

Plant reproductive phenology and floral resources of an Australian subtropical rainforest

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ABSTRACT

A survey of the reproductive features of the rainforest flora of Lamington National Park, based on herbarium records and published floras, is presented to provide a community-wide description of floral morphology and flowering phenology. The flora is predominantly composed of shrubs and trees, but also supports a large diversity of vine species. The majority of species (73.5%) have flowers less than 10 mm in diameter of which 80% are white or green in colour. The greatest number of species are in flower from September through to February, although a number of species flower during the cooler, drier winter months. The data compiled on floral features and phenology for individual plant species were assigned to the species lists derived from the IBISCA-Queensland (Qld) altitudinal gradient in Lamington National Park, Australia. No statistically significant changes in flower colour or size were detected with increasing altitude from 300 m to 1100 m a.s.l., but decreasing trends in the proportions of colourful flowers, flowers less than 5 mm in diameter and unisexual flowers were observed. No pollination studies conducted in Lamington National Park have been published although subtropical forests in general are believed to be predominantly generalist pollinated. Data on the morphology of flowers and timing of flowering provide some support for this idea. Determining the prevalence and species turnover of such generalist pollination systems along altitudinal gradients, such as the IBISCA-Qld gradient, could help determine the reproductive resilience of subtropical rainforest plant species under climate change. □ *Pollination, flower morphology, phenology, altitudinal gradient, subtropical rainforest.*

The flora of any ecosystem contains a wide range of taxa and a concomitant variety of floral traits. This is especially the case in highly complex rainforest systems. The set of flowering plant species that co-occur within a particular forest or, indeed, within a particular stratum within a forest, presents characteristic ranges and distributions of floral traits. At the community level this is the background against which pollination systems operate. In this paper we describe the basic morphological characteristics and flowering patterns of the flowering plants found in the rainforests of Lamington National Park and associated with the IBISCA-Queensland project (see Kitching *et al.* 2011).

AUSTRALIAN SUBTROPICAL RAINFORESTS

Australian subtropical rainforests are widely distributed along the Australian eastern seaboard, but represent a fraction of land cover area. Webb (1959) described the Australian subtropical rainforests as 'an ecological entity in a broad latitudinal sense'. These subtropical rainforests share many structural and floristic elements with tropical rainforests, but extend geographically well beyond the latitudinal delineation of the tropics (Richards 1996) and are therefore considered a separate formation type. Although quasi-tropical rainforests also exist along the Atlantic coast of Brazil and the northern low and mid-elevation regions of South-east Asia at comparable low latitudes (Richards 1996), these are only partially comparable to the Australian systems (Webb 1959).

Extending from approximately 20°S to about 37°S, the Australian subtropical rainforests represent a number of distinctive features, the most notable of which is the dominance of notophyll leaf sizes amongst the trees (i.e. intermediate between the truly tropical meso- and megaphyll, and the cool temperate microphyll forests; Webb 1959). It is generally supposed that rainforests of this kind dominated a

large part of the Australian continent during the Tertiary (Adam 1992), dwindled to a few refuge areas during the last glacial maximum and are now restricted to relatively small discontinuous patches. The present day distribution of subtropical rainforests in Australia results from the interaction of complex rainfall patterns, high altitudes and extant soil types as well as anthropogenic clearing and disturbance (Richards 1996). Floristically, these subtropical rainforests distinguish themselves from their tropical neighbours at the species level (Webb & Tracey 1981) with typical Australian tropical families such as Elaeocarpaceae, Lauraceae and Rutaceae well represented in Australian subtropical rainforests while some of the more abundant species belong to families considered typical of the southern hemisphere such as the Cunoniaceae (Richards 1996). Structurally, these Australian subtropical forests resemble Australian tropical rainforests. The trees reach similar heights and have a comparable presentation of life-forms but with the addition of some more typically temperate groups such as the hemicryptophytes (Richards 1996).

Within the distribution of Australian subtropical rainforests, increasing latitude coincides with a decrease in species diversity and the loss of some tropical characteristics such as cauliflory. The subtropical rainforests of Queensland and New South Wales experience a dry season (five to six months of rainfall less than 100 mm) and a regular and seasonal pattern of substantial temperature variation. As Richards (1996) points out, the coincidence of low temperatures with a dry period, as is the case in Australia's subtropical rainforests, may allow the vegetation to be less affected by water stress than would be the case in seasonal tropical climates. Other microclimatic factors, such as the conditions created by different aspect and topography, also impact on vegetation associations and are important in supporting the survival of subtropical rainforest species.

As with most Australian plant communities (e.g. Boulter *et al.* 2008), there is limited

knowledge of the reproductive systems of these subtropical floras. A collaborative effort to understand these systems by Paul Adam, Geoff Williams and colleagues has contributed a number of significant publications. This includes information on breeding systems (Adam & Williams 2001), wind pollination (Williams & Adam 1999) and the role of insect pollinators (Williams 1995, 1998; Williams & Adam 1995, 2001) in particular thrips (Williams *et al.* 2001). In reviewing pollination in subtropical rainforests, Williams and Adam (1994) identified a number of highly specific plant-pollinator relationships including thrips pollination of *Wilkea hugeliana* (Williams *et al.* 2001), fig-wasp mutualisms in *Ficus* species and weevil-pollination of *Eupomatia laurina* (Williams & Adam 1994). In spite of this, they concluded that generalist pollination is the dominant pollination system, with Diptera, Hymenoptera and Coleoptera the main vectors. The published evidence to support this is limited to very few studies and is largely based on *ad hoc* observations.

