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INCIDENCE, CORRELATES, AND ORIGINS OF DIOECY IN THE ISLAND FLORA OF NEW CALEDONIA

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Premise of research. Because it is an inherently risky sexual system, dioecy is globally rare. Attempts to explain unusually high incidences of dioecy on certain islands have generated a considerable literature on the relationships among dioecy, its ecological correlates, establishment after transoceanic dispersal, and postdispersal speciation. Nevertheless, few studies of dioecy on islands have included considerations of the origins and maintenance of dioecy on islands along with determinations of its incidence.

Methodology. We used the literature, herbarium specimens, and fieldwork to determine the incidence of dioecy in the native angiosperm flora of New Caledonia. We inferred the number and characteristics of colonists needed to account for the extant dioecious flora. We made traditional species-based numerical assessments of associations between dioecy on New Caledonia and woodiness, plain flowers, fleshy fruit, habitat, and endemism, and we constructed a phylogenetic tree for New Caledonia's native angiosperms to investigate correlated evolution of dioecy and those associated traits.

Pivotal results. This study is the first comprehensive survey of sexual systems for the flora of New Caledonia. One-fifth of New Caledonia's native angiosperms are dioecious. Dioecy is numerically overrepresented among species that are woody, have plain flowers, have fleshy fruit, occur in rainforest, or are endemic. However, we found strong evidence for correlated evolution only for dioecy and woodiness, plain flowers, and fleshy fruit. Dioecious groups with more of the widely accepted morphological correlates of dioecy tend to be more speciose. Approximately 90% of the colonists that gave rise to the extant dioecious flora were themselves dioecious. Approximately 60% of the colonists have two or more dioecious descendants, and those descendants comprise more than 90% of the extant dioecious species.

Conclusions. Successful dispersal and establishment of already dioecious colonists and autochthonous speciation of dioecious lineages are primarily responsible for the high incidence of dioecy on New Caledonia. There were relatively few postdispersal transitions to dioecy. The associations of dioecy with woodiness, plain flowers, and fleshy fruit result from correlated evolution that occurred prior to dispersal to New Caledonia, while the associations of dioecy with rainforest habitat and endemism appear to result from autochthonous speciation of dioecious lineages. With ~4% of the world's dioecious species occurring only there, New Caledonia should be a rich source of new information on the evolutionary ecology of dioecy. Realization of this potential will require both further study and concerted efforts to preserve the native flora.

Keywords: dioecy, New Caledonia, island floras, Baker's law.

Online enhancements: supplementary tables, appendixes.

Introduction

Dioecy, in which an individual is either female or male, is the most extreme form of sexual specialization in angiosperms. While dioecy has the unique advantage of completely preventing self-pollination and fertilization, it is also requires transfer of pollen from one particular type of individual to another, making it inherently risky. In addition to the risks of obligate cross-pollination, dioecy imposes several other evolutionary handicaps. Compared to hermaphroditism, dioecy adversely affects seed dispersal (Heilbuth et al. 2001), colonizing ability (Baker 1955), and the evolutionary success of clades (Heilbuth 2000). Consequently, only 4% (Richards 1986) to 6% (Renner and Ricklefs 1995) of the world's angiosperms are dioecious.

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Along with being globally rare, dioecy is unevenly distributed with respect to the ecological characteristics and the biogeography of angiosperms. Dioecious species tend to be tropical and woody and to have small, plain flowers and fleshy fruits (Renner and Ricklefs 1995; Sakai and Weller 1999), and the evolutionary success of dioecious clades compared to nondioecious sister clades increases with the number of these four major ecological correlates present in the dioecious clades (Vamosi and Vamosi 2004).

Continental temperate floras generally have lower incidences of dioecy, whereas woody tropical floras and the floras of certain islands have the highest (Adam and Williams 1994; Sakai and Weller 1999; Carpenter et al. 2003; Gross 2005; Matallana et al. 2005; Vary et al. 2011). With respect to islands, Hawaii received early attention because the high incidence of dioecy there appeared to contradict Baker's law that hermaphroditic, genetically self-compatible species should be the most successful at colonizing islands via long-distance dispersal (Baker 1955; Gilmartin 1968). Proposed explanations for such exceptions to Baker's law have included the hypotheses that postarrival conditions such as inbreeding in small colonizing populations favored the autochthonous evolution of dioecy on islands (Carlquist 1966; Baker 1967) and that certain ecological correlates of dioecy, such as fleshy bird-dispersed fruit, favored transoceanic long-distance dispersal of dioecious colonists to islands (Bawa 1980). Dioecy on islands continues to play a significant role in both empirical and theoretical studies on the evolution of mating systems and dispersal syndromes in plants (Baker and Cox 1984; Thomson and Brunet 1990; Pannell and Barrett 1998; Sakai and Weller 1999; Barrett 2006; Pannell 2006; Cheptou and Massol 2009; Cheptou 2012).

Relatively few studies have gone beyond determinations of the incidence of dioecy to examine both the origins and evolutionary ecology of dioecy in island floras. Those that have were focused on small, geologically young volcanic islands with relatively few native species (e.g., Hawaii: Sakai et al. 1995*a*, 1995*b*; Juan Fernandez Islands: Bernardello et al. 2001) or on specific components of much larger floras (e.g., rainforest trees of New Caledonia: Carpenter et al. 2003; littoral forest of Madagascar: Vary et al. 2011). With the notable exception of New Zealand (Webb et al. 1999), there are no comprehensive studies for geologically older islands with larger floras. Here we examine dioecy in the native flora of New Caledonia, which includes a geologically ancient fragment of Gondwana and has an extremely species-rich, highly endemic indigenous flora.

In an early analysis of dioecy on islands, Baker and Cox (1984) found very strong positive correlations between the incidence of dioecy and two factors: proximity to the equator and maximum island height, with island height as a proxy for mountainous terrain with moist forests (Baker and Cox 1984). New Caledonia has an equable tropical climate and considerable topographic diversity, with mountains rising to 1628 m. It supports a predominantly woody flora with origins dating back to the late Eocene emergence of Grande-Terre and has extensive areas of dense evergreen rainforest (Jaffré et al. 2001; Lowry et al. 2004). Thus, one might expect a high incidence of dioecy there, especially among rainforest species and endemics. Indeed, in their comprehensive review of dioecy in angiosperms, Renner and Ricklefs (1995) noted that a number of entirely or partially dioecious genera were endemic to New Caledonia. While earlier works report high incidences of dioecy for particular taxa (Schlessman et al. 1990*a*, 2001) or ecological groups (Carpenter et al. 2003), prior to this study there has been no attempt to determine the incidence of dioecy or any other sexual system for the entire flora. Here we ask: Is there a high incidence of dioecy in the native angiosperm flora of New Caledonia? Does the flora of New Caledonia provide evidence for correlated evolution of dioecy and woodiness, plain flowers, fleshy fruit, rainforest habitat, and endemism? Does the success of a dioecious group on New Caledonia increase with the number of ecological correlates it possesses? Were most of the colonizing species that established the extant dioecious flora already dioecious, or were they nondioecious as predicted by Baker's law? What is the relative importance of frequent colonization versus postcolonization speciation in accounting for the current number and systematic distribution of dioecious species on New Caledonia? Is there any evidence for dispersal of dioecy from New Caledonia to elsewhere? To address these questions, we have determined the sexual systems of the native species, inferred the ancestry and origins of the dioecious component of the flora, and analyzed the entire flora to seek evidence for correlated evolution of dioecy with endemism, rainforest habitat, woodiness, plain flowers, and fleshy fruit.

Methods

Study Area

New Caledonia is a tropical archipelago spanning the latitudes 18°00′S to 23°50′S and situated ±1200 km E of Australia and ±1500 km NNE of New Zealand. The main island of Grande-Terre (16,595 km^2) is Gondwanan, having separated from Australia and New Zealand as early as 85 Mya (Willford and Brown 1994; Lee et al. 2001). The Loyalty Islands, Isle of Pines, and several smaller islands add another 2377 km^2. New Caledonia is the smallest biodiversity hot spot (Lowry et al. 2004), with more than 3150 indigenous angiosperms, of which 77%–79% are endemic (Lowry 1998; Lowry et al. 2004; Morat et al. 2012). This flora is both larger and less well known than those of Hawaii and New Zealand (table 1). Approximately 40% of the recognized species have not received recent (post-1967) taxonomic treatment (Jaffré et al. 2001), and perhaps 300 or more species are not yet formally recognized (Morat 1993; Swenson et al. 2007). The current checklist of the native flora (Morat et al 2012) includes 3053 recognized angiosperm species, some of which are as yet unpublished.

