Cooperation in non-family groups as a strategy for reproducing in variable climates

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Abstract

The global climate is changing to be more extreme and less predictable, threatening many species. Cooperative breeding is more common under such conditions, indicating it may improve resilience to challenging climates. However, whether specific features of cooperative breeding systems, such as how groups form and how large they become, evolved to cope with particular climates is unclear. We test two predictions using phylogenetic analyses across birds. First, cooperative groups formed by unrelated adults ('nonfamily') are an adaptation to variable environments. Nonfamily groups can form relatively quickly when conditions deteriorate, unlike family groups, which often require offspring retention over multiple generations. Second, species with larger groups are able to breed in more extreme environments. We found that as climates get hotter and precipitation becomes more variable, cooperative breeding with nonfamily is more frequent and groups become larger ($n_{species}$=39). Conversely, cooperative breeding in family groups is more frequent in stable, hot environments ($n_{species}$=128). Additionally, both nonfamily and family cooperative species had broader climatic niches than phylogenetically matched pair breeders ($n_{species}$=456). Our results highlight that cooperation with unrelated individuals may enable species to live in hot environments with variable rainfall that are expected to become more common in the future.

Introduction

Extreme and variable climates make it hard for organisms to survive and reproduce[1,2]. The speed of recent climate change is thought to be outpacing that of genetic adaptation for many species, such as long-lived vertebrates[3,4]. Cooperative breeding can quickly emerge when environments change, which has led to the idea that cooperation may be in helping animals to mitigate the effects of climate change[5,6]. However, cooperative groups vary in how they form, their genetic structure and how large they become, and we lack an understanding of whether this influences the resilience of species to different climatic conditions[7–12].

Cooperative breeding groups can form in different ways[13]. First, groups can form when nonfamily members aggregate after dispersing from their natal territories. These groups typically consist of unrelated individuals who all attempt to breed at some point during their life and mutually benefit from cooperative care[7,9,14–20]. Second, offspring can remain in their natal territory, foregoing independent reproduction, to help their parents raise their siblings, resulting in multi-generational family groups[21,22].

The different mechanisms by which groups form, and the influence this has on relatedness[12], is predicted to change the environments that species can cope with. Nonfamily groups have the potential to form relatively quickly and in environments where high mortality erodes genetic kin structure among potential group members[8,17,19,20,23–26]. Nonfamily cooperative breeders are therefore expected to be in variable climatic regions where independent breeding is difficult and options for cooperating with kin are limited. In contrast, the formation of family groups requires kin associations to be maintained, often over multiple generations, which requires low rates of dispersal and mortality that is more likely in stable environments. Family groups may also be able to colonise more extreme environments due to the benefits of high relatedness[12,27,28]. Helping relatives means that individuals do not have to reproduce to pass on their genes[10,29,30]. This reduces reproductive competition and allows individuals to devote more time to other activities, such as foraging, that may enable groups to successfully raise offspring in extreme climates where food is scarce.

The environments where species persist may also depend on group size[31,32]. Larger groups have the advantages of economies of scale and the division of labour that may be crucial for acquiring the resources to reproduce[33]. For example, having more foraging individuals and partitioning tasks such as predator vigilance and offspring care, may enable larger groups to cope with climatic challenges. Group size can differ between nonfamily and family groups[12,17]: In nonfamily groups, reproductive competition among unrelated individuals can limit group size, which is not the case in family groups with non-reproductive helpers. This can result in family groups being larger, enabling them to potentially inhabit more extreme environments. However, it is currently unclear if the way groups form and how large they become influences the climatic conditions that species are resilient to. This is primarily because the frequency of cooperation (e.g. % of cooperative breeding nests in populations) and the group sizes of species breeding in nonfamily and family groups have not be analysed in relation to climatic conditions or formally compared to pair breeding species[34–38].

Here we use data across birds to test if species that breed in nonfamily and family groups live in environments with different climatic conditions (Supplementary Table 1; Supplementary Table 2). The breeding systems of cooperative species were classified using data on the presence of cobreeders (pairs versus multiple breeders) and the relatedness of helpers, and global climate databases were used to characterise species climatic niches (see Methods section 'Classification of breeding systems'. Table 1). We first tested whether variation in the frequency of cooperative breeding (% nests with 3+ adults) and group size were related to climate, and if this differed between nonfamily and family groups. Second, we tested if the environments that nonfamily and family cooperative breeders inhabit differ from phylogenetically matched pair breeding species (five most closely related species: $n_{species}$=456). Data were analysed using multi-response Bayesian phylogenetic mixed models (MR-BPMM) that enable the coevolution (phylogenetic correlations) of cooperative breeding and climatic variables to be estimated.

Results

Nonfamily cooperation increases with climatic variation

Nonfamily cooperative breeders are broadly distributed across the globe, occurring in northern, southern and equatorial regions (Figure 1). The frequency of cooperative breeding in nonfamily groups increased significantly in environments with more variable precipitation across breeding seasons and higher average temperatures (Figure 2, Extended Data Fig. 3. Variation in precipitation between years (95% credible interval, CI) = 0.29 (0.13, 0.5), pMCMC = 0.001; temperature = 0.28 (0.1, 0.47), pMCMC = 0.001. Supplementary Table 3). Similarly, the group sizes of nonfamily cooperative breeders increased in hotter environments with more variable precipitation across breeding seasons (Figure 2, Extended Data Fig. 4. Variation in precipitation between years (CI) = 1.4 (0.18, 2.58), pMCMC = 0.044. Temperature (CI) = 1.12 (-0.09, 2.34), pMCMC = 0.058. Supplementary Table 4).

In contrast, family group cooperative breeding increased in hotter, more stable environments (Figure 2, Extended Data Fig. 3. Temperature (CI) 0.17 (0.04, 0.28), pMCMC = 0.008. Variation in temperature between years (CI) -0.14 (-0.27, -0.03), pMCMC = 0.024. Supplementary Table 3). This is reflected by the concentration of family cooperative breeders around equatorial regions (Figure 1). The size of family groups were also not related to any climate variables, as in nonfamily cooperative breeders (Figure 2, Extended Data Fig. 4. Supplementary Table 4).

Cooperative breeders occupy more arid environments than pair breeders

When comparing cooperative breeding species to phylogenetically matched pair breeders, we found that both nonfamily and family cooperative breeders inhabit drier environments than pair breeding species (Figure 3, Extended Data Fig. 2). Specifically, cooperative breeders are in significantly drier habitats than pair breeders (Figure 3. Pair vs Nonfamily: Precipitation (CI) = 0.49 (0.06, 0.82), pMCMC = 0.02. Pair vs Family: Precipitation (CI) = 0.28 (0.02, 0.58), pMCMC = 0.042. Supplementary Table 5). Cooperative species also experience consistently drier periods throughout their breeding seasons than pair breeders (Figure 3. Pair vs Nonfamily: Within-year variation in precipitation (CI) = 0.64 (0.24, 1), pMCMC = 0.001. Pair vs Family: Within-year variation in precipitation (CI) = 0.38 (0.1, 0.65), pMCMC = 0.014. Supplementary Table 5). These results were consistent across different classifications of cooperative breeding, for example, sub-setting family cooperative breeders according to the numbers of breeders (pair versus multiple), if helpers were a mix of family and nonfamily members, and which cutoff was used to assign species to breeding categories (>0% versus >30% of nests with cobreeders and helpers. Supplementary Table 6, Supplementary Table 7, Supplementary Table 8, Supplementary Table 9 and Supplementary Table 10).

Cooperative breeders have broader climate niches than pair breeders

To further examine the climates that nonfamily, family and pair breeding species are adapted to, we analysed differences in the correlations between climate variables across breeding systems. For example, it is possible that the benefits of cooperation in dry environments, such as sharing foraging duties, may be even greater in hot areas where being active for long periods is thermally stressful. Comparing differences in temperature and precipitation between breeding systems will not detect such effects. We therefore tested if the correlations between climatic variables differ across breeding systems using eigenvector analysis of phylogenetic variance-covariance matrices of climate variables for nonfamily, family and pair breeders. Here the eigenvectors describe the axes of variation across climate variables and the eigenvalues indicate the amount of variation in each direction. If the first eigenvector explains a greater proportion of variation in the eigenvalues for a given breeding system, such as pair breeders, this indicates that more variation is aligned along a single axis of climatic variation (see Statistical analyses for more details).

We found across pair breeders that the first eigenvector explained a greater proportion of the variation in eigenvalues compared to nonfamily and family cooperative breeders (Figure 4). This indicates that pair breeders are restricted to environments with specific climatic conditions, as indicated by stronger correlations between climate variables (Figure 4). In particular, pair breeders are not found in dry environments with consistently high temperatures (Figure 4). Conversely, nonfamily and family cooperative breeders occupy a broader range of climates than pair breeders, and are less constrained by the relationship between temperature and precipitation (Figure 4. Phylogenetic correlation between precipitation and temperature variation within-years (CI): pair = -0.56 (-0.71, -0.37), pMCMC = 0.001; nonfamily = -0.14 (-0.5, 0.41), pMCMC = 0.754; family = -0.18 (-0.56, 0.17), pMCMC = 0.248 Supplementary Table 11). This is consistent with cooperative breeders having broader climatic niches than pair breeders, irrespective of whether they form nonfamily or family groups (Figure 4).

Discussion

Our results show that cooperation with nonfamily is associated with hot climates with variable precipitation, conditions that also lead to larger group sizes. In contrast, cooperative breeding in family groups is associated with stable hot environments and group sizes are largely decoupled from climatic variation. Compared to pair breeders, both nonfamily and family cooperative breeders occupy a wider range of environments, in particular more arid environments. Together these results highlight the potential importance of social behaviour in determining the resilience of species to climatic challenges.

It has previously been shown that family and nonfamily cooperative breeding species evolved independently with important consequences for the reproductive division of labour[12,13,30,39,40]. Our results indicate that different mechanisms of group formation may also influence the ecological niches of species. Cooperative breeding in vertebrates has repeatedly been associated with high temperatures and variable rainfall, but previous analyses have either considered only family groups or combined family and nonfamily group species[24,27,41–45]. Our results partially align with this work, showing that high temperatures are consistently associated with cooperative breeding. However, our findings highlight that only nonfamily cooperative breeding is associated with increased variation in precipitation and that cooperative breeding with family actually shows the opposite pattern, being more prevalent in stable environments.

