

Co-fruiting plant species share similar fruit and seed traits while phylogenetic patterns vary through time

Onja H. Razafindratsima^{1,2*} and Amy E. Dunham^{1,2}

¹Department of Biosciences, Rice University, 6100 Main St., Houston, TX 77005, USA; and ²Centre ValBio, BP 33, Ranomafana, 312 Ifanadiana, Madagascar

Summary

1. Co-fruiting plant species are subject to a variety of biotic and abiotic processes that may influence patterns of fruiting phenology and the functional and phylogenetic diversity of co-fruiting taxa in a community. Understanding the seasonal patterns of functional and phylogenetic diversity of fruiting in a community will shed new light on potential mechanisms structuring plant communities.

2. Using rain forest trees in south-eastern Madagascar as our system, we predicted there would be clustering of fruit and seed traits and phylogenetic relationships among co-fruiting species because plants are vying for seed-dispersal services from a limited set of generalist frugivore taxa. We also predicted that seasonal variations in rainfall would mediate fluctuations in functional trait and phylogenetic diversity of co-fruiting assemblages.

3. Despite fluctuating patterns in their functional trait diversity over time, co-fruiting assemblages displayed consistent clustering of fruit/seed traits across time. Phylogenetic diversity was not clustered overall, but fluctuated non-randomly in time, between clustered and overdispersed, such that strong shifts in rainfall were associated with the co-fruiting of more closely related species.

4. *Synthesis.* We suggest that it may be more beneficial for co-fruiting plant species to share similar fruit and seed traits than to diversify traits, when they rely on a comparatively small set of generalist frugivorous taxa for seed dispersal. Results also demonstrate that rainfall-driven environmental filtering may cause seasonal fluctuations in the phylogenetic patterns of phenology in a community. Results highlight the importance of a temporal context in examining structural patterns of communities.

Key-words: community assembly, environmental filtering, frugivores, functional diversity, Madagascar, phenology, phylogenetic diversity, plant–plant interactions, seed dispersal, tropical forest

Introduction

Functional traits of fruits and seeds may play a key role in the attraction of seed-dispersing frugivores (Lomáscolo & Schaefer 2010; Schaefer 2011), upon which many plants depend for recruitment, gene flow and colonization of new habitats (Howe & Smallwood 1982; Nathan & Muller-Landau 2000; Jordano 2007; Karubian *et al.* 2010; Carlo & Tewksbury 2014; Razafindratsima & Dunham 2015). Therefore, the composition of fruit and seed traits among co-fruiting plants may mediate competition or facilitation between plants for seed dispersers in a community. In addition, these traits may also influence plant tolerance to different seasonal environmental conditions for reproduction and post-dispersal recruitment. However, we currently know little about how fruit and seed traits are temporally structured within plant communities.

Elucidating such patterns may be important for understanding how seasonal environmental variability and mutualistic interactions with frugivores affect the processes and patterns of plant community structure (Weiher & Keddy 1995; Webb *et al.* 2002; Wiens *et al.* 2010).

Sharing fruit and seed traits with co-fruiting heterospecifics may result in increased competition for frugivores and reduced fruit removal for some species (Carlo, Collazo & Groom 2003; Saracco *et al.* 2005). However, it seems more likely that divergence in fruit traits to attract specialist frugivores is a poor strategy when the number of frugivore species is limited and attracting multiple dispersers is likely advantageous for fruit removal (Blüthgen *et al.* 2007; Whitney 2009; Staggemeier, Diniz-Filho & Morellato 2010). In this case, coexistence may be more likely if the ability to attract the same frugivores differs little between species (Chesson 2000; Mayfield & Levine 2010). Co-fruiting species may even benefit from converging in fruit and seed traits, through facilitation

*Correspondence author. E-mail: onja@ricealumni.net

(Burns 2002; Whitney 2009; Albrecht *et al.* 2015). For example, some studies have shown that heterospecific co-fruited neighbours sharing dispersers can enhance fruit removal (Carlo 2005; Saracco *et al.* 2005). Rare species may especially benefit from converging in fruit traits with abundant species (Albrecht *et al.* 2015; Carlo & Morales 2016). Sharing seed dispersers will also encourage frugivore movement between plant species and thus reduce seed fall under conspecifics (Carlo, Aukema & Morales 2007), where distance- and density-dependent mortality is often high (Janzen 1970; Connell 1971). Finally, divergence patterns of fruit and seed traits of co-fruited species may change across seasons due to fluctuating environmental conditions. For example, species sharing fruit and seed traits may also share seasonal environmental tolerances for reproduction and post-dispersal recruitment (van Schaik, Terborgh & Wright 1993; Oberrath & Bohning-Gaese 2002; Staggemeier, Diniz-Filho & Morellato 2010).

Phylogenetic relationships between species are often used as a proxy for trait similarities in studies of community structure, assembly and diversity (Gerhold *et al.* 2015). However, traits can be labile and lack a phylogenetic signal, or there may be evolutionary convergence in traits among distant lineages (Cavender-Bares *et al.* 2009). Therefore, combining trait-based analyses with phylogenetic information is a more comprehensive approach for studies of community structure. Previous studies have shown that co-fruited assemblages have phylogenetic relationships that do not differ from random or are clustered, suggesting a limited role of competition for seed dispersers in structuring fruiting phenology (Staggemeier, Diniz-Filho & Morellato 2010; Silva *et al.* 2011). However, it is possible that the patterns of traits and phylogenetic structure vary by season and across time because of the seasonally dynamic nature of pressures exerted by the environment and through biotic interactions.

In this study, we conducted a two-year long phenological study of 3320 tree individuals, representing 155 species, in the south-eastern rain forest of Madagascar. Using phylogenetic and trait-based approaches, we examined the structure and diversity of co-fruited assemblages over time and in relation to rainfall. We predicted that fruit and seed traits of co-fruited trees in this highly diverse community would be clustered because they share a limited number of frugivore species. We also predicted that seasonal fluctuations in rainfall would mediate fluctuations in trait and phylogenetic diversity through environmental filtering, with reduced diversity expected during seasonal transitions in rainfall and during periods of heavy rainfall.

