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Assessing intraspecific phenological synchrony in zoochorous trees from the monsoon forests of northern Australia

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Abstract: Intraspecific synchrony in the phenology of tropical forest trees has implications for satiation of browsers and seed predators, pollination, dispersal and interpreting plant responses to environmental cues and stresses. Community phenological studies have been constrained in their consideration of these issues by the lack of concise quantitative measures of intraspecific synchrony. We propose a novel application of Colwell's predictability indices to overcome this deficiency. Its application is demonstrated by evaluating the leaf and reproductive phenologies of 8–16 individuals of each of 20 monsoon forest tree species from northern Australia monthly for 30 mo. The indices yielded substantial additional information over that provided by summaries averaged amongst conspecifics. Marked intraspecific asynchronies in leaf flush or flowering occurred in five evergreen species and two deciduous fig species, and were associated with prolonged individual commitments to these states. Five partly deciduous species exhibited marked intraspecific variation in the seasonal extent of leaf loss. We interpret the observed variation in intraspecific synchrony in terms of contrasting water-use and pollination strategies. The synchronicity indices are concise and robust to small and variable sample sizes, and may thus enhance studies of species-rich assemblages.

Key Words: Colwell's predictability index, deciduousness, dry season, *Ficus*, flowering, fruiting, intraspecific asynchrony, leaf flush, moisture limitation

INTRODUCTION

Phenological events in tropical trees may be cued by day length (Rivera & Borchert 2001, Rivera *et al.* 2002) or driven or modified by rainfall and other weather events (Borchert *et al.* 2002, Holbrook *et al.* 1995). However, there is no a priori necessity that conspecifics will respond identically to these cues. Intraspecific synchrony may arise accidentally in the sense that individuals derive similar independent benefits from response to cues. Thus, if deciduous trees are under selective pressure to maximize the portion of the year in which they are photosynthetically active (Miranda *et al.* 2005), simultaneous release from the constraints of the dry season may yield synchronous leaf flush (Lieberman & Lieberman 1984). Alternatively or additionally, individuals may gain fitness advantages by synchronizing phenophases with conspecifics and/or neighbours. These advantages may arise through cross-pollination (Augspurger 1981,

Calabrese & Fagan 2004, Morellato 2004), mutual attraction of dispersal agents (Howe 1980, Thies & Kalko 2004), and satiation of browsers and seed predators (Aide 1988, 1992; Curran & Leighton 2000, Shibata *et al.* 2002, van Schaik *et al.* 1993). In contrast, and with the notable exceptions of figs (*Ficus* spp.) (Harrison *et al.* 2000, Janzen 1979, Milton *et al.* 1982), intraspecific asynchrony is often regarded as accidental and maladaptive, and its possible advantages have received little attention. Primack (1985) discussed the situations in which intraspecific asynchrony may arise, whilst Dominguez *et al.* (2005) noted that synchronous flowering and fruiting may reduce gene flow by satiating pollinators and frugivores.

Asynchrony amongst conspecifics is more prominent in the wet tropics than the seasonally dry tropics (Borchert 1998, Bullock 1995, Frankie *et al.* 1974, Reich 1995), suggesting that the constraints of an intense dry season are major drivers of synchrony. However, there are remarkably few community phenological studies in either environment that consider levels of intraspecific synchrony, and even fewer that do so systematically and quantitatively. Newstrom *et al.* (1994a, b) argued that

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the uncertainty with respect to state is

$$H(Y) = - \sum_{i=1}^s (Y_i/Z) \log(Y_i/Z),$$

and the uncertainty with respect to the interaction of time and state is

$$H(XY) = - \sum_i \sum_j (N_{ij}/Z) \log(N_{ij}/Z).$$

Then

$$\begin{aligned} \text{Synchronicity } (P) &= C + M \\ &= 1 - [H(XY) - H(X)]/\log(s), \end{aligned}$$

$$\text{Constancy } (C) = P - M = 1 - H(Y)/\log(s), \text{ and}$$

$$\begin{aligned} \text{Contingency } (M) &= P - C \\ &= [H(X) + H(Y) - H(XY)]/\log(s). \end{aligned}$$

Raveh & Tapiero (1980) provided simpler, alternative formulations for P , C and M based on modes.

STUDY AREA AND SPECIES

Data were collected in four small monsoon-forest patches, two spring-fed and two seasonally dry, embedded in a savanna matrix on the low-lying Gunn Point Peninsula (12°24'S, 131°02'E), 40 km north-east of Darwin in the monsoonal 'Top End' of the Northern Territory, Australia. Three seasons are recognized for the purpose of this paper, the wet season (December–April), the dry season (May–September) and the dry-wet transition (the pre-monsoonal or 'build-up' period, October–November) (McDonald & McAlpine 1991). Mean annual rainfall is 1691 mm at Darwin based on 57 y of data, with 84.6% falling in the wet season, 2.8% in the dry season and 12.6% in the dry-wet transition months. Rainfall during the dry-wet transition is particularly unpredictable (Cook & Heerdegen 2001). Mean daily minimum temperatures range from 19.3 °C in July to 25.3 °C in November, with corresponding maximums of 30.4 and 33.1 °C.

