Responses of Primates and Other Frugivorous Vertebrates to Plant Resource Variability over Space and Time at Gunung Palung National Park

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Abstract Identifying patterns of primate diversity and abundance over space and time provides a window into the ecological processes that influence species distributions and community composition. Long-term studies of primate communities across multiple habitat types at small spatial scales are rare, yet can improve our understanding of habitat and resource use. Within primate community ecology, there has been recent interest in studying primate species in the context of the broader faunal communities of which they are a part because interactions with ecologically similar but distantly related species may influence habitat use. We present the results of a 64-mo study of 10 vertebrate frugivore species with highly overlapping diets inhabiting seven distinct forest types at the Cabang Panti Research Station, West Kalimantan, Indonesia. We used survey transects and phenology plots to measure variation in vertebrate population densities (four primate, three hornbill, two squirrel, and one pig species) and fruit resources over space and time. We found little evidence of habitat partitioning or specialization. Densities of all 10 frugivore species, however, varied spatially, due largely to elevation and forest structure. Ordination analyses demonstrated that forest types differed in their structure, floristic composition, plant phenology, and frugivore communities. We also documented substantial temporal variation in orangutan densities, reflecting movements over large spatial scales. The densities of other mammalian and avian frugivores, particularly other primates, varied comparatively little over time.

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Our results demonstrate the importance of forest structure for determining frugivore community structure and highlight the importance of lowland forest types for the conservation of tropical frugivores.

Introduction

A principal goal of ecology is to elucidate how ecological communities are structured (Gause 1934; Hubbell 2001; Hutchinson 1957). Patterns of diversity and abundance over space and time are of particular interest because spatial and temporal patterns provide a window into identifying the ecological processes influencing species distributions and community composition (Diamond 1973; Whittaker 1960). Primatologists have become increasingly interested in community patterns over the last two decades (Fleagle *et al.* 1999; Kamilar and Beaudrot 2013; Reed and Bidner 2004). Research on primate community ecology has highlighted the importance of multiple factors in structuring primate communities, including habitat (Haugaasen and Peres 2005; Peres and Janson 1999), competition with primate and nonprimate taxa (Beaudrot *et al.* 2013a,b; Ganzhorn 1999; Kamilar and Ledogar 2011), dispersal (Beaudrot and Marshall 2011; Beaudrot *et al.* this volume; Kamilar 2009), plant productivity (Kay *et al.* 1997), history (Lehman 2006), and phylogeny (Fleagle and Reed 1996).

Many recent studies in primate community ecology have been conducted at relatively large spatial scales, although studies at smaller spatial scales have provided important insights into primate community dynamics (Chapman *et al.* 2010; Lwanga *et al.* 2011), dietary overlap (Gautier-Hion *et al.* 1985; Marshall *et al.* 2009a), competition (French and Smith 2005; Houle *et al.* 2010), and seed dispersal (Chapman and Onderdonk 1998; Poulson *et al.* 2002; Stevenson 2011). Studies of primate communities at small spatial scales can be particularly illuminating when conducted over extended periods of time (Chapman *et al.* 2010) and across a range of habitat types (Leighton and Leighton 1983; Rodman 1979). For example, they can document relationships between resource availability and primate abundance (Chapman *et al.* 2002; Marshall and Leighton 2006), uncover patterns of habitat partitioning (Rodman 1991; Peres 1993), or detect seasonal movements in response to changes in resource availability over space and time (Buij *et al.* 2002; Haugaasen and Peres 2007; Leighton and Leighton 1983).

The Cabang Panti Research Station in western Borneo is an ideal site at which to investigate variation in primate communities over space and time because it contains seven distinct forest types, which span considerable elevation and soil gradients over the scale of a few square kilometers (Marshall 2009, 2010; Paoli *et al.* 2006). Patterns of fruit availability differ dramatically over space (Cannon *et al.* 2007a,b) as a result of differences in soil, weather, and plant species composition among forest types (Cannon and Leighton 2004), and over time as a result of irregular boom and bust cycles of mast fruiting characteristic of Southeast Asian forests (Ashton *et al.* 1988; Wich and van Schaik 2000). Vertebrate populations at Cabang Panti are diverse and largely unaffected by human disturbance (Blundell 1996; Laman *et al.* 1996; Marshall *et al.* 2009a).

Long-term vertebrate research at the site has focused on frugivores because fruit availability varies considerably over space and time, because fruit is likely a limiting resource for these vertebrates (Marshall and Leighton 2006; Marshall *et al.* 2009b), and because frugivores perform crucial ecological functions, such a seed predation and dispersal (Curran and Leighton 2000; Curran and Webb 2000). We extend our study to nonprimate taxa because they may exert important ecological influences, e.g., competition, on primate communities in Bornean forests (Beaudrot *et al.* 2013a,b; Ganzhorn 1999; Marshall *et al.* 2009a).

Here we examine habitat use, specialization, and partitioning in a community of 10 frugivorous species inhabiting a wide range of habitat types on a small spatial scale at Cabang Panti. We have five primary goals: 1) to determine whether frugivores exhibit strong habitat specialization and spatial partitioning; 2) to model variation in frugivore density among habitat partitions based on abiotic factors, forest structure, and phenology; 3) to characterize spatial and temporal variation in fruit resources; 4) to describe spatial variation in frugivore community structure; and 5) to identify which taxa exhibit temporal fluctuations in population density.

Methods

Site Description

We gathered data at the Cabang Panti Research Station in Gunung Palung National Park, West Kalimantan, Indonesia (1°13′S, 110°7′E, Fig. 1). The site comprises seven distinct, contiguous forest types that differ in geology, soil type, drainage, elevation, plant species composition, forest structure, and plant phenology: 1) peat swamp forest on nutrient-poor, bleached white soils overlain by variable amounts of organic matter (5–10 m asl); 2) freshwater swamp forest on nutrient-rich, seasonally flooded, poorly drained gleyic soils (5–10 m asl); 3) alluvial bench forest on rich sandstone-derived soils recently deposited from upstream sandstone and granite parent material (5–50 m asl); 4) lowland sandstone forest on well-drained sandstone-derived soils with a high clay content and sparse patches of shale (20–200 m asl); 5) lowland granite forest on well-drained, granite-derived soils (200–400 m asl); 6) upland granite forest on well-drained, granite-derived soils (350–800 m asl); and 7) montane forest on largely granite-derived soils (750–1100 m asl; Cannon and Leighton 2004; Marshall 2004; Paoli *et al.* 2006).