Materials and methods

STUDY SITE AND FRUGIVORE GUILD

This study was conducted in the evergreen montane rain forests of Ranomafana National Park (RNP), in south-eastern Madagascar (47°18'–47°37' E, 21°02'–21°25' S). RNP comprises an area of 41 600 ha with an elevation of 600–1500 m (Wright & Andriamihaja

2002) and home to more than 330 species of trees and large shrubs (Razafindratsima & Dunham 2015). The climate in Ranomafana is highly seasonal with average monthly rainfall ranging from 10 to 1200 mm, a peak wet season in January–March, and a peak dry season in June–October (Dunham, Erhart & Wright 2011).

The frugivore assemblage in RNP consists of four large-bodied diurnal lemur species, two small-sized nocturnal lemur species, seven bird species and one frugivorous bat species (Wright *et al.* 2011; Razafindratsima 2014). Three of these large-bodied lemur species (*Eulemur rubriventer*, *Eulemur rufifrons* and *Varecia variegata editorum*) and four of the bird species (*Zosterops maderaspatanus*, *Hypsipetes madagascariensis*, *Philepitta castanea*, *Alectronas madagascariensis*) are known to act as seed dispersers of tree species in RNP and elsewhere in Madagascar (Dew & Wright 1998; Rakotomanana *et al.* 2003; Razafindratsima 2014; Razafindratsima, Jones & Dunham 2014; Razafindratsima & Dunham 2015, 2016a). We focus on lemur- and bird-dispersal modes because we currently have no information on frugivorous bat diets in RNP.

TRAIT DATA

We built a trait data base for tree species in RNP that included measurements of fruit colour (hue, lightness and Chroma), fruit/seed size (length and width), fruit reward (represented by amount of nitrogen, soluble proteins, sugar and lipids) and fruit defence (represented by amount of tannins, polyphenols, fibre and alkaloids). The sampling and measurement methods for each of these trait variables are detailed in Appendix S1 (Supporting Information). We categorized the dispersal mode of each plant species as: (i) primarily bird-dispersed, (ii) primarily lemur-dispersed, or (iii) dispersed by both lemurs and birds, based on frugivory data from the literature (Overdorff 1993; White *et al.* 1995; Dew & Wright 1998; Rakotomanana *et al.* 2003; Razafindratsima, Jones & Dunham 2014) and from knowledge of the long-term local field technicians familiar with the fauna and flora in RNP. A species was considered as 'primarily dispersed' by either one of the frugivore group if it is known to be consumed and/or dispersed by one the taxa but not the other. Plant species dispersed by abiotic means were determined by examining the fruit for presence of plumes and wings, dehiscence or absence of edible aril or pulp (Howe & Smallwood 1982; Seidler & Plotkin 2006).

FRUITING PHENOLOGY

We monitored fruiting phenology in two sites within the southern forest in RNP (Valohoaka and Vatoharanana; see map in Fig. S1). In each site, we set up 10 transects of 100 m long and 4 m wide, which were spaced at least 100 m apart and ran perpendicular to a major trail. All individual canopy trees (≥ 5 cm diameter at breast height, DBH) and understorey trees (≥ 2 cm DBH) were identified in the field by local research technicians familiar with the local flora and marked with numbered aluminium plant tags. In total, we marked 3320 individuals of 155 species belonging to 89 genera and 43 families. Monitoring occurred every 2 weeks for 2 years (July 2012–June 2014), during which we recorded the presence/absence of immature and mature fruits for each tagged individual (Morellato *et al.* 2000, Cortés-Flores *et al.* 2013). Species that were fruiting at the time of our two-week monitoring were considered as co-fruited. We performed circular statistics in MATLAB R2013b (The MathWorks Inc., Natick, MA, USA) using CIRCSTAT toolbox (Berens 2009) to analyse fruiting phenology (Appendix S2).

PHYLOGENETIC TREE RECONSTRUCTION

We used the web-based service `PHYLOMATIC` version 3 (<http://phylodiversity.net/phyloomatic/>) to build a local master phylogenetic tree of all plant species in Ranomafana. This program takes the taxa in our list (with family and genus) to match the most resolved position possible in a stored megatree, developed by the Angiosperm Phylogeny Group III (megatree used: R20120829) (Webb & Donoghue 2005). We added branch lengths to our phylogenetic tree using the *bladj* algorithm implemented in `PHYLOCOM` 4.2 (Webb, Ackerly & Kembel 2008), which adjusts branch lengths with estimated molecular and known fossil ages from Wikström, Savolainen & Chase (2001).

PHYLOGENETIC SIGNAL

We tested for statistical dependence of trait values among tree species due to their phylogenetic relationships ('phylogenetic signal') (Revell, Harmon & Collar 2008). We used different approaches for continuous and categorical trait variables. For continuous variables, we first reduced multiple variables using principal component analysis (PCA), with the package `FACTOMINER` in `R` 3.0.3 (R Core Team 2014), to more concisely represent our traits of interest; for example, Hue, Lightness and Chroma were reduced to fewer PCs to describe 'colour'. We retained principal components with an eigenvalue >1 (Peres-Neto, Jackson & Somers 2005). We tested our reduced variables for phylogenetic signal by estimating Pagel's λ (Pagel 1999), using the package `GEIGER` in `R`. Pagel's λ is a scaling parameter for the correlations between species and is used to assess the phylogenetic associations in traits against random trait distributions and a Brownian motion model of evolution (in which trait divergence increases proportionally with phylogenetic distance), estimated from 1000 randomizations. The value of $\lambda = 0$ indicates evolution of traits that is independent of phylogeny, while a value of $\lambda = 1$ indicates if trait similarity that is proportional to phylogenetic distance (Pagel 1999; Freckleton, Harvey & Pagel 2002). Values above one are undefined. For categorical dispersal modes, we estimated phylogenetic signal of each dispersal mode, using the Fritz and Purvis's D statistic (appropriate for binary variables) (Fritz & Purvis 2010), with the `CAPER` package in `R`. A value of $D = 1$ indicates a trait following a random trait distribution, while a value of $D = 0$ indicates a trait consistent with a Brownian threshold model.