The availability and success of individual potential pollinators will depend on each species' (both pollinator and host plant) morphology, breeding system and phenology or life history. The form of these traits in a plant represent a complex response to a number of evolutionary processes including the success of individual pollinator and predator groups (Wyatt 1983), the phylogenetic history of the plant (Johnson & Steiner 2000) and the plasticity of its character traits (Rathcke & Lacey 1985) as well as the changing influence and nature of these factors over evolutionary time (Feinsinger 1983). Knowing something about a plant's morphology and phenology can provide a useful starting point in understanding the reproductive ecology of a flora in the absence of extensive pollinator records and long-term datasets on plant and pollinator phenology.

The primary purpose of this paper is to provide a community-wide description of flower morphology and flowering phenology. In

addition we consider the extent to which flower morphology and phenology might change naturally along an altitudinal gradient as part of the IBISCA-Queensland (Qld) project (Kitching *et al.* 2011). At the core of the project has been the establishment of four plots at each of five altitudes at which the vegetation within permanently marked 20 m x 20 m quadrats has been surveyed (Laidlaw *et al.* 2011). We use these vegetation surveys in combination with data sets on morphology and phenology to explore changes in floral landscapes with altitude.

MATERIAL AND METHODS

Study site. Lamington National Park is a large, continuous reserve of predominantly subtropical rainforest approximately 100 km south of Brisbane in southeast Queensland at latitude 28°S. Lamington National Park supports several structural types of subtropical rainforest, including the extensive and dominant type, complex notophyll vine forest (Laidlaw *et al.* 2011; *sensu* Webb *et al.* 1984) as well as wet sclerophyll forest, open forest and heathlands. The area experiences average annual rainfall totals of 1600 mm, which at times exceed 3000 mm (Bureau of Meteorology Station Number 040182, 'Green Mountains', 917 m a.s.l.), with summer dominated rainfall and dry winter months (July, August and September).

Database construction. A complete list of the vascular plants of Lamington National Park was drawn up using McDonald and Thomas (1990). A total of 1040 species from 148 families are recorded from the park in all vegetation types of which 603 species occur in rainforest vegetation. Of these, 33 species were classified as 'naturalised' (i.e. introduced or exotic) and 81 species as ferns. These were discarded for the analysis, leaving 489 angiosperm plant species for which we built a database of floral morphology characteristics. Information on floral morphology was extracted from existing

TABLE 1. (Opposite page) Flower visitors and pollinators known for subtropical rainforest plant species. Plant species in bold are known to occur in Lamington National Park. Abbreviations for plant growth habits are as follows: E, epiphyte; H, herb, S, shrub, ST, small tree, T, tree; US, understorey shrub; V, vine.

floral treatments and flowering and fruiting phenology using herbarium records and published floras.

Floral Morphology. Information on each species' inflorescence structure and size, individual flower size, colour, shape and scent, reproductive structures, breeding system (e.g. bisexual, dioecious, monoecious) as well as the plants' growth habit and latitudinal and altitudinal ranges were compiled using published floral accounts (McDonald & Thomas 1990; Harden 2000; Leiper 2008; Floyd 2008; Botanic Gardens Trust 2009). We assessed photographs and descriptions, where available, to assign a dominant flower colour to each species.

Community-Wide Floral Phenology. A database of the flowering and fruiting phenology for the rainforest species of Lamington National Park was constructed using herbarium specimen records. Records of collection date, altitude, and the latitude and longitude of collection of all specimens recorded as having reproductive structures (i.e. flowers and fruits) were extracted from the Queensland Herbarium's collection database HERBRECS. These records were further filtered for those collected between latitudes 20°S and 37°S to represent collection within the distribution of subtropical rainforests. In addition, we compiled a second list of flowering phenology for each species using published floras (McDonald & Thomas 1990; Harden 2000; Leiper 2008; Floyd 2008; Botanic Gardens Trust 2009) to assign flowering months. From each of these datasets (i.e. herbarium records and published floras) we calculated two measures associated with flowering phenology for each plant species. First, mean flowering times or flowering midpoints were calculated using circular vector statistics (Batschelet 1981; Boulter *et al.* 2006). This was necessary as flowering events for individual species

frequently span the calendar break between years, making it inappropriate to use linear models based on a simple numbering of months. Species that flowered in all 12 months or for a discontinuous period were excluded from these calculations. Second, the length of flowering season of each species was calculated. For the data collated from herbarium records, flowering length was calculated as the mean vector length, r , as a measure of the concentration of flowering times for each species for which flowering midpoint was calculated (Batschelet 1981). For the information collected from published sources, which was expressed as month(s) of flowering, this was simply a count of the number of months.

IBISCA-QLD Vegetation Survey. All trees greater than or equal to 5 cm diameter at breast height (dbh) were surveyed by staff of the Queensland Herbarium on each of the 20 IBISCA-Qld 20 m x 20 m plots, i.e. four replicate plots at each of five altitudes; 300, 500, 700, 900 and 1100 m a.s.l. In addition all species found in the understorey of each plot were recorded. The complete survey methodology and results are described in Laidlaw *et al.* (2011). We used the data from the herbarium surveys to construct a species list for each plot at each altitude and, using the morphology and phenology databases we had prepared, collated flower morphology and phenology characteristics for each altitude.

Analyses. Estimates of flowering season length and mid-flowering peak using both the herbarium data and information derived from published floras were used to determine if the two sources of data provided comparable patterns. The first estimate, flowering midpoint was circular and was compared using a circular correlation analysis (Batschelet 1981). The second estimate – flowering season length – was linear and we compared these using a paired *t*-test.

