	52	45	9	8
Year 42	34	27	4	4
Years 70–75	53	46	8	8
Glacier Bay				
Early	34	23	11	4
Mid	10	9	3	2
Late	17	15	2	1
Olson's sand dune				
Pioneer	8	5	3	2
Seral	31	26	4	3
Climax	50	45	4	4
Mixed	58	50	4	4
Pine forest				
Shrubland	9	6	3	3
Early	26	21	3	3
Mid	26	20	3	3
Late	24	18	1	1
Forbes Forest				
Immature	55	50	5	5
Mature	53	49	3	3
Oregon Cascades				
Year 2	73	60	6	6
Year 5	74	58	2	2
Year 10	59	49	3	3
Year 15	76	59	3	3
Year 20	76	63	3	3
Year 30	67	57	3	3
Year 40	55	48	3	3
Old Growth	50	46	2	2
Lichter's sand dune				
Year 25	9	9	1	1
Year 55	18	16	3	1
Year 95	18	16	3	1
Year 145	34	32	4	3
Year 175	31	29	1	1
Year 225	41	36	4	3
Year 285	46	43	3	2
Year 345	41	39	4	3
Year 400	31	29	4	4
Year 440	28	27	2	2
Year 835	29	27	4	4
Year 1465	22	20	2	2
Year 1975	17	16	2	2
Year 2375	16	15	3	3

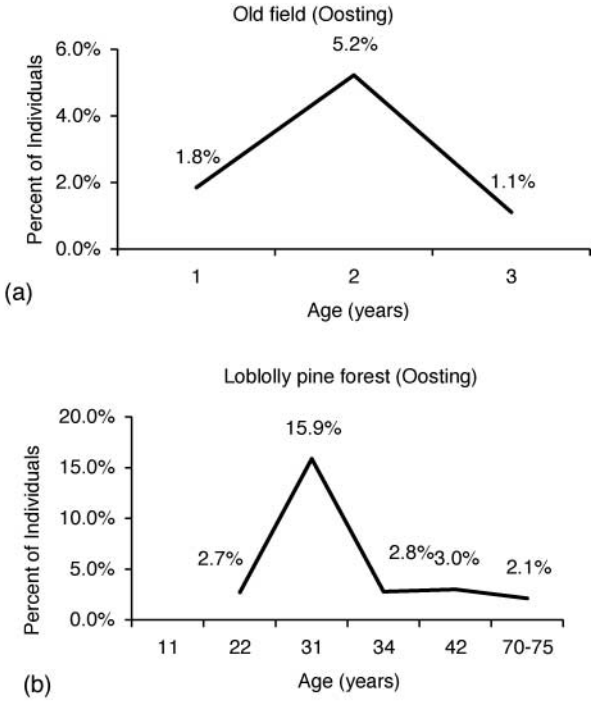


Fig. 2. Percent of individuals (population composition) that are dioecious at various successional stages in Oosting's old field (a) and loblolly pine studies (b).

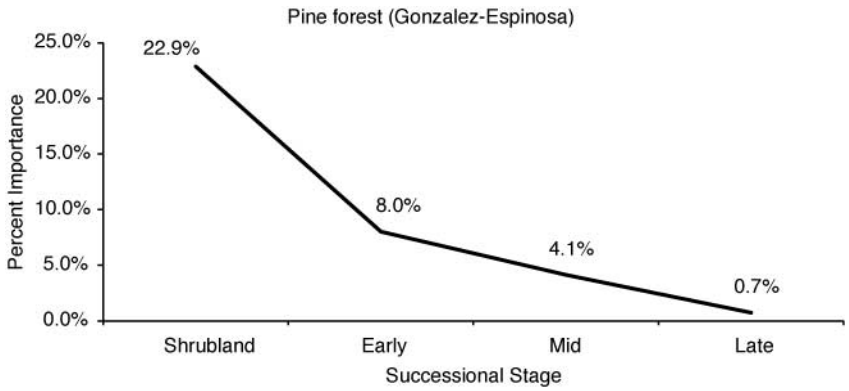


Fig. 3. Relative importance of dioecious individuals in the Mexican pine forest system over successional time.

Individuals experiencing inbreeding depression are less competitive at every stage of their life history (Charlesworth and Charlesworth, 1987; Sakai *et al.*, 1989). As a result, we hypothesized *a priori* that dioecious species would become increasingly important as succession progressed.

Our data clearly do not support this hypothesis. Dioecious species in the successional series did not become either more common or more important in any climax communities

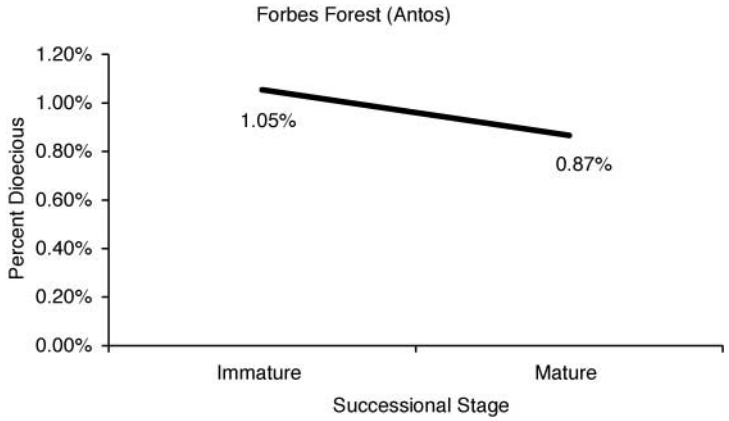


Fig. 4. Relative importance of dioecious individuals in the Forbes Forest system over successional time.

