

Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change

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ABSTRACT

We demonstrate that within-year climatic variability, particularly rainfall seasonality, is the most significant variable explaining spatial patterns of bird abundance in Australian tropical rainforest. The likely mechanism causing this pattern is a resource bottleneck (insects, nectar, and fruit) during the dry season that limits the population size of many species. The patterns support both the diversity–climatic–stability hypothesis and the species–energy hypothesis but clearly show that seasonality in energy availability may be a more significant factor than annual totals or means. An index of dry season severity is proposed that quantifies the combined effect of the degree of dryness and the duration of the dry season. We suggest that the predicted increases in seasonality due to global climate change could produce significant declines in bird abundance, further exacerbating the impacts of decreased range size, increased fragmentation, and decreased population size likely to occur as a result of increasing temperature. We suggest that increasing climatic seasonality due to global climate change has the potential to have significant negative impacts on tropical biodiversity.

Keywords

Abundance, birds, climate change, macroecology, rainforest, seasonality.

INTRODUCTION

Tropical forests generally experience relatively little or no seasonal changes in temperature and photoperiod compared to temperate habitats. However, seasonal fluctuations in rainfall are common and most tropical forests experience alternating wetter and drier seasons to a varying degree (Kato *et al.*, 2000). In addition to seasonal rainfall fluctuations, much of the humid tropics are periodically affected by drought conditions associated with the El Niño Southern Oscillation (ENSO) (Ropelewski & Hapert, 1987). Anthropogenic climate change is predicted to result in not only increases in temperature but also increased rainfall seasonality. This would result in an increase in the average length and/or severity of the dry season and the incidence of ENSO-related droughts in many tropical areas, including north-eastern Australia (Walsh & Ryan, 2000; Hughes, 2003).

It is now widely accepted that anthropogenic climate change has had widespread impacts on many biological patterns and processes in all ecosystems and that these impacts will increase with continued acceleration in global climate change (Walther, 2002; Hughes, 2003; Parmesan & Yohe, 2003; Root *et al.*, 2003). Previous studies have demonstrated the potential for increasing temperatures to have severe impacts on global biodiversity (e.g. Thomas *et al.*, 2004; papers in Lovejoy & Hannah, 2005) and

more specifically on the distribution and abundance patterns of tropical rainforest birds in Australia (Williams *et al.*, 2003; Shoo *et al.*, 2005a). These studies suggest that many species will experience significant range reductions, increased population fragmentation, and declines in population size; all leading to an increased risk of extinction (Williams *et al.*, 2003; Thomas *et al.*, 2004; Shoo *et al.*, 2005a; Walther *et al.*, 2005). Although there has been considerable research into predicting the impacts on biodiversity of increasing temperature due to global climate change, there has been little consideration of the potential impacts of altered within-year levels of variability of rainfall or temperature, that is, changing seasonality. Changing patterns of rainfall and temperature could have significant impacts on the continuity or temporal reliability of resources and levels of productivity.

There have been numerous ecological studies relating various aspects of macroecology (biodiversity, abundance, biomass, etc.) to primary productivity with most effort concentrating on the diversity/productivity/stability relationships (e.g. Loreau *et al.*, 2001; Evans *et al.*, 2005). Net primary productivity (NPP) is notoriously difficult to measure; therefore, surrogates are commonly used in analyses (Sanders *et al.*, 2003). Annual rainfall and temperature are the most commonly used surrogates and most indices of NPP use these variables (see reviews in Cramer *et al.*, 1999; Schloss *et al.*, 1999). Previous studies, both empirical and

modeling, have demonstrated that measures of annual rainfall and temperature provide a reasonable surrogate of primary productivity (e.g. Schloss *et al.*, 1999). Basically the hypothesis is that primary productivity is related to the solar energy input (indexed by mean temperature) and rainfall. Species-energy theory predicts that sites with greater available energy are able to support more individuals and therefore more species (Wright *et al.*, 1993). Numerous studies show that the local population size of birds is positively correlated with food availability or other measures of energy availability (Poulin *et al.*, 1993; Monkkonen *et al.*, 2006). These results support the argument that greater levels of environmental energy allow a larger resource pool that can sustain more individuals, permitting more species to maintain viable population sizes and, therefore, greater species richness (Pautasso & Gaston, 2005). However, using annual measures of energy availability such as NPP (or climatic surrogates of NPP) may hide important relationships in species where seasonal fluctuations in resources are significant (Hurlbert & Haskell, 2003). Generally, in the tropics, temperature is not limiting and it is rainfall patterns that have the greatest influence on variation in productivity: seasonal variability in rainfall is a key factor in determining the overall primary productivity and its temporal variability (Schloss *et al.*, 1999).