Many New Caledonian angiosperm groups have both disjunct distributions involving other fragments of Gondwana and generalized (plesiomorphic) traits that led systematists to characterize them as ancient. Botanists and biogeographers have debated the relative importance of vicariance (Raven and Axelrod 1972) and long-distance dispersal (Carlquist 1966) as explanations for the present distributions of these ancient Gondwanan taxa. The geologic record shows that after separation from Australia and New Zealand, Grande-Terre was submerged during the late Cretaceous and Paleocene and then

Table 1

Species Richness, Endemism, and Dioecy in the Native Floras of New Caledonia, Hawaii, and New Zealand

	New Caledonia	Hawaii	New Zealand
Land area (km^2)	19,103	16,887	268,680
Angiosperm species	3051	971	2066
% of species endemic	78	89	84
Dioecious species:			
Total	640	143	±225
Endemic (%)	567 (89)	136 (95)	NA
% of world's dioecious species (total ± 14,620):			
Total	4.4	1.0	1.5
Endemic	3.9	.9	NA

Sources. New Caledonia: Morat et al. (2012) and this study; Hawaii: Sakai et al. (1995*a*, 1995*b*); New Zealand: Godley (1979); total world's dioecious species: Renner and Ricklefs (1995).

Note. NA = not available.

resurfaced during the late Eocene (Brothers and Lillie 1988; Willford and Brown 1994; Hall 2001; Cluzel et al. 2006; Schellart et al. 2006). While some authors have suggested that the extant Gondwanan component of the flora could be descended from pre-submergence ancestors that survived on emergent portions of Grande-Terre (Lee et al. 2001; Ladiges and Cantrill 2007) or on geologically ephemeral nearby islands (Pelletier 2006), the emerging consensus is that the extant flora has evolved from colonists that arrived via transoceanic dispersal after the resurfacing of Grande-Terre ±37 Mya (Aitchison et al. 1995; McLoughlin 2001; Grandcolas et al. 2008; Cruaud et al. 2012).

Incidence of Dioecy on New Caledonia

Our attention to information on the sexual systems of New Caledonian angiosperms has spanned more than a decade, and we consulted hundreds of publications. We used three types of literature to determine sexual systems: (*a*) the Flore de la Nouvelle-Calédonie et Dépendances (Aubréville et al. 1967–) and other floras of the Pacific region, (*b*) primary taxonomic literature for families not covered in the floras, and (*c*) secondary references (Kubitzki 1990–) to corroborate information from *a* and *b* or for families not covered there. We also examined specimens in the herbaria of the Muséum National d'Histoire Naturelle in Paris (P; in 2003 and subsequently) and the Institut de Recherche pour le Développement in Nouméa, New Caledonia (NOU; in 2004 and subsequently). In the herbaria, we focused on taxa for which the literature was lacking, unclear, or conflicting and also made spot checks of other taxa to confirm determinations from the literature.

During 2 wk of fieldwork in New Caledonia (Grande-Terre; January 4–18, 2004), we evaluated the accuracy of our assessments and attempted to resolve questions that had arisen from our literature and herbarium studies. At each of 10 sites chosen to provide a representative sampling of substrate and vegetation types, we examined and collected all accessible indigenous species that were flowering (excluding protected species and those whose sexual system was impossible to determine in the field). We focused especially on four problematic families: Euphorbiaceae, Primulaceae, Rutaceae, and Sapindaceae. We deposited voucher specimens at NOU, P, and the Missouri Botanical Garden in St. Louis (MO). We were able to assign most collections to a genus in the field. We completed species identifications at NOU and P, consulting experts when necessary. In the field, we examined the sex expression of 155 species, i.e., 5% of the indigenous angiosperm flora. For the few cases in which our field determinations contradicted information from the literature, newer publications or consultations with colleagues confirmed our fieldwork.

We classified each species as hermaphroditic, all individuals bearing bisexual flowers (bisexual = perfect, with both pistils and stamens); monoecious, all individuals bearing both female (pistillate) and male (staminate) flowers; andromonoecious, all individuals bearing both bisexual and male flowers; gynomonoecious, all individuals bearing both bisexual and female flowers; dioecious, separate male (staminate flowers, occasionally also a few bisexual or pistillate flowers) and female (pistillate flowers, occasionally also a few bisexual or staminate flowers) individuals; androdioecious, some individuals bearing only male flowers, others with bisexual flowers (or both staminate and pistillate flowers); gynodioecious, some individuals bearing only female flowers, others with bisexual flowers (or both male and female flowers); or undetermined. This classification encompasses the range of variation that we encountered. It is necessarily morphological (but see below), and it follows well-accepted definitions of flowering plant sexual systems (Darwin 1877; Lloyd and Bawa 1984; Richards 1986; Sakai and Weller 1999).

Hermaphroditism, monoecy, andromonoecy, and gynomonoecy are monomorphic sexual systems; i.e., the distribution of sexual phenotypes is unimodal. All individuals presumably have the same genotype for sex expression and can potentially exhibit the same range of sex expression (Lloyd and Bawa 1984; Barrett 2002). Dioecy, androdioecy, and gynodioecy are forms of sexual dimorphism; i.e., the distribution of sexual phenotypes is bimodal, and there are presumably two genotypes for sex expression (Lloyd and Bawa 1984; Barrett 2002). Sexual dimorphism can involve leakiness (Baker and Cox 1984) or inconstancies (Lloyd and Bawa 1984), i.e., the occasional production of flowers with atypical sex expression. For example, Tirel and Veillon (2002) reported that some New Caledonian species of *Pittosporum* (Pittosporaceae) were strictly dioecious (all individuals studied bore either staminate flowers or pistillate flowers but not both), while in other species some individuals bore pistillate flowers, some bore staminate flowers, and others bore both types of flowers. Here we treat the latter group as dioecious (with inconstancies or leakiness) rather than placing them in a separate category such as paradioecious, polygamodioecious, or subdioecious. Finally, several relatively well-studied species, e.g., *Polyscias pancheri* (Schlessman et al. 1990*b*), that appeared on first inspection to be androdioecious (males and hermaphrodites with apparently bisexual flowers) have been shown to be functionally dioecious because the pollen in the apparently bisexual flowers of the female plants is nonfunctional or absent. Here we also classify such cryptically dioecious species as dioecious.

Correlates of Dioecy on New Caledonia

Scoring traits. We scored species with determined sexual systems for five ecological traits: endemism (from Morat et al. 2012), habitat (seven vegetation types; Morat et al. 2012), habit (woody vs. herbaceous; literature and personal observations), flower type (petals <10 mm and white, green, or greenish white = plain; petals >10 mm or brightly colored = showy; following Vamosi and Vamosi 2004; literature, personal observations, images from the internet when necessary), and fruit type (fleshy or not, following Vamosi and Vamosi 2004; literature and personal observations). A few species with determined sexual systems were excluded from analyses of endemism and habitat because those data were absent from Morat et al. (2012).

Evidence for associations of dioecy with other traits. We sought evidence for associations between dioecy and purported ecological correlates through the traditional method of species-based contingency table analyses. We interpreted overrepresentation of dioecious species among all species with the purported correlate (observed > expected) to suggest that the purported correlate might favor one or more of the following: transitions from other sexual systems to dioecy, speciation of already dioecious lineages, or persistence of dioecious lineages.

For woodiness, plain flowers, fleshy fruit, and endemism, we used two-by-two contingency tables, e.g., dioecious or not by woody or not. We also performed a two-by-seven contingency table analysis for association of dioecy with the seven possible combinations of presence or absence of the three morphological traits: e.g., woody, plain, and fleshy; woody, plain, and dry; woody, showy, and dry, and so on. Last, we performed a two-by-seven analysis for the distribution of dioecious species among the seven vegetation types recognized by Morat et al. (2012). We scored species that occurred in more than one habitat as present in each of them.