We divided forest types into two distinct partitions when each partition contained at least three phenology plots and vertebrate transects that did not overlap with transects in the other partition within the same forest type. These conditions were met in five of the seven forest types; the remaining two forest types (freshwater swamp and peat swamp) each contained a single partition, which resulted in a total of twelve partitions (Fig. 1; Table I). Habitat partitions did not overlap within or among forest types, and are considered independent samples. Habitat partitions varied in several biotic and abiotic factors, including rainfall, temperature, elevation, and the stem density and total basal area (TBA) of different plant forms, i.e., trees, lianas, and figs (Fig. 2). Generally, there was less variation between partitions within the same forest type than there was among partitions in different forest types (Fig. 2). In each habitat partition we conducted
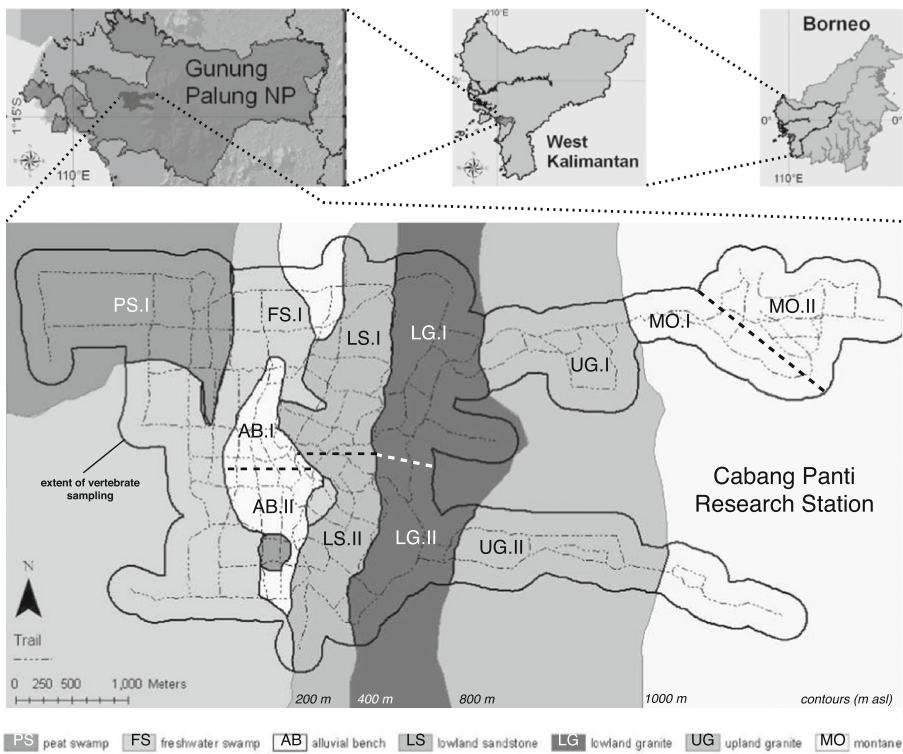
Fig. 1 The Cabang Panti Research Station. Top panels show the position of West Kalimantan on the island of Borneo and the location of Gunung Palung National Park. Lower panel shows distribution of forest types at the study site. The seven forest types are indicated by distinct shades of gray; the legend below the figure lists each forest type, its associated color on the map, and its two-letter code. Dashed lines indicate the research trail system. The solid black line indicates the extent of the vertebrate sampling, i.e., the edge of the study site. Codes on the map, e.g., PS.I, LG.II, indicate habitat partitions; heavy dashed lines indicate divisions between contiguous partitions within a forest type (AB, LS, LG, MO). The montane forest east of UG.II is not included in any partition, as there are no phenology plots in this area. Numbers in italics along the bottom of the map show approximate contour lines in meters above sea level.

vertebrate surveys, gathered monthly phenology data, and monitored temperature and rainfall.

Field Methods

All data presented in this article were collected by A. J. Marshall and a team of dedicated, highly proficient, long-term field assistants between October 2007 and February 2013.

Vertebrate Censuses In 2000 A. J. Marshall established a series of 14 vertebrate survey transects across the 7 forest types at Cabang Panti (Marshall 2004, 2010). Mean length of the survey routes was $3.4 \pm SD\ 0.24$ km and routes followed existing trails through the forest. We walked each route twice per month (starting at opposite ends) at the same speed and time of day (beginning at 05:30 h), and gathered standard line transect data for all vertebrates encountered, e.g., perpendicular sighting distance, group size, group
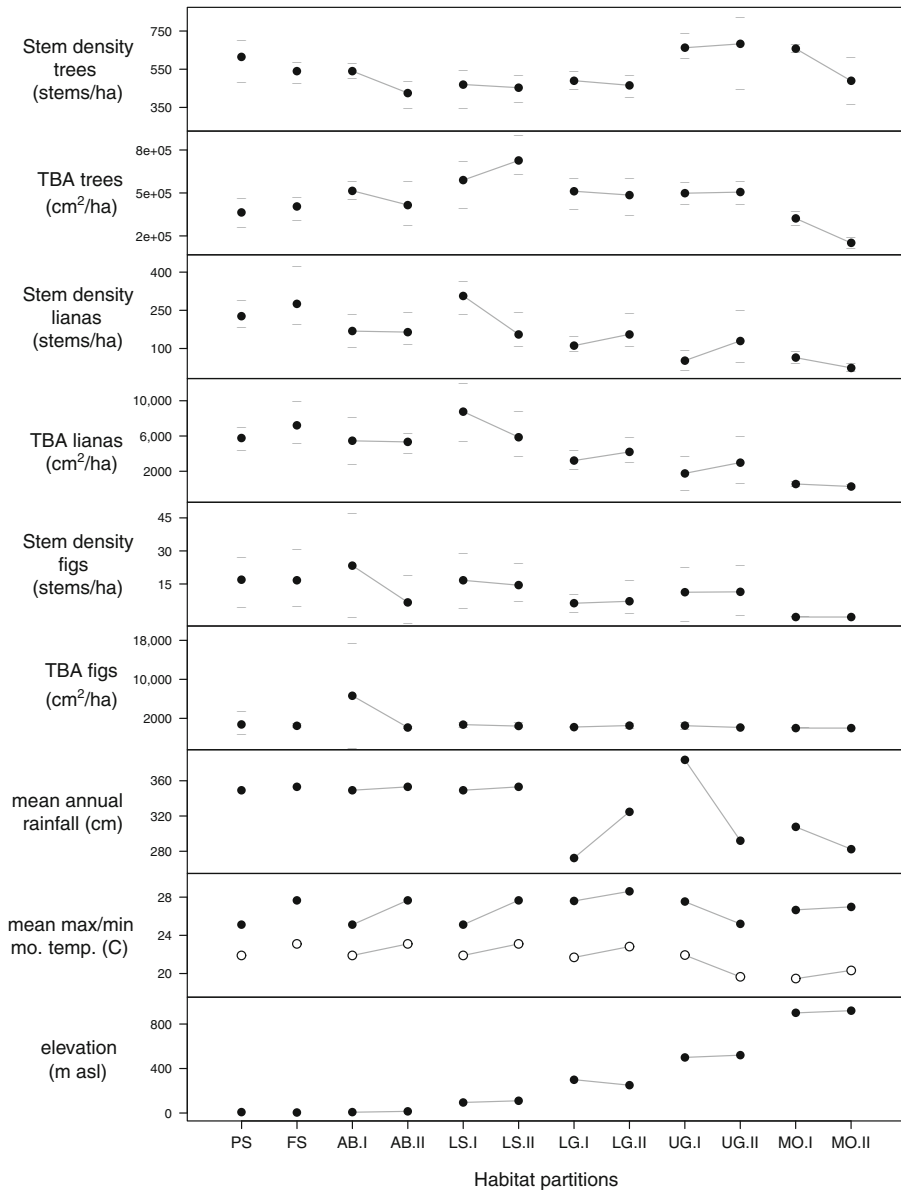
Table I Sampling effort for vertebrate surveys and phenology plots in 12 habitat partitions at the Cabang Panti Research Station, Gunung Palung National Park, West Kalimantan from October 2007 to February 2013