Climatic stability has been widely suggested to have a positive influence on species diversity over a range of temporal scales (Pianka, 1966; Fjeldsa & Lovett, 1997; Graham *et al.*, 2006). Previous research in the Australian tropical rainforest has suggested that within-year climatic seasonality is an important determinant of the spatial pattern of species richness of frogs (Williams & Hero, 2001). Rainfall seasonality in particular was an important environmental correlate of the patterns of distribution and species richness of microhylid frogs that rely on a consistently moist leaf litter (Williams & Hero, 1998; Williams & Hero, 2001). Furthermore, a number of studies have demonstrated close relationships between insect abundance and rainfall patterns in tropical rainforest, e.g. (Frith & Frith, 1985). Increases in the seasonality of both temperature and rainfall can cause significant disruption to the phenology of tropical forest trees (Corlett & Lafrankie, 1998), and thus, to the temporal availability of food resources for birds, such as insects, nectar, and fruit. The availability of fruit, flowers, seeds, and new flush leaves fluctuates seasonally in almost all tropical forests (Shaik van *et al.*, 1993). Seasonal fluctuation in rainfall and associated soil moisture cycles are thought to be a major factor influencing the phenology of fruiting, flowering, and new leaf production in tropical forests (Shaik van *et al.*, 1993; Corlett & Lafrankie, 1998). In aseasonal habitats it has been demonstrated that insect abundances remain relatively stable throughout the year (Janzen, 1973; Buskirk & Buskirk, 1976). However, insect populations in tropical forests typically exhibit seasonal variation in abundance, which has been correlated with rainfall and with availability of food resources, such as new leaves and fruit (Fogden, 1972; Levings & Windsor, 1982). In areas with pronounced wet and dry seasons, insect abundance typically peaks during the wet season and is lowest during the dry season (Fogden, 1972; Levings & Windsor, 1982; Frith & Frith, 1985). Therefore, dry seasons are potentially times of scarce resources

potentially resulting in ecological bottlenecks that limit species abundances and biotic interactions and processes.

Wiens (1977) hypothesized that 'ecological crunches' or 'bottlenecks' in resources may be important in structuring bird communities in variable environments. Spatial and temporal variations in abundance characterize most tropical avian communities that have been studied in detail (e.g. Poulin *et al.*, 1993). Changes in abundances can result from demographic processes, such as reproduction and mortality (Faaborg *et al.*, 1984), or from individual movements both within and between habitats (Loiselle & Blake, 1991). The availability of food resources in tropical forests has been positively correlated with bird abundance for various feeding guilds, including insectivores, frugivores, and nectivores (Loiselle, 1988; Karr & Brawn, 1990). Most studies have found that bird species in tropical forests have distinct breeding seasons, which often correlate with periods of high food availability, such as the beginning of the wet season (Fogden, 1972; Poulin *et al.*, 1992).

Here, we use standardized surveys of rainforest birds in the Australian Wet Tropics World Heritage Area across a gradient of climatic seasonality to examine the relationship between bird abundance and climate. We show that although the species composition and richness do not significantly vary across this gradient, there are significant differences in total abundance. Our analyses suggest that rainfall seasonality is the most significant variable explaining differences in bird abundance and suggest the hypothesis that the mechanism causing this pattern is a resource bottleneck during the dry season that limits the population size of many species of rainforest birds.

METHODS

Study area description

The Australia Wet Tropics bioregion consists of a narrow strip of coastal plains and a series of disjunct mountain ranges, ranging from sea level to *c.* 1600 m, running parallel to the North Queensland coast between 19°30' S and 15°30' S (Fig. 1). The rainfall in the region is distinctly spatially and seasonally variable, ranging from between 1500 m and 4000 m annually with approximately 75–90% falling between November and April (McDonald & Lane, 2000). The dominant vegetation type is tropical rainforest, which covers an area of *c.* 10,000 km² (McDonald & Lane, 2000).

Site selection

A total of 21 sites were selected as part of an ongoing systematic study of the macroecology of the Wet Tropics rainforest vertebrates. A major change in bird species assemblage structure is known to occur below 600 m (Williams, 2006), therefore all sites were located between 600 and 1000 m a.s.l. to minimize the confounding effects of altitude. All sites were located within upland rainforest of similar vegetation structure (notophyll vine forest – Tracey, 1982) across four biogeographical subregions (Spec, Kirrima, Atherton, and Carbine uplands; Fig. 1).