Traditionally, the statistical significance of such contingency table comparisons has been evaluated with tests of independence such as the χ^2 (Bawa 1980; Renner and Ricklefs 1995; Sakai et al. 1995*a*; Carpenter et al. 2003; Gross 2005; Matallana et al. 2005). However, using such tests of independence to evaluate hypotheses about correlated evolution is inappropriate because phylogenetic history violates the assumption that a particular combination of traits (e.g., dioecious and woody) may occur in each species independently of its presence in any other species (Felsenstein 1985; Harvey and Pagel 1991). To address this concern, we used contingency table comparisons solely as a heuristic method for identifying associations that might be biologically important and for generating hypotheses about correlated evolution. We refrained from using overrepresentation of dioecy among species with a purported correlate as evidence for correlated evolution of dioecy with that trait (see below). Here we report statistical tests of independence (χ^2 tests, JMP 10.0.0, SAS, Cary, NC) solely for illustrative and comparative purposes.

Tests for correlated evolution of dioecy with other traits. To assess evidence for correlated evolution of dioecy with other traits, we employed Pagel's maximum likelihood method for two binary characters as implemented in Mesquite 2.75 (Pagel 1994; Maddison and Maddison 2003). This test compares the likelihoods for two models of transitions between character states, one in which transitions between the two states of each character are independent of those in the other and one in which changes in the hypothesized dependent character (here sexual system, dioecious or not) depend on the state of the independent character (e.g., woody or not). Statistical significance for rejecting the null hypothesis of independence is determined by the magnitude of the difference between the two likelihoods.

With Mesquite 2.75, we manually constructed a phylogenetic tree for 3040 of the 3053 species in Morat et al. (2012; 3047 with determined sexual systems minus 7 lacking habitat data). For each species, we included data on sexual system (dioecious or not), endemism (endemic or not), habitat (occurs in rainforest or does not), habit (woody or herbaceous), flower type (plain or showy), and fruit type (fleshy or dry).

We followed Soltis et al. (2011) for phylogenetic relationships among families, and we consulted numerous other publications to resolve relationships within families and genera as fully as possible (see literature cited and table S1; tables S1–S3 available online). Because we needed to draw on a number of sources to construct the topology of our tree, it was impossible to assign meaningful relative branch lengths; therefore, we set all branch lengths to 1.

As with most phylogenetic tests for correlated evolution, the Pagel (1994) method requires a completely resolved tree. However, some New Caledonian genera and most New Caledonian species have not been included in molecular phylogenetic studies, so initially our tree included numerous polytomies, especially at the infrageneric level. We made every effort to minimize the number of polytomies while retaining all of the meaningful information we had about relationships among taxa. We collapsed phylogenetically uninformative polytomies and clades (all species with identical states for all characters) into single terminal taxa. When infrageneric polytomies could not be fully collapsed, we reduced the number of terminal taxa by collapsing species with the same sets of character states into single operational taxonomic units. A Nexus file for our tree, a key to taxon abbreviations, and a list of additional sources we consulted are provided in appendixes A–C, available online.

Our final tree still had many polytomies, and it was necessary to generate randomly resolved trees for analysis. We generated a set of 100 different randomly resolved trees and ran tests for correlated evolution on each one. For each of those 500 tests (5 possible correlates × 100 trees), we based estimates of statistical significance (*P* values) on the recommended minimum of 1000 simulation replicates (Maddison and Maddison 2003).

Morphological correlates and species richness. We used linear regression (JMP 10.0.0; SAS) to examine the relationship between the species richness of a dioecious group (genus or clade with two or more genera) and the number of major morphological correlates of dioecy (woodiness, plain flowers, fleshy fruit) possessed by that group. We defined species richness as the number of extant dioecious species on New Caledonia. If we determined that two or more ancestral colonists had given rise to a dioecious group, we apportioned species among ancestors when the literature provided a basis for doing so (e.g., *Ficus* in tables 3, S1), or we simply divided the species equally among the ancestors (e.g., *Canarium* in tables 3, S1).

Table 2

Frequencies (%) of Sexual Systems among Species of Angiosperms in the Native Floras of Three Pacific Island Groups and the World

Sexual system	New Caledonia	Hawaii	New Zealand	World
Dioecy	21.0	14.7	12–13[G] ± 19[W]	4[Y], 6[RR]
Gynodioecy	.1	3.8	2[G] ± 7[W]	7[R]
Androdioecy	.1	0	NA	NA
Total dimorphic	21.2	18.5	14–16[G] ± 23[W]	10[L]
Hermaphroditism	61.2	62.4	NA	72[R]
Monoecy	12.8	7.6	9[G]	5[R]
Andromonoecy	3.7	4.5	NA	1.7[Y]
Gynomonoecy	1.0	3.9	NA	3[R]
Total monomorphic	78.8	78.4	84–86[G] ± 77[W]	90[L]

Sources. New Caledonia: this study; Hawaii: Sakai et al. (1995*b*); New Zealand: G = Godley (1979), W = Webb et al. (1999); world: L = Lloyd and Bawa (1984), R = Richards (1986), RR = Renner and Ricklefs (1995), Y = Yampolsky and Yampolsky (1922).

Note. In sexually dimorphic systems, the distributions of sexual phenotypes within populations are bimodal, presumably reflecting the expression of two distinct sexual genotypes, while in monomorphic systems, the distribution of sexual phenotypes is unimodal, presumably reflecting the expression of a single sexual genotype (Lloyd and Bawa 1984; Barrett 2002).

We predicted that the evolutionary success of a group on New Caledonia would increase with the number of major correlates possessed by the group.

Origins of Dioecy on New Caledonia

The sources used to determine sexual systems and construct the phylogenetic tree also provided information to estimate the number of ancestral colonist species (i.e., species that arrived on New Caledonia following long-distance dispersal) required to account for origins of the extant dioecious flora, to infer the sexual systems and ecological traits of those ancestral colonists, and to assess the extent of autochthonous speciation that occurred after colonists became established. In many cases, traits were invariant within genera or even families, and no further analysis was necessary to assign character states to hypothesized ancestors. When traits varied, we compared the distributions of character states within and among clades containing the extant dioecious taxa (in-groups) and their established or likely sister clades (out-groups). We considered the character state common to an in-group and its out-group as ancestral for the in-group and assigned that state to the ancestral colonist (or colonists) for the in-group. Our ability to determine the exact numbers of colonizing ancestors and autochthonous speciation events was frequently hampered by insufficient phylogenetic data. In several cases it was clear that some autochthonous speciation within a genus had occurred, but we could not infer the exact number of colonizing ancestors involved. Thus, the numbers of hypothesized ancestors we report are often minimum estimates. Synopses of our reasoning on colonizing ancestors and their attributes, including literature citations, are given in table S1. During our examinations of published phylogenetic and biogeographic studies, we also sought evidence for the dispersal of dioecy from New Caledonia to elsewhere.

Results

Incidence of Dioecy in New Caledonian Angiosperms

Using the published literature and our herbarium and field observations, we were able to assign sexual systems to 99.8% of the indigenous angiosperm flora (3047 of the 3053 species listed in Morat et al. 2012; table S2). We found that a remarkable 21% of the indigenous species were dioecious (640 of 3047; tables 1–3, S1, S2). Dioecious species occurred in one-third (52 of 158) of the angiosperm families and in one-sixth of the genera (108 of 690). Instances of leakiness or inconstancy, i.e., occasional production of unisexual flowers and bisexual flowers or both kinds of unisexual flowers on the same individual (see Methods), were reported for seven genera representing six families: *Casuarina* and *Gymnostoma* (Casuarinaceae), *Myrtastrum* (Myrtaceae), *Canarium* (Burseraceae), *Euroshinus* (Anacardiaceae), *Myrsine* (Primulaceae), and *Pittosporum* (Pittosporaceae; tables 3, S1). Rare occurrences of andro- and gynodioecy brought the incidence of sexual dimorphism (dioecy + androdioecy + gynodioecy) to 21.2% (table 2).