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Plant Family and species	Habit	Sexual system	Flower colour	Flower diameter	Flower shape	Pollinators	Flower visitors	Habitat/location sampled	Source
ANACHARDIACEAE <i>Eurochinus falcata</i>	T	Bisexual or dioecious	Cream	6 mm	Dish	N/A	bees; <i>Glycyphana brunnipes</i> (Scarabaeidae: Cetoniinae); <i>Polistes humilis</i> (Hymenoptera: Vespidae); <i>Myrmecia nigrocincta</i> (Hymenoptera: Formicidae); <i>Amata</i> sp. (Lepidoptera: Arctiidae); <i>Apis mellifera</i> ; <i>Castiarina producta</i> (Coleoptera: BUPRESTIDAE)	Subtropical rainforest, NSW	Williams 1995
ATHEROSPERMATACEAE <i>Daphnandra micrantha</i>	ST	Bisexual	White/Green	8 mm	Dish	Nematocera?		Riparian rainforest, Lortien Wildlife Refuge, NSW	Williams 1995
COMMELINACEAE <i>Pollia crispata</i>	H	Bisexual	White	10 mm	Open/Dish		Syrphid flies, halictid bees, <i>Trigonia carbonaria</i>	Subtropical rainforest, Lortien Wildlife Refuge, NSW	Williams & Walker 2003
CUNONIACEAE <i>Davidsonia johnsonii</i>	T	Bisexual	Pink	7 mm	Dish	unknown	bees (native included), beetles and ants	Subtropical rainforest, NSW	Department of Environment and Conservation NSW 2004
EBENACEAE <i>Diospyros australis</i>	S/T	Dioecious	Cream	5 mm	Tube		bees - Anthophoridae, <i>Hylaeus ?primulipictus</i>	Subtropical rainforest, NSW	Williams 1995
EUPOMATIACEAE <i>Eupomatia bennetti</i>	S	Bisexual	Yellow	25 mm	Complex structure	<i>Elleschodes</i> spp. (weevils)		Subtropical rainforest, NSW	Endress 2003
<i>Eupomatia laurina</i>	S/T	Bisexual	White	20 mm	Complex structure	<i>Elleschodes</i> spp. (weevils)	ptiliid beetle, cockroach, thrips	Subtropical rainforest, NSW	Endress 2003; Williams & Adam 1994 and various references cited therein
FABACEAE <i>Senna acclinis</i>	S	Bisexual	Yellow	?	Cup-shaped	<i>Amphylaeus nubilosellus</i> , <i>Hylaeus turgtollaris</i> , <i>Lasioglossum polygoni</i>	diverse assemblage of native bees	Littoral rainforest, Halidays Point, NSW	Williams 1998
LAURACEAE <i>Neolitsea dealbata</i>	T	Dioecious	Cream	2 mm	Tube		Coleoptera, Hymenoptera, Diptera	Tropical rainforest	House 1985, 1989

TABLE 1. cont...

Plant Family and species	Habit	Sexual system	Flower colour	Flower diameter	Flower shape	Pollinators	Flower visitors	Habitat/location sampled	Source
MONIMIACEAE <i>Wilkiea huegeltiana</i>	S/T	Dioecious	Cream	3 mm	Urceolate	Thrips setipennis	<i>Trigona carbonaria</i> (Apidae) ? <i>Crematogaster</i> and <i>Camponotus</i> ants	Subtropical rainforest, NSW	Williams 1995
MORACEAE <i>Ficus macrophylla</i>	T	Monoeious	Orange	22.5 mm	Fig	Pleistodonites froggatti			Lopez-Vaa- monde et al. 2002
<i>Ficus obliqua</i>	T	Monoeious	Orange	9 mm	Fig	<i>Pleistodonites greenwoodii</i> ; <i>Pleistodonites xanthocephalus</i>			Lopez-Vaa- monde et al. 2002; Dixon et al. 2001
<i>Ficus rubiginosa</i>	T	Monoeious	Yellow	15 mm	Fig	<i>Pleistodonites imperialis</i>			Lopez-Vaa- monde et al. 2002; Dixon et al. 2001
<i>Ficus watkinsiana</i>	T	Monoeious	Purple/Black	30 mm	Fig	<i>Pleistodonites nigricentris</i>			Lopez-Vaa- monde et al. 2002
<i>Maclura cochinchinensis</i>	V	Dioecious	Yellow	1 mm	Inflorescence: Globulose head	thrips		Subtropical rainforest, NSW	Williams et al. 2001
<i>Streblus brunonianus</i>	T	Dioecious	Cream	4 mm	Dish	facultatively wind pollinated		Subtropical rainforest, NSW	Williams & Adam 1993
MYRSINACEAE <i>Rapanea howittiana</i>	S/T	Bisexual	Cream	3 mm	Closed; fused perianth	thrips		Riverine rainforest, Landsdowne Reserve, NSW	Williams 1995
<i>Rapanea subsessilis</i>	US	Gynodioecious	Cream	3 mm	Closed; fused perianth	thrips	<i>Trigona</i> sp.; thrips	Tropical rainforest	Harrison 1987; Jackes 2005
<i>Rapanea variabilis</i>	S/T	Bisexual	Cream	2 mm	Closed; fused perianth	thrips		Subtropical rainforest, NSW	Williams 1995
MYRTACEAE <i>Acmena smithii</i>	T	Bisexual	Cream	7 mm	Cup-shaped Dish		bees	Littoral rainforest, Harrington, NSW	Williams 1995
<i>Tristaniaopsis laurina</i>	T	Bisexual	Yellow	10 mm	Dish		bees	Subtropical rainforest, NSW	Williams 1995

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TABLE 1. cont...