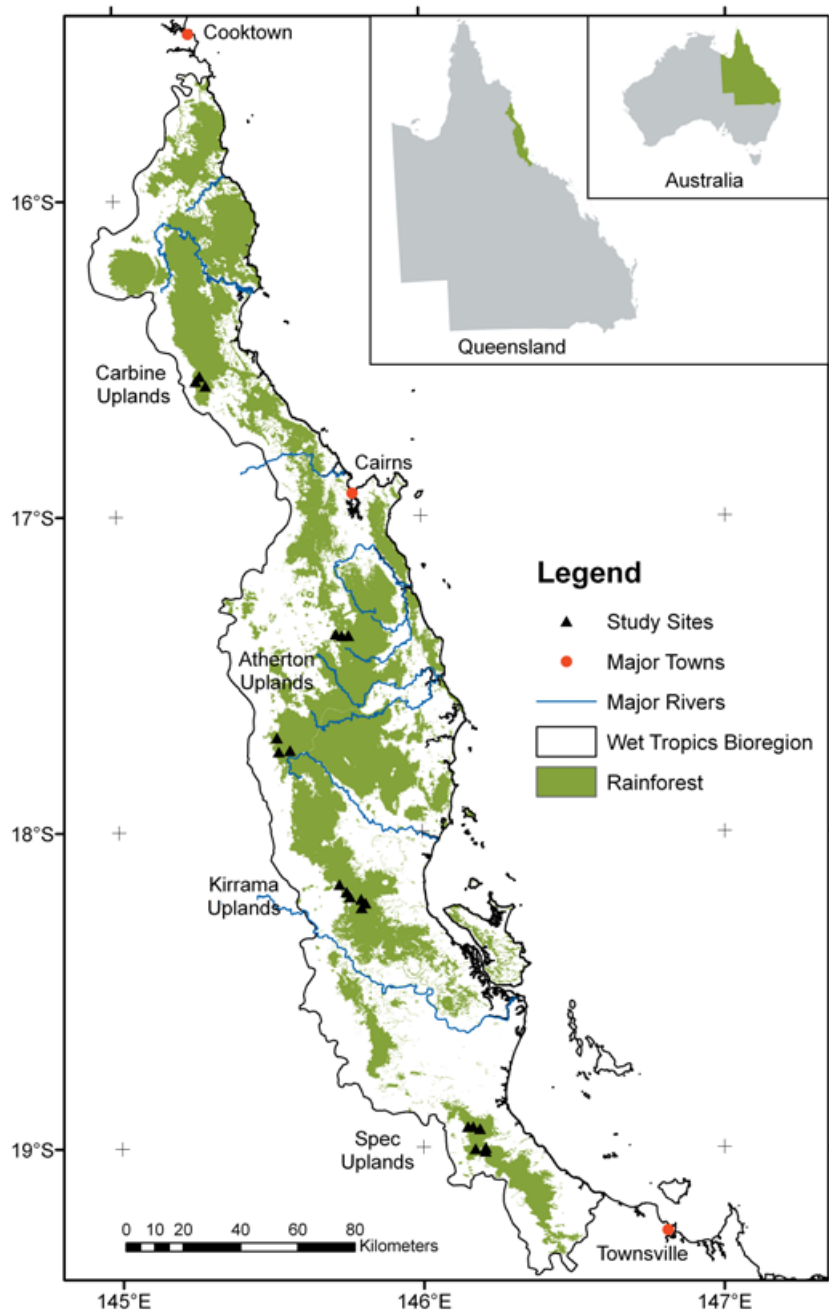


Figure 1 Map of Wet Tropics biogeographical region showing the current extent of closed forest and the location of the study sites.

Survey methodology

Relative abundance and species richness for the rainforest bird fauna were derived from standardized bird surveys. At each site, surveys were conducted at six points spaced at least 200 m apart to maximize independence. Surveys were undertaken by two persons (one observer and one data recorder) walking for 30 min along a 150-m transect through the rainforest perpendicular to the track, using both visual observations and bird calls to identify species. As much care as possible was taken to avoid double-counting of calling individuals. Observers were randomly rotated with all observers surveying all sites, therefore removing any systematic observer bias in the abundance counts across the

gradient. Surveys were conducted between the years 2000–02 during the late dry and wet seasons (September to April), that is the time of year when the majority of the Wet Tropics rainforest-bird species (including migratory species) are known to breed, thus maximizing the likelihood that surveys were conducted during periods of peak activity and calling. Counts were repeated between three and six times at each point over the period of the study, giving a total of 359 counts. A total of 101 species were recorded from the standardized surveys. Surveys were only conducted if environmental conditions on the day were suitable to ensure that daily conditions did not bias the results, for example, no surveys were conducted in rain or strong winds.