Ecological Traits Associated with Dioecy on New Caledonia

Major correlates of dioecy. The four widely accepted ecological correlates of dioecy are tropical distribution, woody habit, plain flowers, and fleshy fruit (Vamosi et al. 2003). By definition, all indigenous New Caledonian angiosperms have tropical distributions. In addition, we found that 76% of the indigenous angiosperm species are woody, 56% have plain flowers, 46% have fleshy fruit, and 25% have all three traits (table S2). Even though the overall frequency of woodiness was very high, dioecy was still more common than expected among woody species (fig. 1, W). Similarly, the observed numbers of dioecious species with plain flowers and fleshy fruit are both much greater than expected (fig. 1, P, F). To make

Table 3

Origins and Ecology of the Indigenous Dioecious Flora of New Caledonia

Order, family, and genus	Species (endemic)		Ancestors		Ecology of extant species			
	Total	Dioecious	No.	SS	Habitat	Woody?	Plain flowers?	Fleshy fruit?
Amborellales:								
Amborellaceae:[a]								
Amborella[a]	1 (1)	1	1	u	F	+	+	+
Chloranthales:								
Chloranthaceae:								
Ascarina	2 (2)	2	2	d	F	+	+	+
Piperales:								
Piperaceae:								
Piper	4 (3)	4	1	d	F	–	+	+
Laurales:								
Lauraceae:								
Litsea[b]	15 (15)	15	1	d	M	+	+	+
Adenodaphne[a]	4 (4)	4			M	+	+	+
Monimiaceae:								
Hedycarya[b]	9 (9)	9	1	d	F	+	+	+
Kibaropsis[a]	1 (1)	1			F	+	+	+
Alismatales:								
Cymodoceaceae:								
Cymodocea	2 (0)	2	2	d	R	–	+	–
Halodule	2 (0)	2	2	d	R	–	+	–
Syringodium	1 (0)	1	1	d	R	–	+	–
Thalassodendron	1 (0)	1	1	d	R	+	+	–
Hydrocharitaceae:								
Enhalus	1 (0)	1	1	d	R	–	+	+
Halophila	3 (0)	2	2	d	R	–	+	+
Thalassia	1 (0)	1	1	d	R	–	+	+
Vallisneria	1 (0)	1	1	d	R	–	+	+
Dioscoreales:								
Dioscoreaceae:								
Dioscorea	1 (0)	1	1	d	F	–	+	+
Pandanales:								
Pandanaceae:								
Frecinetia	24 (19)	24	1	d	F	+	+	+
Pandanus	21 (20)	21	1	d	F	+	+	+
Liliales:								
Smilacaceae:								
Smilax	6 (6)	6	1	d	F	+	+	+
Asparagales:								
Asparagaceae:								
Lomandra	1 (1)	1	1		M	+	+	–
Asteliaceae:								
Astelia	1 (1)	1	1	d	F	–	+	+
Poales:								
Poaceae:								
Spinifex	1 (0)	1	1	d	G	–	+	–
Ranunculales:								
Menispermaceae:								
Hypserpa	3 (2)	3	1	d	F	+	+	+
Pachygone	2 (2)	2	1	d	F	+	+	+
Stephania	1 (0)	1	1	d	F	+	+	+
Tinospora	1 (1)	1	1	d	F	+	+	+
Ranunculaceae:								
Clematis	3 (1)	3	1	d	L,M,N	+	–	–
Fabales:								
Polygalaceae:								
Balgoya[a]	1 (1)	1	1	H	F	+	+	+
Rosales:								
Moraceae:								
Ficus	35 (27)	4 (0)	2	d	L	+	+	+
Maclura	1 (0)	1	1	d	L,G,N	+	+	+

Table 3

(*Continued*)

Order, family, and genus	Species (endemic)		Ancestors		Ecology of extant species			
	Total	Dioecious	No.	SS	Habitat	Woody?	Plain flowers?	Fleshy fruit?
Sparattosyce[a]	2 (2)	2	1	d	F	+	+	+
Streblus	2 (1)	2	1	d	F	+	+	+
Trophis	1 (0)	1	1	d	F,L,G,N	+	+	+
Urticaceae:								
Dendrocnide	3 (0)	3	1	d	F	–	+	–
Nothocnide	1 (0)	1	1	d	F,G,N	–	+	–
Pipturus	2 (0)	2	1	d	N	–	+	–
Fagales:								
Myricaceae:								
Canacomyrica[a]	1 (1)	1	1	d	F	+	+	+
Casuarinaceae:								
Casuarina[c]	3 (2)	3	1	d	M,G	+	+	–
Gymnostoma[c]	8 (8)	8	1	d	F,M,R	+	+	–
Cucurbitales:								
Cucurbitaceae:								
Zehneria	3 (1)	3	1	d	N	–	+	+
Celastrales:								
Celastraceae:								
Celastrus	1 (0)	1	1	d	,M,N	+	+	–
Elaeodendron	6 (5)	3 (2)	1	d	F	+	+	+
Menepetalum[a]	4 (4)	4	1	H	F	+	+	–
Salaciopsis[a]	6 (6)	6	1	u	F	+	+	–
Oxalidales:								
Cunoniaceae:								
Hooglandia[a]	1 (1)	1	1	H	F	+	+	+
Pancheria[a]	27 (27)	27	1	d	M	+	+	–
Malphigiales:								
Euphorbiaceae:								
Acalypha	4 (3)	1 (1)	1	m?	F	+	+	–
Baloghia	13 (12)	9 (8)	1	u	F	+	+	–
Bocquillonia[a]	14 (14)	14	1	d	F	+	+	–
Claoxylon	1 (1)	1	1	d	F	+	+	–
Cleidion	12 (12)	10	1	u	F	+	+	–
Excoecaria	1 (0)	1	1	d	F	+	+	–
Fontainea	1 (0)	1	1	d	F	+	+	+
Macaranga	5 (5)	5	1	d	F	+	+	–
Mallotus	1 (0)	1	1	d	F	+	+	–
Picrodendraceae:								
Austrobuxus	15 (15)	15	1	u	F	+	+	+
Phyllanthaceae:								
Antidesma	1 (1)	1	1	d	F	+	+	+
Bischofia	1 (0)	1	1	d	F	+	+	+
Malpighiaceae:								
Rhyssopterus	4 (3)	4	1	d	M	+	+	–
Balanopaceae:								
Balanops	7 (7)	7	1	d	F	+	+	+
Putranjivaceae:								
Drypetes	1 (0)	1	1	d	F	+	+	+
Salicaceae:								
Xylosma[b]	20 (20)	20	1	d	F	+	+	+
Lasiochlamys[a]	11 (11)	11						
Calophyllaceae:								
Mammea	2 (1)	2	1	d	F,G	+	–	+
Clusiaceae:								
Garcinia	13 (13)	13 (13)	1	d	F	+	–	+
Myrtales:								
Myrtaceae:								
Carpolepis	3 (3)	1	1	H	F,M	+	–	–
Myrtastrum[a,c]	1 (1)	1	1	H	F	+	+	+

Table 3

(*Continued*)