Plant family and species	Habit	Sexual system	Flower colour	Flower diameter	Flower shape	Pollinators	Flower visitors	Habitat/location sampled	Source
<i>Waterhousea floribunda</i>	T	Bisexual	White	3 mm	Cup-shaped		bees	Subtropical rainforest, NSW	Williams 1995
ORCHIDACEAE <i>Dendrobium monophyllum</i>	E	Bisexual	Yellow	10 mm	Orchidaceous	<i>Trigona</i>		Herberton, Atherton Tablelands-Tropical rainforest	Bartreau 1993
PROTEACEAE <i>Hicksbechia pinnatifolia</i>	S/T	Bisexual	Pink	15 mm	Tube		Native & introduced bees, moths None seen to contact pollen presenter	Lismore, NSW	Goldingay & Bowen 2003
<i>Triumia youngiana</i>	S	Bisexual	White/pink	15 mm	Tube		Butterflies & moths (contacted pollen presenter) Flies, ants & beetles (no contact with pollen presenter)	Lismore, NSW	Goldingay & Bowen 2003
RHAMNACEAE <i>Alphitonia excelsa</i>	T	Bisexual	White	4.5 mm	Dish		bees	Littoral rainforest, Harrington, NSW	Williams 1995
ROUSSEACEAE <i>Cutisia viburnea</i>	S/T	Bisexual	White	4 mm	Dish		Colletidae-Colletinae (? <i>Leioproctus</i>)	Subtropical rainforest, Lorient Wildlife Refuge, NSW	Williams 1995
RUTACEAE <i>Acradenia euodiformis</i>	S	Bisexual	White	8 mm	Dish		bees	Subtropical rainforest, NSW	Williams 1995
SAPINDACEAE <i>Alectryon coriaceus</i>	S/T	Monocious	White	2 mm	Cup-shaped	Facultatively ant-pollinated?	bees	Littoral rainforest, Harrington, NSW	Williams 1995
<i>Guioa semiglauc</i>	T	Monocious/dioecious	Cream	3 mm	Dish		bees, <i>Apis mellifera</i> , <i>Phyllostictus australis</i> (Scarabaeidae)	Littoral rainforest, Harrington, NSW	Williams 1995
SMILACACEAE <i>Smilax glycyphylla</i>	V	Dioecious	White	4 mm	Cup-shaped	thrips		Subtropical rainforest, NSW	Williams 1995
VITACEAE <i>Cissis antarctica</i>	V	Bisexual	Yellow	5 mm	Dish	generalist		Subtropical rainforest, NSW	Williams 1995

The statistical significance of associations between flower colour, habit and flower size were tested using chi squared analyses. The association between altitude and different proportions of habit, flower colour and category of flower size were also tested using chi squared analyses.

RESULTS

Whole Flora

Habit. Of the 570 plant species found in the rainforests of Lamington National Park, approximately 21% are trees, 23% shrubs and a further 7% can take the form of either a small tree or a tall shrub (Fig. 1). Vines made up about 14% of the total, as did ferns. Other life forms included forbs (7%), epiphytes (7%), graminoids (3.5%) and parasites (i.e. mistletoes) (1%).

Flower size. Floral diameter could be determined for 448 plant species, with almost three quarters (73.7%) having flowers less than 10 mm in diameter. Fewer than 10% of plants had flowers greater than 20 mm in diameter. The distribution of flower sizes appeared more or less uniform across all growth habits with the exception of parasites (Fig. 1) with no significant relationship between the two variables ($c^2 = 24.78$, d.f. = 21, $P = 0.26$).

Flower colour. Dominant flower colour was determined for 350 of the target species which were grouped into the following categories: white/green, yellow/orange, pink/red, blue/purple and brown. These groupings were based on colour groups generally associated with pollination syndromes (e.g. red or pink associated with bird pollination syndromes (Faegri & van der Pijl 1979)). The overwhelming majority of flowers were white/green (73%). Of the remaining species, 12.5% have yellow/orange flowers, 6% pink/red, 6% blue/purple and 2% brown. When we considered the proportional representation of flower colour groups within each plant growth habit type (Fig. 2), not surprisingly, white/green flowers dominated

across all types. There was a strong association between colour and habit type ($c^2 = 170.11$, d.f. = 28, $P < 0.0001$), largely due to the colour bias in graminoids and parasites. When these were omitted from the analysis there was no significant association ($c^2 = 9.6$, d.f. = 12, $P = 0.65$). Flower size and colour showed a clear association ($c^2 = 36.69$, d.f. = 12, $P = 0.0003$). The proportion of white/green flowers decreased with increasing flower size (Fig. 3) with small flowers more often a dull white or green colour and large flowers more often colourful.

Sexual Systems. Most plant species in the Lamington rainforests are bisexual (ca. 67%, $n = 479$). Most of the remainder of species have unisexual flowers although about 5% can have both bisexual and unisexual flowers (e.g. Asteraceae). Of the 127 unisexual species, more than half ($n = 71$) are monoecious.

Phenology. Preliminary analysis showed good congruence between flowering estimates derived from herbarium data and those derived from published floras. There was a strong positive correlation between flowering midpoints derived from the two data sources ($R_+ = 0.49$, $P < 0.001$, $n = 393$), suggesting that the herbarium records provided a reliable basis on which to assess the flowering times of species. In contrast, the independent assessments of flowering season length differed slightly (paired $t = 1.83$, $P = 0.06$). Flowering season length averaged 5.58 and 5.26 months for the herbarium records and published flora data respectively. This suggests that the herbarium records overestimate flowering season compared to published floras. This may reflect the fact that the herbarium records were collected across the entire distribution of subtropical rainforests, while published floras may be based more on local records and knowledge. For the rest of the analyses, we used the data derived from the herbarium collections.