For each survey location, the following climatic variables: mean annual temperature, intra-annual temperature seasonality [coefficient of variation (CV) of mean monthly temperature], mean annual precipitation, and intra-annual precipitation seasonality (coefficient of variation of mean monthly precipitation), mean monthly rainfall, and mean number of rain days per month were extracted from GIS climate surfaces provided by the Wet Tropics Management Agency. The climate surfaces were based on a GIS digital elevation model with an 80-m pixel resolution and were derived using ANUCLIM/ESOCCLIM software (Houlder *et al.*, 2000) from long-term meteorological data sets, including 78 years of monthly rainfall means estimated from serially incomplete rainfall records from 265 rainfall stations.

Data analysis

Local species richness was estimated using rarefaction methods (Colwell, 2005). The data set was sufficiently large that the estimates of total local species richness were almost identical using any estimator, so we have presented Chao's estimates as an example. Multiple linear regression was used to examine the relationship between the total bird assemblage abundance and the following climatic variables: mean annual temperature, mean annual rainfall, and the coefficient of variation of mean monthly rainfall and temperature. We calculated an index of dry season severity that combines the degree of dryness and the duration of the dry season. The degree of dryness was estimated as the frequency of rain days each month and dry season duration by the number of months where this frequency was below the 25th percentile of the mean number of rain days per month across all sites and months. The dry season severity index was the cumulative sum of days per month below the 25th percentile of the annual mean number of rain days per month. We used one-way analysis of variance to test for significant differences in dry season severity across the subregions.

RESULTS

Climate

Mean annual rainfall varied between ~1500 mm and 3300 mm across the sites, although most of the sites were around 2000 mm (Fig. 2a). Annual mean temperature varied between ~19 °C and 21 °C (Fig. 2a). Variation in the annual means was generally as great within each subregion as across subregions. Basically, there is no consistent difference in the mean annual rainfall or temperature across the sites in different subregions. Differences in annual mean temperature are primarily the result of variation in elevation which varied between ~ 600 and 900 m a.s.l. In contrast, the level of within-year seasonality in both rainfall and temperature was different in each subregion, resulting in a clear pattern of subregional clustering of the sites in the seasonality plot (Fig. 2b). The Spec Uplands have the highest seasonality in both temperature and rainfall, the Atherton Uplands were the least seasonal, the Kirrima Uplands were intermediate, and the Carbine Uplands had relatively low temperature seasonality but relatively high rainfall seasonality (Fig. 2b).

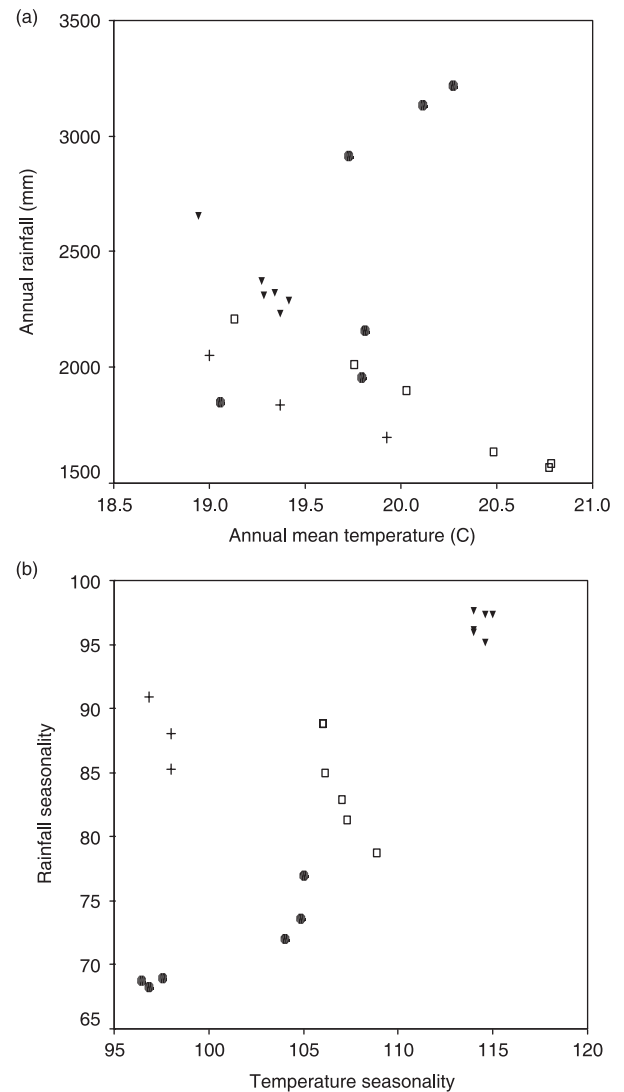


Figure 2 (a) Annual mean rainfall and temperature for each of the sites used in the analysis. (b) Rainfall and temperature seasonality of each of the sites used in the analysis (Atherton Uplands — ●; Spec Uplands — ▲; Kirrima Uplands — □; Carbine Uplands — +).