As this study forms part of a larger study into the role of vertebrates in maintaining viability in populations of tree species which occur in only small numbers in any given patch (Bach & Price 2005, Shapcott 2000), the species considered (Table 2) are all zoochorous, being selected for their relevance to mobile vertebrates, namely birds and flying foxes (Pteropodidae). Community phenological patterns with no species-specific information were presented by Bach (2002).

Table 2. Study species with number of individuals (n) tagged in wet and dry monsoon forests.

Species	Family	n	
		wet	dry
<i>Buchanania arborescens</i> (Blume) Blume	Anacardiaceae	11	0
<i>Canarium australianum</i> F. Muell.	Burseraceae	0	12
<i>Carallia brachiata</i> (Lour.) Merr.	Rhizophoraceae	5	9
<i>Carpentaria acuminata</i> (H. Wendl. & Drude) Becc.	Arecaceae	8	0
<i>Cupaniopsis anacardioides</i> (A. Rich.) Radlk.	Sapindaceae	0	11
<i>Diospyros calycantha</i> O. Schwarz	Ebenaceae	6	6
<i>Diospyros compacta</i> (R.Br.) Kosterm.	Ebenaceae	2	10
<i>Drypetes deplanchei</i> (Brongn. & Griseb.) Merr.	Euphorbiaceae	0	11
<i>Elaeocarpus arnhemicus</i> F. Muell	Elaeocarpaceae	0	9
<i>Exocarpos latifolius</i> R.Br.	Santalaceae	0	10
<i>Ficus racemosa</i> L.	Moraceae	10	0
<i>Ficus virens</i> Aiton	Moraceae	11	0
<i>Gmelina schlechteri</i> H.J. Lam	Verbenaceae	8	0
<i>Maranthes corymbosa</i> Blume	Chrysobalanaceae	9	0
<i>Miliusa brahei</i> (F. Muell.) Jessup	Annonaceae	0	8
<i>Mimusops elengi</i> L.	Sapotaceae	0	9
<i>Myristica insipida</i> R.Br.	Myristicaceae	9	0
<i>Strychnos lucida</i> R.Br.	Loganiaceae	3	8
<i>Syzygium nervosum</i> DC.	Myrtaceae	10	0
<i>Terminalia microcarpa</i> Decne.	Combretaceae	10	6

METHODS

Data collection

Eight to sixteen mature individuals of each of 19 species of tree and one arborescent palm, 211 individuals in total, were tagged along transects (Table 2). Only females of dioecious species were tagged.

Phenological assessments were conducted by CSB in the first half of the month for each of the 30 mo of the study period. Assessments were visual estimates following examination of the individual canopy, using binoculars or telescope where needed. Phenological characters estimated were: % canopy fullness; % of canopy consisting of new leaves, number of flowers, number of fruits, and % of fruits that were unripe/ripe, the latter based on fruit colour. Per cent classes were to the nearest 10%, whilst numeric estimates were in classes of 0, 1–10, 11–50, 51–100, 101–500, 501–1000, . . . 1 000 001–5 000 000.

The following exceptions to the above are noted. Leaf phenology was not assessed for the palm *Carpentaria acuminata* because visibility of new fronds was obscured by the older fronds – the species is evergreen (*pers. obs.*). Flowering in *Ficus* spp. was not assessed because the flowers are aggregated within a syconium that is indistinguishable from an unripe fruit (Janzen 1979) – such observations are here treated as unripe fruit. No specimens of *Gmelina schlechteri* were assessed in November 1994.

Analysis

For quantitative analysis other than the synchronicity indices, flowering and fruiting abundance estimates were converted to classes 0, 1, 2, 3, 4, 5, . . . 14 corresponding to the numeric estimate classes above. As indicated by subsequent fruiting, flowering was under-reported in *Drypetes deplanchei*, *Miliusa brahei* and *Myristica insipida*. These species along with *Ficus* spp. have therefore been deleted from most quantitative analyses but the available data are included in Figure 1. For each phenological parameter, species averages were calculated for each month.

The synchronicity indices P , C and M were calculated for each of canopy fullness, leaf flush, flowering and fruiting following Colwell (1974). Because of the number of combinations (20 species by four phenological measures) we generated a simple computer program to perform the calculations. We recognized two states for each phenological parameter. Canopies were treated as either full (defined as $\geq 85\%$) or not. Leaf flush, flowers and fruit were either present or absent, presence of leaf flush being defined as $\geq 5\%$ of the canopy.