Partition	Total distance walked (km)	Mean ± SD effort (km/mo)	N plots (0.1 ha)	N plots (0.2 ha)	Total plot area (ha)
PS.I	921.0	14.4 ± 4.1	4	3	1.0
FS.I	534.9	8.4 ± 1.6	5	5	1.5
AB.I	250.9	3.9 ± 1.0	0	3	0.6
AB.II	422.3	6.6 ± 1.4	5	2	0.9
LS.I	399.1	6.2 ± 1.1	2	2	0.6
LS.II	258.8	4.0 ± 1.0	3	3	0.9
LG.I	388.6	6.1 ± 1.3	2	3	0.8
LG.II	429.9	6.7 ± 1.4	3	2	0.7
UG.I	514.2	8.0 ± 2.4	2	3	0.8
UG.II	735.0	11.5 ± 2.8	3	2	0.7
MO.I	307.2	4.8 ± 1.3	5	0	0.5
MO.II	706.0	11.0 ± 6.6	0	5	1.0
Mean	489.0	7.6	2.8	2.8	0.8
SD	205.8	3.2	1.7	1.4	0.3

Habitats are indicated by two-letter codes; see Fig. 1. Columns depict total survey distance walked across the study period, mean survey effort in kilometers per month, the number of plots in each of two size classes, and the total sampling area per partition.

spread. Some transects were contained entirely in a single habitat partition, and others spanned multiple partitions and/or forest types. In our analyses, we separated vertebrate survey data based on habitat partition, and estimated vertebrate population densities in each. We surveyed each habitat partition a mean of 7.6 ± SD 3.2 km per month (Table I). Here we present habitat partition specific densities for the 10 frugivorous vertebrate species with the highest known dietary overlap at the study site (Marshall *et al.* 2009a). These species included four primates, three hornbills, two squirrels, and bearded pigs, listed in Table II, along with the number of independent observations and body size of each. Hereafter we refer to species by their genus names, with the exception of the two *Buceros* species, *Buceros rhinoceros* and *Buceros vigil*.

Plant Phenology and Forest Structure We monitored 10 randomly placed plant plots in each forest type. Three of these plots were not located in the habitat partitions studied here, so we present data from a total of 67 plots. Plots were either 0.1 or 0.2 ha in size. Mean sampling per habitat partition was 5.6 ± SD 1.8 plots and 0.8 ± SD 0.3 ha (Table I). In these plots trees larger than 14.5 cm DBH, all lianas larger than 3.5 cm DBH, and all hemi-epiphytic figs whose roots reached the ground were identified, measured, and tagged (Marshall 2004, 2009, 2010; Marshall and Leighton 2006; Marshall and Wich 2013). Botanical nomenclature followed APGII (Angiosperm Phylogeny Group 2003). Plots were placed in the mid-1980s (Cannon *et al.* 2007a) and updated by A. J. Marshall and staff in 2007. Each month we monitored the reproductive status of all tagged tree, fig, and liana stems located in the plots. We carefully examined each stem each month with binoculars and assigned it to one of six

Fig. 2 Summary of biotic and abiotic characteristics of habitat partitions at the Cabang Panti Research Station, Gunung Palung National Park, West Kalimantan (partition codes as in Fig. 1). Plots show with black dots overall stem density (stems/ha) and TBA (cm^2/ha) of trees, lianas, and figs; mean annual rainfall (cm/yr); mean max/min monthly temperature (°C); and elevation (meters above sea level) in each partition from October 2007 to February 2013. We ran all models using these overall values calculated by combining all plots within a partition. To depict within-partition variance, we also plot with gray bars the mean ± standard deviation of plot-specific measures in each partition. Partitions in the same forest type are connected by a solid line.

reproductive states: reproductively inactive, bearing flower buds, flowers, immature, mature, or ripe fruits (Cannon *et al.* 2007a; Marshall *et al.* 2009a).

Table II Vertebrate frugivore taxa included in this study

Code	Species's	Common name	N_{obs}	Body size (kg)
Ag	*Anorrhinus galeritus*	Bushy-crested hornbill	138	1.17
Sb	*Sus barbatus*	Bearded pig	222	150
Cp	*Callosciurus prevostii*	Prevost's squirrel	173	0.38
Mf	*Macaca fascicularis*	Long-tailed macaque	221	5.00
Ha	*Hylobates albibarbis*	Bornean white-bearded gibbon	943	5.70
Bv	*Buceros vigil*	Helmeted hornbill	58	2.89
Pr	*Presbytis rubicunda*	Red leaf monkey	772	6.25
Pp	*Pongo pygmaeus*	Orangutan	319	67.5
Ra	*Ratufa affinis*	Giant squirrel	239	11.9
Br	*Buceros rhinoceros*	Rhinoceros hornbill	199	2.38

Table lists each species' code (used in Fig. 4 ordinations), their scientific and common name, the number of independent observations of the taxon on censuses during the study period, and body size (kg). Body size data from Beaudrot *et al.* (2013a) and Curran and Webb (2000).

Weather and Elevation We recorded maximum and minimum temperature and cumulative rainfall every 10 d in each habitat partition. We measured elevation at the approximate midpoint of each habitat partition using a Suunto Vector Altimeter. Elevation measurements corresponded to estimates on maps of the area produced in the 1980s, and more recent maps produced using GIS software.

Analyses

Modeling Frugivore Densities For each of the 10 vertebrate species presented (Table II), we calculated mean density estimates per km^2 for 12 habitat partitions (D_{SPACE}) and 16 4-mo periods across the entire study site (D_{TIME}) and evaluated the effects on frugivore densities of variation in habitat characteristics along an elevation gradient (habitat covariates, COV_{SPACE}). We used linear regression to determine whether D_{TIME} was a significant predictor of D_{SPACE}.

We used the "unmarked" package (Fiske and Chandler 2011) in R, which is designed to estimate densities of nonindividually identified animals (as opposed to MARK, which is designed for estimating densities of known individuals). We used the unmarked package because both detection and observation covariates can be modeled simultaneously via a hierarchical maximum likelihood approach. This is in contrast to traditional distance sampling methods, such as DISTANCE (Buckland *et al.* 1993), which only allow for evaluation of the effects of detection probabilities on densities. Specifically, we used the distsamp function to investigate the influence of environmental characteristics on animal densities (Royle *et al.* 2004). The distsamp function can be used for data recorded in discrete distance intervals. We binned the data into 10-m intervals and included observations up to 50 m from the transect. We used the hazard detection function to model the detection process as a multinomial distribution and modeled the latent habitat partition specific abundances as Poisson distributed using a

number of models with abiotic and biotic environmental characteristics. We based density estimates on 4-mo periods to reduce the number of zeros in the data matrix because the Poisson distribution used by the distsamp function is inappropriate for heavily zero-inflated data, and analysis of data on monthly intervals produced implausible or nonconverging density estimates. We were unable to analyze movement over both space and time concurrently for the same reasons, as division of species specific data by habitat partition and time led to an abundance of zeros that proved prohibitive using the functions currently available in the unmarked package.

We used AIC model comparisons (Burnham and Anderson 2002) to select the best models predicting habitat partition specific density (D_{SPACE}) based on habitat partition specific site covariates (COV_{SPACE}). These comprised abiotic covariates ($N = 4$; elevation, minimum monthly temperature, maximum monthly temperature, and mean monthly rainfall), structural covariates ($N = 8$, stem density and TBA of stems for trees, lianas, figs, and all forms combined), and the mean values of phenological covariates over the duration of the study (64 mo) for each partition ($N = 45$). Phenological covariates were combinations of three components: reproductive stage (flowers, immature fruits, mature fruits, ripe fruits), plant form (trees, figs, lianas, all stems), and abundance measures (TBA, stem density). We used a similar model selection approach to predict site-wide species densities over 4-mo intervals (D_{TIME}). The D_{TIME} models included only phenological covariates, each of which was calculated as the mean site-wide value for each 4-mo interval.