Species richness and composition

There was no significant difference in species richness or the species composition of rainforest birds across the study sites. Over the space of the study, all species were recorded in all of the subregions sampled in this study except for the Atherton scrubwren which is not known to be present in the Spec Uplands. There are 82 species of rainforest bird in the region for which the sampling technique was suitable (Table 1). We conducted sufficient sampling in all subregions to ensure that all 82 species were observed in the Carbine, Atherton, and Kirrima Uplands and 81 species in the Spec Uplands. The mean species richness observed at a site (local species richness) was not significantly different across the subregions in either observed species richness or when using rarefaction techniques to estimate the total species richness at each site (Table 1). Local species richness is estimated to be

Table 1 Summary of species richness in each subregion and estimates of mean local species richness at each site. Mean local species richness is the mean species richness at that site across six locations each sampled three times, that is, a mean of 18 surveys with 95% confidence intervals rounded to nearest species.

	Spec Uplands	Carbine Uplands	Kirrima Uplands	Atherton Uplands
Total observed subregional species richness	81	82	82	82
Mean local species richness				
Observed	48 ± 6	46 ± 6	56 ± 7	48 ± 5
Chao estimate	72 ± 2	71 ± 1	71 ± 1	71 ± 1
Total number of surveys	116	36	118	116
Number of points surveyed	36	18	36	36
Number of sites	6	3	6	6

Table 2 Multiple regression (backward removal) results with total bird abundance at each site ($n = 21$) as the dependent variable and four climate variables (productivity surrogates) as the independent variables (mean annual rainfall, mean annual temperature, rainfall seasonality, and temperature seasonality). Analysis shows that both mean annual temperature and rainfall seasonality were significant, although seasonality explained more of the variance than mean annual temperature. Final model includes mean annual temperature and rainfall seasonality ($F = 20.473$; $P = 0.000$; d.f. = 20, 2; total model $r^2 = 0.695$; adjusted $r^2 = 0.661$); mean annual rainfall and temperature seasonality did not contribute and were removed by the analysis.

Variable	Unstd coeff. (B)	Std error	Std coeff. beta	<i>T</i>	<i>P</i>	Partial <i>r</i>	Partial r^2
(constant)	-32.384	37.001		-0.875	0.393		
Mean annual temperature	0.564	0.172	0.444	3.271	0.004	0.611	0.373
Rainfall seasonality	-0.407	0.093	-0.591	-4.357	0.000	-0.716	0.513

71 species (Table 1). Since observed species richness is so strongly dependent on the number of individuals recorded, we used 'EstimateS' (Colwell, 2005) to estimate the total species richness at each local site (Table 1). Using EstimateS to estimate Chao estimates or MMM estimates of total species richness at each site gave almost identical estimates of mean local species richness $\sim 71 \pm 2$ species.

Abundance

Although species richness and composition did not vary across the sites, there was a significant difference in the abundance of birds observed in each subregion, with the Spec Uplands having significantly lower abundance than either Kirrima or Atherton and Carbine being somewhat intermediate and variable (Carbine Uplands had fewer samples, therefore, greater variability) (Fig. 3). Abundance data were tested for spatial autocorrelation and there was no consistent pattern of correlation that affected the observed patterns, therefore, all analyses were subsequently conducted on the raw abundance data.