PATTERNS OF DIVERSITY AND STRUCTURE OF CO-FRUITING PLANT ASSEMBLAGES

We characterized the functional trait diversity of each co-fruiting assemblage by measuring how functional dispersion (FDis, Laliberté & Legendre 2010) differed from null expectations (FD package in `R`). FDis computes the mean distance of co-fruiting species in a multidimensional trait space from the centroid of all species (Laliberté & Legendre 2010; Ding *et al.* 2012; Chamberlain *et al.* 2014). For each assemblage, null expectations were estimated from 1000 randomly generated assemblages drawn from a pool of all the tree species in our sample, by shuffling taxon names and maintaining species richness. We then calculated standardized effect sizes of FDis (ZFDIs) (Ding *et al.* 2012; Satdichanh *et al.* 2015) for each trait category. ZFDIs were calculated as follows: $ZFDis = [(FDis_{obs} - FDis_{null})/SD(FDis_{null})]$, in which the subscripts *obs* and *null* refer to the means of observed and null assemblages, respectively, and *SD* refers to the standard deviation of the metric for the null assemblages. Negative ZFDIs values indicate trait dispersion is larger than expected by chance (overdispersion), and positive values indicate that the trait

dispersion is smaller than expected by chance (clustering). Values of ZFDIs are in units of standard deviation; thus, the significance of a single metric is contained in its value (<-1.96 is significantly overdispersed, and >1.96 is significantly clustered at $\alpha = 0.05$) (Vamosi *et al.* 2009; Satdichanh *et al.* 2015).

We used two phylogenetic indices to quantify the community-wide phylogenetic structure of co-fruiting assemblages (i.e. relatedness patterns of species that have overlap in fruiting time): Nearest Taxon Index (NTI) and Net Relatedness Index (NRI) (Webb *et al.* 2002). NTI is the standardized effect size of the mean phylogenetic distance between nearest taxa (mean nearest neighbour distance, MNND) across all species in an assemblage, and NRI is a standardized effect size of the mean pairwise phylogenetic distance (MPD) across all species in an assemblage. NTI and NRI were calculated in `PHYLOCOM` 4.2 (Webb, Ackerly & Kembel 2008) using the following equations: $NTI = -1 \times [(MNND_{obs} - MNND_{null})/SD(MNND_{null})]$ and $NRI = -1 \times [(MPD_{obs} - MPD_{null})/SD(MPD_{null})]$, in which the subscripts *obs* and *null* refer to the means of observed and null assemblages, respectively. To generate null assemblages, we used the null model #1 in `Phylocom`, in which species richness within each assemblage was maintained and the species names were drawn from a pool containing all species present in at least one assemblage (Webb, Ackerly & Kembel 2008). Species names were randomly shuffled without replacement 999 times, and the values of MNND and MPD were calculated each time for each null assemblage. Negative values of NTI or NRI indicate that co-fruiting species are less phylogenetically related than expected by chance ('phylogenetic overdispersion'), whereas positive values of NTI or NRI indicate phylogenetic clustering (i.e. co-fruiting species are more phylogenetically related than expected by chance) (Webb *et al.* 2002). Similar to ZFDIs, individual values of NRI and NTI will be significantly different from zero when the absolute value is >1.96.

We measured the diversity of co-fruiting assemblages by calculating species richness (S) and $\exp H$, which is an exponential of the value of Shannon entropy diversity index H representing an 'effective number of species' (Hill 1973; Jost 2006).

We performed serial runs tests (Zar 1999) to assess temporal independence of each metric over time (ZFDIs, NRI, NTI, S , $\exp H$), using the `LAWSTAT` package in `R`, testing the null hypothesis that the distribution of the values of the metric over time is random (Levey 1988; Santorelli *et al.* 2014).

SEASONAL EFFECTS ON THE STRUCTURE OF CO-FRUITING ASSEMBLAGES

We used generalized least-squares (gls) function in the `NLME` package in `R` to determine the relationships between the shifts in rainfall patterns and each community metric (NTI, NRI, species richness, $\exp H$), allowing for autoregressive correlation within our time-series data. Rainfall shifts were represented by the absolute value of a rainfall differential D , which is calculated as $R_t - R_{t+1}$ (Ramírez *et al.* 2015), in which R_t is the sum of rainfall at time interval t . Rainfall data were from available daily measurements in RNP (<http://www.teamnetwork.org/>).

Results

FRUIT TRAITS AND SEED-DISPERSAL STRATEGIES

Zoochorous plant species accounted for 84.4% of the tree species with known dispersal mode ($n = 141$) within our phenological transects, of which 11.8% are primarily dispersed

by birds, 69.8% primarily dispersed by lemurs, and 18.5% dispersed by both birds and lemurs. At the individual tree level, an average 91.5% ($n = 3270$) were zoochorous, among which 8.4% were primarily bird-dispersed, 63.2% were primarily lemur-dispersed, and 28.3% were with mixed dispersal mode.

The three major dispersal modes differed significantly in fruit and seed traits (PERMANOVA; $F_{2,81} = 3.23$, $P = 0.002$). Bird-dispersed fruits were found to have smaller seed and fruit sizes, richer sugar content, and lower protein, fibre and polyphenols than lemur-dispersed fruits (Table S1). A non-metric multidimensional scaling (nMDS) analysis on the variation of fruit traits relative to the different dispersal modes (Appendix S3) showed a specialization of birds on small-sized fruits and seeds, darker coloured fruits and with high sugar content; these traits are nested within the wide spectrum of trait distribution associated with dispersal by lemurs; mixed dispersal mode showed an overlap in traits with bird- and lemur-dispersed species.

FRUITING PHENOLOGY

Fruiting occurred year-round (Fig. 1) with no significant seasonal peak in the number of co-fruiting species (i.e. co-fruiting species did not differ from uniformity across time, Table 1, Rayleigh test $P = 0.84$). We also did not detect a seasonal peak in the number of species fruiting with bird, lemur or mixed dispersal mode (Fig. 1b–d, Table 1). However, overall and for each dispersal mode, fruiting was seasonal by abundance of trees fruiting, with a significantly unimodal peak occurring in April (Fig. 1e–h, Table 1).