We use the term 'deciduous' as a description, defined as any species in which *some* individuals lost at least 50% of their canopy; there is no a priori implication concerning functional type (cf. Singh & Kushwaha 2005).

RESULTS

Canopy patterns from species-average data

Twelve species were evergreen or very nearly so (*Buchanania arborescens*, *Carallia brachiata*, *Carpentaria acuminata*, *Cupaniopsis anacardioides*, *Diospyros calycanthera*, *Diospyros compacta*, *Diospyros deplanchei*, *Exocarpos latifolius*, *Maranthes corymbosa*, *Mimusops elengi*, *Myristica insipida*, *Syzygium nervosum*). Two species were more or less fully deciduous during the mid-to-late dry season (*Canarium australianum*, *Miliusa brahei*), whilst five were partially deciduous at that time (*Elaeocarpus arnhemicus*, *Ficus virens*, *Gmelina schlechteri*, *Strychnos lucida*, *Terminalia microcarpa*). *Ficus racemosa* was brevideciduous with canopy reduction concentrated in the late-wet or early dry season in most individuals (Figure 1).

In most deciduous and some evergreen species, leaf flush was brief and coincident with, or up to 3 months before, the onset of the wet season, earliest in the evergreen *S. nervosum* (Figure 1). The evergreens *C. brachiata* and *M. elengi* flushed at low levels throughout the wet season, whilst the evergreens *C. anacardioides* and *E. latifolius* and the deciduous *F. racemosa* flushed at low levels for most of the year.

Canopy synchrony

Synchronicity indices for canopy state and leaf flush (Table 3) illustrate variation in canopy strategy (Figure 2). The two *Ficus* spp. are clearly aberrant. Canopy state was (by definition) highly synchronous in evergreen species (Colwell's $P > 0.95$), and was also moderately high in deciduous species ($P: 0.79-0.90$) except the *Ficus* spp. Extreme asynchrony of canopy state in *F. virens* was the product of variation among individuals in the commencement of leaf loss and thus of the period with less than full canopy (mean = 2.1 mo y^{-1} , range 0-9). Leaf flush was moderately synchronized in deciduous species ($P: 0.57-0.85$) except *F. racemosa* ($P: 0.31$), but variable amongst evergreens ($P: 0.34-0.77$) with two discrete leaf flush strategies evident (Figure 2). A strong negative relationship between the per cent of time in leaf flush and its synchrony (Figure 3a; $n = 19$ spp., $r = -0.81$; ANCOVA $F = 29.1$, $P \ll 0.001$) did not differ significantly between deciduous and non-deciduous species ($F = 0.14$, $P = 0.72$).

Evergreen and seasonally deciduous species form a continuum from canopy constancy to contingency (Table 3: evergreen species, $C/P: 94-100\%$; partially deciduous species, $C/P: 23-85\%$; fully deciduous species, $C/P: 12-13\%$). Examination of individual records of partially deciduous species demonstrates much variability within species in the seasonal extent of canopy loss. We are unable to establish helpful interpretations for C/P and M/P for leaf flush.

Reproductive patterns from species-average data

Fourteen species had well-defined flowering periods which collectively spanned the entire year, though most flowered between the middle of the dry season and the middle of the wet season (Figure 1: *B. arborescens*, *C. australianum*, *C. brachiata*, *C. anacardioides*, *D. calycanthera*, *D. compacta*, *D. deplanchei*, *E. arnhemicus*, *G. schlechteri*, *M. elengi*, *M. corymbosa*, *S. lucida*, *S. nervosum*, *T. microcarpa*). *Carpentaria acuminata* and *E. latifolius* flowered throughout the year though *C. acuminata* exhibited seasonal fluctuations in abundance with peak activity in the late dry season. Fruiting patterns suggest that *M. brahei* may also have had a well-defined flowering period but that *F. racemosa* and *F. virens* did not. The flowering seasonality of *M. insipida* was unclear.

Two annual peaks in flowering activity are evident in four species in particular (Figure 1: *C. australianum*, *C. brachiata*, *E. arnhemicus* and *T. microcarpa*). Examination of individual records showed that individual trees of these species often flowered twice per year.

Fruiting was continuous or nearly so in seven species (Figure 1: *C. australianum*, *C. acuminata*, *D. calycanthera*, *E. latifolius*, the two *Ficus* spp. and *M. insipida*). However,