There are several possible reasons for why nonfamily cooperative breeding is associated with more variable precipitation across breeding seasons. First, fluctuating environmental conditions can erode population genetic structure, limiting opportunities for cooperating with kin[5,19,46,47]. Kin structure can be reduced by higher dispersal and mortality, which are known to increase in cooperative breeders in high and low rainfall years[20,48–50]. The interaction between temperature and rainfall can also influence patterns of adult and juvenile mortality directly, for instance through cold and heat stress[3,26,47], and indirectly by affecting prey species abundances[51,52]. Second, in variable environments the benefits and costs of cooperation can vary over space and time[53,54]. As nonfamily groups can potentially form relatively quickly, it is possible that individuals adjust their cooperative behaviour in response to environmental change more easily than individuals in family groups, which can take longer to form. For example, in Taiwan yuhinas, *Yuhina brunneiceps*, females increase their cooperative behaviour towards unrelated cobreeders in years when rainfall makes independent breeding harder[48]. Nonfamily cooperative breeding systems may therefore be favoured in environments where variable climatic conditions reduce kin structure and select for relatively fast group formation and breakdown.

Similar to frequencies of cooperative breeding, the size of nonfamily groups was linked to hot climates with fluctuating precipitation, whereas family group size varied independently of climate. The costs of reproductive competition amongst unrelated individuals in nonfamily groups may mean that groups only become larger when environmental conditions increase the benefits of cooperation, resulting in group size closely tracking climatic variation[31,32]. For example, in nonfamily groups of the greater ani, *Crotophaga major*, it has been shown that dry years favour small groups because of competition over food, whereas larger groups are more successful in wet years because of better protection against predators[31]. In contrast, family group sizes are rarely found to vary with environmental conditions (e.g.[26,47]) and may instead be determined by diminishing indirect fitness returns that are capped by the reproductive output of breeding females[8,55].

Extreme climatic conditions, where high temperatures are combined with periods of drought can lead to reproductive failure and even the collapse of entire communities[3,26,47]. Cooperative breeding is one way species may cope with such adverse climates[6,49]. Climate change is expected to magnify environmental variation and it has been proposed that cooperative breeding can help reduce the impact of such variation on reproductive success[53]. However, recent work shows that variable environments do not always select for cooperative behaviour among relatives[54]. In line with this, our results show that family cooperative breeding is associated with hot, stable climates and only cooperation with unrelated individuals is associated with variable environments.

Cooperation amongst unrelated individuals may therefore be an important strategy that allows animals to cope with climatic conditions that are becoming ever more frequent.

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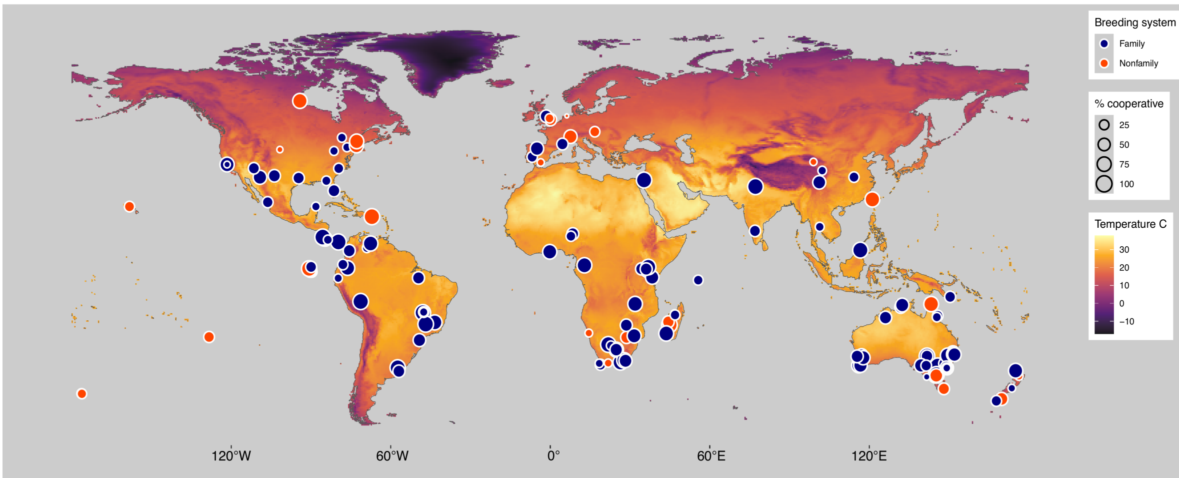
Figures

A



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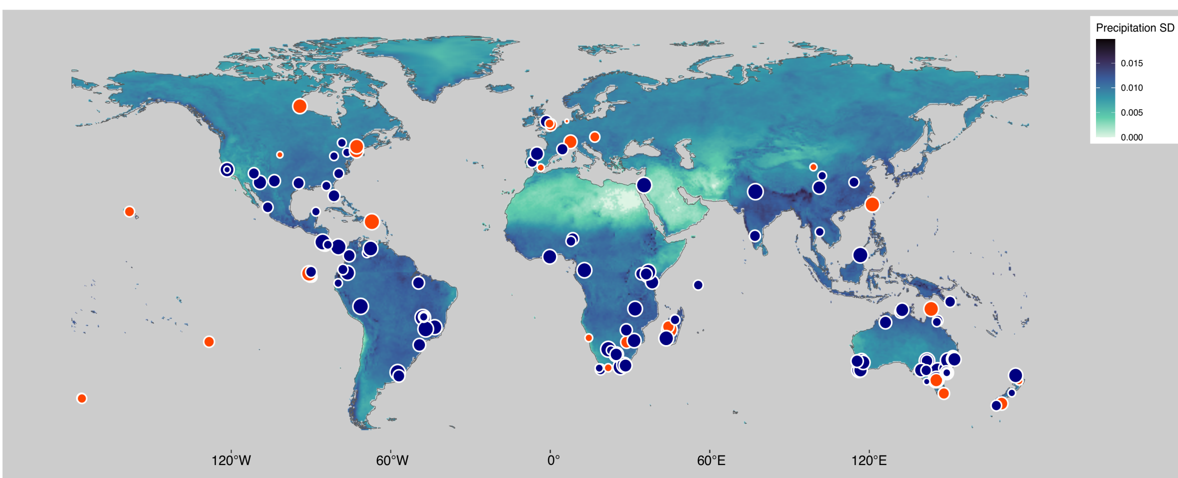

Fig. 1: The areas where family and nonfamily cooperative breeders occur in relation to (A) median temperature and (B) variation in precipitation across years. Points represent study sites, the colour of the circles represents the breeding system, and the size of the circle

represents the % of cooperative nests in the population. Maps of all climatic variables with points labelled by species are presented in Extended Data Fig. 1.

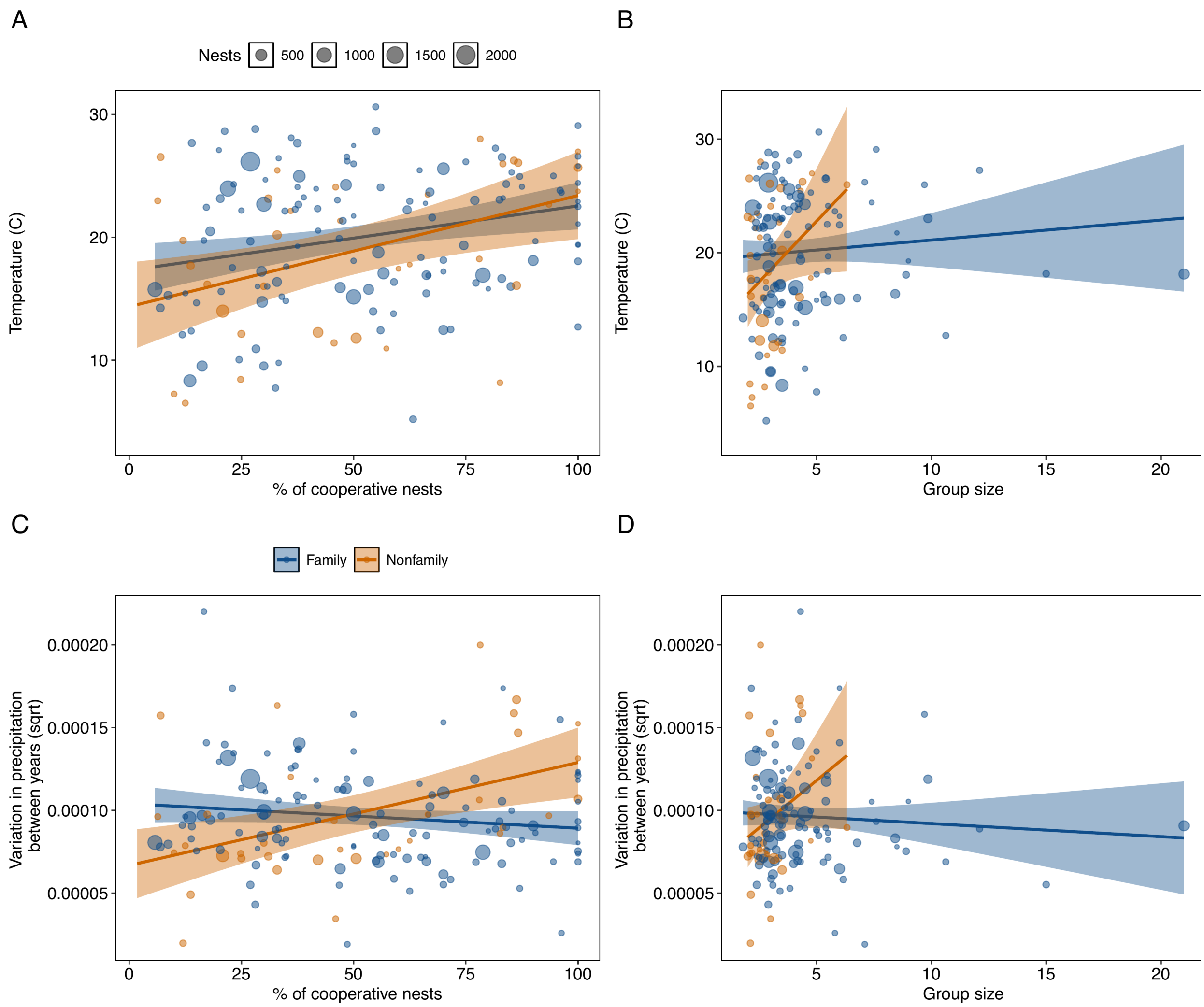

Fig. 2: The frequency of non-family cooperative breeding (% nests with >2 adults) and group sizes increases in environments with higher temperatures (A-B) and variable precipitation across years (C-D). The frequency of family cooperative breeding only increases in relation to median temperature (A) and group size are independent of climate (B, D). Points represent species with the size of circles proportional to the number of nests studied to ascertain % of cooperative nests and group sizes. Regression lines with 95% confidence

intervals are plotted. For relationships between all climatic variables and the % of cooperative nests and group sizes see Extended Data Fig. 3 and Extended Data Fig. 4.