PHYLOGENETIC SIGNAL

We used principal component scores resulting from PCA of each trait type to examine the phylogenetic signal for each

trait; variations explained by each retained principal scores are detailed in Table 2. For fruit colour, PC1 explained 44% of the variance and was most correlated with hue (load = -0.807) and lightness (load = 0.817); PC2 explained 36.12% of the variance, with Chroma as the largest loading (0.947). For fruit size, both length and width had the same loadings (0.936). Likewise, for seed size, seed length and seed width had the same loadings (0.961). For fruit reward, PC-1 explained 38.55% of the variance with percentage of lipid as the largest loading (0.732) followed by nitrogen (0.662) and sugar (-0.648); for PC-2, the largest loading was protein (0.817) followed by nitrogen (-0.530). For fruit defence, PC-1 explained 42.66% of the variance and was most correlated with fibre content (ADF: 0.942 ; NDF: 0.922); for PC-2, which accounted for 24.26% of the variance, the

Table 1. Peak date of fruiting as represented by the mean angle α in a circular year (starting with July 1 as 0° and with 30° increment in month) and occurrence of seasonality in fruiting as represented by the concentration of resultant vector r around the mean angle (the closer the value of r is to 1, the more concentrated the data are around the mean), for each and all the three major dispersal modes, based on number of species and number of individual trees fruiting. A Rayleigh test was used to test the null hypothesis that fruiting is uniformly distributed around the year

	Dispersal mode	Peak of fruiting (α , in degrees)	Vector r	Rayleigh Z	P -value
Based on number of species fruiting	All	279.39	0.05	0.916	0.401
	Bird	273.43	0.20	1.846	0.158
	Lemur	104.61	0.02	0.080	0.924
Based on number of individual trees fruiting	All	257.63	0.37	359.859	<0.001
	Bird	283.09	0.47	71.090	<0.001
	Lemur	292.57	0.16	21.150	<0.001
	Mixed	247.56	0.52	381.454	<0.001

Bold indicate significant P -values at $\alpha = 0.05$.

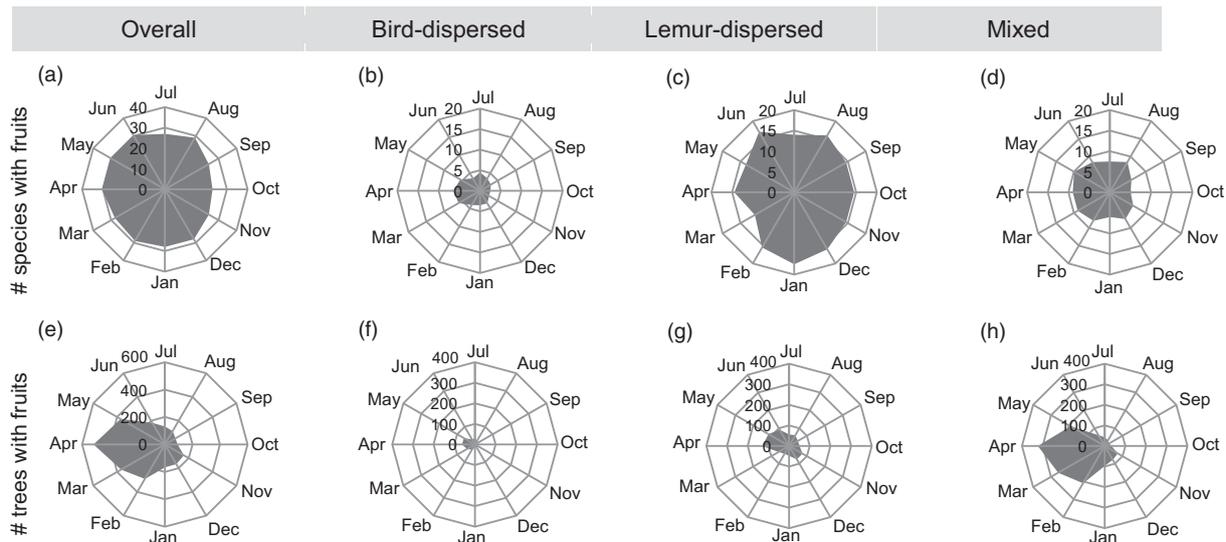


Fig. 1. Absolute frequency distribution of fruiting species (a–d) and individual trees (e–h) (averaged across years), considering all species (a) and all individuals (e), and by dispersal mode (b, f: bird-dispersed; c, g: lemur-dispersed; and d, h: mixed).

Table 2. Eigenvalues and percentage of variance accounted by each principal component for phenology variables and each trait type, resulting from PCA and CATPCA (for defence traits with discrete variable), and phylogenetic signal in phenology and each trait type using Pagel's λ . Value of λ equals 0 if there is no phylogenetic signal and approaches 1 with increasing phylogenetic pattern

Component for each trait type	PCA results		Phylogenetic signal	
	Eigenvalue	% variance	λ	<i>P</i> -value
Phenology PC-1	1.729	57.64	0.135	0.19
Fruit colour PC-1	1.320	44.00	0.118	0.23
Fruit colour PC-2	1.084	36.12	0.261	0.02
Fruit size PC-1	1.751	87.53	<0.0001	1.00
Seed size PC-1	1.847	92.33	0.873	<0.001
Fruit reward PC-1	1.542	38.55	0.289	0.003
Fruit reward PC-2	1.122	28.06	0.274	0.005
Fruit defence PC-1	2.133	42.66	0.092	0.31
Fruit defence PC-2	1.213	24.26	<0.0001	1.00

Bold indicate significant *P*-values at alpha = 0.05.

largest loadings was condensed tannin (0.725), followed by polyphenols (0.530) and alkaloid (−0.498).