Habitat Specialization and Variation in Frugivore Densities over Time We used the coefficients of variation (CV) for population density estimates to examine differences in vertebrate abundance among habitat partitions and changes in abundance over time. We used the CV of population density among habitat partitions for a species (CV_{SPACE}) as an index of its degree of habitat specialization, that is, the degree to which individuals are heavily concentrated in a subset of habitat partitions. When CV_{SPACE} is large, the species is relatively specialized; when CV_{SPACE} is small, a taxon is spread more evenly across the entire study site. The CV in population density among periods for a species (CV_{TIME}) is an indication of the stability of its population size within the study site over time. Large values of CV_{TIME} indicate fluctuations in density, resulting from individuals moving in and out of the study site, rather than changes in dispersion among habitat partitions within the study site. In contrast, small values of CV_{TIME} suggest that the total population size in the study site remains relatively stable, and that individuals are not moving in and out of the study site. We used linear regressions to ascertain whether CV_{SPACE} or CV_{TIME} was influenced by species specific sample size or body size and whether CV_{TIME} was a significant predictor of CV_{SPACE}.

Habitat Partitioning Two species may use different habitats for a number of reasons, one of which is that past competition may have resulted in habitat (and thus resource) partitioning. Species pairs exhibiting spatial habitat partitioning in its most extreme form would not co-occur in the same forest type. Less extreme forms of habitat partitioning would be indicated by a low degree of habitat use overlap between species pairs. We evaluated habitat partitioning by examining the densities of vertebrate species pairs across habitats. Habitat partitioning would produce negative correlations in D_{SPACE} among taxa. Negative correlations in D_{SPACE} among species pairs would be

consistent with interspecific competition, but would not definitively demonstrate it as alternative explanations are possible for such patterns. The absence of negative correlations in D_{SPACE} would suggest that competition has not resulted in habitat partitioning among these vertebrate species pairs.

Ordination Analyses Ordination techniques are a category of multivariate analysis that orders ecological communities. Ordination uses attributes of communities, e.g., species composition, population density, to arrange sites along axes in such a way that proximity indicates similarity; sites that are more similar are displayed more closely together in an ordination diagram (ter Braak and Šmilauer 1998). Principal component analysis (PCA) is a form of ordination that can, but does not necessarily, include conditioned variables. Conditioned variables are those whose effects have been statistically removed prior to analysis, i.e., they are "partialed out." Redundancy analysis (RDA) is an extension of PCA that can include conditioned variables but also includes constrained variables. Constrained variables are those whose effects are assessed by the analysis. The effects of constrained variables can be plotted as arrows on ordination diagrams with the length of the arrow indicating the explanatory strength of the variable. When PCA and RDA include conditioned variables they are considered partial PCA and partial RDA, respectively (Legendre and Gallagher 2001).

We performed PCA, partial PCA and partial RDA with the rda function in the vegan package in R (Oksanen *et al.* 2013) to display variation in plant and animal communities across habitat partitions on two ordination axes. We report the cumulative variance explained (*cve*) by each of these axes, and the orthonormal species scores (*v*) to describe the influence of variables on each ordination axis (Oksanen *et al.* 2013). Orthonormal species scores (*v*) are comparable to factor loadings in PCA, representing the correlations of each species with axes of variation. In our analyses, "species" may be vertebrate species or any of the COV_{SPACE} variables; large $|v|$ values indicate factors that are important in determining the position of habitat partitions on cluster diagrams relative to the origin. Factors with large $|v|$ values, and thus stronger influences, cause habitat partitions to be located farther from the origin.

We used ordination analyses to investigate variation across habitat partitions in the following plant characteristics: forest structure, floristic composition, plant reproductive phenology, and a combined measure of these characteristics. The forest structure PCA used six simple measures of structure across habitat partitions (COV_{SPACE}). The forest structure measures were the TBA of trees (TBAt), figs (TBAf), and lianas (TBAl) and the stem density of trees (SDt), figs (SDf), and lianas (SDl). The floristic composition PCA used the habitat partition specific stem density of each plant genus ($N = 154$ genera). The plant reproductive phenology PCA used simple phenology measures that varied among habitat partitions. The phenology measures were the mean and coefficient of variation for the percentage of tree, fig, and liana stems bearing immature, mature, and ripe fruit. Lastly, we conducted a PCA to assess the combination of how forest structure, phenology, and elevation are differentiated among habitat partitions and forest types.

We also used ordination analyses to investigate variation in frugivore densities across habitat partitions using 1) partial PCA conditioned on elevation and 2) partial RDA conditioned on elevation and constrained by forest structure. For the ordination analyses, we estimated habitat partition densities using only elevation as a covariate in

the distsamp model to depict the effects of forest structure independently from the modeled densities.

We conducted all analyses in R 3.0.2 (R Core Team 2013). All data were collected in accordance with the laws of Indonesia and regulations of the University of California.

Results

Frugivore Habitat Specialization and Spatial Partitioning

None of the 10 frugivore species exhibited strong habitat specialization. With the exception of *Macaca*, which was virtually absent (density < 0.005 individuals/km^2) from both upland granite and both montane partitions, each species was found in all 12 habitat partitions (Fig. 3). There were, nevertheless, differences in the degree of habitat specialization among taxa. CV_{SPACE} was highest for *Macaca* ($CV_{SPACE} = 1.55$), indicating that this was the most specialized of the taxa we examined. *Callosciurus*, *Ratufa*, and *Sus* ($CV_{SPACE} = 0.80, 0.66$, and 0.65) were the next most specialized taxa. The primate species *Pongo*, *Hylobates*, and *Presbytis* showed consistent and lower specialization (CV_{SPACE} for each was 0.57–0.59). The three hornbills, *Buceros rhinoceros* ($CV_{SPACE} = 0.55$), *Anorrhinus* ($CV_{SPACE} = 0.51$), and *B. vigil* ($CV_{SPACE} = 0.37$), were the least specialized. CV_{SPACE} was not related to the number of observations of a species (linear regression of $\log(CV_{SPACE}) \sim \log(N_{obs})$, $\beta = 0.08$, $R^2_{adj} = -0.09$, $N = 10$, $P = 0.61$) or body size (linear regression of $\log(CV_{SPACE}) \sim \log(\text{body size})$, $\beta = -0.002$, $R^2_{adj} = -0.12$, $N = 10$, $P = 0.97$).

We found no evidence of spatial partitioning across habitats among the 10 frugivore species. As every species except *Macaca* was found in every habitat partition, presence–absence data showed an absence of complete spatial partitioning at the habitat-partition scale. All pairwise correlations of partition specific densities between species were positive (mean $r = 0.66 \pm SD\ 0.24$), indicating a lack of evidence for less extreme forms of spatial partitioning. Indeed, the best habitats for one species were generally also the best for other species (Fig. 3).