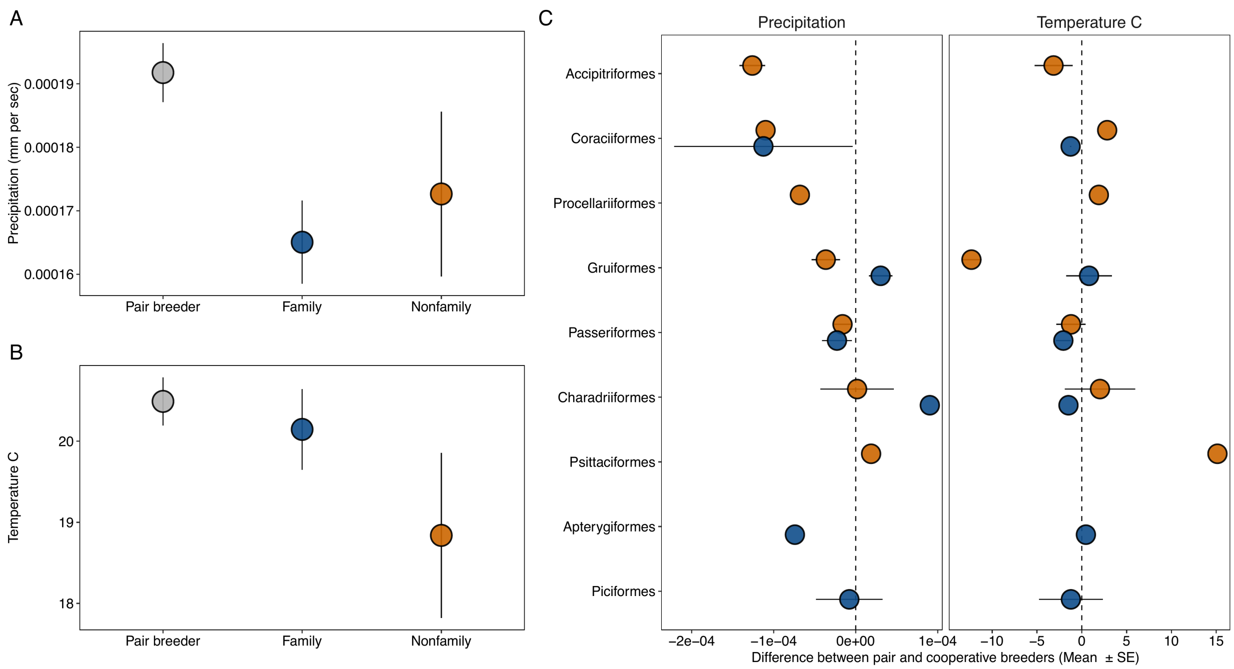

Fig. 3: The environments where nonfamily group, family group and pair breeding species occur. Different breeding systems in relation to (A) median precipitation (mm per second) and (B) median temperature. Nonfamily and family cooperative breeders occur in environments with significantly less precipitation but similar temperatures to closely related pair breeders. Points are means ± SEs. (C) The difference in climates between breeding systems. Orange dots show mean ± SEs of pair - nonfamily species and blue dots show pair - family species for different bird orders. In five out of seven bird orders nonfamily cooperative breeders were in environments were lower precipitation than pair breeders (left of dashed line, B left panel) and were also in a wide variety of thermal environments (C right panel). In contrast, family cooperative breeders occur in environments with similar temperatures to pair breeders (C right panel) and in four out of six bird orders environments had less precipitation (C left panel). For plots with more breeding system classifications that distinguish between species with multiple breeders and a combination of family and nonfamily members see Extended Data Fig. 5.

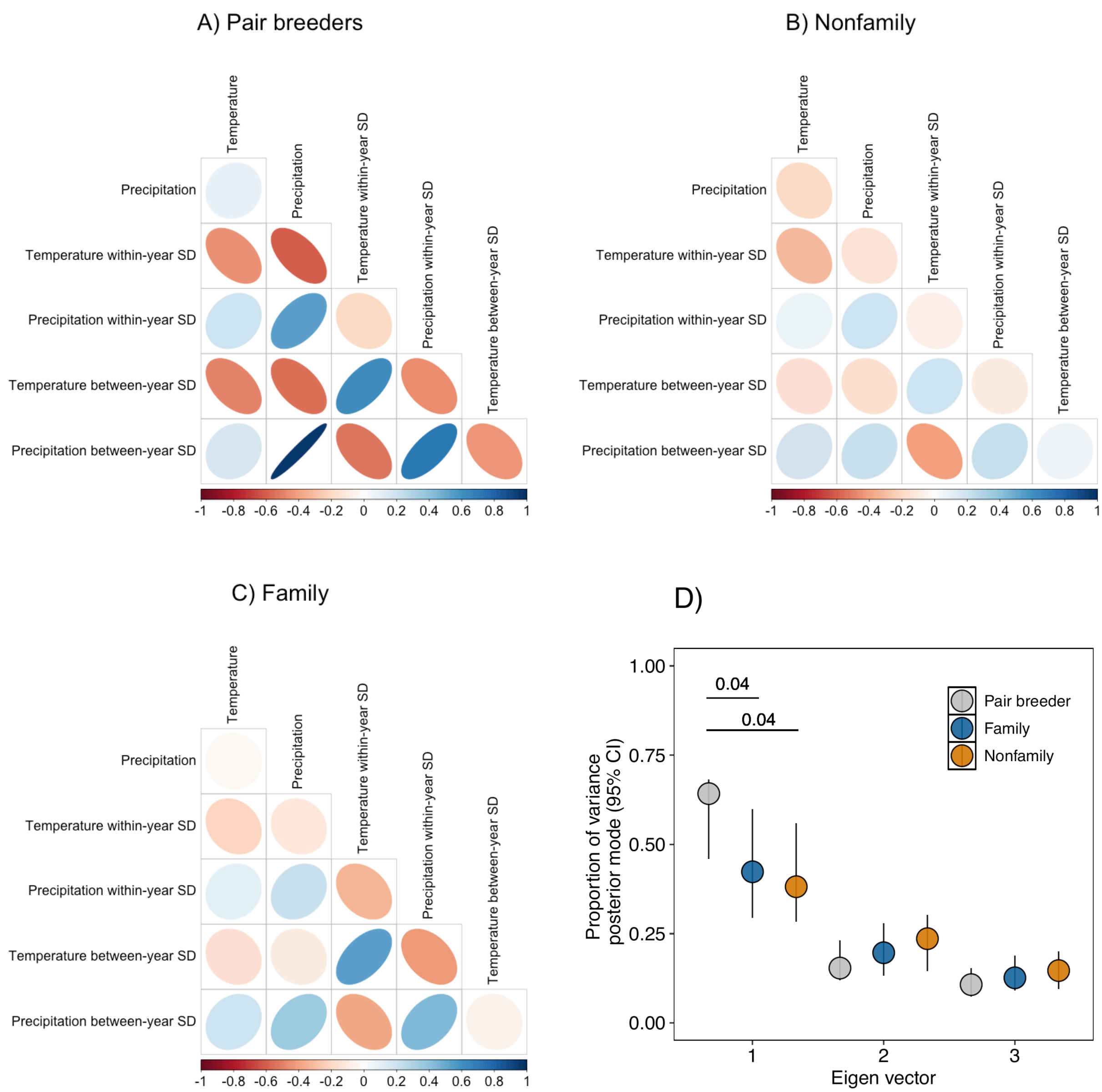

Fig. 4: Nonfamily and family cooperative breeders occupy a broader range of climates than pair breeding species. (A-C) The correlational structure of climate variables across the different breeding systems. Ellipses show the direction and strength of correlations (tighter ellipses represent stronger correlations) with more intense blue colours indicating stronger positive correlations and more intense red colours indicating stronger negative correlations. D) The proportion of variation in eigenvalues explained by each eigenvector across breeding

systems. If the first eigenvector explains a greater proportion of variation in the eigenvalues for a particular breeding system (pair breeders, family cooperative breeders or nonfamily cooperative breeders) this indicates that more variation is aligned along a single axis of climatic variation. Lines represent significant differences (95% CI of difference does not included 0) with pMCMC values (proportion of iterations greater or less than 0).

Methods

To quantify variation across cooperative breeding systems, we used published papers to collect data on the how groups form, relatedness among group members, the presence of cobreeders, the presence of non-reproductive adults that assisted with offspring care, the frequency of nests in the population where group breeding was observed and the size of cooperative groups. To compare cooperative breeders to pair breeders, we selected the five most closely related pair breeding species to each cooperative species using phylogenetic information from Jetz *et. al* 2012[56] and breeding system information from Cockburn 2006[57]. To quantify the environments where species live we extracted climate data for breeding and nonbreeding seasons from study sites and breeding ranges (i.e. temperature and precipitation) from 1979 to 2018 using the ERA5 global bioclimatic indicators dataset derived from reanalysis[58]. We analyzed our data using Bayesian phylogenetic mixed models.

Data collection

We used the species list of cooperative breeders and corresponding literature from Downing et al. 2020[12], supplemented with additional literature (full list of references in Supplementary Table 1). To find additional species the following search terms were used: “cooperative breeding” OR “helper” OR “related” OR ”unrelated” OR “kin” OR “nonkin” OR “nonfamily” OR “family” AND “bird” OR “avian”. Where required data were missing for specific species, we also searched for references using only the common and Latin names of the species as given by BirdLife and Handbook of Birds of World. For our searches we used Google Scholar, PubMed and the library database at Lund University.

Data on breeding systems, helpers and helper relatedness

Classification of breeding systems

Species were classified according to the presence of cobreeders in groups (pair or multiple breeders) and the presence of related and/or unrelated individuals that helped raise offspring (Table 1). Pairs within cooperative species were socially monogamous pairs with one or more helpers. Multiple breeders were any species where more than two adults contribute offspring to the brood, ascertained using information on joint nesting females and rates of within-group multiple paternity. Classifications were based on species-specific articles and available information in review articles on avian breeding systems (supptbl-datacoop and Supplementary Table 2)[12,16,27,57]. Data were only included if exact percentages of nests with cobreeders (pair versus multiple) and the presence of nonfamily and family helpers (yes versus no) were recorded (but see section 'Sensitivity to breeding system classficiations' for relaxation of this criteria). This reduced the number of species from 39 to 32 for nonfamily cooperative breeders and 128 to 58 for family cooperative breeders. Classifications of breeders and helpers were made at a threshold of >10% of nests, for example, species were recorded as having multiple breeders if there were more than two breeding adults at more than 10% of nests.