The phylogenetic pattern of fruiting phenology did not differ significantly from a random distribution on the phylogeny (Table 2). For fruit traits, closely related species tended to be more similar than expected by chance in their colour Chroma (colour PC2), seed size and fruit rewards (both principal components), but not in colour hue and lightness (colour PC1), fruit size and defence (Table 2). For dispersal mode, we also found significant phylogenetic signal of being dispersed by birds ($D = 0.223$, $P < 0.0001$), lemurs ($D = 0.560$, $P < 0.0001$) and both ($D = 0.653$, $P < 0.0001$). However, this signal was weaker than expected under genetic drift (Brownian motion evolution) for lemur ($P < 0.0001$) and mixed dispersal mode ($P < 0.0001$), but not for bird-dispersal mode ($P = 0.32$).

TEMPORAL PATTERNS OF DIVERSITY AND STRUCTURE OF CO-FRUITING ASSEMBLAGES

The measurements of trait diversity within co-fruiting plant assemblages revealed fluctuating patterns over time, such that the distribution of the ZFDis values was significantly non-random with respect to time (runs tests, $P < 0.05$) (Fig. 2). Despite a low incidence of individual ZFDis values exceeding absolute values of 1.96 (indicating significance) for any of the traits measured, each trait displayed an overall pattern of trait clustering (84–100% of ZFDis values were positive for each trait).

The estimated indices of standardized phylogenetic diversity of co-fruiting plant assemblages exhibited fluctuating patterns over time, from clustered to overdispersed. We rejected the null hypothesis that the distribution of NRI (Net Relatedness Index) values over time was random (runs tests; $P < 0.0001$), but not for NTI (Nearest Taxon Index, $P = 0.669$) (Fig. 3). Similarly, species richness and the modified Shannon entropy fluctuated over time and were significantly non-random with respect to time (Fig. 3).

SEASONAL EFFECTS ON THE DIVERSITY AND STRUCTURE OF CO-FRUITING ASSEMBLAGES

There was a significant positive correlation between the rainfall differential D and the values of the NRI of the co-fruiting assemblages, indicating that higher change in rainfall corresponds to more phylogenetic clustering at the base of the phylogenetic tree within co-fruiting assemblages (Fig. 4). However, this pattern was driven primarily by the three phenology sampling points with the most extreme rainfall differentials. We found no association of the rainfall differential D with NTI, species richness, the modified Shannon entropy (Fig. 4) or the ZFDis values of co-fruiting assemblages (Fig. S2). For absolute rainfall, we found no significant relationships with most of our metrics; however, the Shannon entropy index of diversity declined and the ZFDis of fruit colour increased with higher rainfall levels (Table S3). These no longer remained significant with a Bonferroni adjustment for multiple tests.

Discussion

Fruit and seed traits often play an important role in the attraction of animal mutualists and may mediate competition or facilitation for seed-dispersal services among co-fruiting plant species within a community (Schaefer, Schaefer & Levey 2004; Whitney 2009). However, we know relatively little about how these traits are structured within a community in a temporal context. To address this, we examined the patterns of phylogenetic relatedness and trait similarities among co-fruiting tree species in the south-eastern rain forest of Madagascar over a period of 2 years. We predicted that the limited number of frugivore taxa relative to animal-dispersed tree species in the system would make trait divergence through limiting similarity unlikely. Instead, we predicted there would be temporal clustering of traits and phylogenetic relationships among co-fruiting species vying for shared dispersers. We also predicted that because of the strong role of rainfall in the seasonal patterns of plant phenology, temporal variation in rainfall would mediate temporal fluctuations in fruit traits and phylogenetic relationships of co-fruiting assemblages.

We found that the patterns of functional (trait) diversity and phylogenetic structure of co-fruiting assemblages varied over time. Despite fluctuations, fruit/seed traits of co-fruiting trees were clustered across time. Phylogenetic diversity of co-fruiting trees was not clustered overall, and, unlike functional diversity, decreased during extreme shifts in rainfall.

The overall clustered patterns of functional diversity among co-fruiting plant species in time may be a result of facilitation, seasonal environmental filtering, mimicry, competition for similar frugivores or a combination of pressures (Chesson 2000; Burns 2002; Saracco *et al.* 2005; Cavender-Bares *et al.* 2009; Whitney 2009; Albrecht *et al.* 2015). This pattern differs from floral trait patterns, studies of which tend to show overdispersion within co-flowering communities (McEwen & Vamasi 2010; Heystek & Pauw 2014; Muchhala, Johnsen & Smith 2014). Unlike fruits, flowers often have less