Regression analysis of abundance and climate variables

Rainfall seasonality and mean annual temperature explained $\sim 70\%$ of the variation in bird abundance across the study sites (Table 2). Multiple regression analysis was used to determine the relative contribution and significance of the climate variables (NPP surrogates) in explaining abundance patterns. The strongest relationship was the negative relationship between rainfall seasonality and bird abundance (Table 2), that is, sites with the highest degree

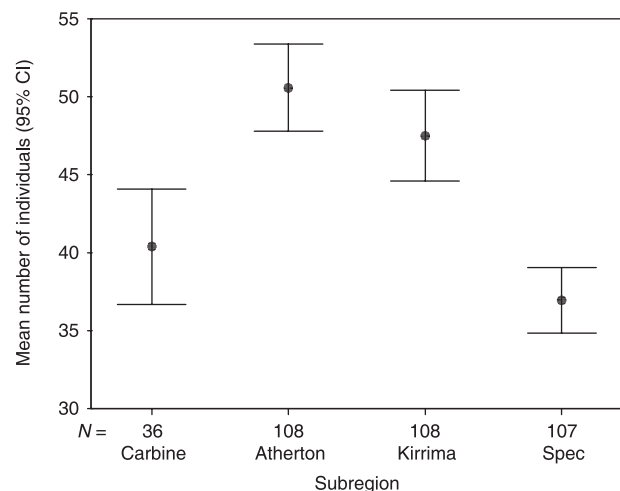


Figure 3 Mean local density of birds in each upland subregion showing significantly lower bird density in the Spec and Carbine Uplands compared to the Atherton and Kirrima Uplands. Mean is based on all standardized surveys in that subregion with the number of surveys (n) shown on the axis.

of rainfall seasonality had the lowest abundance of birds (Fig. 4b). Abundance increased with mean annual temperature (Fig. 4a) but was a weaker relationship than rainfall seasonality (Table 2).

Quantification of dry season severity

Dry season severity (indexed by the cumulative number of days across months where the number of rain days was below the 25th

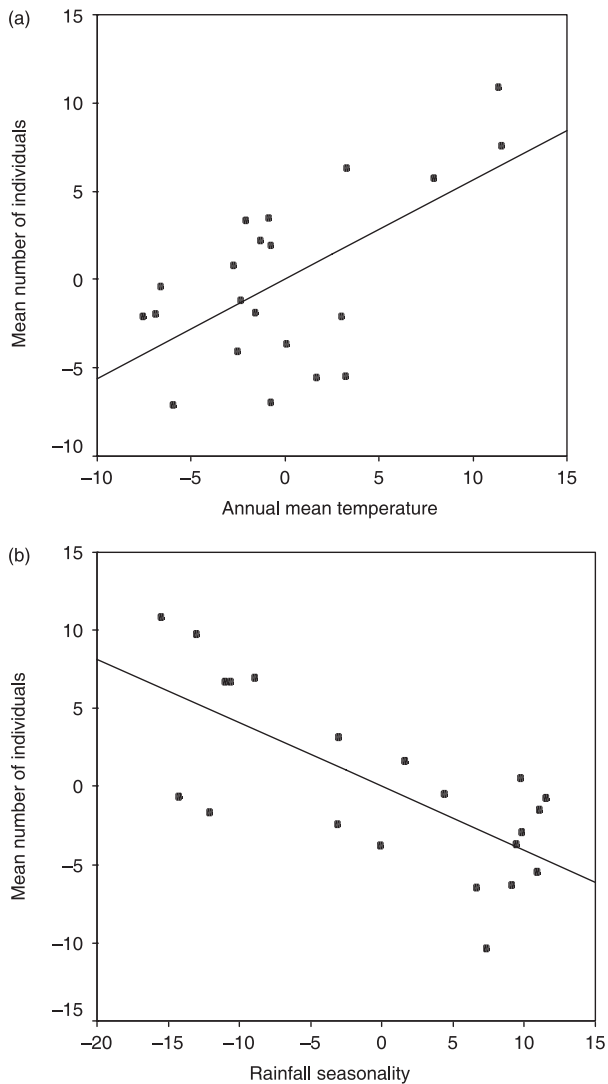


Figure 4 Partial regression plots of bird abundance and (a) annual mean temperature ($r^2 = 0.37$) and (b) rainfall seasonality ($r^2 = 0.51$) based on the multiple regression analysis presented in Table 2.

percentile of all locations and months, see Fig. 5) was significantly greater in the Spec (9.1) and Carbine Uplands (9.9) compared to the Atherton (0.9) and Kirrima Uplands (1.3) (Fig. 5, one-way analysis of variance, between groups d.f. = 3, $F = 345.3$, $P < 0.001$). Dry season severity was not significantly different between Spec and Carbine or between Atherton and Kirrima (Tukey HSD post-hoc test for homogenous subsets).