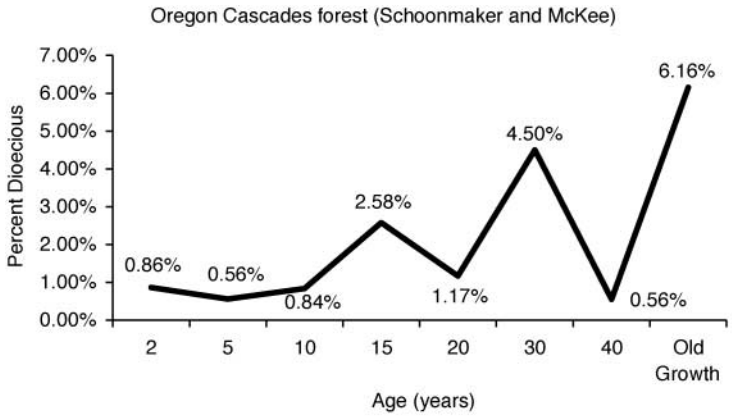


Fig. 5. Relative importance of dioecious individuals in the Oregon Cascades system over successional time.

that we examined. Rather, the distribution throughout the successional stages did not statistically differ from random, and in six of the eight studies trends suggested a decline in the representation and abundance of dioecy as succession progressed.

We find it telling that in no case were dioecious species represented in the canopy of the climax forests. Species such as *Sassafras albidum* are found in the understory of some climax forests, but as Bazzaz (1968) has shown, this species is really a seral species adapted for colonizing. Similarly, *Smilax* occasionally appears in patches in the understory of climax forests, but there it tends to reproduce clonally, with both sexes rarely occurring together (D.C. Freeman, personal observation).

Darwin (1877) argued that specialization played an important role in the evolution of dioecy. A number of dioecious species have evolved from species that had a pre-existing outcrossing mechanism. Ornduff (1966) examined a case of dioecy that evolved following

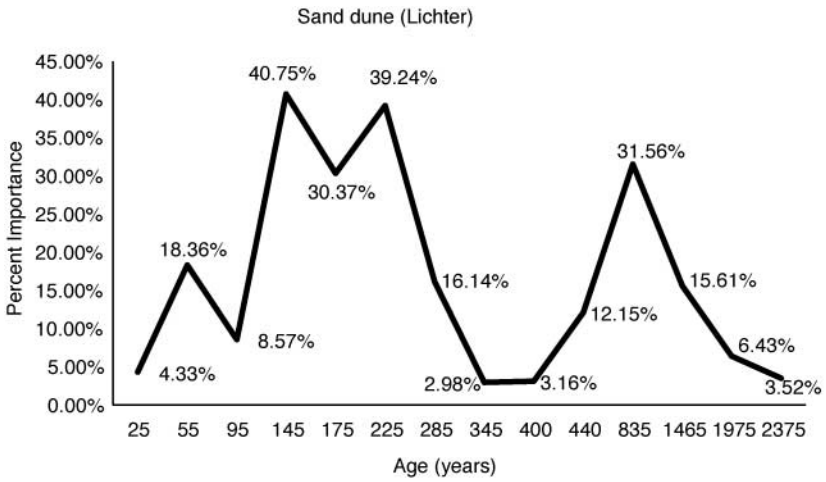


Fig. 6. Relative importance of dioecious individuals based on cover in Lichter's sand dune system over successional time.

a simple case of diochogamy. Pendleton *et al.* (2000) provided evidence for an evolutionary pathway from hermaphroditism to dioecy via heterodichogamy (see also Muenchow and Grebus, 1989). Pannell and Verdu (2006) present a theoretical model in which specialization in the form of heterodichogamy relaxes conditions required for the evolution of androdioecy, which can then proceed to dioecy. And recently Sinclair *et al.* (2013) found that neither inbreeding nor specialization alone is likely to facilitate the evolution of dioecy, but they do so when acting together. If dioecious species are more important in early successional stages – a hypothesis that needs further studies but one strongly suggested by our results – then the claim that sexual specialization in the form of dispersal ability plays an important role in the ecology of dioecious plants would accrue considerable support.

There are conflicting reports regarding environmental stability and the presence of dioecy. Barrett (2003) found that monoecious individuals of the species *Sagittaria latifolia* occupied the more frequently disturbed sites, while dioecious individuals were found in the stable, older habitats. On the other hand, Ashman (2006) and Barrett (1992) found that dioecy occurs in extreme environments or at the edge of a species' range – presumably places with less stable conditions. Furthermore, rather than being highly competitive, dioecious species face higher extinction rates than their hermaphrodite counterparts (Heilbuth, 2000; Heilbuth *et al.*, 2001). Because dioecious species appear to be locally ephemeral, those that persist are likely to have superior dispersal abilities that counter local extinction.

Dioecy occurs in a large number of diverse species. These species experience and rely on a variety of environmental conditions, which, in turn, result in different life strategies. Our analysis of eight successional studies clearly suggests that a dioecious mating system is not more common late in succession, but may well be more important in early to mid successional stages in North America. It would be extremely interesting to see if this same pattern prevails in the tropics.

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