Table 1: Classification of different cooperative breeding systems.

Breeders[1]	Family Helpers[2]	Nonfamily Helpers[2]	Group size[3]	Detailed Classification[4]	Broad Classification
Pair	Yes	No	>2	Pair Family	Family
Pair	Yes	Yes	>2	Pair Mixed	Family
Multiple	Yes	No	>2	Multiple Family	Family
Multiple	Yes	Yes	>2	Multiple Mixed	Family
Multiple	No	Yes	>2	Multiple Nonfamily	Nonfamily
Pair	No	No	2	Pair	Pair

[1]Breeders = reproducing individuals

[2]Helpers = adult individuals foregoing reproduction

[3]Group size >2 = cooperative species

[4]Note there were no species with clear evidence of a pair of breeders with nonfamily helpers.

Classification of helpers and helper behaviour

Helpers were defined as adult non-reproducing individuals that assisted with offspring care. Immature individuals were disregarded in this study and not included in any data or analyses. For example, if a species had helpers at 100% of nests but 50% of the helpers were juveniles, species were recorded as having helpers at 50% of nests. If it was clear that both juvenile and adult helpers were present at nests, but it was not possible to disentangle the exact percentage of helper presence for each age group from any references, we assumed an estimate of 50% for each helper age group. While helping traditionally includes a wide range of behaviours (e.g., nest construction, incubation, provisioning of the incubation female, nest and chick defence and provisioning of chicks), our data collection only included verified accounts of incubation and/or feeding of chicks or fledglings. Studies including other accounts of helping behaviour were excluded. Studies in which observations of incubation or feeding were rare (i.e. only for one nest or only observed on one occasion) were also excluded.

Relatedness of helpers to breeders

The relatedness of helpers to the breeding pair and chicks they helped raise was assessed as high, medium or low using information on genetic markers and pedigrees constructed from ringing data. In cases of multiple studies on the same species using different methods, we first used information from genetic markers to assess relatedness, followed by pedigree data (Supplementary Table 5). For species with polygamous, polyandrous or polygynandrous mating systems, we assumed that breeding/adult individuals were unrelated unless genetic analyses of the population specifically state otherwise. If data on relatedness was too sparse to assess if groups members were nonfamily or family, species were excluded from analyses.

Sensitivity to different breeding system classifications

The quality of data we were able to extract from the available literature varied across species. For the analyses presented in the manuscript we used a threshold of >10% nests where citeria were met. However, to assess the sensitivity of our results to excluding species without data on the exact percentages of nests with cobreeders and the presence of nonfamily and family helpers, we classified as many species as possible using a summary of available information from all references for a given species (Supplementary Table 1). In cases of discrepancies between references, we implemented a hierarchical decision-making process with advantage given to information based genetic data, then ringing data, then observational data and lastly anecdotal or referred to information (i.e. information based on other studies, unpublished data, personal communication or references of unclear origin).

We also examined the sensitivity of our results to classifying species at a 10% threshold by reclassifying breeding systems at a threshold of >30% of nests (Supplementary Table 1). For example, if a species had multiple breeders at 15% of nests, nonfamily helpers at 20% of nests and family helpers at 40% of nests it would be classified at the 10% threshold as “multiple mixed” (main analyses) whereas it would be reclassified at a >30% threshold as “pair family”.

Breeding seasons

As some cooperative species have widespread distributions, breeding seasons can vary widely between study sites. We therefore applied a two-step approach in assessing breeding seasons. First, we assessed the breeding season for each species at the study sites given in references (Supplementary Table 1). In the few cases where a breeding season was not stated in the reference, we used breeding seasons given for the same species at identical study sites, or sites within reasonable proximity in different references, or lastly from Handbook of Birds of the World[59]. In cases where breeding seasons given for species at the same location did not match across references, we recorded all months where breeding was reported to occur across references. For the breeding seasons of pair breeding species we used Handbook of Birds of the World[59] (Supplementary Table 2).

Climate data

Information on temperature and precipitation was extracted from the ERA5 global bioclimatic indicators dataset[58]. This dataset combines multiple sources of observational data with forecast models to accurately reconstruct the global weather conditions between 1979 to 2018 at a resolution of 0.5° x 0.5°. We extracted data on monthly mean air temperature at 2m above the surface in units of Kelvin (converted to centigrade for analyses) and monthly mean precipitation as accumulated liquid and frozen water, comprising rain and snow, falling onto the Earth's surface in meters per second.

The primary benefit of using the ERA5 reanalysis data over observational data is gap-free coverage in both space and time. This approach assimilates a vast array of observational weather data from different sources, e.g. from satellites and weather stations, into a model that accounts for how different climatic variables interact, resulting in highly reliable estimates of past climatic conditions[60]. Precipitation datasets based purely on *in-situ* direct observations, such as the CRU dataset (one of the longest running observational climate datasets that has previously been used in studies of cooperative breeding e.g.[27,43,61]), are more influenced by individual rain-gauge estimates, which are sensitive to factors such as local topological features[62]. Reanalysis data may be less impacted by anomalies in single sources of observational data[60,62,63].

For all species we extracted information on temperature and precipitation for study sites for cooperative breeding species and centroid coordinates for pair breeding species. We also examined temperature and precipitation values across entire distributions by intersecting climate data with range maps from BirdLife International[64] and Handbook of Birds of the World[59]. The map shapefiles contain information on the seasonal distribution of each species, allowing us to separate breeding and wintering ranges. To extract the climatic data for the relevant coordinates for each species from the gridded ERA5 dataset the R package 'Raster' was used[65]. This resulted in datasets containing monthly mean estimates of temperature and precipitation for each species between 1979-2018. For the data extracted using species ranges (ii) we then calculated a median value across the range for each time point. From each of these datasets, we selected only the breeding season months for each species (see 'Breeding seasons'). Three summary values were then calculated for each dataset for each species: (i) the median breeding season temperature and precipitation across the full 40 year period (calculated from yearly medians); (ii) the within breeding season variation in temperature or precipitation as the median of the standard deviation within years of each of these variables; and (iii), the between breeding season variation in temperature or precipitation as the standard deviation of the yearly medians of each of these variables.

There was strong correspondence between measurements at study sites/centroid values and measurements across whole ranges (correlation coefficients across datasets (r): temperature median and variation r >0.79; precipitation median and variation r >0.73. See R script 'data_nonfam.R'. Therefore, we analysed climate data from study sites/centroid values.

Data compilation

Raw data on cooperative breeding species is presented in Supplementary Table 1 with references. Data on breeding seasons and climate data for all species, together with summarised information on cooperative breeders, is presented in Supplementary Table 2. Datasets were compiled using the R script 'data_nonfam.R'.

Statistical analyses

General Overview

Three sets of analyses were conducted using multi-response Bayesian Phylogenetic mixed models (MR-BPMM) with Markov chain Monte Carlo (MCMC) estimation implemented in the R package MCMCglmm[66]. First, we analysed if the percentage of nests with cooperative breeding and the number of individuals in groups were related to climate across nonfamily and family cooperative breeders. Second, we tested if there were mean differences in the climates occupied by different types of cooperative breeders and pair breeders. Third, we examined if the relationships between climate variables differed between cooperative and pair breeders. See R script 'analyses_nonfam.R'.

Model settings

For MR-BPMMs default priors were used for fixed effects (independent normal priors with zero mean and large variance (10^10)) and for random effects inverse-gamma priors were used (V = diag(n), nu = n − 1 + 0.002, where nu is the degree of belief and n was equivalent to the number of response traits). Phylogenetic relationships were modelled by fitting a variance-covariance matrix constructed from the phylogeny as a random effect. To account for uncertainty in phylogenetic relationships, we ran models across a sample of 1500 trees. Estimates from the last iteration from tree i were used as starting values for tree i+1. Estimates from the last iteration of each tree were saved, with samples from the first 500 trees being discarded as a burn-in. Each tree was sampled for 2000 iterations with a burn-in of 1999 and a thinning interval of 1. Model convergence was examined by repeating each analysis three times and examining the correspondence between chains using the R package 'coda'[67] in the following ways: (i) visually inspecting the traces of the MCMC posterior estimates and their overlap; (ii) calculating the autocorrelation and effective sample size of the posterior distribution of each chain; and (iii) using Gelman and Rubin's convergence diagnostic test that compares within- and between- chain variance using a potential scale reduction factor (PSR). PSR values substantially higher than 1.1 indicate chains with poor convergence properties.

Parameter estimation

The global intercept was removed from MR-BPMMs to allow trait specific intercepts to be estimated. Parameter estimates from models are presented as posterior modes (PM) with 95% credible intervals (CIs). P values (pMCMC) were estimated as the number of posterior samples above or below a specified value divided by the total number of posterior samples, corrected for the finite number of MCMC samples. For correlations and fixed effects, the specified value was 0, and for testing differences between fixed effect levels (e.g. breeding systems) it was the number of posterior samples where one level was greater than the other.

Phylogenetic and residual correlations between traits were calculated using the variance and covariance estimates from the unstructured phylogenetic and residual variance-covariance matrices. We estimated the amount of variation in response variables explained by random effects (RE), including phylogenetic effects, as the intraclass correlation coefficient (ICC) estimated as: $V_i / V_{RE} + V_e$

where V_i is the focal random effect, V_{RE} is the sum of all random effects and V_e is the residual variance on the latent scale[68,69].

Specific analyses

Differences in the % of nests with cooperative breeder and number of individuals in groups in relation to climate

To test if the proportion of nests where there was cooperative breeding was related to the climate, we re-ran model mod_bs10 including the proportion of nests with more than two individuals (logit transformed) as a covariate interacted with each climate variable separately for nonfamily and family cooperative breeders using the 'at.level' notation in MCMCglmm (Rcode model mod_nests). Finally, the relationship between the number of individuals in groups and climate across family and nonfamily cooperative breeders was estimated using the same setup as model mod_nests, but including the number of individuals in groups instead of the proportion of cooperative nests (Rcode model mod_groupsize).

Median climatic differences across cooperative breeders and pair breeders

To test for climatic differences across breeding systems a MR-BPMM was used with the responses of median, variation within years and variation between years for temperature and precipitation (six responses) and breeding system (nonfamily cooperative breeders, family cooperative and pair breeders) as a fixed effect. The "at.level" notation in MCMCglmm was used to estimate each response variable at the level of each breeding system. For details see model mod_bs10 in R code.