All surveyed species from Lamington National Park showed distinct seasonality in their flowering patterns with most flowering in November

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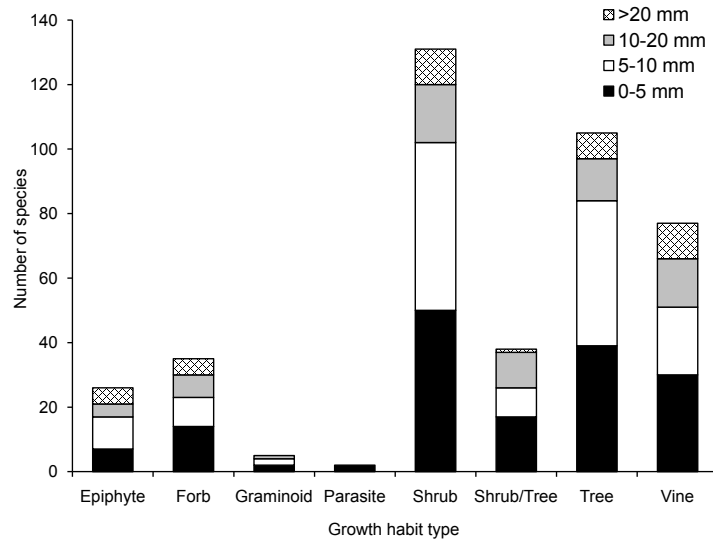


FIG. 1. Number of species in each of four flower diameter size classes within growth habit types for angiosperm species found in the rainforests of Lamington National Park.

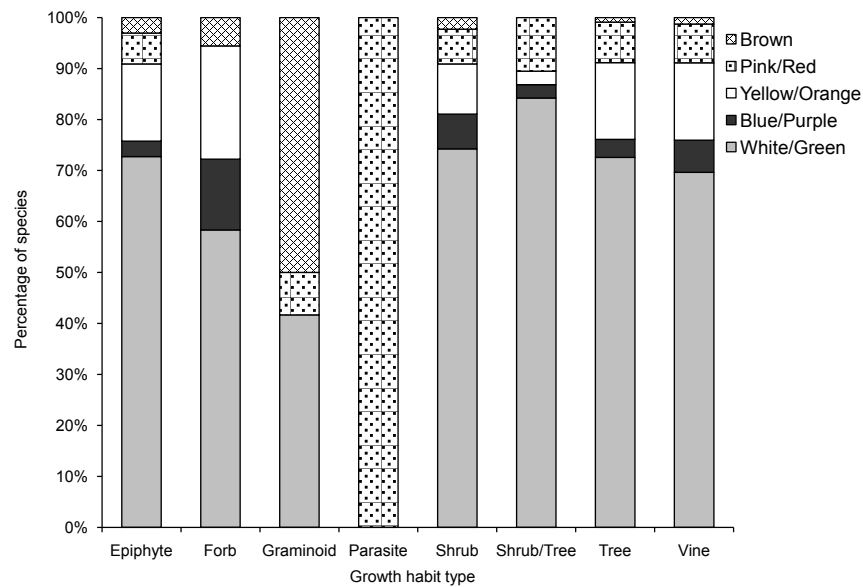


FIG. 2. Proportions of Lamington National Park rainforest species displaying different flower colours within eight different plant growth habit types. See figure 1 for the number of plant species within each habit type.

($n = 285$) and December ($n = 287$) and the least in June ($n = 129$) and July ($n = 125$). Using the calculated flowering peak for all species, flowering activity is clearly at its most intense around November (Fig. 4).

Changes in Floral Morphology with Altitude

Including both understorey and tree species, the twenty IBISCA-Qld vegetation plots (situated between 248 m a.s.l. and 1142 m a.s.l.) contained a total of 287 plant species from 82 families. Looking at the total number of species recorded at each altitude (Fig. 5), there was a clear decrease in diversity with increasing altitude. At the 900 m and 1100 m altitudes this appeared to coincide with a decrease in the number of tree species, fern species and the absence of forb species (Fig. 5). However, of note is that species classified as graminoids were present at higher altitudes and included *Drymophila moorei* which was only found at the 1100 m altitude plots. No epiphyte species were recorded at the 300 m sites. However the proportion of each plant habit type was not dependent on altitude ($\chi^2 = 22.07$, d.f. = 28, $P = 0.78$). The proportion of species with flowers less than 5 mm in diameter appeared to decrease slightly with increasing altitude (Fig. 6) but no significant statistical relationship was detected between flower size and altitude ($\chi^2 = 7.74$, d.f. = 12, $P = 0.80$). While no significant association between flower colour and altitude was detected ($\chi^2 = 6.78$, d.f. = 16, $P = 0.98$) there appeared to be an increase in the proportion of species with white/green flowers, and a decrease in the proportion of yellow flowers, the higher along the altitudinal gradient we sampled (Fig. 7).

The proportion of bisexual and dioecious species appeared to increase with increasing altitude (Fig. 8) although neither showed a statistically significant relationship with altitude (bisexuality vs altitude, $\chi^2 = 14.74$, d.f. = 8, $P = 0.07$; dioecy vs altitude, $\chi^2 = 10.54$, d.f. = 8, $P = 0.22$).

Using flowering midpoints derived from herbarium specimens to determine average

flowering patterns for the species present at each of the IBISCA-Qld altitudes, it can be seen that the proportion of species flowering in any given month (Figure 9) is highly seasonal at all altitudes. The seasonal pattern is more or less consistent across all altitudes with a dramatic increase in flowering starting in August and maintenance of this level of activity until February. A chi square test demonstrated there was no significant difference in the pattern of flowering between altitudes ($\chi^2 = 17.8$, d.f. = 44, $P = 0.99$). Repeating the analysis on low altitude (300, 500 and 700 m a.s.l.) and high altitude (900 and 1100 m a.s.l.) data sets, again no significant association was found between the number of species flowering and altitude ($\chi^2 = 5.63$, d.f. = 11, $P = 0.90$).

DISCUSSION

Our results are of interest from three perspectives. First those that relate to the Lamington rainforest flora as a whole, second, those that quantify altitudinal trends, and third, those which can be used to erect hypotheses about likely pollinators and pollination syndromes. The first is useful in understanding the floral landscape of the Lamington rainforests. The second addresses the impacts of closely adjacent climates upon floral biology and is relevant to predicting likely impacts of climate change. The third, concerning pollination, is most useful in informing future, focussed studies and will be relevant to both spatial comparisons and in predicting future changes of pollination in subtropical rainforests.

The Lamington Rainforest as a whole.