Order, family, and genus	Species (endemic)		Ancestors		Ecology of extant species			
	Total	Dioecious	No.	SS	Habitat	Woody?	Plain flowers?	Fleshy fruit?
Sapindales:								
Burseraceae:								
Canarium[c]	4 (4)	4	2	d	F	+	+	+
Anacardiaceae:								
Euroschinus[a,c]	7 (7)	7	1	d	F	+	+	+
Pleiogynium	1 (0)	1	1	d	L	+	+	+
Semecarpus	6 (6)	6	1	d	F	+	+	+
Sapindaceae:								
Allophylus	2 (0)	2	1	d	F	+	+	–
Dodonaea	2 (0)	1	1	d	F	+	+	–
Rutaceae:								
Comptonella[a]	8 (8)	8	1	u	F,M	+	+	+
?*Picrella*[a,b]	3 (3)	3			L	+	+	+
Crossosperma[a]	2 (2)	2	1	H	F	+	+	+
Medicosma	15 (15)	11	1	H	M	+	+	–
Melicope	6 (6)	6	1	d	F	+	+	+
Sarcomelicope	9 (8)	9	1	d	F	+	+	+
Zanthoxylum	8 (8)	8	1	d	F	+	+	+
Simaroubaceae:								
Soulamea	11 (11)	11	1	d	F	+	+	–
Meliaceae:								
Aglaia	1 (0)	1	1	d	F,L	+	+	+
Anthocarapa	1 (0)	1	1	d	F	+	+	+
Dysoxylum	9 (8)	9	1	d	F	+	+	–
Xylocarpus	2 (0)	2	2	d	G	+	+	–
Malvales:								
Thymelaeaceae:								
Lethedon	15 (15)	15	1	d	F	+	+	+
?*Solmsia*[a,b]	2 (2)	2						
Santalales:								
Balanophoraceae:								
Hachettea[a]	1 (1)	1	1	d	F	–	+	–
Caryophyllales:								
Nepenthaceae:								
Nepenthes	1 (1)	1	1	d	F	+	–	–
Phytolaccaceae:								
Monococcus	1 (0)	1	1	d	F,L,N	+	+	–
Nyctaginaceae:								
Pisonia	4 (2)	3 (1)	1	u	F,L	+	+	–
Ericales:								
Ebenaceae:								
Diospyros	32 (29)	32	4	d	F	+	+	+
Primulaceae:								
Myrsine[c]	39 (37)	39	1	d	F	+	+	+
Lamiales:								
Boraginaceae:								
Cordia	2 (0)	2	2	u	G	+	–	+
Gentianales:								
Rubiaceae:								
Antirhea	2 (2)	2	1	d	F	+	+	+
Guettarda	11 (10)	11			F	+	+	+
Timonius	1 (0)	1			G	+	+	+
Tinadendron	2 (1)	1			FL	+	+	+
Atractocarpus	12 (12)	12	1	d	F	+	–	+
Randia	9 (9)	9				+	–	+
Gardenia	7 (7)	1				+	–	+
Cyclophyllum	16 (16)	13	1	d	F	+	–	+
Gea	6 (6)	6	1	d	FM	+	+	+

Table 3

(*Continued*)

Order, family, and genus	Species (endemic)		Ancestors		Ecology of extant species			
	Total	Dioecious	No.	SS	Habitat	Woody?	Plain flowers?	Fleshy fruit?
Aquifoliales:								
Aquifoliaceae:								
Ilex	2 (0)	2	1	d	F	+	+	+
Asterales:								
Phellinaceae:[a]								
Phelline[a]	14 (14)	14	1	H	F	+	+	+
Apiales:								
Araliaceae:								
Meryta	16 (16)	16	1	d	F	+	+	+
Polyscias	26 (25)	18 (18)	1	Am	F	+	+	+
Pittosporaceae:								
Pittosporum[c]	45 (45)	40	1	u	F	+	–	–
Totals		640 (566)	109					

Note. Orders follow APG III (2009); families and genera follow FLORICAL (Morat et al. 2012, which also follows APG III). Underlined taxa signify that all taxa included are likely in the same clade. Numbers of endemic dioecious species given in parentheses only if not clear from data for the entire genus. Ancestors: S = sexual system, d = dioecious, H = hermaphroditic, Am = andromonoecious, m = monoecious, u = unknown; the total number of colonists is the minimum estimate. Habitats according to Morat et al. (2012); whenever possible, only the predominant habitat is listed: F = rainforest, L = sclerophyll forest, M = maquis, G = halophytic, N = disturbed, R = wetland. For other ecological traits, a plus sign indicates yes, minus no. Inferred ecological traits of ancestors are the same as the ecological traits for the extant taxa in all cases except *Crossosperma*, for which we infer that the ancestor had dry rather than fleshy fruit (see table S1).

[a] Endemic to New Caledonia.

[b] Autochthonous derivation of the second genus from an ancestor resembling the first genus.

[c] “Leakiness” or “inconstancy” reported.

the comparison another way, 98% of the dioecious species are woody, 84% have plain flowers, and 69% have fleshy fruit. Traditional species-based tests for independence of trait combinations (presented here for illustrative purposes only, not hypothesis testing) indicated very strong associations between dioecy and each of the three traits ($\chi^2 = 218$ for woodiness, 234 for plain flowers, 161 for fleshy fruit; df = 1, P always <0.0001, $n = 3049$). Similarly, in all tests for correlated evolution of dioecy with woodiness, plain flowers, and fleshy fruit, differences between the likelihoods for independent and dependent models were always large and very highly significant (P always 0; table 4).

The distribution of character state combinations for woodiness, plain flowers, and fleshy fruit among dioecious species differed significantly from expectation based on the frequencies of the combinations in the entire flora (fig. 1, right-hand group of bars; $\chi^2 = 568$, df = 7, $P < 0.0001$). Species with all three traits are very strongly overrepresented, while those that were woody with plain flowers and dry fruit are only moderately overrepresented and all other trait combinations were underrepresented.

Species richness of dioecious groups, and hence the amount of postcolonization speciation that probably occurred in those groups, increased with the number of major morphological correlates of dioecy that they possessed (fig. 2). However, the differences among means were not statistically significant because the genus *Pittosporum*, with only one correlate (woodiness) and 40 dioecious species, was a clear outlier (linear regression; $F = 2.10$, df = 1, 97, $P = 0.151$). When we excluded *Pittosporum* (for illustrative purposes only), the mean species richness for groups with only one correlate decreased substantially, and differences among means became statistically significant (linear regression; $F = 7.09$, df = 1, 96, $P = 0.009$).

Habitat and endemism. The distribution of dioecious species among habitats shows that dioecy is noticeably more common than expected in rainforest, slightly overrepresented in maquis, minimally overrepresented in sclerophyll, and underrepresented in all other vegetation types (fig. 3; table S3). Our traditional test of independence suggested that dioecious species are indeed significantly overrepresented in rainforest ($\chi^2 = 17$, df = 1, $P < 0.0001$, $n = 3041$), but the results of our phylogenetic tests for correlated evolution were decidedly mixed. Because most of the unresolved polytomies in our phylogenetic tree included both forest taxa and nonforest taxa, rejection of the null hypothesis of independent character state transitions depended strongly on how those polytomies were resolved. Just 44 of the 100 randomly resolved trees gave statistically significant differences between log likelihoods for the independent and dependent models (table 4).

Even though the overall proportion of endemics on New Caledonia is very high at 78% (Morat et al. 2012), dioecy was still overrepresented among endemic taxa (fig. 1). While our traditional test of independence indicated statistical significance ($\chi^2 = 54$, df = 1, $P < 0.0001$, $n = 3049$), our phylogenetic tests did not support correlated evolution of dioecy and endemism. Only nine of the 100 randomly resolved trees produced statistically significant P values (table 4).

Eight of the nine randomly resolved trees that supported correlated evolution of dioecy and endemism also supported correlated evolution of dioecy and occurrence in the rainforest habitat. Thus, while all 100 randomly resolved trees provided