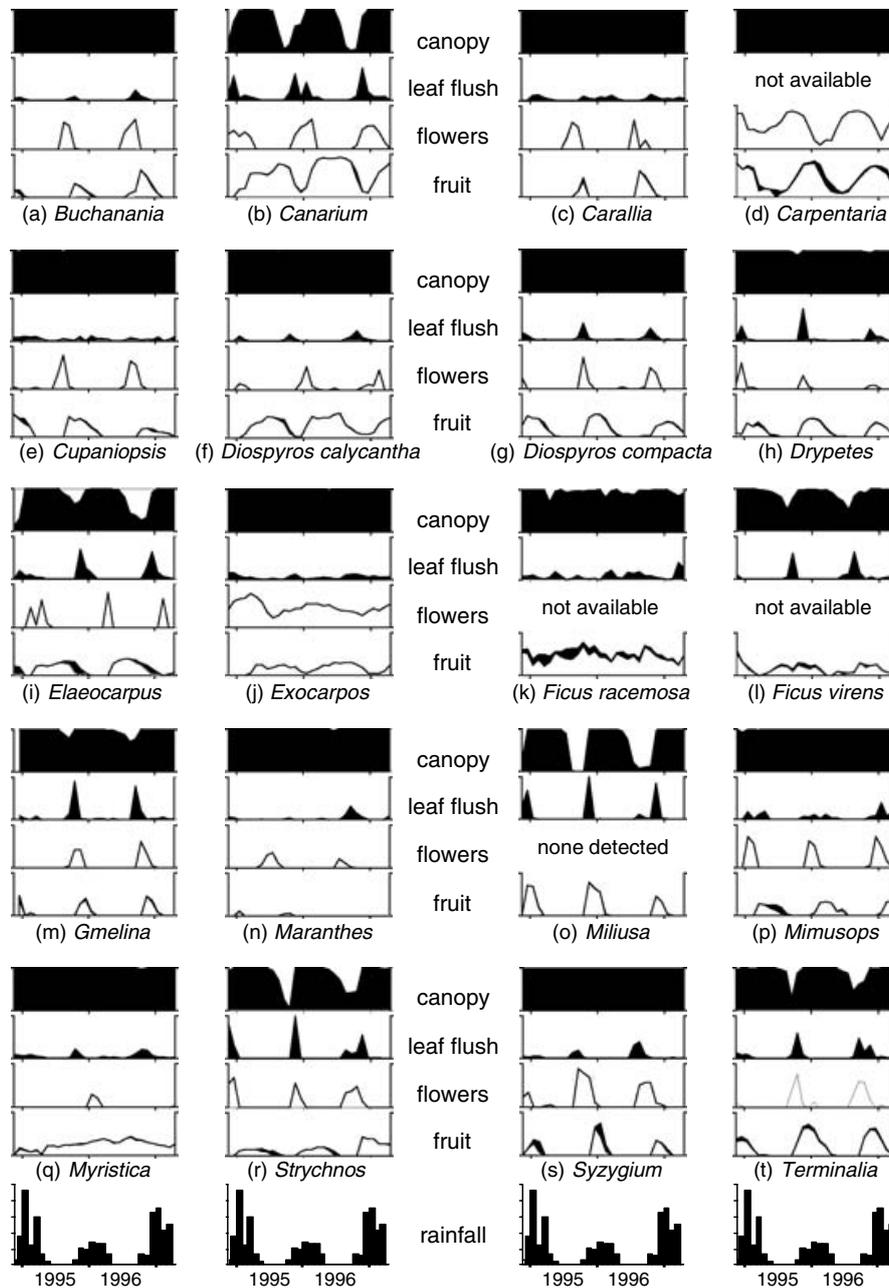


Figure 1. Thirty-month timelines for canopy fullness, leaf flush, flowering and fruiting of 20 monsoon forest tree species (Table 2) from the Northern Territory, Australia. X-axis ticks correspond to ends of years – see lower (rainfall) graphs for details. Species values are means of individual values. Canopy and leaf flush are scaled from 0–100%. Flower and fruiting are indexed on a scale from 0 to the maximum abundance class observed at any time for any individual of that species, so that absolute values are not comparable between species. The indices have an approximately logarithmic distribution, reducing emphasis on peak values. Fruit classes are: unripe = white; ripe = black. Canopy fullness for *Carpentaria acuminata* (d) is based on general observation only. The rainfall graphs (lowest line) are monthly totals for Darwin, 40 km south-west of the study sites, with the y-axis ticks corresponding to 200-mm intervals.

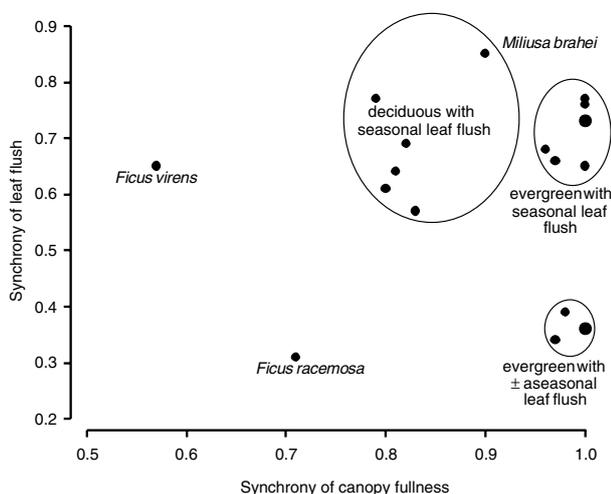
ripe fruit were observed only infrequently in most species, though some were available through most of the study period on *C. acuminata*, *F. racemosa* and to a lesser extent *F. virens* and *E. arnhemicus*. *Canarium australianum* and *D. calycantha* exhibited long ripening periods such that seasonal flowering followed soon after ripening of the previous year’s fruit.