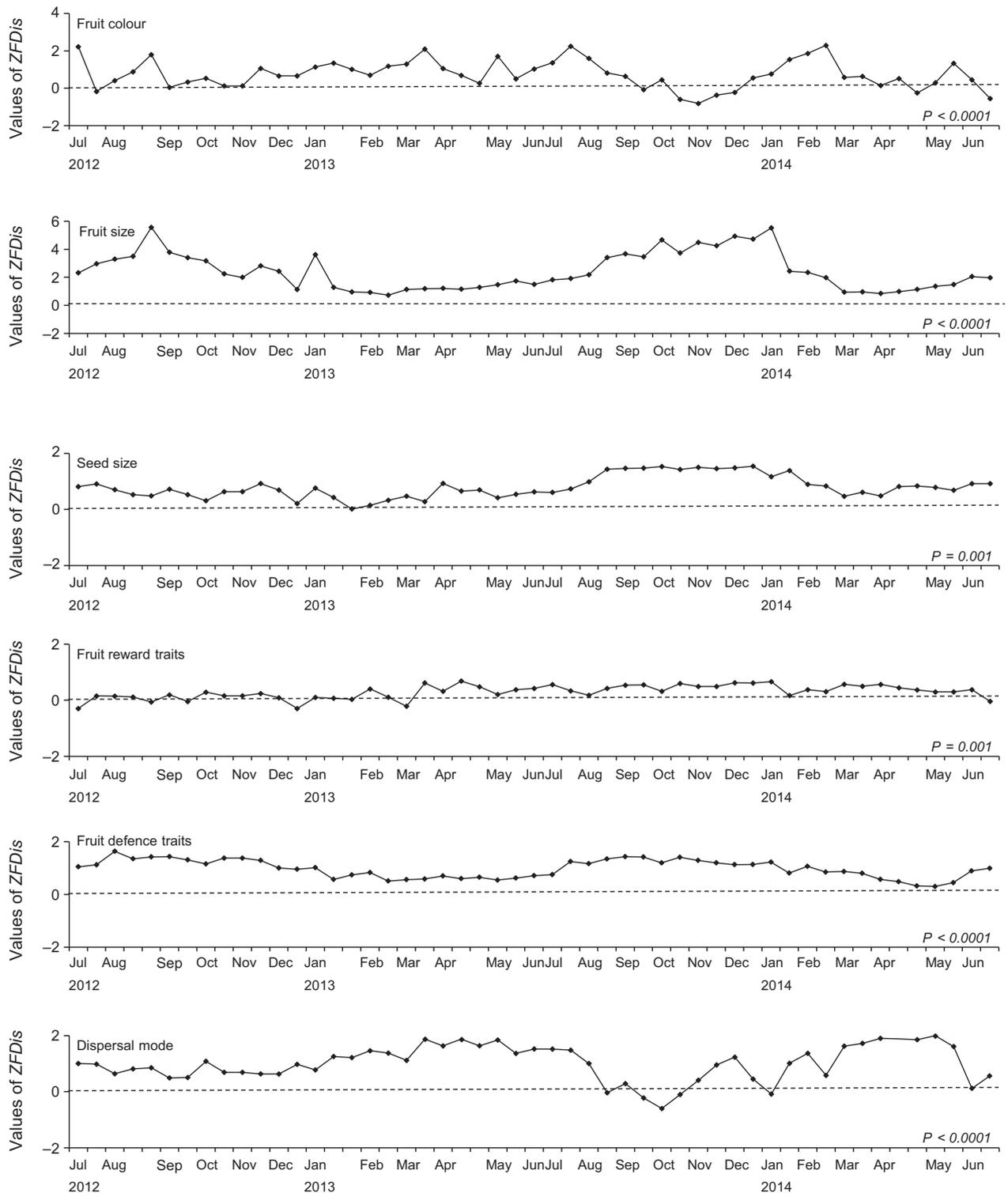


Fig. 2. Standardized effect size of the functional diversity (ZFDIs) of co-fruiting assemblages over time, for all traits. Negative ZFDIs values indicate that trait dispersion is larger than expected by chance (overdispersion), and positive values indicate that the trait dispersion is smaller than expected by chance (clustering). P -values correspond to runs tests used to assess temporal independence of each index.

generalized relationships with their animal mutualists and sharing pollinators has higher costs to fitness than sharing seed dispersers, such as interspecific pollen clogging (Blüthgen *et al.* 2007; Whitney 2009). Frugivores tend to have generalist diets (Fleming 1986; Howe 1993), which may be even

more generalized than expected based on fruit availability (Carlo & Morales 2016). Co-fruiting species are, therefore, likely to share dispersers with many species such that divergence of fruit, and seed traits is unlikely to enhance coexistence. Trait convergence and mimicry among co-fruiting