Modeling Density Variation Among Habitat Partitions

Habitat covariates (COV_{SPACE}) explained spatial variation in density (D_{SPACE}) for each vertebrate species (Table III). While models varied among taxa, several consistent patterns emerged. First, elevation was a strong and highly significant negative predictor of habitat specific frugivore densities (D_{SPACE}) for all 10 taxa (although somewhat less significant for *B. vigil*, Table III). Second, forest structure covariates, such as the stem density and total basal area of certain growth forms, were frequently important predictors. The effects of some were consistent across taxa in the models in which they appeared, e.g., negative effect of liana stem density, positive effect of fig stem density, whereas others, e.g., tree stem density, had variable effects (Table III). Third, neither temperature nor rainfall was important for any taxon; all models including these variables had $\Delta AIC > 5$ and model weights < 0.05, suggesting that elevation was the only important abiotic spatial covariate. Finally, mean phenological measures were largely unimportant in determining D_{SPACE}; for no species did phenological habitat
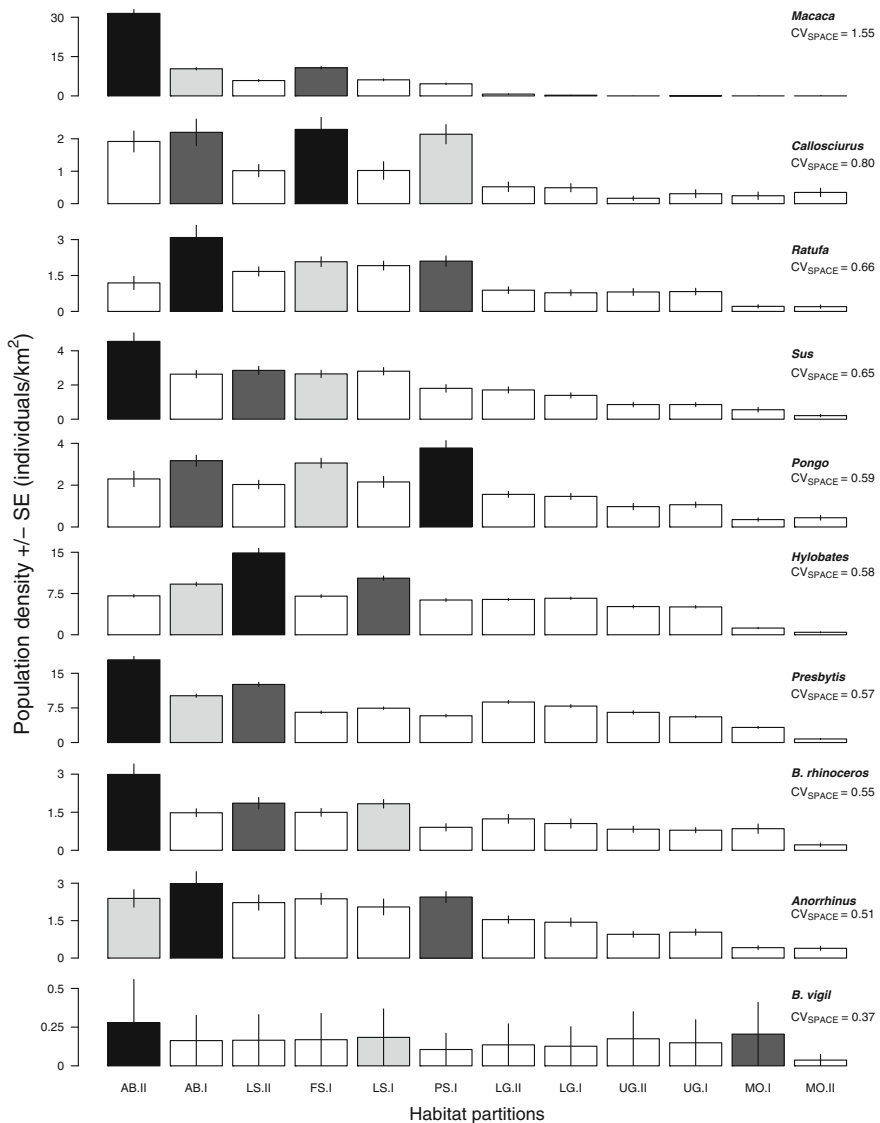
Fig. 3 Spatial variation in frugivore population densities at the Cabang Panti Research Station, Gunung Palung National Park, West Kalimantan from October 2007 to February 2013. Mean (±SE) model averaged population density (individuals/km^2) for each vertebrate frugivore by habitat partition (D_{SPACE}). Note that the y-axis scale differs among plots, therefore the height of bars reflects relative habitat quality of partitions within each taxon. The highest partition specific mean population density for each taxon is shown with a black bar, second highest in dark gray, third highest in light gray, and all others in white. Taxon names are given on the right side of the figure, along with the coefficient of variation for model averaged population density among partitions (CV$_{SPACE}$, an index of habitat specialization). Species are listed from top to bottom in descending order of habitat specialization; habitat partitions are listed from left to right in descending order of mean population density for the 10 frugivore species shown. Lowland forest types contain the highest densities of all 10 frugivorous species.

covariates contribute to any top models (all models including phenology had $\Delta AIC > 3$ and model weight < 0.15).

Table III Top models of spatial variation in population density across habitat partitions for each frugivore species at the Cabang Panti Research Station, Gunung Palung National Park, West Kalimantan from October 2007 to February 2013

Taxon	Model (elevation +)	Cumul. Weight	Δ AIC	Elevation	Stem density all	Stem density trees	Stem density lianas	Stem density figs	TBA all	TBA trees	TBA lianas	TBA figs	Interaction	Δ AIC next model
Macaca fascicularis														
	Tree SD	0.69	0	−4.89***		−0.98***								191
	Tree SD + E * tree SD	1.00	1.62	−4.60***		−0.64*							−0.39*	
Callosciurus prevostii														
	TBA lianas + E * TBA lianas	0.53	0	−2.09***							−0.72**		−1.00***	2.26
Ratufa affinis														
	Fig SD	0.52	0	−0.43**				0.45***						6.48
	Fig SD + E * fig SD	0.89	0.7	−0.37***				0.54***					0.14	
Sus barbatus														
	Tree SD + E * tree SD	0.99	0	−0.82***		−0.15*							0.36***	9.53
Pongo pygmaeus														
	Tree SD + E * tree SD	0.73	0	−0.76***		0.13*							−0.18*	4.03
Hylobates albibarbis														
	TBA all + E * TBA all	0.56	0	−0.41***					0.51***				0.17***	17.5
	TBA trees + E * TBA trees	1.00	0.46	−0.42***						0.50***			0.17***	
Presbytis rubicunda														
	All stems SD + E * all stems SD	1.00	0	−0.51***	−0.09**								0.45***	52.6
Buceros rhinoceros														
	Tree SD + E * tree SD	0.96	0	−0.56***		−0.15*							0.50***	6.27

Table III (continued)

| Taxon	Model (elevation +)	Cumul. Weight	Δ AIC	Elevation	Stem density all	Stem density trees	Stem density lianas	Stem density figs	TBA all	TBA trees	TBA lianas	TBA figs	Interaction	Δ AIC next model
Anorrhinus galeritus														
	Liana SD	0.17	0	−0.86***			−0.22*							2.14
	TBA figs	0.32	0.19	−0.61***								0.13**		
	Fig SD	0.45	0.44	−0.51***				0.20*						
	TBA all	0.54	1.38	−0.64***					0.14*					
	TBA Trees	0.62	1.41	−0.64***						0.14*				
	Liana SD + E * liana SD	0.69	1.79	−0.81***			−0.19						−0.05	
Buceros vigil														
	Tree SD + E * tree SD	0.64	0	−0.70*		0.20							0.89**	3.33

*P < 0.05, **P < 0.01, ***P < 0.001; E = elevation, SD = stem density, TBA = total basal area, all = all stems (trees + lianas + figs)

Species listed in the same order as in Fig. 3. All models include elevation. Listings for each model show model parameters, the cumulative model weight, ΔAIC, and β for each parameter. For models containing interactions, e.g., E * TBA lianas; β for the interaction term is given in the penultimate column. All models with ΔAIC < 2 are listed. The final column shows the ΔAIC of the next best model after those listed for each species.