DISCUSSION

We suggest that within-year climatic variability, particularly rainfall seasonality, is the most significant variable explaining differences in bird abundance in upland tropical rainforest in Australia. Our hypothesis is that in areas with higher levels of temporal variability in rainfall, there is a greater probability of more frequent and/or more severe bottlenecks in productivity of resources (particularly insects and fruit). The seasonal bottlenecks

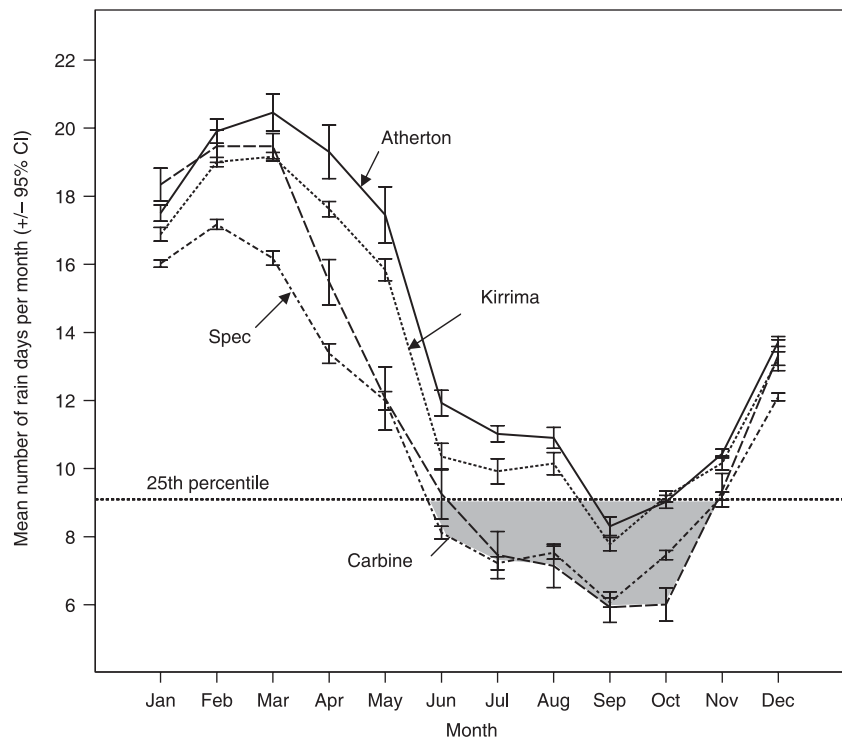
in available resources limit the population density of birds with less seasonal areas supporting more individuals. The patterns support the species–energy hypothesis and suggest that temporal bottlenecks in productivity can be a more significant factor in the tropics than annual totals or means. Our findings also provide support for the ‘more-individuals’ mechanism of species–energy theory, that is, that more energy input to the system results in more individuals and generally higher species richness (Srivastava & Lawton, 1998). However, our results suggest that in the rainforests of the Australian Wet Tropics, seasonal variation in available resources and energy has a stronger influence than the annual mean available energy (i.e. indexed by mean annual temperature) on bird density.

Our results also provide support for the climatic–stability–diversity hypothesis (Pianka, 1966) where more climatically stable areas are more diverse. In this study at the within-year temporal scale, the effect is only represented by more individuals rather than more species; it might be expected that over longer time-scales, this would also be expressed in greater species richness in the more stable areas. Seasonal estimates of environmental energy availability have previously been shown to influence bird species richness patterns (e.g. Githaiga-Mwici *et al.*, 2002; Hurlbert & Haskell, 2003). The differences in abundance between the lowest rainfall seasonality subregion, the Atherton and, and the highest rainfall seasonality subregion, the Spec Uplands, were significant but apparently not sufficient to translate into more species. Unlike our findings, other studies have found that a positive relationship between available energy and assemblage abundance is also associated with an increase in species richness (Pautasso & Gaston, 2005; Monkkonen *et al.*, 2006) but were conducted at continental scales and covered a wide gradient in total available environmental energy.

Several studies have examined climatic effects on bird species richness at continental scales (Pautasso & Gaston, 2005; Bini *et al.*, 2004), but few have examined these relationships at regional scales in the tropics as we have done in this study (but see Cueto & de Casenave, 1999). Habitat heterogeneity has been shown to be an important determinant of bird species richness at regional scales in the tropics (Williams *et al.*, 1996; Cueto & de Casenave, 1999). The Wet Tropics bioregion provides a unique opportunity to examine the relationship between abundance, species richness, and environmental energy at regional scales without the confounding effects of different habitat types due to the presence of a gradient in rainfall seasonality across areas of upland rainforest with the same habitat and bird species present. This gradient represents a unique natural experiment to test relationships between the fauna and the climate, specifically the role of seasonality and resource bottlenecks as a limiting mechanism. The Wet Tropics is also unique among tropical rainforest ecosystems, in possessing finescale (80 m) climatic layers based on at least 30 years of accurate rainfall and temperature records across the entire region that allows many aspects of the role of climate on bird macroecology to be examined.