To verify that our results were not dependent on how breeding systems were classified we re-ran model mod_bs10 with the breeding system defined as: i) 'pair breeders', 'pair with family helpers', 'pair with family and nonfamily helpers', 'multiple breeders with family helpers' and 'nonfamily' (Table 1. Rcode model mod_bsdetailed. Supplementary Table 6); ii) 'pair breeders', 'pair with helpers', 'multiple breeders' (Rcode model mod_breeders. Supplementary Table 7); and iii) 'pair breeders', 'family helpers', 'family and nonfamily helpers' and 'nonfamily' (Rcode model mod_helpers. Supplementary Table 8). We also tested whether classifying species as having multiple breeders, family helpers and nonfamily helpers using all information and a 30% threshold influenced our results by re-running model mod_bs10 including all species (Rcode models mod_bs. Supplementary Table 9) and 30% classifications (Rcode models mod_bs30. Supplementary Table 10). Across these analyses we found qualitatively and quantitatively similar results (Supplementary Table 5, Supplementary Table 6, Supplementary Table 7, Supplementary Table 8, Supplementary Table 9 and Supplementary Table 10).

Differences in the relationships between climate variables across cooperative and pair breeders

To examine if the correlations between climatic variables differed across breeding systems we re-ran model mod_bs10 including separate phylogenetic variance-covariance matrices for each breeding system (nonfamily cooperative breeders, family cooperative and pair breeders). This was done using the "at.level" notation in MCMCglmm and variance-covariance estimates were used to calculated phylogenetic correlations between all climate variables for each breeding system (Rcode model mod_climcorrs).

It is possible that including more pair breeding species (456 versus 39 nonfamily and 128 family) may bias variance and covariance estimates across climate variables. We therefore verified that our phylogenetic variance-covariance estimates for pair breeders were not different from cooperative breeders by down-sampling our data to the same number of species as family cooperative breeders and re-running analyses (Rcode model mod_climcorrsdown). The results were qualitatively and quantitatively similar (Supplementary Table 12).

To analyse the structure of the phylogenetic covariance matrices across breeding systems we calculated the eigenvectors and their eigenvalues for each posterior sample from model mod_climcorrs for each breeding system using the R function 'eigen'. To test if the structure of the covariances between climate variables was different across breeding systems, we calculated the posterior mode and 95% CIs of the pairwise differences between pair, family cooperative and nonfamily cooperative breeders in the proportion of variance in eigenvalues explained by each eigenvector (Figure 4). Differences where the 95% CIs did not span 0 and less than 5% of iterations was greater or less than 0 were considered statistically significant.

Data and code availability

All code, data and analysis results are available at the open science framework (osf.io project number qhvs5) and can be located at doi.org using the doi number (https://doi.org/10.17605/OSF.IO/QHVS5).

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Author contributions

Conceptualization - CKC, CHW, EO, PD, ASG. Methodology: CKC, CHW, EO, PD. Investigation: CKC, CHW, EO. Visualization: CKC, EO. Funding acquisition: CKC, CHW. Project administration: CKC. Supervision: CKC. Writing – original draft: CKC, CHW. Writing – review & editing: CKC, CHW, EO, PD, ASG.

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Ethics declarations

Competing interests

The authors have no competing interests.

Supplementary Information

Supplementary Tables are provided in xlsx format in the file "SupplementaryTables.xlsx". Full citations of references in Supplementary Tables are given in the method references[70-510].

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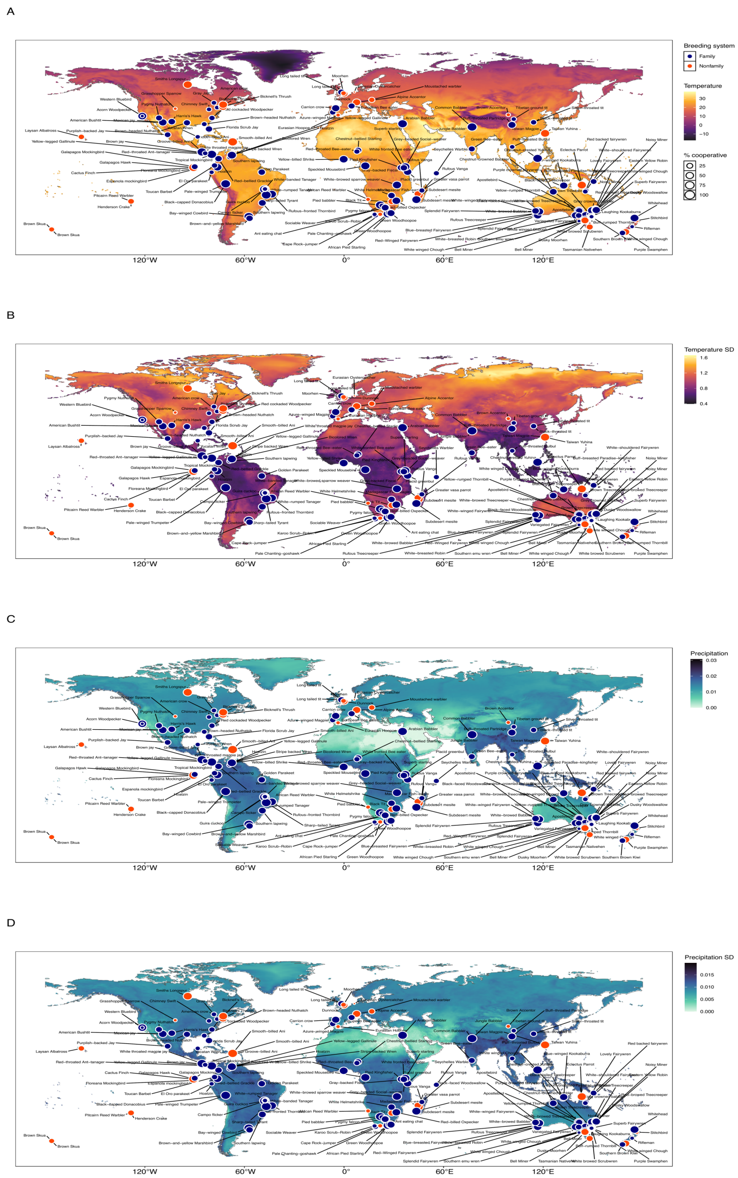
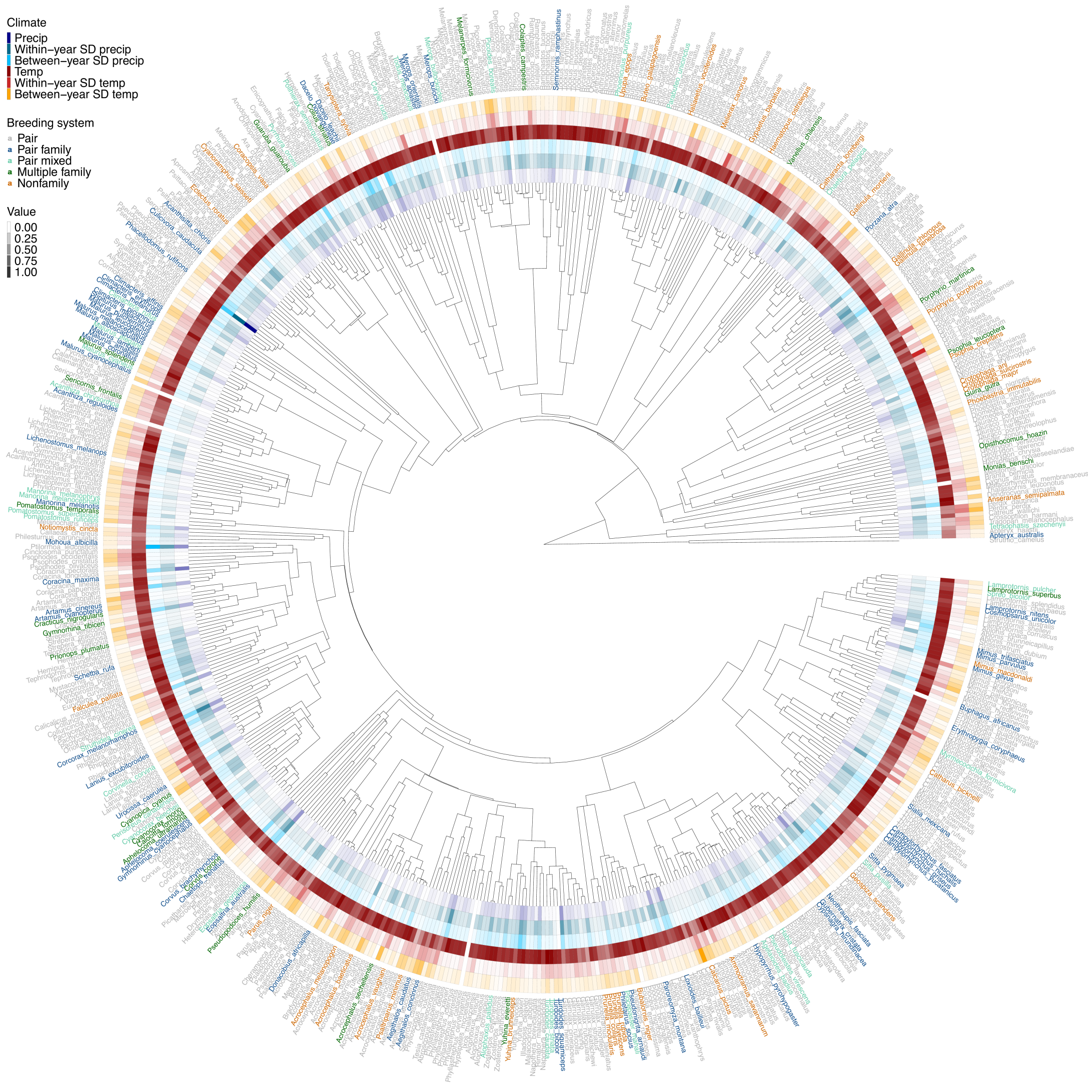
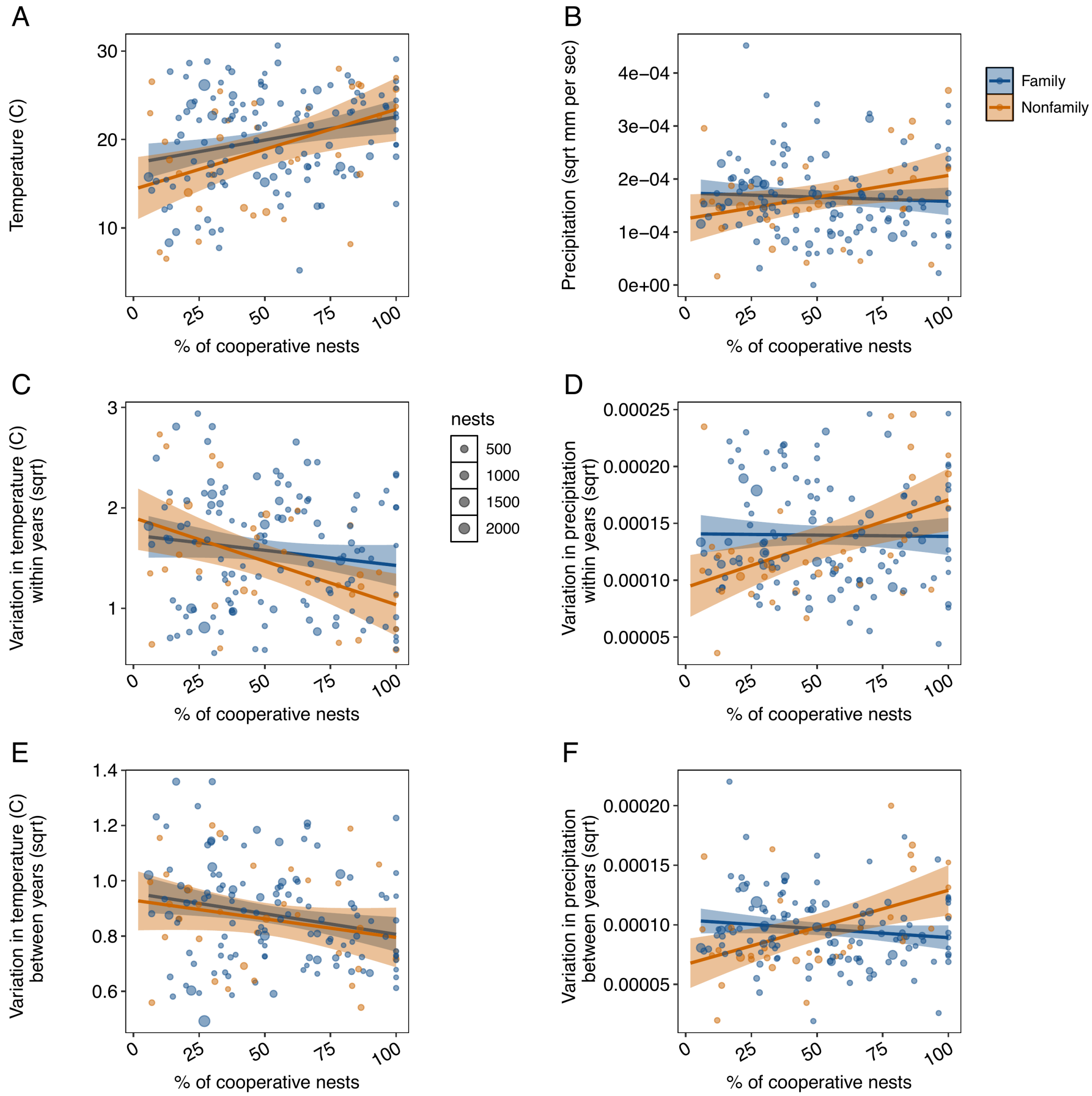
Extended Data Figures