Plant Ordinations: Spatial and Temporal Variation in Frugivore Resource Availability

Ordination analyses demonstrated that habitat partitions differed across space in forest structure and floristic composition and varied over time in patterns of plant phenology. The forest structure ordination showed that forest types differed substantially: habitat partitions within a forest type tended to cluster relatively close together (Fig. 4a). The first principal component (PC1) of forest structure explained a large proportion of the variance ($cve > 0.99$) and was influenced primarily by TBA of trees ($v = -0.99$) and lianas ($v = -0.01$); PC2 ($cve = 1.00$) was primarily influenced by TBA of lianas ($v = 0.94$) and figs ($v = 0.34$).

The floristic ordination showed that taxonomic composition clearly distinguished some partitions, e.g., freshwater swamp, peat swamp, but not others, e.g., lowland sandstone, lowland granite (Fig. 4b). Floristic composition explained a substantially
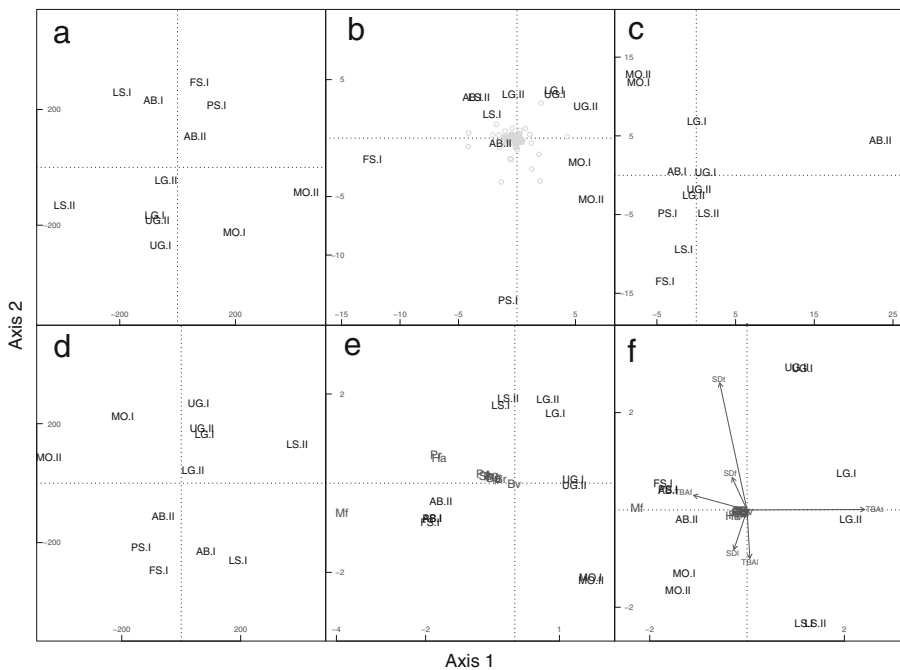
Fig. 4 Ordination diagrams depicting comparisons of habitat partitions at the Cabang Panti Research Station, Gunung Palung National Park, West Kalimantan from October 2007 to February 2013. The x- and y-axes depict, respectively the first and second principal component (plots a–e) or first and second redundancy analysis axis (RDA, plot f). Panels depict clustering based on **(a)** forest structure (TBA trees, fig, and lianas, stem density of trees, fig, and lianas); **(b)** floristic composition (number of stems of each plant genus, circles indicate plant genera); **(c)** plant phenology (mean and CV of percent tree, fig, and liana stems bearing immature, mature, and ripe fruit); **(d)** combined forest structure, phenology, and elevation (components of A and B plus elevation); **(e)** frugivore population densities conditioned on elevation; and **(f)** frugivore population densities conditioned on elevation and constrained by forest structure variables listed in **(a)**. Black two letter codes indicate habitat partitions (as in Fig. 1). In **(e)** and **(f)**, frugivores are listed in gray with two-letter codes listed in Table II; only *Macaca fascicularis* (Mf, in **e** and **f**), *Hylobates albibarbis* (Ha, in **e**), and *Presbytis rubicunda* (Pr, in **e**) are visible at this scale. Gray arrows in f indicate loadings for the following constraining variables: TBA of figs (TBAf), lianas (TBAl), and trees (TBAt); and stem density of figs (SDf), lianas (SDl), and trees (SDt).

smaller portion of the cumulative variance (*cve* PC1 = 0.34, *cve* PC2 = 0.54) than forest structure, phenology, or mammal covariates (*cve* PC1 ≥ 0.95 for each).

The plant reproductive phenology ordination showed that habitat partitions were best clustered based on the CV in phenological measures over time within a partition. PC1 (*cve* = 0.98) was influenced primarily by the CV in the availability of fruit from figs (*v* = 1.00) and lianas (*v* = –0.05); PC2 (*cve* = 0.99) was largely influenced by the CV in the availability of fruit from lianas (*v* = –0.82) and trees (*v* = –0.57). Most pairs of habitat partitions within a forest type were quite similar, e.g., montane forest, upland granite, while one differed substantially (alluvial bench, Fig. 4c).

The combined plant characteristics PCA suggested that structural variables and elevation were most important in distinguishing habitat partitions (PC1: *cve* = 0.99, TBA trees *v* = –0.99, TBA lianas *v* = –0.01, elevation *v* = –0.001; PC2: *cve* = 1.00, TBA lianas *v* = –0.93, TBA figs *v* = –0.34, elevation *v* = 0.11; Fig. 4d).

Animal Ordinations: Spatial Variation in Frugivore Communities

The partial PCA of habitat partition specific vertebrate densities conditioned on elevation, an important predictor for all taxa (Table III), demonstrated clear differences among forest types and high concordance among partitions within forest types. Partitions within lowland sandstone, lowland granite, upland granite, and montane forests were extremely similar within but different among forest types, whereas alluvial bench, freshwater swamp, and peat swamp partitions clustered closely together in the ordination diagram (Fig. 4e). PC1 for vertebrate ordinations explained most of the variance (*cve* = 0.95), with *Macaca* (*v* = –0.81), *Presbytis* (*v* = –0.37), and *Hylobates* (*v* = –0.36) being most influential; PCA2 (*cve* = 1.00) was also most heavily loaded on these species (scores *v* = –0.58, 0.56, and 0.50 respectively).

The partial RDA of frugivore population densities conditioned on elevation and constrained by the forest structure variables illustrated the effects of stem density and TBA of trees, lianas, and figs on frugivore densities across habitat partitions (Fig. 4f). Frugivore densities were primarily differentiated based on the TBA of trees (*v* = 0.69) and figs (*v* = –0.31) in RDA1 (*cve* = 0.85). In RDA2 (*cve* = 0.86) densities were differentiated by the stem density of trees (*v* = 0.74) and lianas (*v* = –0.23) and the TBA of lianas (*v* = –0.28). As with the partial PCA on vertebrate densities, lowland sandstone, lowland granite, upland granite, and montane partitions were very similar within forest type, and the remaining three forest types, i.e., alluvial bench, freshwater swamp, and peat swamp, clustered together (Fig. 4f).