The likely mechanism driving the relationship between bird abundance and climatic seasonality is a resource bottleneck (insects, nectar, and fruit) during the dry season that limits the

Figure 5 Mean number of rain days per month across the year for the sites within each subregion. Dotted threshold line represents the minimum 25th percentile of all data to illustrate the longer and more severe period of dryness in the Spec and Carbine uplands compared to the Atherton and Kirrima Uplands. Essentially, the shaded area between the line for each subregion and the 25th percentile is an index of both dry season severity and duration. Error bars are 95% confidence intervals to easily visualize significant differences.



breeding success and hence population size of many species. Long-term studies of birds in the region have shown that insect abundance was correlated with monthly rainfall, with the lowest abundances being during the dry seasons (Frith & Frith, 1985). In 1979, there was an exceptionally harsh dry season resulting in many species of birds failing to breed that year (Frith & Frith, 2005). Our hypothesis is that the dry season severity, a combination of dry season length and relative dryness, will result in a period of low insect abundance resulting in a bottleneck of available resources especially for insectivorous birds. This bottleneck is the factor that limits bird abundance even if there is no shortage of food throughout the remainder of the year. The mechanism may well be that the severity of the dry season determines the breeding success of insectivorous birds, as noted by Frith & Frith (2005). We suggest that mean population size is determined by this bottleneck, rather than annual averages of resource productivity. That is, that insectivorous bird population size is limited by a minimum threshold of resource availability rather than maximums or annual means, as commonly used indices of environmental productivity. This hypothesis is currently being tested in ongoing field experiments targeting spatial and temporal patterns of insectivore and insect abundance.

Temporal stability of habitats and resources has had great significance within this regions fauna across a variety of spatial and temporal scales, taxa, and ecological processes. Paleo-climatic stability over the Quaternary has been suggested as the major determinant of current patterns of biodiversity and distribution in the vertebrate fauna (Winter, 1988; Williams & Pearson, 1997; Schneider & Williams, 2005; Graham *et al.*, 2006). Long-term stability has influenced the biogeography of the region via the interactions between stability, species-specific extinction proneness,

and dispersal/colonization dynamics (Schneider & Williams, 2005). Long-term stability mediated by species-specific extinction proneness and dispersal/colonization potential determines the subregional species pool (species richness and composition) (Williams, 1997; Graham *et al.*, 2006). Intra-annual patterns of seasonality based on long-term averages influence the species richness of some groups (Williams & Hero, 2001) and abundances (this paper). Increasing our understanding of the relationships between environmental stability and biodiversity is a crucial aspect of being able to improve our predictions of climate change impacts.

We predict that increases in seasonality due to global climate change could cause significant declines in bird density in the rainforests of the Australian Wet Tropics. This impact could interact with, and further exacerbate, the impacts of decreased range size, increased fragmentation, and decreased population size previously predicted to occur as a result of increasing temperature (Williams *et al.*, 2003; Shoo *et al.*, 2005a,b). Regional climate change predictions suggest that annual rainfall will not change markedly but that seasonality will increase (Walsh & Ryan, 2000). Our results clearly show that it is vital that we explore the impact of climatic seasonality on biodiversity in addition to more generally considered annual totals and averages. Although we have only demonstrated a relationship between seasonality and abundance of rainforest birds here, it seems likely that expanding the geographical and taxonomic scope of the analysis would also show significant impacts on species richness. Previous studies in this region have shown that areas with a highly seasonal rainfall pattern have lower species richness of microhylid frogs (Williams & Hero, 2001). It is also certain that the impacts of increasing seasonality will influence different

species to varying extents and that there will be time lags associated with changes in productivity that may be more beneficial to those species with fast response times.

Future research

Our results highlight that it is necessary to include measures of climatic variability and minimum thresholds, and not rely on means and totals, in any predictive models estimating future impacts of climate change. It is important to examine the relationships and interactions between seasonality, measurements of resource fluctuations, and different functional guilds to improve understanding of the mechanisms and likely impacts of increasing seasonality with climate change (e.g. species that are leaf litter foragers vs. canopy foragers vs. frugivores). We need empirical measurements of the temporal variability in resource levels, environmental variables, and the dependent fauna. It will be important to examine the temporal time lags between resource changes and the biotic response. These results also make it clear that we need more studies on the interactions between primary productivity, energy, abundance, species richness, and climate in order to make more robust predictions about the impacts of future global climate change.

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