Reproductive synchrony

Seasonal flowering at the species level implies at least a moderate level of intraspecific synchrony, and for the 12 of the 13 seasonal-flowering species listed above for which a synchrony measure is available, Colwell’s *P* ranged from 0.70 to 0.91 (Table 3). Contingency, anticipated

Table 3. Synchrony (Colwell's P) and its components, constancy (C) and contingency (M), for canopy and reproductive parameters of 20 monsoon forest tree species in the Northern Territory, Australia. Constancy and contingency are expressed as a percentage of Colwell's P .

Species	Canopy fullness			Leaf flush			Flowering			Fruiting		
	P	C/P (%)	M/P (%)	P	C/P (%)	M/P (%)	P	C/P (%)	M/P (%)	P	C/P (%)	M/P (%)
Evergreen species												
<i>Buchanania arborescens</i>	1	100	0	0.77	37	63	0.87	47	53	0.65	48	52
<i>Carallia brachiata</i>	1	100	0	0.36	11	89	0.87	55	45	0.86	55	45
<i>Carpentaria acuminata</i>	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.44	28	72	0.44	17	83
<i>Cupaniopsis anacardioides</i>	0.97	97	3	0.34	9	91	0.82	53	47	0.56	19	81
<i>Diospyros calycantha</i>	1	100	0	0.65	41	59	0.73	58	42	0.41	14	86
<i>Diospyros compacta</i>	1	100	0	0.73	34	66	0.86	59	41	0.55	2	98
<i>Drypetes deplanchei</i>	0.96	94	6	0.68	40	60	n.a.	n.a.	n.a.	0.44	10	90
<i>Exocarpos latifolius</i>	1	100	0	0.36	2	98	0.33	68	32	0.24	33	67
<i>Maranthes corymbosa</i>	1	100	0	0.76	33	67	0.81	80	20	0.95	96	4
<i>Mimusops elengi</i>	0.97	97	3	0.66	6	94	0.84	34	66	0.51	50	50
<i>Myristica insipida</i>	0.98	98	2	0.39	0.04	99.6	n.a.	n.a.	n.a.	0.29	61	39
<i>Syzygium nervosum</i>	1	100	0	0.73	26	74	0.77	23	77	0.78	34	66
Fully deciduous, partly deciduous and brevi-deciduous species												
<i>Canarium australianum</i>	0.81	12	88	0.64	3	97	0.70	6	94	0.68	40	60
<i>Elaeocarpus arnhemicus</i>	0.82	15	85	0.69	12	88	0.91	49	51	0.27	29	71
<i>Ficus racemosa</i>	0.71	76	24	0.31	1	99	n.a.	n.a.	n.a.	0.45	81	19
<i>Ficus virens</i>	0.57	55	45	0.65	57	44	n.a.	n.a.	n.a.	0.32	49	51
<i>Gmelina schlechteri</i>	0.80	77	23	0.61	36	64	0.84	63	37	0.77	60	40
<i>Milusa brahei</i>	0.90	13	87	0.85	35	65	n.a.	n.a.	n.a.	0.89	21	79
<i>Strychnos lucida</i>	0.79	30	70	0.77	37	63	0.78	50	50	0.39	42	58
<i>Terminalia microcarpa</i>	0.83	57	43	0.57	42	58	0.76	54	46	0.63	8	92

**Figure 2.** Synchrony (Colwell's P) of canopy and leaf flush among individuals of 19 monsoon forest tree species in northern Australia. Larger symbols represent two species with identical scores. Deciduous species are those in which some individuals lost at least 50% of their canopy, modified here to exclude the two *Ficus* species.

to be high in seasonally flowering species, varied from 37% to 94% (Table 3), low values reflecting a contribution of constancy to some species where individuals did not flower each year, or were not detected to do so.

Synchrony was low in the two species that flowered throughout the year (*C. acuminata* and *E. latifolius*, Colwell's $P = 0.44$ and 0.33 respectively), indicating that not all individuals flowered continuously, as was indeed the case (Figure 4). The seasonality evident in the species-averaged flowering of *C. acuminata* was the product of somewhat synchronized cessation of flowering by individuals rather than synchronized fluctuations in flower abundance (Figure 4a), and this is reflected in the contingency of flowering ($C/P = 72\%$, cf. 51% for *E. latifolius*).