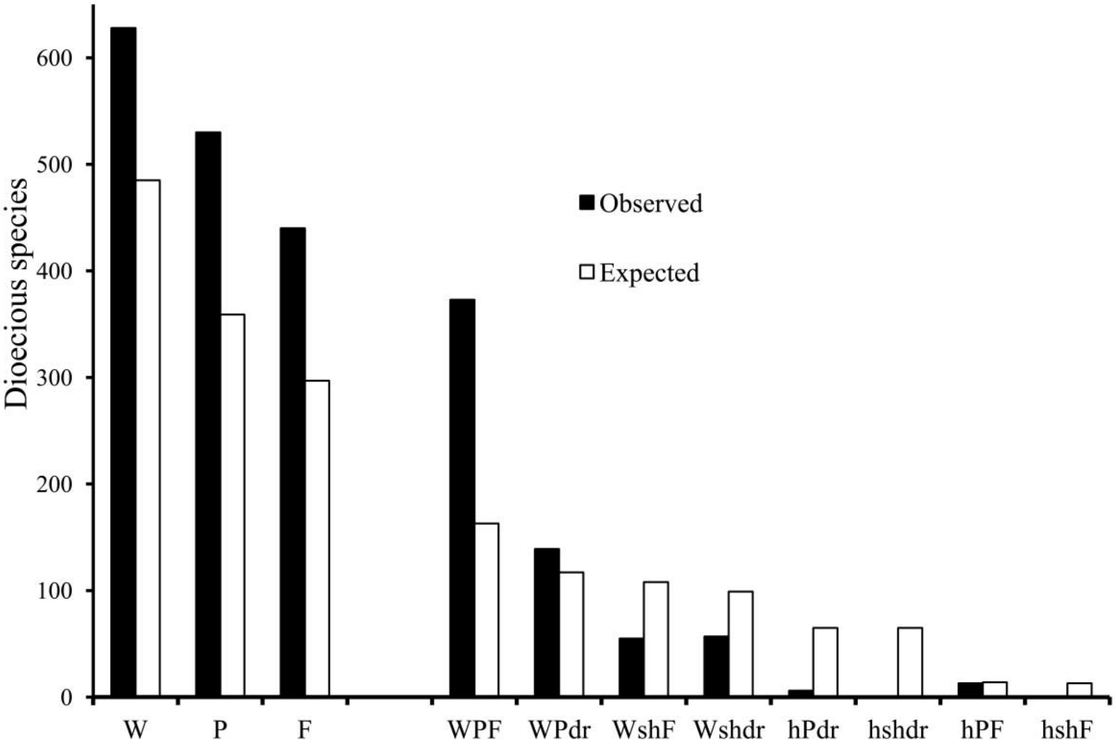

Fig. 1 Numbers of dioecious angiosperms native to New Caledonia exhibiting the three morphological traits considered major ecological correlates of dioecy. Single traits (three groups on left) and combinations of traits (eight groups on right) arranged in decreasing order of expected frequencies in the entire native angiosperm flora. W = woody, h = herbaceous, P = plain flowers, sh = showy flowers, F = fleshy fruit, dr = dry fruit.

support for correlated evolution of dioecy and the three morphological correlates (woodiness, plain flowers, fleshy fruit), only eight supported correlated evolution of all five of the purported correlates that we evaluated.

Origins of Dioecious Lineages on New Caledonia

Characteristics of ancestral colonists. We estimated that a minimum total of 109 ancestral colonist species was required to account for the extant indigenous dioecious flora (table 3). We were able to infer the sexual systems for 104 of the colonists and concluded that 95 of them (91%) were dioecious, while only 9 had some other sexual system (7 hermaphroditism, 1 monoecy, 1 andromonoecy). Even if all of the ancestors with unknown sexual systems were found to be nondioecious, the dioecious proportion would remain very high at 87% (95/109). Eight of the inferred ancestors (7%) may have exhibited leaky or inconstant dioecy (tables 3, S1). Except for *Crossosperma* (ancestor with dry fruit to New Caledonian descendants with fleshy fruit; table S1), we found no evidence that the morphological traits of ancestors differed from those of their extant descendants; thus, 99 (91%) had plain flowers and 90 (83%) were woody, but only 67 (61%) had fleshy fruit.

Postcolonization speciation in dioecious groups. While the quality of phylogenetic information varied considerably among groups, we were able to infer that 46 (42%) of our hypothesized ancestral colonists have just one extant descendant (indeed, the hypothesized ancestor and the extant species may be the same), while as many as 63 (58%) may have two or more descendants (table 3). Since the later 58% of colonists account for 93% (595/640) of the extant dioecious species, it appears that autochthonous speciation (i.e., postcolonization speciation on New Caledonia) has contributed substantially to the current high incidence of dioecy. Groups that appear to have undergone the most extensive autochthonous speciation are *Pittosporum* (Pittosporaceae, 45 spp.); *Myrsine* (formerly *Rapanea*; Primulaceae, 39 spp.); *Xylosma* + *Lasiochlamys*

Table 4

Tests for Correlated Evolution of Dioecy with Other Traits

	Difference		*P* value	
Trait	Mean	Range	Range	No. <.05
Plain flowers	23.65	21.66–24.89	0	100
Woody	21.67	21.19–22.65	0	100
Fleshy fruit	15.51	13.29–17.03	0	100
Rainforest	4.08	2.13–7.15	.002–.730	44
Endemic	4.25	3.44–6.27	.015–.980	9

Note. Maximum likelihood tests (Pagel 1994) implemented with Mesquite 2.75 (Maddison and Maddison 2003). Differences in log likelihoods (independent model − dependent model) and their associated *P* values were determined for 100 different random resolutions of the polytomies in our phylogenetic tree.

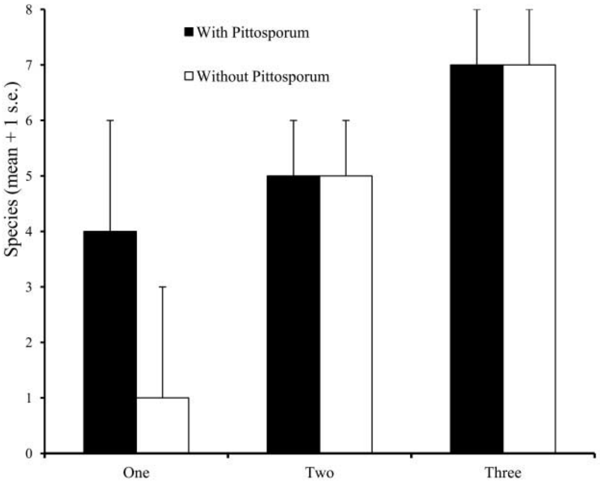

Fig. 2 Species richness of dioecious groups (single genera or groups of related genera) in the indigenous angiosperm flora of New Caledonia with different numbers of the three major morphological correlates of dioecy (woodiness, plain flowers, fleshy fruits). The trend of increasing numbers of species with increasing numbers of correlates is not statistically significant (filled bars) unless the outlier group *Pittosporum* (1 correlate, 40 species) is excluded (filled bars; linear regressions).

(Salicaceae, 31 spp.); *Pancheria* (Cunoniaceae, 27 spp.); *Freycinetia* (Pandanaceae, 24 spp.); *Pandanus* (Pandanaceae, 21 spp.); *Litsea* + *Adenodaphne* (Lauraceae, 19 spp.), each perhaps derived from a single colonizing ancestor; and *Diospyros* (Ebenaceae, 32 spp.), for which there were probably four different colonists (tables 3, S1).

New Caledonia as a Source of Dioecy Elsewhere

We found evidence for dispersal of dioecious taxa from New Caledonia to elsewhere for the genera *Sarcomelicope* (Rutaceae), *Soulamea* (Simaroubaceae), *Polyscias* (Araliaceae), and *Pittosporum* (Pittosporaceae). All species of *Sarcomelicope* except one are endemic to New Caledonia. The exception, *Sarcomelicope simplicifolia*, occurs also on Australia, Lord Howe Island, and Norfolk Island. The most recent molecular phylogenetic results are consistent with dispersal from New Caledonia elsewhere, but further work is necessary to confirm this (Bayly et al. 2013). Phylogeographic analysis suggests that the ancestor of *Soulamea terminaloides*, a dioecious species endemic to the Seychelles, may have dispersed from New Caledonia (Clayton et al. 2009). For *Polyscias*, there may have been three separate dispersals from New Caledonia: *Polyscias cissodendron* to Vanuatu and Lord Howe Island, *Polyscias jokesii* to Fiji, and *Polyscias schmidii* to Vanuatu (Plunkett et al. 2001; Plunkett and Lowry 2010). For *Pittosporum*, Gemmill et al. (2002) suggested possible dispersal from New Caledonia to Figi/Tonga and then to Hawaii. More recent analyses (C. E. C. Gemmill, personal communication) appear to confirm that suggestion (though independent dispersals to Figi/Tonga and Hawaii cannot be ruled out). More recent work also indicates dispersal from New Caledonia to New Zealand (C. E. C. Gemmill, personal communication).

Discussion

Incidence of Dioecy on New Caledonia

At 21%, the incidence of dioecy on New Caledonia is more than three times that for angiosperms as a whole and among the highest known for island floras. The incidence of sexual dimorphism (dioecy + androdioecy + gynodioecy) is 21.2%, which is similar to Hawaii and New Zealand (table 2), where gynodioecy is more common. The combination of great species richness and a high incidence of dioecy gives New Caledonia perhaps the highest concentration of dioecious angiosperms per unit area in the world (table 1). New Caledonia has 2.5 times as many dioecious species as New Zealand, which is 14 times larger, and more than 4 times as many as Hawaii, which is only 12% smaller. We estimated that 4.4% of the world's dioecious species occur on New Caledonia and 3.9% of the world's dioecious species are found only there.