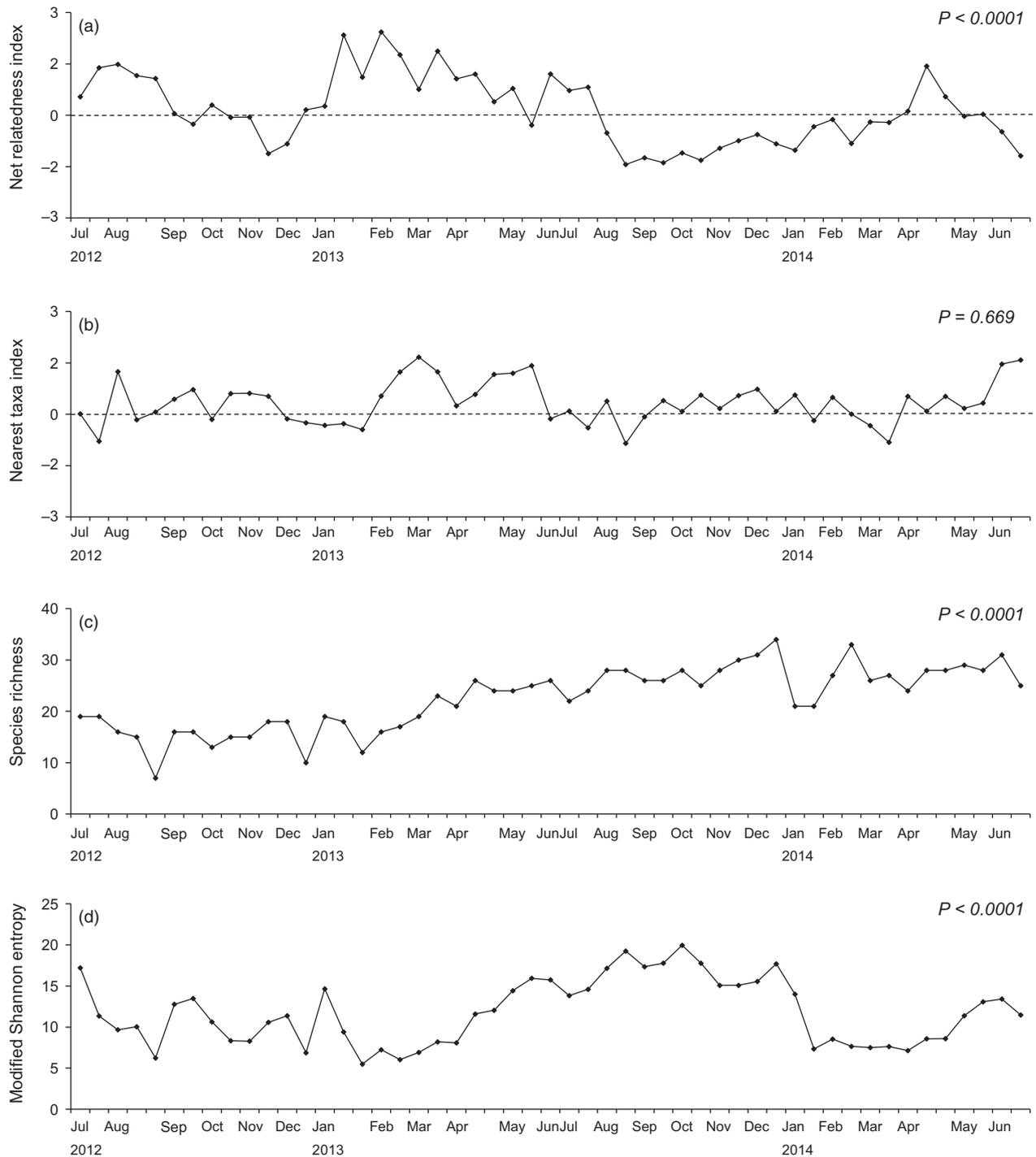


Fig. 3. Fluctuating patterns of the indices of phylogenetic diversity (a: NRI, b: NTI), species richness (c) and the modified Shannon entropy (d) of co-fruiting species assemblages. Negative values of NTI or NRI indicate phylogenetic overdispersion, and positive values indicate phylogenetic clustering. P -values correspond to runs tests used to assess temporal independence of each index.

species may be an effective evolutionary strategy in diverse plant communities, especially for low density species, which are likely to profit from being similar to more common co-fruiting species (Albrecht *et al.* 2015). Indeed, the potential benefit of fruit mimicry has been shown in studies of wild birds, which will readily try novel mimetic fruits (Galetti 2002).

Environmental filtering due to seasonal abiotic variation or interactions with antagonists and natural enemies may also cause patterns of temporal clustering in fruit and seed traits. Timing of fruiting will affect the post-dispersal conditions for germination and early seedling growth and mortality. Fruit and seed traits can affect outcomes under different abiotic conditions and can also serve as attracting cues or defences

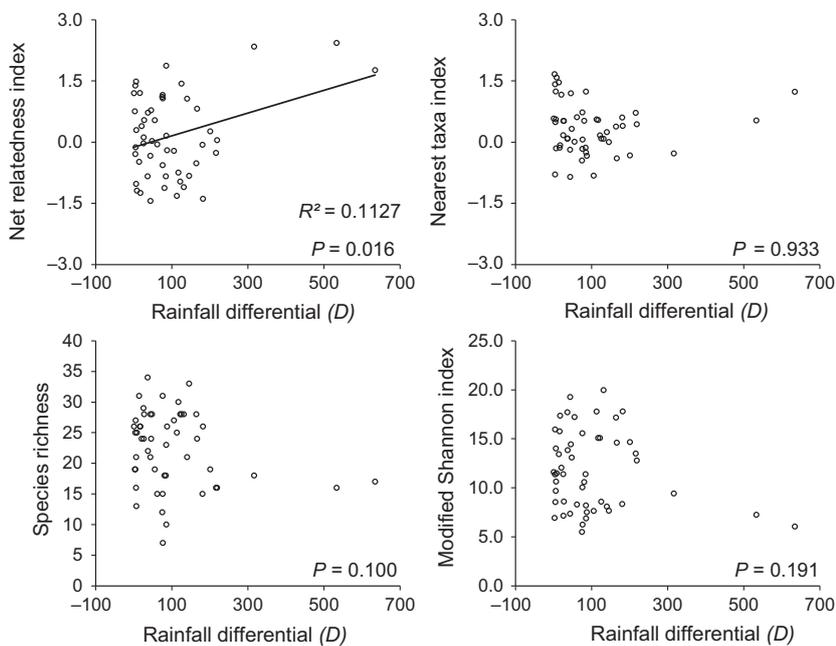


Fig. 4. Relationships between the shifts in rainfall patterns (differential of rainfall D between time intervals) and each community metric (NRI, NTI, species richness and the modified Shannon entropy). P -values correspond to significance of generalized least-squares models.

against natural enemies (Schaefer, Schaefer & Levey 2004; Whitney & Stanton 2004).

Despite clustering of fruit and seed traits in time and the presence of strong phylogenetic signal (i.e. closely related species had similar traits) in seed-dispersal mode and in some fruit and seed traits (seed size and nutritional reward), we found no phylogenetic signal in fruiting phenology (i.e. closely related species do not tend to have synchronous fruiting time). The lack of phylogenetic signal in fruiting phenology we observed for plant species in Ranomafana is consistent with previous studies on evolution of fruiting phenology (Staggemeier, Diniz-Filho & Morellato 2010; Silva *et al.* 2011). This finding supports recent theoretical work that predicts evolutionary lability of phenological traits in the tropics because of the broad temporal niche axis afforded by less extreme seasonality (Pau *et al.* 2011). Competition for seed dispersal services (Wheelwright & Janson 1985) or factors affecting flowering or post-dispersal mortality such as natural enemies (Whitney 2009) could then drive divergence in fruiting times. It has also been suggested that closely related plant species sharing seed dispersers will benefit from divergent fruiting times because it would help maintain disperser populations (Staggemeier, Diniz-Filho & Morellato 2010); however, since selection acts on individuals, this hypothesis remains controversial.

The patterns of phylogenetic structure of co-fruiting species fluctuated over an annual cycle ranging from clustered (i.e. co-fruiting species were more closely related than expected by chance) to overdispersed (i.e. co-fruiting species were more distantly related than expected by chance). These fluctuations were non-random with respect to time when looking at net relatedness (NRI), but not for patterns of closest related taxa (NTI). This suggests significant seasonal fluctuations of phylogenetic structure at the base of the phylogenetic tree, but not at the tips. These fluctuating patterns of NRI were associated with shifts in rainfall, such that stronger shifts in

either direction were associated with more closely related co-fruiting assemblages. This pattern may be explained by environmental filtering if closely related species tend to share environmental tolerances related to germination and early survival (Burns & Strauss 2011). Periods of shifting rainfall may represent difficult or unpredictable environments for newly dispersed seeds, and some taxonomic groups may tolerate these conditions better than others resulting in patterns of phylogenetic clustering of co-fruiting species.