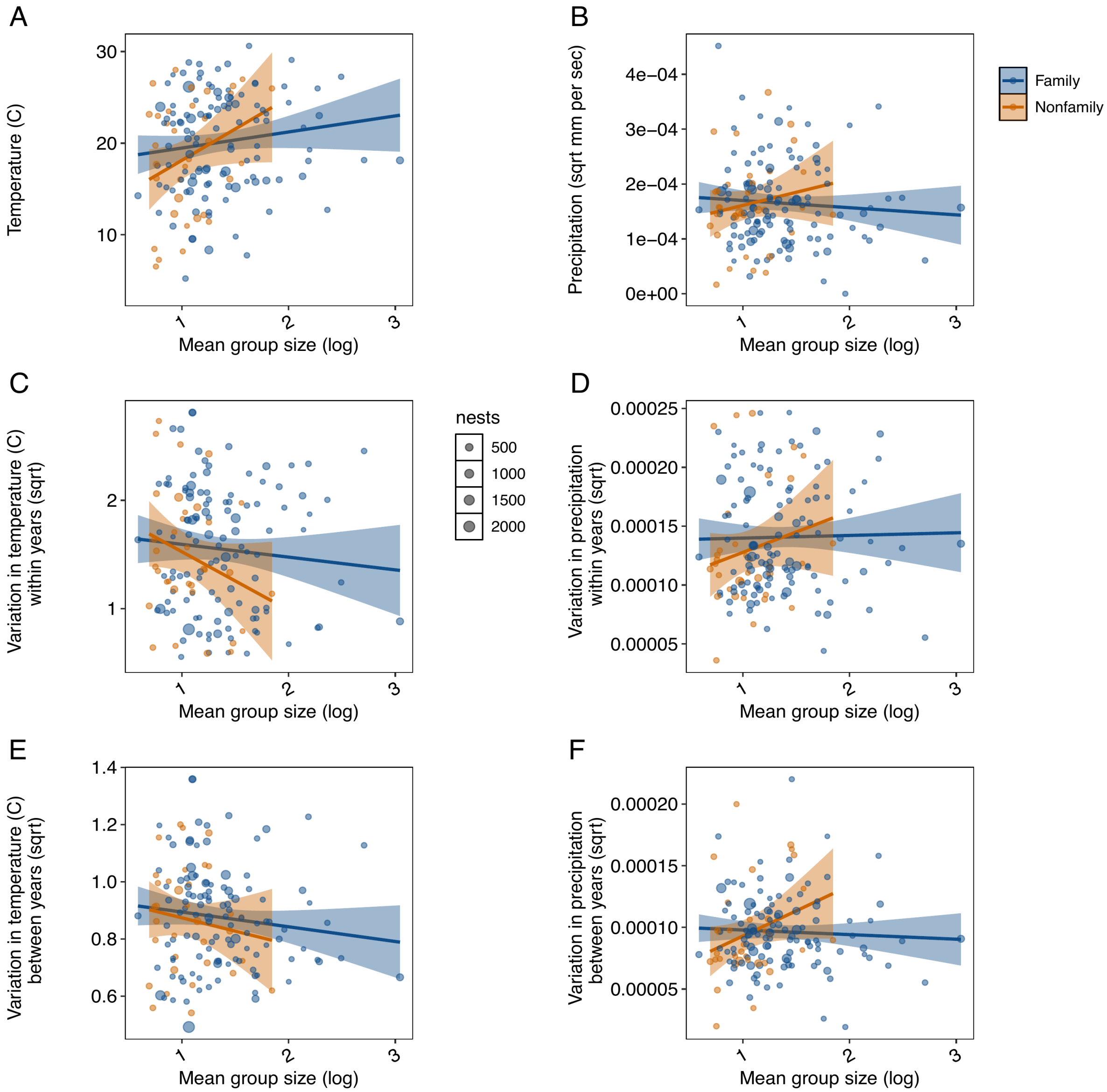
Extended Data Fig. 1: The areas where family and nonfamily cooperative breeders occur in relation to median temperature (A) and precipitation (B) and variation across years in temperature (C) and precipitation (D). Points represent study sites and are labelled by species common names with the colour of the circle representing breeding system and the size of the circle represent % of cooperative nests in the population.



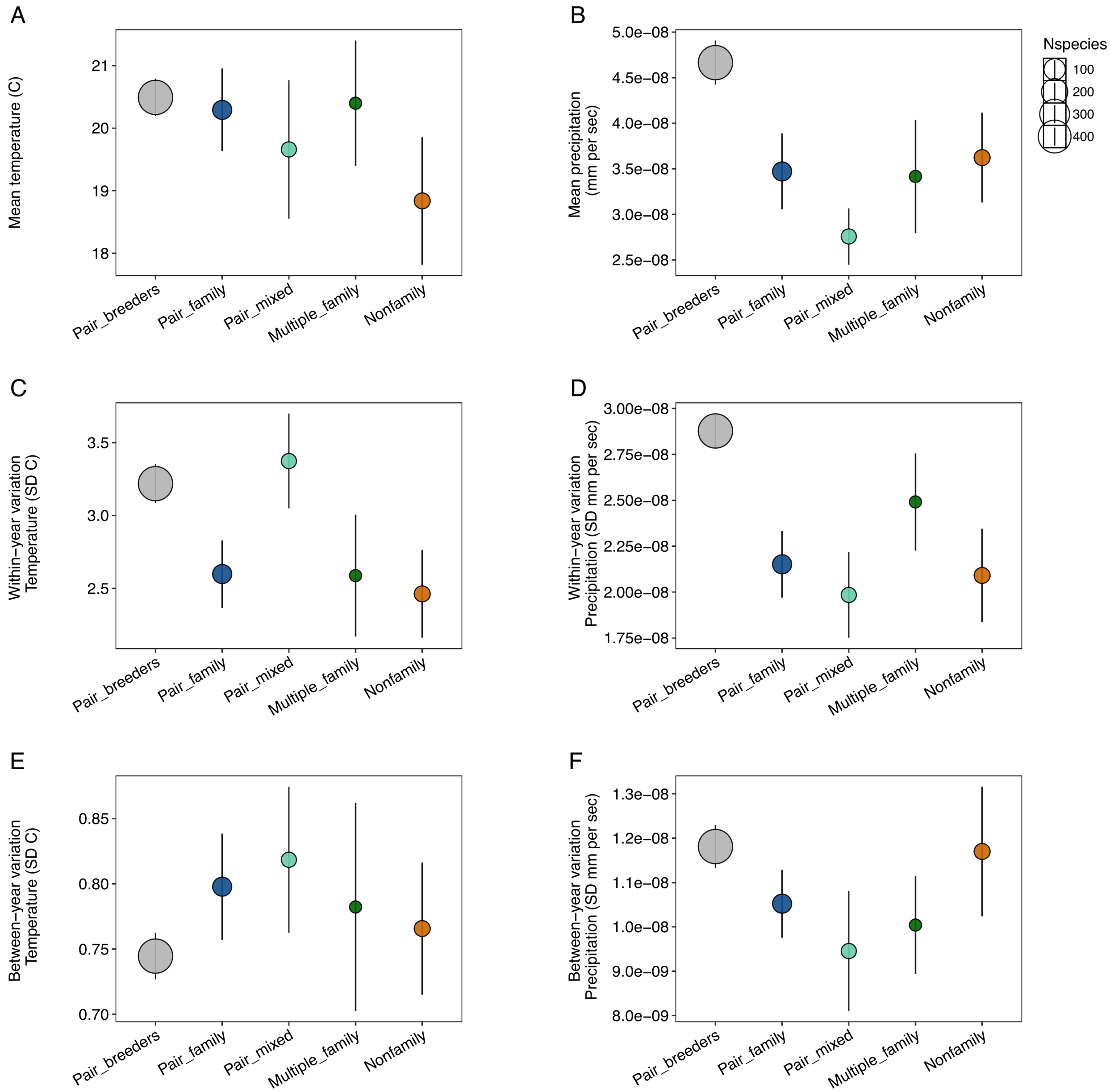
Extended Data Fig. 2: The evolution of different cooperative breeding systems in relation to climatic variation. Tip label colours indicate different breeding systems and colour rings represent (inner to outer circle) median precipitation (dark blue), precipitation variation within breeding seasons (aqua), precipitation variation across breeding seasons (turquoise), median temperature (dark red), temperature variation within breeding seasons (pink), and temperature variation across breeding seasons (orange). Climate data was restricted to the months each species has been found breeding.