The strong negative relationship between per cent time in flower and synchrony (Figure 3b; $n = 15$ spp., $r = -0.95$; ANCOVA $F = 107$, $P \ll 0.001$) did not differ significantly between deciduous and non-deciduous species ($F = 0.003$, $P = 0.96$).

There was a wide spectrum of synchrony in fruiting with no discrete classes (Table 3). Fruiting in the two *Ficus* spp. was markedly asynchronous (Colwell's $P = 0.45$ and 0.32), constancy being markedly greater in *F. racemosa* than *F. virens* ($C/P = 81$ and 49% respectively), a pattern confirmed in Figure 5. Interpretation of synchrony, constancy and contingency was complicated by the failure of some individuals to flower or set fruit, or our failure to detect these events. In particular, high levels of synchrony and constancy in the flowering and fruiting of *M. corymbosa* (Table 3) reflect their relatively predictable absence (flowers and fruit are obvious), and the species may flower supra-annually.

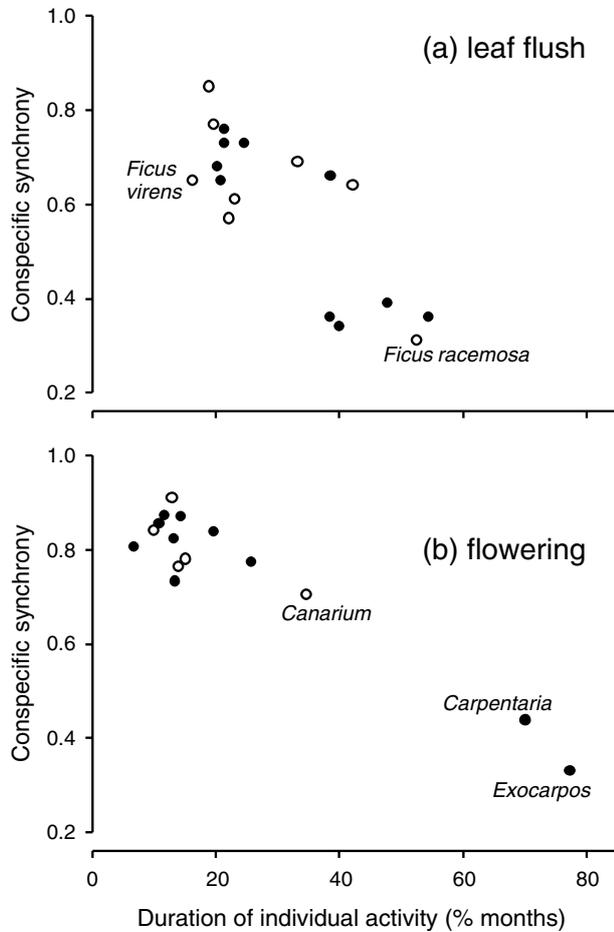


Figure 3. Leaf flush (a) and flowering (b) characteristics of monsoon forest tree species in northern Australia: relationship between time active and the level of synchrony (Colwell's *P*) among individuals. Closed circles are evergreen and open circles deciduous species as defined in the text. The duration of individual activity has been calculated as the number of months in leaf flush or flowering summed across individuals and divided by the number of months of records summed across individuals.

DISCUSSION

Measuring intraspecific synchrony in community phenological studies

This study has demonstrated the feasibility and value of incorporating a quantitative measure of intraspecific synchrony into phenological studies involving a considerable number of species. With the qualifications discussed below, it has demonstrated the efficacious nature of this novel application of Colwell's (1974) predictability indices in so doing. Whilst the simple description of population patterns can proceed by graphical and other summaries, we have in addition been able to offer fresh quantitative perspectives on differences between evergreen and deciduous species, identify contrasting