Additionally, several studies have shown that co-fruiting individuals may serve as focal points for dispersal by frugivores (Clark *et al.* 2004; Kwit, Levey & Greenberg 2004; Blendinger, Blake & Loiselle 2011; Carlo & Tewksbury 2014; Razafindratsima & Dunham 2016a), which may bias phylogenetic relationships between dispersed seeds and neighbouring adult trees (Razafindratsima & Dunham 2016a). In consequence, the phylogenetic distance between seeds and neighbouring adults may alter recruitment outcomes because of shared habitat affinities of closely related species or the negative effects of competition and shared natural enemies (Webb, Gilbert & Donoghue 2006; Liu *et al.* 2012; Lebrija-Trejos *et al.* 2014).

Conclusions and implications

Our findings suggest that the interactions of frugivores with fruiting phenology can be an important component for structuring communities and could explain some of the variation in patterns of community structure across studies. A temporal context is particularly important in tropical forests, where fruiting occurs year-round (van Schaik, Terborgh & Wright 1993; Oberrath & Bohning-Gaese 2002). Our findings also open new avenues for further studies to address the combined importance of ecological and evolutionary factors for plant interactions, recruitment and community structure.

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Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.g4n11> (Razafindratsima & Dunham 2016b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Map of Ranomafana National Park showing the field sites.

Figure S2. Relationships between the shifts in rainfall patterns (differential of rainfall D between time intervals) and ZFDIs for all traits.

Table S1. Average value (\pm SD) of each morphological and biochemical trait for the three major dispersal modes.

Table S2. Relationships between rainfall and all metrics.

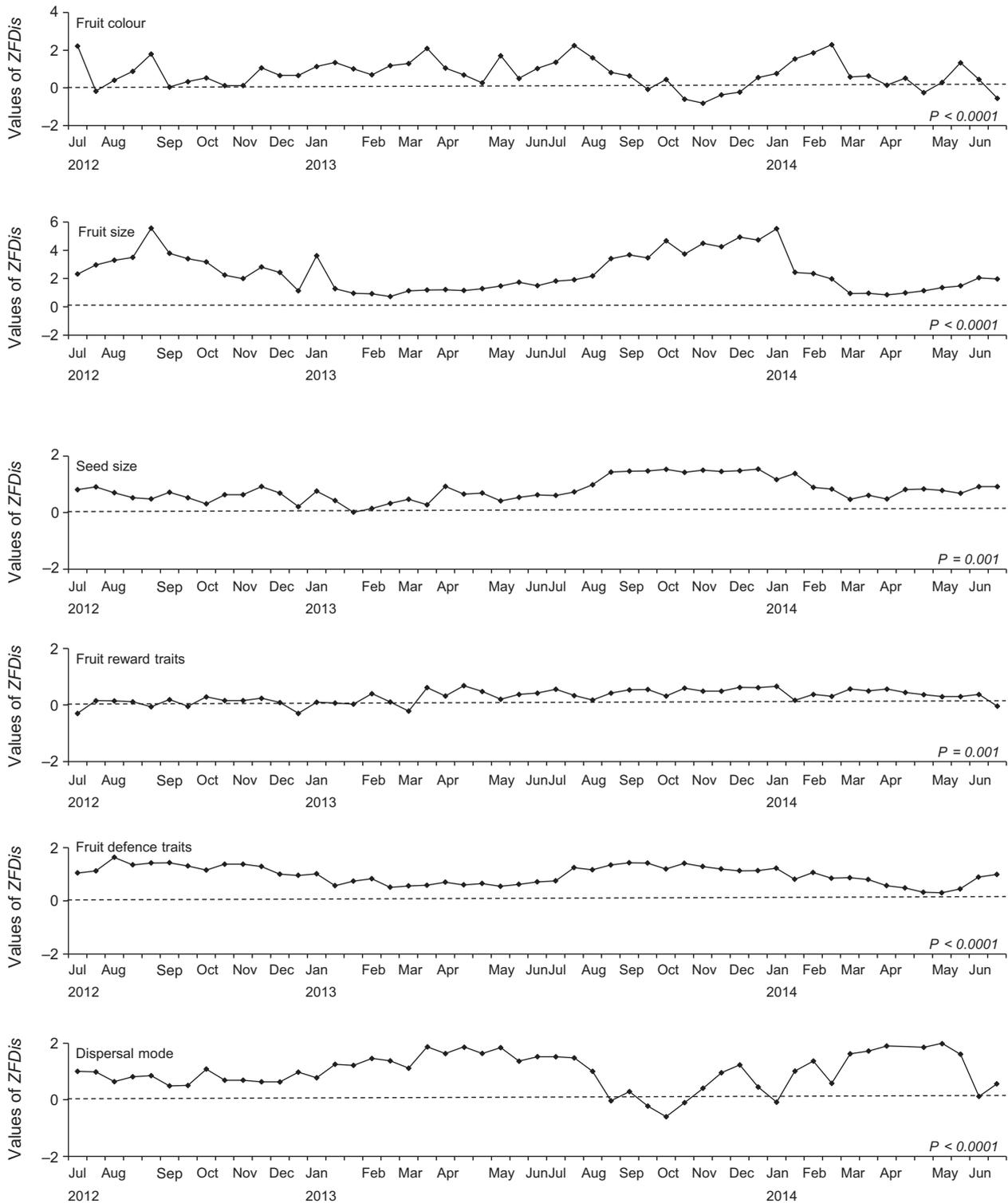
Appendix S1. Methods for sampling fruit trait data.

Appendix S2. Analyses of fruiting phenology.

Appendix S3. Differences in fruit and seed traits among the three major known dispersal modes.

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main.



We suggest that it may be more beneficial for co-fruiting plant species to share similar fruit and seed traits than to diversify traits, when they rely on a comparatively small set of generalist frugivorous taxa for seed dispersal. Results also demonstrate that rainfall-driven environmental filtering may cause seasonal fluctuations in the phylogenetic patterns of phenology in a community. Results highlight the importance of a temporal context in examining patterns of community structure.