Fig. 5 Temporal variation in frugivore population densities (D_{TIME}) at the Cabang Panti Research Station, ▶ Gunung Palung National Park, West Kalimantan. Model averaged population density (individuals/km^2) for each vertebrate frugivore between October 2007 and January 2013 with mean shown in solid lines and standard errors shown in dashed lines. Data are grouped into 4-mo periods; tick marks are labeled with the first month of each period. The *y*-axis labels for each plot depict zero, the mean density, and twice the mean density of the taxon across all habitat partitions. Taxon names are given on the right side of the figure, along with the CV for model averaged population density over time (CV_{TIME}, an index of movement in and out of the study site). Species are listed from top to bottom in descending order of CV_{TIME}.
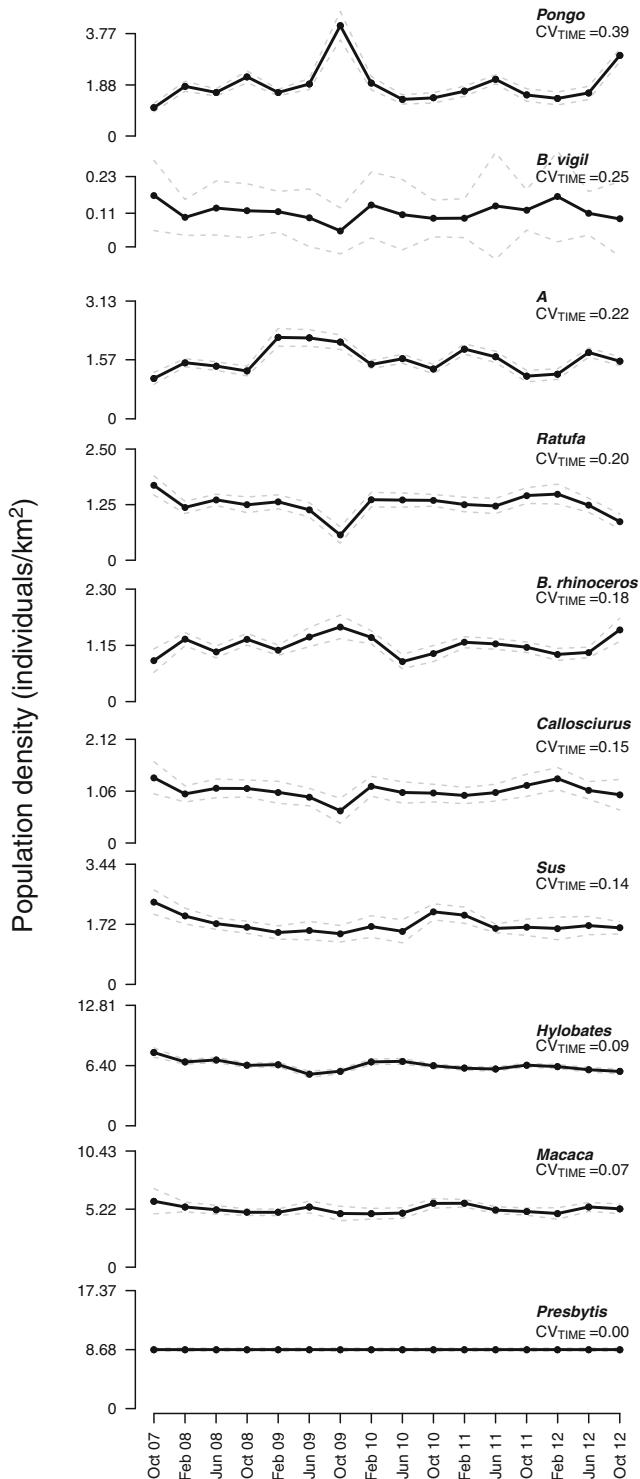
Frugivore Movements in and out of the Study Site

There was substantial variation among taxa in temporal fluctuations in density, with CV_{TIME} varying from 0.00 to 0.39. The species known to be territorial or to confine movements to quite restricted areas, e.g., *Hylobates*, *Macaca*, *Presbytis* (Marshall 2004; Rodman 1979) exhibited the lowest variation over time (CV_{TIME} < 0.10; Fig. 5). In contrast, the species known to range widely and over large distances, i.e., *Pongo* (Leighton and Leighton 1983) exhibited the highest variation over time (CV_{TIME} = 0.39). There was no relationship between body size and temporal fluctuations in density (linear regression of $\log(CV_{TIME}+1) \sim \log(\text{body size})$, $\beta = 0.007$, $R^2_{adj} = -0.10$, $N = 10$, $P = 0.69$); this result was consistent across comparisons for mammals and birds. Estimates of CV_{TIME} did not strongly correlate with the number of observations (linear regression of $\log(CV_{TIME}+1) \sim \log(N_{obs})$, $\beta = -0.06$, $R^2_{adj} = 0.16$, $N = 10$, $P = 0.13$).

   Among the 10 taxa examined, there was no relationship between habitat specialization and movement in and out of the study site (linear regression of $\log(CV_{TIME}) \sim \log(CV_{SPACE})$, $\beta = -0.10$, $R^2_{adj} = 0.05$, $N = 10$, $P = 0.27$). Overall density estimates for each species calculated by taking the mean of partition specific density estimates (D_{SPACE}) and the mean of period-specific density estimates (D_{TIME}) were essentially identical (linear regression of $\log(D_{TIME}+1) \sim \log(D_{SPACE})$, $\beta = 1.10$, $R^2_{adj} = 0.99$, $N = 10$, $P < 0.0001$), indicating that our density estimates were robust.

Discussion

Our analyses show that there was little evidence of habitat specialization or partitioning by 10 vertebrate frugivores inhabiting 12 habitat partitions over a period of >5 yr; the densities of frugivores varied greatly across the partitions, with variation largely due to elevation and forest structure; habitat partitions varied substantially in their forest structure, floristic composition, plant reproductive phenology, and vertebrate densities; and there were pronounced temporal fluctuations in the density of *Pongo*.

Frugivore Habitat Specialization and Spatial Partitioning

All but one of the study taxa inhabited all 12 habitat partitions (Fig. 3), indicating that these species in our study area did not exhibit strong habitat specialization, did not partition habitats spatially, and did not avoid interspecific competition by occupying distinct habitats. *Macaca* showed the greatest habitat specialization, largely confining their ranging to the alluvial bench habitat partitions, although they also used freshwater swamp, and to a lesser extent lowland sandstone and peat swamp partitions (Fig. 3). This comparative habitat specialization is clearly evident in Fig. 4e,f, showing *Macaca* clustered most closely with these partitions (*cf.* Peres 1997), replicating results from a study conducted in East Kalimantan (Rodman 1979, 1991).

   We chose to include only a subsample of the frugivores present at Cabang Panti, limiting our analysis to species with high dietary overlap. The 10 species included were also among the most well sampled. Although none of the 10 frugivores we examined exhibited strong habitat specialization, there may be other frugivorous vertebrate

species that are habitat specialists at Cabang Panti. Extreme habitat specialists would, by definition, be confined to a single forest type, meaning that they would be more rarely observed in our vertebrate censuses, and therefore not well sampled. In addition, their dietary overlap would be difficult to assess accurately owing to small sample sizes and therefore they would have been excluded from consideration of high dietary overlap (Marshall *et al.* 2009a). Broad-scale comparisons, however, suggest that elevational specialists are relatively rare in tropical Asia, and that mammals and birds, the taxa we examined here, are less likely to be upper elevation specialists than other taxa, perhaps because endotherms have wider tolerances than ectotherms (Laurance *et al.* 2011).