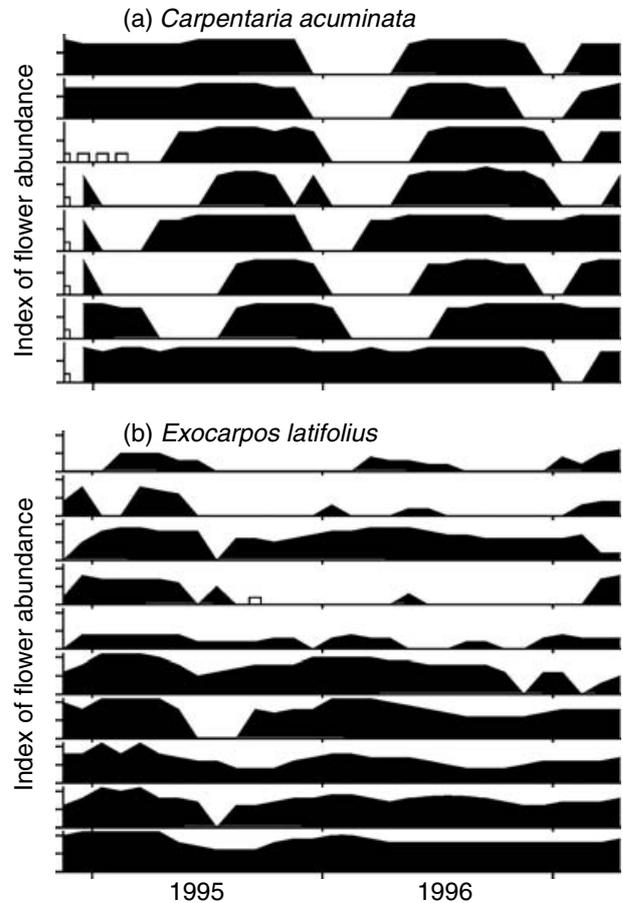


Figure 4. Timing and extent of flowering over 30 mo in: (a) eight *Carpentaria acuminata* palms, and (b) ten *Exocarpos latifolius* trees. The flowering index is shown with grey shading, with y-axis ticks indicating increments of five. Open bars indicate missing data.

canopy strategies within evergreen species, distinguish individual from population commitments to a phenophase, explore the relationship between individual time commitments and population synchrony, and explore the nature of aberrant phenological strategies in figs.

In community studies, samples of each species may of necessity be small, and the robustness of Colwell's indices with small samples is one of its strengths. In this study, as few as eight replicates appear to have been adequate for useful analysis. In a traditional time-series application to phenological data, Williams-Linera (1997) applied Colwell's indices to 5 y of data, suggesting that even smaller samples than ours may prove satisfactory. An evaluation of the robustness of Colwell's indices with small samples may be made by trial-and-error or simulation, and would appear useful for the design of future studies. Another virtue of Colwell's indices is that they are not seriously compromised by missing data.

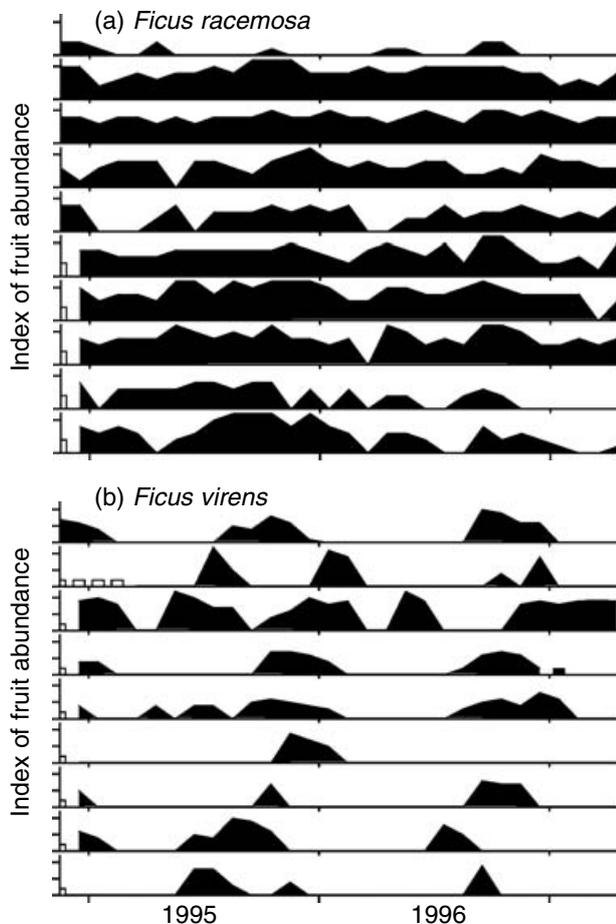


Figure 5. Timing and extent of fruiting in figs over 30 mo in: (a) ten *Ficus racemosa* trees, and (b) nine *Ficus virens* trees. The fruit index is shown with gray shading, with y-axis ticks indicating increments of five. Open bars indicate missing data. Two *F. virens* trees did not fruit during the study and have been excluded.

In other respects as well, future studies may be designed to make optimal use of Colwell's indices. Sampling targeted at intervals that avoid missing annual events such as flowering will improve interpretation of results. It should also be possible to compare levels of intraspecific synchrony amongst life forms, communities or other groups by comparing median index values, or generate index values for these groups by treating species within groups as replicates. Comparisons among species or other groups are, of course, only possible if the intervals between assessments are similar; synchrony is a scale-dependent phenomenon.

A limitation of Colwell's indices is that when quantitative data are reduced to more than two states, no information is retained from the rank order of states. Furthermore, employment of more than two states can be fraught because some species may rarely or never achieve a state and will thus be adjudged more highly synchronous and constant than would otherwise be the

case. For example, if a species routinely loses part of its canopy but rarely all of it, employment of three canopy states – full canopy, partial canopy and no canopy – in the analysis will result in an overestimation of predictability and constancy relative to a species that loses its entire canopy. For these reasons, we recommend two-state analyses in the assessment of synchrony, and judicious choice of states to match the aims of the study. From this it is also evident that, in the comparison of species or other groups, the number of states should be identical.