Extended Data Fig. 3: Variation in the frequency of cooperation across nonfamily and family groups in relation to (A) median temperature, (B) median precipitation (C) temperature and (D) precipitation variation within breeding seasons, and (E) temperature and (F) precipitation variation across breeding seasons. Climate data was restricted to the months each species has been found breeding. Regression lines with 95% confidence intervals are plotted. Points represent species with size proportional to the number of nests studied.



Extended Data Fig. 4: Variation in group size in nonfamily and family groups in relation to (A) median temperature, (B) median precipitation (C) temperature and (D) precipitation variation within breeding seasons, and (E) temperature and (F) precipitation variation across breeding seasons. Climate data was restricted to the months each species has been found breeding. Regression lines with 95% confidence intervals are plotted. Points represent species with size proportional to the number of nests studied.



Extended Data Fig. 5: The environments inhabited by cooperative breeding species with cobreeders (pair versus multiple breeders) and the relatedness of group members (presence of nonfamily, family & mixed helpers) compared to pair breeding species. Means ± SEs across different breeding system are presented with the size of circles proportional to the number of species in each category.

Supplementary Information

Supplementary Tables

Data used for analyses

Supplementary Table 1: See SItablesXL.xlsx

Supplementary Table 2: See SItablesXL.xlsx

Results of analyses

To estimate the variation in response variables explained by random effects the percentage of total random effect variance explained by each random term was calculated on the latent data scale (I2).

Supplementary Table 3: Variation in the frequency of cooperative breeding (% nests with group breeding, logit transformed) in nonfamily and family groups in relation to climate.

Fixed Effects	Posterior Mode (CI)	pMCMC
Family temp	-0.02 (-0.2, 0.18)	-
Family precip	0 (-0.2, 0.18)	-
Family temp within-year	0.11 (-0.11, 0.26)	-
Family precip within-year	0.08 (-0.19, 0.2)	-
Family temp between-year	0.08 (-0.1, 0.27)	-
Family precip between-year	-0.01 (-0.19, 0.19)	-
Nonfamily temp	-0.28 (-0.52, 0.12)	-
Nonfamily precip	-0.03 (-0.37, 0.3)	-
Nonfamily temp within-year	-0.13 (-0.39, 0.26)	-
Nonfamily precip within-year	-0.2 (-0.47, 0.17)	-
Nonfamily temp between-year	-0.09 (-0.37, 0.3)	-
Nonfamily precip between-year	-0.03 (-0.36, 0.31)	-
Family temp: coop frequency	0.17 (0.04, 0.28)	0.008
Family precip: coop frequency	-0.04 (-0.12, 0.12)	0.858

Family temp within-year: coop frequency	-0.11 (-0.21, 0.03)	0.124
Family precip within-year: coop frequency	0.02 (-0.12, 0.12)	0.948
Family temp between-year: coop frequency	-0.14 (-0.27, -0.03)	0.024
Family precip between-year: coop frequency	-0.07 (-0.17, 0.06)	0.29
Nonfamily temp: coop frequency	0.28 (0.1, 0.47)	0.001
Nonfamily precip: coop frequency	0.19 (0.01, 0.38)	0.028
Nonfamily temp within-year: coop frequency	-0.25 (-0.44, -0.09)	0.008
Nonfamily precip within-year: coop frequency	0.29 (0.09, 0.47)	0.004
Nonfamily temp between-year: coop frequency	-0.12 (-0.33, 0.05)	0.154
Nonfamily precip between-year: coop frequency	0.29 (0.13, 0.5)	0.001
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.57 (0.28, 0.82)	53.24 (32.97, 74.77)
Phylogeny temp within-year	0.53 (0.25, 0.84)	51.22 (22.62, 74.47)
Phylogeny temp between-year	0.58 (0.26, 0.84)	50.59 (25.62, 75.8)
Phylogeny precip	0.55 (0.23, 0.89)	52.15 (25.61, 80.46)
Phylogeny precip within-year	0.54 (0.21, 0.89)	49.2 (24.57, 71.85)
Phylogeny precip between-year	0.56 (0.21, 0.83)	51.79 (23.97, 76.15)
Residual temp	0.45 (0.27, 0.75)	46.76 (25.23, 67.03)
Residual temp within-year	0.53 (0.24, 0.8)	48.78 (25.53, 77.38)
Residual temp between-year	0.5 (0.28, 0.87)	49.41 (24.2, 74.38)
Residual precip	0.49 (0.22, 0.85)	47.85 (19.54, 74.39)
Residual precip within-year	0.42 (0.19, 0.86)	50.8 (28.15, 75.43)
Residual precip between-year	0.43 (0.2, 0.8)	48.21 (23.85, 76.03)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	-0.57 (-0.73, -0.17)	0.004

Phylogeny temp between-year : Phylogeny temp	-0.45 (-0.69, -0.1)	0.03
Phylogeny precip within-year : Phylogeny precip	0.67 (0.28, 0.82)	0.008
Phylogeny precip between-year : Phylogeny precip	0.66 (0.33, 0.83)	0.002
Phylogeny precip : Phylogeny temp	0.13 (-0.39, 0.41)	0.826
Phylogeny precip within-year : Phylogeny temp	0.34 (-0.04, 0.65)	0.122
Phylogeny precip between-year : Phylogeny temp	0.27 (-0.12, 0.6)	0.206
Phylogeny temp within-year : Phylogeny precip	-0.58 (-0.73, -0.02)	0.066
Phylogeny temp between-year : Phylogeny precip	-0.41 (-0.67, 0.08)	0.154
Residual temp within-year : Residual temp	-0.53 (-0.72, -0.11)	0.028
Residual temp between-year : Residual temp	-0.38 (-0.64, 0.02)	0.1
Residual precip within-year : Residual precip	0.64 (0.22, 0.79)	0.006
Residual precip between-year : Residual precip	0.68 (0.32, 0.81)	0.001
Residual precip : Residual temp	0 (-0.41, 0.43)	0.978
Residual precip within-year : Residual temp	0.4 (-0.12, 0.65)	0.178
Residual precip between-year : Residual temp	0.36 (-0.19, 0.59)	0.288
Residual temp within-year : Residual precip	-0.47 (-0.72, -0.04)	0.06
Residual temp between-year : Residual precip	-0.45 (-0.66, 0.07)	0.15

Supplementary Table 4: Variation in the mean group size (log transformed) of nonfamily and family groups in relation to climate.

Fixed Effects	**Posterior Mode (CI)**	**pMCMC**
Family temp	-0.24 (-0.91, 0.25)	-
Family precip	0.07 (-0.38, 0.82)	-
Family temp within-year	0.41 (-0.23, 0.9)	-
Family precip within-year	0.13 (-0.64, 0.55)	-
Family temp between-year	0.36 (-0.12, 1.04)	-
Family precip between-year	0.06 (-0.44, 0.74)	-
Nonfamily temp	-1.28 (-2.87, -0.19)	-
Nonfamily precip	-1.03 (-2, 0.61)	-
Nonfamily temp within-year	1.32 (-0.43, 2.25)	-
Nonfamily precip within-year	-0.91 (-2.29, 0.4)	-
Nonfamily temp between-year	0.73 (-0.63, 1.99)	-
Nonfamily precip between-year	-1.24 (-2.81, -0.09)	-
Family temp: group size	0.29 (-0.11, 0.72)	0.152
Family precip: group size	-0.18 (-0.59, 0.27)	0.482
Family temp within-year: group size	-0.32 (-0.62, 0.17)	0.296
Family precip within-year: group size	0.06 (-0.4, 0.43)	0.848
Family temp between-year: group size	-0.3 (-0.72, 0.1)	0.15
Family precip between-year: group size	-0.07 (-0.51, 0.31)	0.56
Nonfamily temp: group size	1.12 (-0.09, 2.34)	0.058
Nonfamily precip: group size	0.69 (-0.45, 1.94)	0.306
Nonfamily temp within-year: group size	-0.88 (-2.01, 0.42)	0.146
Nonfamily precip within-year: group size	0.54 (-0.49, 1.9)	0.24
Nonfamily temp between-year: group size	-0.81 (-1.75, 0.67)	0.402
Nonfamily precip between-year: group size	1.4 (0.18, 2.58)	0.044
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.64 (0.31, 0.88)	53.66 (30.33, 74.25)
Phylogeny temp within-year	0.53 (0.24, 0.88)	51.91 (23.83, 76.36)

Phylogeny temp between-year	0.58 (0.26, 0.86)	51.33 (24.7, 75.83)
Phylogeny precip	0.63 (0.28, 0.97)	52.77 (24.2, 78.61)
Phylogeny precip within-year	0.61 (0.26, 0.99)	50.29 (25.59, 72.13)
Phylogeny precip between-year	0.69 (0.25, 0.95)	52.6 (25.18, 78.17)
Residual temp	0.46 (0.24, 0.78)	46.34 (25.75, 69.67)
Residual temp within-year	0.46 (0.25, 0.87)	48.09 (23.64, 76.17)
Residual temp between-year	0.45 (0.27, 0.86)	48.67 (24.17, 75.3)
Residual precip	0.46 (0.26, 0.93)	47.23 (21.39, 75.8)
Residual precip within-year	0.49 (0.24, 0.92)	49.71 (27.87, 74.41)
Residual precip between-year	0.43 (0.21, 0.83)	47.4 (21.83, 74.82)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	-0.53 (-0.74, -0.18)	0.01
Phylogeny temp between-year : Phylogeny temp	-0.51 (-0.71, -0.09)	0.032
Phylogeny precip within-year : Phylogeny precip	0.72 (0.29, 0.82)	0.01
Phylogeny precip between-year : Phylogeny precip	0.71 (0.33, 0.83)	0.001
Phylogeny precip : Phylogeny temp	0.18 (-0.36, 0.47)	0.806
Phylogeny precip within-year : Phylogeny temp	0.38 (0.01, 0.69)	0.084
Phylogeny precip between-year : Phylogeny temp	0.34 (-0.13, 0.62)	0.196
Phylogeny temp within-year : Phylogeny precip	-0.59 (-0.74, -0.04)	0.064
Phylogeny temp between-year : Phylogeny precip	-0.42 (-0.67, 0.05)	0.132
Residual temp within-year : Residual temp	-0.43 (-0.71, -0.06)	0.042
Residual temp between-year : Residual temp	-0.45 (-0.65, 0.03)	0.102
Residual precip within-year : Residual precip	0.69 (0.27, 0.81)	0.002