Modeling Density Variation Among Habitat Partitions

Densities of most species declined dramatically at higher elevations (Table III; Fig. 3), mirroring patterns found at other sites in Southeast Asia (Caldecott 1980; O'Brien *et al.* 2004). It seems reasonable to expect that these effects are at least in part due to declines in food abundance at higher elevations (Marshall 2004, 2009), although elevation-related changes in forest structure are likely also important for some taxa (Caldecott 1980; Kappeler 1984). Indeed, forest structure covariates, such as stem density and TBA of certain growth forms, were frequently important predictors of density (Table III). It is not surprising that the effects of forest structure on frugivore densities differed among species, given variation in locomotor adaptations (flight, terrestrial quadrupedalism, arboreal quadrupedalism, suspensory locomotion). For example, different structural components were important for *Hylobates* and *Macaca*, species exhibiting distinct locomotor behaviors. *Hylobates* populations were best predicted by the TBA of plants, particularly trees, reflecting their preference for travel in large trees (Cannon and Leighton 1994). These results are consistent with those found on the same species in central Kalimantan (Cheyne *et al.* 2013; Hamard *et al.* 2010). Density of *Macaca*, in contrast, was not related to tree TBA; instead, it was negatively related to the stem density of trees, although this pattern, while highly significant, was not especially strong in the best model. This is perhaps a reflection of the relatively nonselective use of trees based on size by *Macaca* (Cannon and Leighton 1994). Mean measures of temperature, rainfall, and phenology among habitat partitions were not important for explaining variation in frugivore densities between habitat partitions. This is also unsurprising because the effects of climate and food variability were obscured when their values are averaged over time.

Plant Ordinations: Spatial and Temporal Variation in Frugivore Resource Availability

Ordination analyses demonstrated that habitat partitions differed in their forest structure, floristic composition, and plant reproductive phenology. Primary structural differences among habitat partitions were the TBA of trees and lianas. Floristic comparisons clearly separated peat swamp and freshwater swamp forests from each other and other partitions (Fig. 4b), reflecting the floristic distinctness of these forest types, particularly the peat forest (Cannon and Leighton 2004). It is important to note, however, that these ordinations were based on genera, not species. Given the high degree of habitat associations among tree species at Cabang Panti (Cannon and Leighton 2004), ordinations based on species would have likely further separated other forest types.

Phenological ordination clustered habitats primarily on the basis of temporal variation in phenology, rather than mean values of productivity. This is interesting, because the degree of variation in productivity over time can have important effects in determining animal abundance, e.g., *Pongo* (Marshall *et al.* 2009b).

The ordination diagrams indicate that the ecological patterns we report are not largely driven by spatial proximity of habitat partitions. For example, in most ordinations habitat partitions are more similar to the other habitat partition in the same forest type than they are to spatially closer partitions in other forest types. The ordination diagrams also demonstrate that habitat partitions were quite distinct even after removing the effects of elevation, a major axis of variation in this forest. These comparisons highlight the ecological distinctness of the seven forest types at Cabang Panti, and validate comparisons of vertebrate community structure and the group size, population density, and demographic structure of frugivores among them (Marshall 2010).

Animal Ordinations: Spatial Variation in Frugivore Communities

The partial PCA of frugivore population densities demonstrated high concordance among partitions within forest types and clear differences among forest types (with the exception of alluvial bench, freshwater swamp, and peat swamp partitions, which clustered together; Fig. 4e). Indeed, frugivore communities separated most forest types more cleanly than did the plant ordinations (compare Fig. 4e with Figs. 4a, b, and c). As there was little evidence of habitat specialization at our site, these differences are due to differences in species abundances among partitions, rather than distinct species compositions. The partial RDA showed that frugivore communities were primarily differentiated based on the TBA of trees and figs (axis 1, Fig. 4f) and the stem density of trees and lianas and the TBA of lianas (axis 2, Fig. 4f). Groupings of habitat partitions in the partial RDA were consistent with those from the partial PCA (Fig. 4e, f), although the clustering resulting from the partial PCA more closely mapped onto the spatial proximity of habitat partitions. These results are broadly consistent with those reported from Western Amazonia, where vertebrate communities were more similar among sites within a forest type than between sites in distinct forest types (Haugaasen and Peres 2007), perhaps due in part to differences in habitat structure (Haugaasen and Peres 2005).

Frugivore Movements in and out of the Study Site

We detected substantial temporal changes in the population densities of *Pongo* and very little variation in *Macaca*, *Hylobates*, and *Presbytis*. Temporal changes reflect movements of individuals in and out of the study site, and detection of such patterns was not unexpected for *Pongo*, which are known to travel widely in response to spatiotemporal variation in fruit abundance (Buij *et al.* 2002; Leighton and Leighton 1983). In contrast, *Macaca*, *Hylobates*, and *Presbytis* live in stable social groups and limit their ranging to relatively small, exclusive areas. These species therefore appear unable to move in and out of the study site, and must instead respond to periods of fruit scarcity by eating fallback foods (Marshall and Wrangham 2007; Marshall *et al.* 2009c). These results suggest a link between social system and the response to food scarcity

(Hemingway and Bynum 2005) that is mediated by social constraints on movement. An alternative explanation that could be postulated is that differences in dietary adaptations influence movement. This would imply that orangutans move over greater areas than the other primate taxa at Cabang Panti because they are more committed to frugivory than the taxa that do not travel widely. This explanation seems unlikely, as orangutans are highly adapted to processing nonfruit, nonfig fallback foods (Harrison and Marshall 2011) and at Cabang Panti gibbons appear to maintain more frugivorous diets during periods of fruit scarcity than orangutans (Knott 1998; Marshall 2004), likely due to their more efficient locomotor adaptations and greater day ranges (Marshall *et al.* 2009a).

Conservation Implications

Our results have a number of implications for conservation. First, monitoring a diverse guild of frugivores across a complex environmental gradient highlights the importance of lowland forests for the maintenance of all taxa sampled. Patterns of density variation and demographic structure at Cabang Panti have shown that montane forests are demographic sinks for *Hylobates* (Marshall 2009) and perhaps also *Presbytis* (Marshall 2010); given our results, it is conceivable that this pattern holds more broadly. Whether or not high elevation forests are true demographic sinks, they clearly support very low population densities of the frugivores we examined, and therefore will contribute relatively little to their conservation. This is a concern, because higher quality lowland forests are being disproportionately lost at Gunung Palung and across much of Kalimantan (Curran *et al.* 2004; Dennis and Colfer 2006; Fuller *et al.* 2004). Second, although a subset of the lowland habitat partitions (primarily alluvial bench and lowland sandstone), appear to have the highest mean densities for virtually every taxon, this should not diminish the importance of protecting the full diversity of forest types, as they are highly distinct ecologically and some, such as the peat swamp, may serve as keystone habitats during certain periods (Cannon *et al.* 2007b; Haugaasen and Peres 2005). Finally, our study demonstrates the importance of forest structure in determining the composition and relative abundance of species in frugivore communities. This suggests that the structural changes occurring as a result of logging may have effects on frugivore community structure beyond the effects on food availability associated with the removal of fruit trees, lianas, and figs.

G. Bell, A. D. Busran, E. Tang, Hanjoyo, J. R. Harting, S. M. Jaffe, S. R. Lemoine, Mian, Rhande, J. R. Sweeney, and Surya. Statement of contributions: L. Beaudrot and A. J. Marshall conceived of project ideas, designed the study, and analyzed the data; A. J. Marshall was responsible for, and H. U. Wittmer contributed to, data collection; L. Beaudrot wrote the R code for the majority of the data analysis; A. J. Marshall produced the figures and tables; A. J. Marshall and L. Beaudrot wrote the manuscript; and H. U. Wittmer edited the manuscript.

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