We have already noted the problem that may arise particularly with analysis of flowering and fruiting in which phenological events are missed or do not occur in all individuals regardless of an otherwise well-synchronized seasonality. If the problem of missing events due to insufficiently frequent sampling is overcome, exploration of the non-occurrence of events may be profitably explored with larger samples, and may prove to be of considerable ecological interest.

The indices of Primack (1980) and Augspurger (1983) assess synchrony in activity, whereas this application of Colwell's indices assesses synchrony in states. In intense studies of flowering or leaf flush such as daily monitoring for a small portion of a year, an activity index is likely to be preferable. However, in the assessment of phenological states at less frequent intervals and for a full annual cycle or longer, where canopy state is being considered, and where the spectrum of species considered includes those that flush or flower over extended periods, Colwell's indices will generally prove more useful because they provide additional information (constancy and contingency) and give weight to states representing an absence of activity (e.g. 'not flowering') or which do not involve activity (canopy state).

Intraspecific synchrony and moisture stress in monsoon forest trees

In this study, marked asynchronies in either or both leaf flush or reproductive phenology were identified in 7 of 20 tree species, of which two were figs. In addition, five partly-deciduous species in which leaf flush and flowering were relatively synchronous exhibited marked variation among individuals in the seasonal extent of leaf loss. This frequency of phenological asynchrony appears without parallel in monsoon forest or tropical savannas, although comparable analyses are scarce. However, it is acknowledged that this study may not be representative of the monsoon forests of the study area. We selected zoochorous species known to be important to vertebrates, and trees that fruit asynchronously provide keystone resources for frugivore assemblages in a variety of ecosystems (Bleher *et al.* 2003, Lambert & Marshall 1991, Shanahan *et al.* 2001). Nevertheless, 84% of

the 166 tree species in Top End monsoon forests are zoochorous (Russell-Smith & Dunlop 1987).

Using synchrony indices, we identified a continuum between evergreen and fully deciduous species, but discrete patterns of leaf flush. The latter, we suggest, reflects contrasting water-use strategies. Deciduous species other than figs flushed synchronously during or about the time of the dry-wet transition, suggesting a response constrained by the severity of the dry season. Furthermore, the apparently facultative loss of canopy in partly deciduous species is best explained as a direct response to moisture stress. In contrast, some evergreens flushed at low levels throughout the year, and since none has evident moisture-storage capacity and several were not associated with spring-fed monsoon forests (Table 2; *Cupaniopsis anarcardioides*, *Exocarpos latifolius*), these species are likely to be deep-rooted, though we note also that *E. latifolius* is a root hemiparasite (Hewson & Georges 1984). Leaf flush during the dry season is a feature of a number of nearby savanna species (Williams *et al.* 1997) that are deep-rooted and access deep soil moisture during the dry season (Kelley 2002).

Stem hydration is also essential for flowering (Holbrook *et al.* 1995), and it is notable that in this study, deciduous species flowered synchronously and only during the dry-wet transition and wet seasons. In contrast, flowering when leafless is a feature of some deciduous species (Janzen 1967) including a number in savannas near our study area. The latter are fully deciduous, shed leaves early in the dry season and retain high water potential in terminal twigs (Myers *et al.* 1997, Williams *et al.* 1999).

As with leaf flush, intraspecific synchrony of flowering was negatively correlated with the length of individual commitment to flowering with the likely exception of *F. virens*. Prolonged flowering may provide an alternative out-crossing strategy to synchronous flowering, and intermediate or mixed strategies (e.g. brief but asynchronous flowering) may not be viable because of pollination limitations. Our data suggest two discrete flowering strategies rather than the continuum from synchrony to asynchrony identified by Augspurger (1983) among six shrubs in a Neotropical semi-deciduous forest, but we note the very different temporal scale of Augspurger's study. If asynchronous flowering leads to asynchronous fruiting, it may be advantageous for zoochorous plants whose dispersal agents are specialists occurring at low densities, a relationship that may be further enhanced by prolonged individual fruiting (McKey 1975). An alternative explanation for the observed asynchronies is that the species involved – *Carpentaria acuminata* and *E. latifolius* – can flower continuously, as two individuals of the latter species did, and thus asynchrony is an accidental product of unknown and aseasonal environmental limitations.

We conclude that moisture stress during the dry season may indeed limit the potential for monsoon forest trees to develop asynchronous leaf flush and flowering strategies. However, the exceptions were surprisingly numerous and are likely associated with the ability to access moisture during the dry season. The frequency of exceptions also suggests that phenological asynchrony may be adaptive rather than accidental. The drivers of phenological asynchrony in monsoonal systems warrant further investigation.

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