Small, white or green flowers dominate the Lamington flora with, as would be expected, the majority bisexual. Small, dull-coloured, simple flowers are often associated with generalist pollination systems (Faegri & van der Pijl 1979). Williams and Adam (1994) suggested that generalist pollination (defined in this case as having pollinators drawn from a wide range of small insects) prevails in subtropical rainforest

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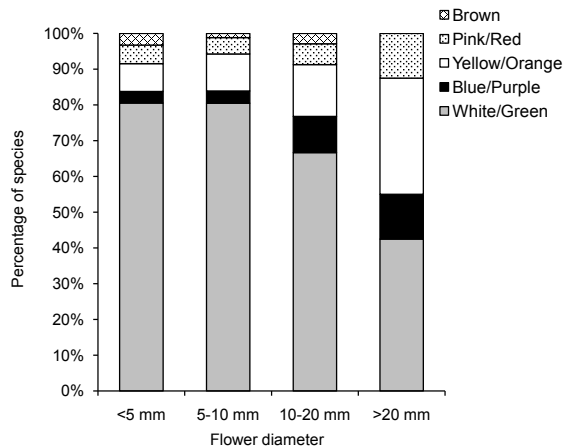


FIG. 3. Proportions of Lamington National Park rainforest species displaying different flower colours within four different classes of flower diameter.

systems and this is associated with a dominance of unspecialised flower structures. As flowers become larger they also become more colourful with flowers greater than 10 mm in diameter displaying more colour than their smaller counterparts. About a third of the species in the Lamington rainforests for which information was available (109 species out of 350) had flowers greater than 10 mm in diameter, and of those 109 species, more than 40% were a colour other than white or green. Families with a number of species with large, coloured flowers were Orchidaceae (6 spp.), Fabaceae (6 spp.), Moraceae (5 spp.), Solanaceae (4 spp.) and Asteraceae (4 spp.) all of which also include species with smaller, non-colourful flowers with the exception of Fabaceae. This suggests that the incidence of large, colourful flowers may not necessarily be phylogenetically constrained. Larger, more colourful flowers are generally associated with bird, butterfly and beetle pollination (Faegri & van der Pijl 1979), although the attraction of pollinators to

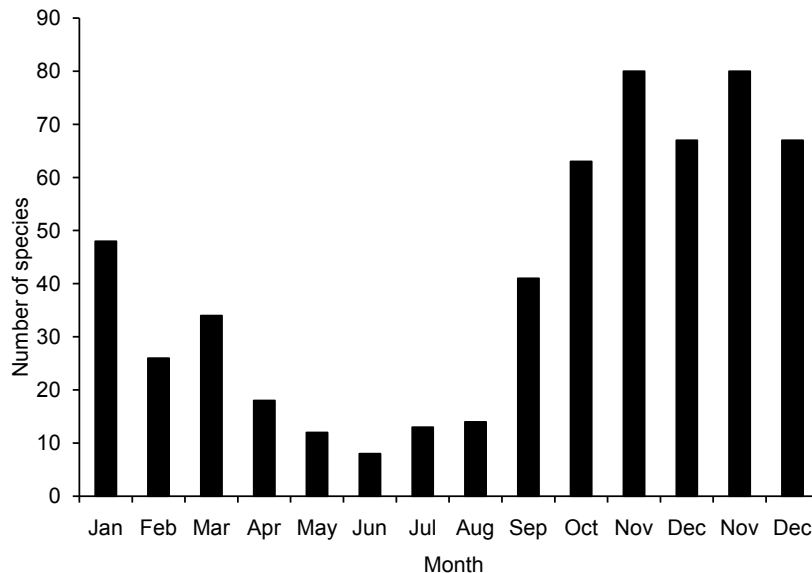


FIG. 4. The distribution of mean flowering times ('peak' flowering) for all species of angiosperm known from the rainforests of Lamington National Park derived from herbarium collections between 20°S and 37°S.

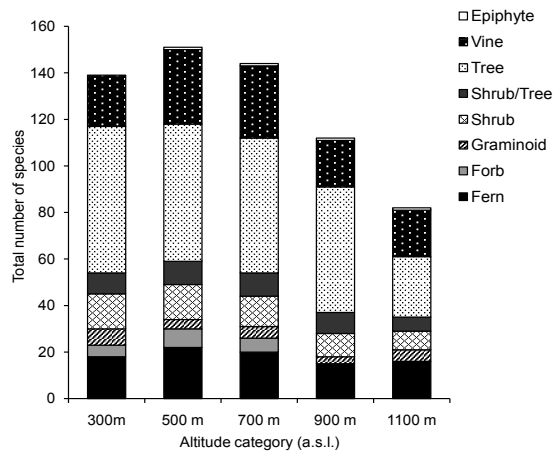


FIG. 5. Total number of vascular plant species, classified according to their growth habit types, recorded from all four replicate plots across the five IBISCA-Qld altitude categories (m a.s.l.).

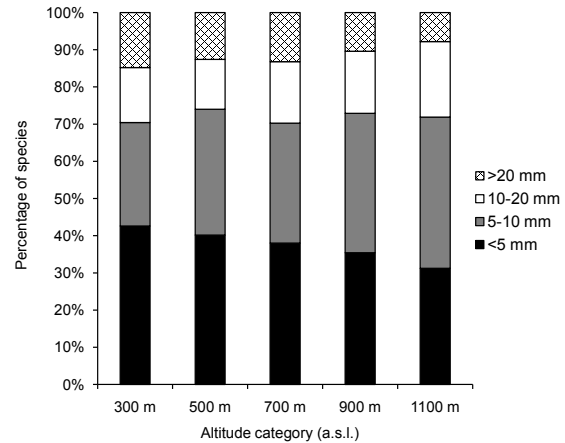


FIG. 6. Proportions of plant species in each of four flower size categories, across the five IBISCA-Qld altitude categories (m a.s.l.).

the flowers of particular species is also related to other attractants like scent, and the success of pollination will depend on more complex morphological characteristics such as flower shape and the position of reproductive structures. Flower colour was strongly related to growth habit for parasites, graminoids and forbs. All five species of parasites, from two families, have red flowers. Brightly coloured flowers are common in species from these families (Loranthaceae and Viscaceae) and have been associated with bird pollinators. Among the graminoids, mainly consisting of members of the families Cyperaceae and Poaceae, flowers were found to be white, green or brown with the exception of the spectacular pink flowers of *Helmholtzia glaberrima* (J.D. Hook) Caruel (Philydraceae).