This study is the first to assess the diversity of sexual systems in the entire native flora of New Caledonia. We believe that our multipronged approach of combining literature search, herbarium work, and direct observation in the field has yielded the most accurate assessment possible at this time. While the numbers of species with various sexual systems will surely change as more detailed studies of floral biology are completed and new taxa are discovered and described, we expect the relative proportions to remain largely the same.

Correlates of Dioecy on New Caledonia

In our study, explicitly phylogenetic tests strongly supported correlated evolution of dioecy with woodiness, plain flowers, and fleshy fruit, thus confirming that each of those morphological traits as an ecological correlate of dioecy. Our work also supports the finding that dioecious lineages are most speciose when they posses all three of these morphological traits

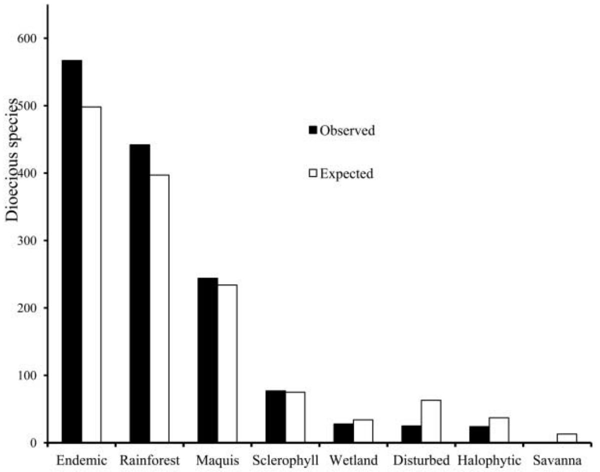

Fig. 3 Observed and expected numbers of dioecious angiosperms native to New Caledonia that are endemic or that occur in each of the seven habitats (vegetation types) recognized by Morat et al. (2012). Expected numbers are based on the overall frequency of endemics or the frequencies of species occurring in each habitat for the entire flora.

and also occur in the tropics (Vamosi and Vamosi 2004). Our analyses indicate that ~90% of the colonists that established the extant dioecious lineages on New Caledonia were themselves dioecious and that each of those dioecious colonists possessed at least two of the morphological correlates. From this, we conclude that with respect to the dioecious lineages that successfully colonized New Caledonia and left extant descendants, essentially all of the events of correlated evolution of dioecy and the three morphological correlates occurred elsewhere, prior to dispersal to New Caledonia. Thus, dispersal to New Caledonia and successful establishment there has been an important ecological sieve (Pannell 2006) through which dioecious species with the most correlates are the most likely to be successful colonists. Moreover, low floristic diversity soon after the Eocene reemergence of Grande-Terre may have limited competition of dioecious colonists with nondioecious ones, mitigating the disadvantages of dioecy relative to hermaphroditism and facilitating establishment of the dioecious colonists (Heilbuth et al. 2001). Therefore, we discuss the significance of fleshy fruits, plain flowers, woodiness, and tropical habitat for dioecy on New Caledonia in terms of dispersal, establishment, and subsequent speciation of already dioecious lineages.

Fleshy fruit. Bawa (1980), Givnish (1980), and others (see Sakai and Weller 1999) have argued that since dioecy is associated with fleshy fruits and endozoochorous dispersal of seeds by birds, dioecy may be especially common on islands with native floras derived from transoceanic dispersal. Inferences about the colonists that gave rise to the extant flora of Hawaii appear to support this, as the incidence of fleshy fruit was only 35% among all hypothesized colonists but rose to 52% for dioecious colonists that gave rise to extant dioecious groups and to 65% for all dioecious colonists (Sakai et al. 1995*b*). For New Caledonia we have so far considered only those colonists that gave rise to the extant dioecious flora. Of those, 62% overall (68/109) had fleshy fruits, as did 67% (64/95) of the colonists that were dioecious.

Of course, the absence of fleshy fruits does not preclude dioecy or prevent transoceanic dispersal. In our analyses, 80% (32/40) of colonists with dry fruits were also dioecious, and a number of them would have been well adapted for long-distance dispersal of diaspores. Examples include *Macaranga* and *Mallotus* (Euphorbiaceae), with dry, capsular fruits containing fleshy seeds (Esser 2003); *Austrobuxus* (Picrodendracee), with arillate seeds (McPherson and Tirel 1987); and *Pittosporum* (Pittosporaceae), with bright orange or red seeds embedded in sticky resin (Cayzer et al. 2000).

Plain flowers. Small, radially symmetrical, plainly colored flowers visited by generalist pollinators are thought to favor dioecy because they facilitate (1) gender specialization without substantial morphological differentiation between male and female flowers, reducing the ability of pollinators to discriminate between them (Charlesworth 1993), and (2) pollen-packaging strategies that allow increases in male reproductive investment (e.g., larger male inflorescences) without saturation of the relationship between investment and actual reproductive success (the male gain curve; Charlesworth and Charlesworth 1987). These factors should facilitate the establishment of males in hermaphroditic populations (Thomson and Brunet 1990) and the establishment of females in hermaphroditic populations when pollen is the only floral reward (Charlesworth 1993; Vamosi et al. 2003). Plain flowers should also reduce the likelihood of extinction caused by infrequent pollinator visits to females of populations with extreme sexual dimorphism in floral display (Vamosi and Otto 2002). Scarcity of specialized pollinators has been suggested as a factor favoring plain flowers and dioecy on both Hawaii (Bawa 1980; Sakai et al. 1995*a*) and New Zealand (Godley 1979; Lloyd 1985).

The entomofauna of New Caledonia is rather poorly known, with as much as 80% of the species not yet described (J. Chazeau and H. Jourdan, personal communication). The bee fauna (Apoidea) is now known to include at least 45 species (Donovan et al. 2013), which is comparable to New Zealand and Hawaii (40 and 54 species, respectively; Pauly and Munzinger 2003). Excluding three recent introductions (*Apis mellifera* and two megachilids) there are 32 species of long-tongued bees, but none of them is common. In contrast there are only 524 described species of Lepidoptera on New Caledonia (Chazeau 1993), compared to 1203 for Hawaii (Bishop Museum 2002). There are just 17 species of nocturnal moths (Sphingidae) and no long-tongued flies (Nemestrinidae). The New Caledonian avifauna includes just six species of nectar feeders (all honeyeaters; Meliphagidae), and only three of those are found in the rainforests of Grande-Terre (Hannecart and Létocart 1980, 1983).

Broad, community-level studies of plant-pollinator interactions on New Caledonia are almost nonexistent. In their study of 123 rainforest tree species, Carpenter et al. (2003) reported that ±61% had white or pale-colored flowers and that 81% were pollinated by insects, 13% by wind, and 6% by birds. In a study of 95 indigenous species distributed among rainforest, sclerophyllous forest, maquis, savanna, and mangrove vegetation, Kato and Kawakita (2004) reported ±80% insect, 3% wind, 12% bird, and 3% bat pollination. While the most frequent primary insect pollinators were bees (46.3% of the plant species), the overwhelming majority of visits were by introduced honeybees (*Apis mellifera*). Other insect visitors were moths (20% of plant species), beetles (8.4%), and flies (3.2%). The available data suggest that on New Caledonia, a relative paucity of some groups of specialized pollinators may have contributed to the high incidence of dioecy by favoring the establishment of colonists with plain flowers over those with showy ones. This is consistent with our estimate that 91% of the ancestors of New Caledonia's dioecious flora already had plain flowers.

Woody habit. Woodiness is thought to favor dioecy primarily through indirect means. The large inflorescences produced by many woody plants may result in substantial geitonogamy, which could cause pollen-stigma interference and inbreeding (de Jong et al. 1993). If inflorescences are sufficiently large, mechanisms such as herkogamy and dichogamy may be ineffective in reducing geitonogamy, and selection would then favor dioecy (Harder and Barrett 1996; Barrett 2002; Vamosi et al. 2003). Since woody plants are perennial and may have numerous opportunities for successful mating, the riskiness of dioecy could be mitigated (Pannell and Barrett 1998).