A strong seasonal pattern of flowering was demonstrated in the rainforest of Lamington National Park at the scale of analysis presented here. Dramatic increases in the number of species in flower occur from around September with the greatest flowering activity in November,

coinciding with the end of an extended dry period and start of the wet season (Strong *et al.* 2011). Flowering is frequently influenced by rainfall and it is likely that flowering in many of the Lamington subtropical rainforest species is in response to proximate environmental cues. Seasonal cues other than rainfall include day length and temperature, and individual species are likely to respond differentially to different cues. This seasonal flowering activity is likely to coincide with the seasonal activity of pollinator insect species. A considerable number of plant species flower outside of this peak flowering time and these may represent species that have been influenced by different selection pressures to those experienced by other species. Flowering during cooler periods equates to a lower availability and diversity of pollinators (Williams & Adam 1994). This might suggest avoidance of a detrimental pressure (e.g. conspecific competition for pollinators) that outweighs flowering to optimise pollinator visitation, i.e. flowering during the peak pollinator activity season.

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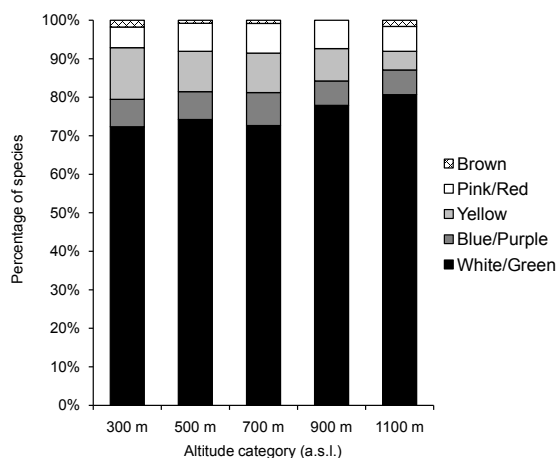


FIG. 7. Proportions of plant species in five dominant flower colour categories, across the five IBISCA-Qld altitude categories (m a.s.l.).

Altitudinal Changes. By global standards the IBISCA-Qld Lamington transect is a rather short one, spanning an altitudinal range of just 800 vertical metres (Beck *et al.* 2008). Accordingly, although we might hope to identify clear

trends, the low magnitude of altitudinal change along the transect mitigates against dramatic contrasts. In addition, here we have measured averages (e.g. average flowering period rather than actual first flowering date) across species and so proximate responses to microclimatic cues could not be detected. However, given that patterns of flowering phenology (Boulter *et al.* 2006) and pollinator movements (Torres-Diaz *et al.* 2007) are driven by climatic cues, we would expect that the microclimatic variation along the altitudinal gradient would give rise to variation in pollination systems. Whether this has translated into different floral morphologies is more difficult to determine and our data have not provided conclusive evidence to support this supposition.

Although not statistically significant, some trends were apparent, even along this short altitudinal gradient: more 'medium'-sized flowers (and less tiny and large flowers), more dull-coloured flowers and less yellow flowers, more bisexual flowers and increase in the likelihood of species with unisexual flowers to be dioecious with increasing altitude. Field-based studies are required to confirm these trends, but they present some possible support for the notion

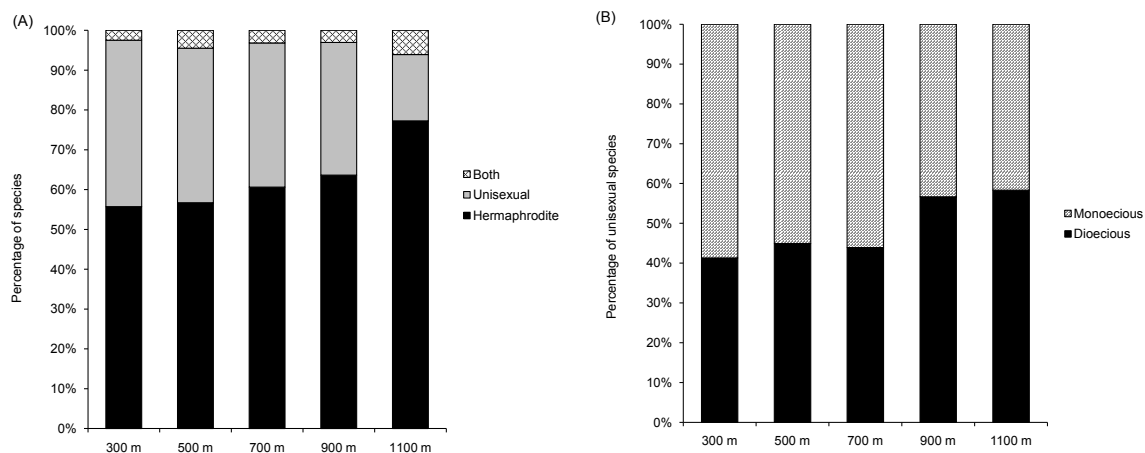


FIG. 8. Proportions of (a) plant species with different breeding systems and (b) plant species with unisexual flowers showing dioecy or monoecy, across the five IBISCA-Qld altitude categories (m a.s.l.).

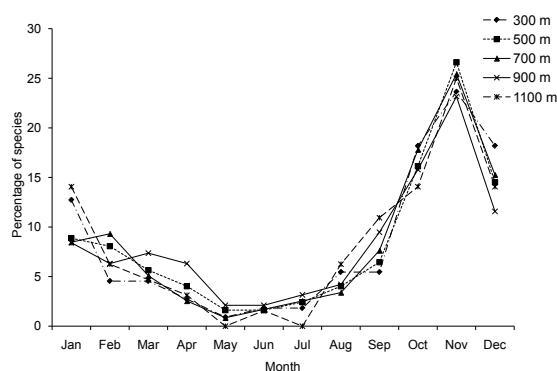


FIG. 9. Percentage of angiosperm species in peak flowering in each month of the year, based on flowering midpoint calculated from herbarium records, within each of the five IBISCA-Qld altitude categories (m a.s.l.).

that the floral display at higher altitudes might be a response to a reduction in available pollinators. Floral traits have been shown to be under selection pressure from pollinators (Waser 1983) and as a result these flower traits have been traditionally thought to demonstrate a significant association with the dominant pollinator of the plant species, i.e. the pollination syndrome concept. With increasing altitude we would expect a decrease in the abundance and diversity of some insect groups in general, with some less able to function at higher altitudes. As a result, the dominant pollinator groups will change with increasing altitude. Generally, a decreasing number of plants are pollinated by Hymenoptera with increasing altitude, whereas Lepidoptera and Diptera in particular, are increasingly important pollinators along the same gradients (Warren *et al.* 1988; Arroyo *et al.* 1982; Kearns 1992). Previous studies have found more blue flowers in upland sites (Weevers 1952), higher proportions of, and increased visitation to, white and yellow flowers (reviewed in Arnold *et al.* 2009). However, Arnold *et al.* (2009) did not find a relationship between altitude and flower colour according to ecologically relevant models of insect vision (as opposed to human perception of colour).

Likely pollinators and pollination syndromes.

As already highlighted, the subtropical rainforests of Australia are considered to be dominated by generalist pollination systems (Williams & Adam 1994). These systems are usually characterised by white or dull-coloured flowers with simple, general flower structures (e.g. bowl or dish-shaped flowers). Under the pollinator syndrome concept, white or dull-coloured flowers are usually associated with beetles, flies, non-specialised bees, moths, bats and thrips (Ollerton & Watts 2000). Based on the pollination syndrome concept then, we might conclude, that over seventy percent of the flowers in the subtropical rainforest of Lamington National Park should be visited by these groups. The distinction between flower types matching each of these pollinator groups generally comes down to flower structure, scent and anthesis. So for example, a night flowering species with a white, musky-odoured, brush-like flower would be associated with bats. Coloured flowers are more often associated with butterflies, bees, birds and other vertebrates. However, caution must be exercised in relying too heavily on flower colour as an indication of likely pollinators, as the success of a flower visitor also relates to their behaviour, the structure of the flower, the presence and accessibility of rewards and so on. The traditional pollinator syndrome should be used with caution when interpreting floral diversity or inferring pollinators, as a recent test of the concept has shown limited match between predicted and actual pollinators (Ollerton *et al.* 2009). Ollerton *et al.* (2009) suggest that rather than abandoning the concept of pollination syndromes, how traits of flowers and pollinators relate to visitation and pollen transfer needs reconsidering to determine if a new categorisation of floral functional diversity can be more successfully used than the traditional syndromes.

To date there have been no published studies of pollination conducted in Lamington National Park. However, the flower visitors and pollinators of 27 plant species that are found in Lamington National Park have been studied in

other locations (Table 1). A further five plant species found in subtropical rainforests, but not in Lamington, have had pollinators or flower visitors identified (Table 1). Of these 33 plant species, 18 have a named pollinator species or group of taxa. Only one was described as having a generalist pollination system, although many of the plants with only flower visitors recorded may, in fact, have generalist pollinators e.g. *Euroschinus falcata* which is visited by a number of different insect orders. The identification of Nematocera, a large and diverse group of primitive flies, as pollinators of *Daphnandra micrantha* may also suggest a general pollination system in this plant species. However, the overwhelming majority of reported studies describe specialised pollination, in that a single species or closely related taxa are identified as pollinators. We would suggest that this presents a biased picture of the dominant pollination system in subtropical rainforests, as these studies were all made on plants with complex flower structures not suited to a wide variety of pollinators.

CONCLUSIONS

This study provides a broad overview of the general floral morphology and phenology of the subtropical rainforest flora of Lamington National Park. In addition, a preliminary exploration of the variety of these characteristics among plant species at different altitudes was undertaken. A search of the pollination literature revealed that very little is known about the pollinators of, and flower visitors to the plant species of subtropical rainforests. Variation of flower morphologies found at different altitudes could have implications for the identity of different effective pollinators. If the dominance of specialised interactions seen in the literature reflects that of the flora as a whole, then these systems may be more vulnerable to changes in climate, with the uncoupling of mutualistic interactions a key threat. However, if subtropical rainforest plants are indeed predominantly generalist pollinated

as suggested by Williams and Adam (1994) and with some support from our own findings, then this might confer these forests with a degree of reproductive robustness under a changing climate. Altitudinal studies of changes in flower visitors and pollinator assemblages to plant species identified as potentially generalist could help determine the resilience of these systems under different climate conditions.

A study of the type presented here, provides an opportunity to gain a broad understanding of a flora and its phenology and reproduction in the absence of fine-scale studies that would take many years of effort to achieve. However, the information derived at this scale cannot reveal many of the intricate and complex interactions between plant species and their pollinators in Lamington National Park. A limitation of this type of study is an inability to demonstrate site specific characteristics e.g. phenology of individual species across altitudes, and more detailed studies are essential in order to better understand the reproductive functioning of subtropical rainforests.

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