New Caledonia's equable, tropical climate has clearly been favorable for woody plants. Prior to the arrival of humans, extensive evergreen forests likely covered more than 70% of the land area (~13,000 km^2; Jaffré et al. 2001; Lowry et al. 2004). Though rainforests are now reduced to only ~4000 km^2 (Lowry et al. 2004), ~60% of New Caledonia's angiosperms are still found there (Morat et al. 2012). As we noted above, the incidence of dioecy among woody rainforest species is extremely high, both on New Caledonia as we have shown here and elsewhere.

Tropical climate. Vamosi and Vamosi (2004) argued that tropical climate per se favors dioecy independently of its associations with morphological correlates such as woodiness. They suggested that the absence of a severely unfavorable season permits less synchrony of flowering and fruiting among species, decreasing interspecific competition for pollinators and dispersers. Since dioecious species cannot self-pollinate and have fewer fruit-producing individuals than sexually monomorphic species, reduction of such interspecific competition should be especially advantageous for dioecious species (Heilbuth et al. 2001). There are few comprehensive phenological studies of New Caledonian rainforest plants, but Carpenter et al. (2003) found that as a group, 123 species of rainforest trees on ultramafic soils flowered and bore fruit continuously throughout the year. Understanding the reproductive phenologies of dioecious species may help explain the association of dioecy with woodiness and rainforest habitats.

Habitat and endemism. The extremely high incidence of dioecy among New Caledonia's rainforest species, 27%, is at the upper end of the range previously reported in studies restricted to tropical forest vegetation (±18%–26%; Adam and Williams 1994; Sakai and Weller 1999; Carpenter et al. 2003; Gross 2005; Matallana et al. 2005; Vary et al. 2011). Marked overrepresentation of dioecy among endemics and rainforest species seems to suggest that the high incidence of dioecy on New Caledonia is due in part to a climate that supports an extensive rainforest. Indeed, all but two of the more speciose dioecious groups mentioned above occur solely or primarily in rainforest, the exceptions being *Litsea* + *Adenodaphne* (Lauraceae) and *Pancheria* (Cunoniaceae), which occur primarily in maquis. The lack of support for correlated evolution of dioecy and occurrence in rainforest habitat or endemism suggests that while the New Caledonian environment may have favored postcolonization speciation of already dioecious lineages, it has not favored postcolonization transitions from other sexual systems to dioecy.

Origins of Dioecy on New Caledonia

Dioecious colonists versus nondioecious colonists. We estimated that a minimum of 87% of the colonizing species that gave rise to the extant dioecious flora of New Caledonia were themselves dioecious. Sakai et al. (1995*b*) inferred a similarly high proportion of dioecy among colonists that produced the dioecious flora of Hawaii (86%; treating polygamo- and subdioecy as dioecy). For New Zealand, Webb et al. (1999) concluded that dioecy arose autochthonously (i.e., on New Zealand after colonization) in 22% (15/69) of the entirely or partially dioecious genera, implying that ancestors of the remaining 78% were probably dioecious. Clearly, our results, as well as those for Hawaii and New Zealand, do not support the prediction, derived from Baker's law (Baker 1955), that dioecy on these islands should be largely derived from hermaphroditism or another cosexual system after dispersal to the island. Rather, the available data for all three island groups favor the alternative view that dioecy itself usually originated elsewhere and then reached the islands because it was associated with other traits (e.g., fleshy fruit) that facilitated long-distance dispersal (Bawa 1980). Our results for New Caledonia provide new empirical support for the recent theoretical work of Cheptou and Massol (2009), who, contrary to Baker's law, predicted evolutionarily stable associations between outcrossing and high dispersibility and also between selfing and low dispersibility.

As we noted above, limited competition soon after the Eocene reemergence of Grande-Terre may have mitigated the disadvantages of dioecy relative to hermaphroditism and other monomorphic sexual systems, thus facilitating establishment of dioecious lineages. Nevertheless, 79% of the extant native flora is sexually monomorphic, and it is likely that a strong majority of those species are derived from sexually monomorphic ancestors. While it is beyond the scope of this study, it would be interesting to infer sexual systems for ancestors of the sexually monomorphic flora and to determine the relative ages of monomorphic and dimorphic lineages.

Similarly, leakiness or inconstancy may also have facilitated establishment after long-distance dispersal (Humeau et al. 1999). Though we found that only 7% of the colonizing ancestors that gave rise to the extant dioecious flora may have exhibited leaky dioecy, leakiness does occur in two of the most speciose dioecious groups (*Myrsine*, 39 species, and *Pittosporum*, 40 species).

Autochthonous speciation versus frequent colonization. We found that autochthonous speciation played a significant role in the evolution of New Caledonia's extant dioecious flora, with more than nine-tenths of the extant dioecious species derived from just 58% of the ancestral colonists. As this conclusion is based on our inferences of the minimal number of ancestors needed to account for the extant dioecious flora, it is subject to revision if new phylogenetic studies provide evidence for multiple colonizations by species in the same genus. However, we note that extensive autochthonous speciation appears to have occurred in the evolution of the dioecious native flora of Hawaii. We calculated that 85% of the dioecious flora (134 of 158 dioecious, polygamodioecious, or subdioecious species; Sakai et al. 1995*b*) was derived via autochthonous speciation from just 46% (17/37) of the inferred colonists. We could not obtain a comparable estimate for any other island group.

Dioecy Out of New Caledonia?

In all but one of the cases we discovered, it appears that dispersal of dioecy from New Caledonia to elsewhere has left just one (*Sarcomelicope*, *Soulamea*, *Polyscias*) or at most two (*Pittosporum* to Fiji/Tonga, *Pittosporum* to New Zealand) extant descendants. For *Sarcomelicope* and *Polyscias*, within-species disjunctions indicate rather recent dispersals with very little morphological change. At present, the only possible case of dispersal of dioecy from New Caledonia leading to a significant radiation of dioecious species elsewhere is that of *Pittosporum* dispersing directly from New Caledonia to Hawaii. However, it seems more likely that the ancestor of the Hawaiian clade of *Pittosporum* arrived from Fiji/Tonga rather than directly from New Caledonia (Gemmill et al. 2002).

Future Prospects

With 3.9% of the world's dioecious angiosperms occurring only there (table 1), New Caledonia presents an especially rich and potentially important source of new information for elucidating the maintenance of dioecy and the conditions under which dioecious lineages have diversified. While this study focused specifically on the origins of the extant dioecious species, there are many questions remaining. Expanding our analyses of numbers and traits of ancestral colonists and postcolonization speciation to the entire native flora would provide a more comprehensive assessment of Baker's law and perhaps reveal losses of dioecy after dispersal to New Caledonia. It would also be interesting to compare the ages of dioecious and nondioecious lineages to test the prediction that most dioecious lineages were established relatively soon after the Eocene emergence of Grande-Terre, when the flora was relatively sparse and competition somewhat limited.

As we noted above, knowledge of New Caledonia's flora is far from complete. New taxa are described regularly, and for many species there is little information beyond the original taxonomic descriptions. Yet even as new species are recognized and described, conservationists have recognized New Caledonia as a priority hot spot in which anthropogenic fire, invasive species, logging, mining, and urbanization continue to threaten natural vegetation (Bramwell 2011). The once extensive humid evergreen forest, in which the large majority of endemic dioecious species occur, has been reduced by at least 70%, from more than 13,000 to ~4,000 km^2 (Lowry et al. 2004). Truly protected natural areas comprise only 3.4% of the land area (Morat et al. 2012).

The same attributes of dioecy that make it rare among angiosperms, including the necessity of pollen transfer between two particular types of individuals, the inability of many individuals to produce seeds, and the need for at least two individuals to establish a new population, should also make dioecious species especially vulnerable to anthropogenic extinction. Recently, Vamosi and Vamosi (2005) showed that exclusively dioecious families had higher proportions of threatened species than their nondioecious sister groups and that woodiness also contributes to the high likelihood that dioecious species are listed as threatened. The very high incidence of dioecy in New Caledonia's remaining rainforest, along with the high incidence of dioecy overall, makes the conservation of New Caledonia's remaining natural vegetation an even greater priority.

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