Residual precip between-year : Residual precip	0.68 (0.29, 0.82)	0.001
Residual precip : Residual temp	0.07 (-0.41, 0.43)	0.966
Residual precip within-year : Residual temp	0.37 (-0.11, 0.64)	0.178
Residual precip between-year : Residual temp	0.25 (-0.2, 0.57)	0.328
Residual temp within-year : Residual precip	-0.44 (-0.74, -0.06)	0.054
Residual temp between-year : Residual precip	-0.38 (-0.64, 0.07)	0.118

Supplementary Table 5: Differences in the environments of nonfamily, family and pair breeding species.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.09 (-0.13, 0.31)	0.356
Pair temp vs Nonfamily temp	0.27 (-0.07, 0.52)	0.164
Pair precip vs Family precip	0.28 (0.02, 0.58)	0.042
Pair precip vs Nonfamily precip	0.49 (0.06, 0.82)	0.02
Pair temp within-year vs Family temp within-year	0 (-0.26, 0.22)	0.948
Pair temp within-year vs Nonfamily temp within-year	0.16 (-0.19, 0.49)	0.358
Pair precip within-year vs Family precip within-year	0.38 (0.1, 0.65)	0.014
Pair precip within-year vs Nonfamily precip within-year	0.64 (0.24, 1)	0.001
Pair temp between-year vs Family temp between-year	-0.26 (-0.53, 0)	0.036
Pair temp between-year vs Nonfamily temp between-year	-0.15 (-0.49, 0.19)	0.446
Pair precip between-year vs Family precip between-year	0.06 (-0.22, 0.35)	0.606
Pair precip between-year vs Nonfamily precip between-year	0.25 (-0.11, 0.66)	0.116
Family temp vs Nonfamily temp	0.19 (-0.22, 0.5)	0.51

Family precip vs Nonfamily precip	0.23 (-0.34, 0.59)	0.56
Family temp within-year vs Nonfamily temp within-year	0.11 (-0.24, 0.58)	0.42
Family precip within-year vs Nonfamily precip within-year	0.33 (-0.13, 0.77)	0.188
Family temp between-year vs Nonfamily temp between-year	0.1 (-0.27, 0.59)	0.504
Family precip between-year vs Nonfamily precip between-year	0.21 (-0.22, 0.68)	0.306
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.26 (0.19, 0.4)	50.3 (34.56, 68.88)
Phylogeny temp within-year	0.43 (0.22, 0.61)	50 (24.42, 75.87)
Phylogeny temp between-year	0.37 (0.23, 0.65)	50.48 (27.51, 72.71)
Phylogeny precip	0.45 (0.23, 0.77)	50.18 (26.23, 73.05)
Phylogeny precip within-year	0.48 (0.24, 0.7)	50.19 (28.41, 74.22)
Phylogeny precip between-year	0.55 (0.22, 0.77)	50.44 (24.11, 76.44)
Residual temp	0.31 (0.18, 0.39)	49.7 (31.12, 65.44)
Residual temp within-year	0.38 (0.23, 0.61)	50 (24.13, 75.58)
Residual temp between-year	0.45 (0.23, 0.66)	49.52 (27.29, 72.49)
Residual precip	0.55 (0.24, 0.78)	49.82 (26.95, 73.77)
Residual precip within-year	0.5 (0.24, 0.7)	49.81 (25.78, 71.59)
Residual precip between-year	0.46 (0.22, 0.76)	49.56 (23.56, 75.89)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	-0.5 (-0.64, -0.16)	0.01
Phylogeny temp between-year : Phylogeny temp	-0.44 (-0.58, -0.08)	0.026
Phylogeny precip within-year : Phylogeny precip	0.65 (0.24, 0.77)	0.004
Phylogeny precip between-year : Phylogeny precip	0.8 (0.58, 0.89)	0.001
Phylogeny precip : Phylogeny temp	0.2 (-0.3, 0.37)	0.752
Phylogeny precip within-year : Phylogeny temp	0.32 (-0.07, 0.52)	0.16

Phylogeny precip between-year : Phylogeny temp	0.2 (-0.15, 0.48)	0.234
Phylogeny temp within-year : Phylogeny precip	-0.62 (-0.74, -0.19)	0.008
Phylogeny temp between-year : Phylogeny precip	-0.53 (-0.72, -0.08)	0.038
Residual temp within-year : Residual temp	-0.42 (-0.62, -0.11)	0.01
Residual temp between-year : Residual temp	-0.37 (-0.6, -0.07)	0.026
Residual precip within-year : Residual precip	0.59 (0.24, 0.77)	0.006
Residual precip between-year : Residual precip	0.82 (0.59, 0.88)	0.001
Residual precip : Residual temp	0.08 (-0.28, 0.39)	0.85
Residual precip within-year : Residual temp	0.24 (-0.06, 0.51)	0.164
Residual precip between-year : Residual temp	0.25 (-0.14, 0.48)	0.3
Residual temp within-year : Residual precip	-0.55 (-0.72, -0.17)	0.012
Residual temp between-year : Residual precip	-0.54 (-0.71, -0.08)	0.042

Supplementary Table 6: Differences in the environments of pair breeding species and cooperative breeding species with cobreeders (pair versus multiple breeders) and nonfamily, family and a mix of both nonfamily and family group members.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Pair_family temp	0.12 (-0.24, 0.4)	0.542
Pair temp vs Pair_mixed temp	0.1 (-0.24, 0.55)	0.468
Pair temp vs Multiple_family temp	0.02 (-0.3, 0.47)	0.74
Pair temp vs Nonfamily temp	0.22 (-0.09, 0.49)	0.154
Pair precip vs Pair_family precip	0.36 (-0.2, 0.6)	0.268
Pair precip vs Pair_mixed precip	0.27 (-0.13, 0.85)	0.13
Pair precip vs Multiple_family precip	0.36 (-0.15, 0.88)	0.14

Pair precip vs Nonfamily precip	0.52 (0.08, 0.83)	0.024
Pair temp within-year vs Pair_family temp within-year	-0.06 (-0.38, 0.36)	0.874
Pair temp within-year vs Pair_mixed temp within-year	-0.04 (-0.48, 0.35)	0.772
Pair temp within-year vs Multiple_family temp within-year	0.17 (-0.34, 0.56)	0.766
Pair temp within-year vs Nonfamily temp within-year	0.15 (-0.18, 0.54)	0.384
Pair precip within-year vs Pair_family precip within-year	0.55 (0.23, 1.01)	0.002
Pair precip within-year vs Pair_mixed precip within-year	0.29 (-0.24, 0.74)	0.256
Pair precip within-year vs Multiple_family precip within-year	0.19 (-0.31, 0.65)	0.562
Pair precip within-year vs Nonfamily precip within-year	0.65 (0.28, 1.01)	0.001
Pair temp between-year vs Pair_family temp between-year	-0.34 (-0.82, -0.03)	0.034
Pair temp between-year vs Pair_mixed temp between-year	-0.29 (-0.59, 0.35)	0.526
Pair temp between-year vs Multiple_family temp between-year	-0.22 (-0.73, 0.25)	0.36
Pair temp between-year vs Nonfamily temp between-year	-0.18 (-0.49, 0.22)	0.438
Pair precip between-year vs Pair_family precip between-year	0.23 (-0.22, 0.62)	0.378
Pair precip between-year vs Pair_mixed precip between-year	0.06 (-0.47, 0.48)	0.948
Pair precip between-year vs Multiple_family precip between-year	0.04 (-0.53, 0.52)	0.976
Pair precip between-year vs Nonfamily precip between-year	0.2 (-0.03, 0.73)	0.104
Pair_family temp vs Pair_mixed temp	0.05 (-0.48, 0.55)	0.816
Pair_family temp vs Multiple_family temp	-0.1 (-0.54, 0.48)	0.914
Pair_family temp vs Nonfamily temp	0.15 (-0.3, 0.58)	0.55
Pair_family precip vs Pair_mixed precip	0.08 (-0.45, 0.79)	0.592

Pair_family precip vs Multiple_family precip	0.34 (-0.45, 0.79)	0.644
Pair_family precip vs Nonfamily precip	0.22 (-0.32, 0.7)	0.444
Pair_family temp within-year vs Pair_mixed temp within-year	0.03 (-0.55, 0.53)	0.944
Pair_family temp within-year vs Multiple_family temp within-year	0.06 (-0.45, 0.66)	0.722
Pair_family temp within-year vs Nonfamily temp within-year	0.23 (-0.3, 0.69)	0.5
Pair_family precip within-year vs Pair_mixed precip within-year	-0.27 (-0.9, 0.28)	0.314
Pair_family precip within-year vs Multiple_family precip within-year	-0.35 (-1.08, 0.16)	0.168
Pair_family precip within-year vs Nonfamily precip within-year	-0.04 (-0.42, 0.61)	0.854
Pair_family temp between-year vs Pair_mixed temp between-year	0.29 (-0.35, 0.85)	0.402
Pair_family temp between-year vs Multiple_family temp between-year	0.21 (-0.46, 0.75)	0.566
Pair_family temp between-year vs Nonfamily temp between-year	0.35 (-0.27, 0.82)	0.3
Pair_family precip between-year vs Pair_mixed precip between-year	-0.28 (-0.79, 0.43)	0.574
Pair_family precip between-year vs Multiple_family precip between-year	0.04 (-0.8, 0.45)	0.592
Pair_family precip between-year vs Nonfamily precip between-year	0.09 (-0.42, 0.67)	0.642
Pair_mixed temp vs Multiple_family temp	-0.03 (-0.63, 0.42)	0.78
Pair_mixed temp vs Nonfamily temp	0.06 (-0.41, 0.51)	0.756
Pair_mixed precip vs Multiple_family precip	0.04 (-0.67, 0.66)	0.986
Pair_mixed precip vs Nonfamily precip	0.16 (-0.5, 0.69)	0.852
Pair_mixed temp within-year vs Multiple_family temp within-year	0.22 (-0.48, 0.77)	0.64
Pair_mixed temp within-year vs Nonfamily temp within-year	0.22 (-0.32, 0.73)	0.47

Pair_mixed precip within-year vs Multiple_family precip within-year	-0.11 (-0.81, 0.53)	0.72
Pair_mixed precip within-year vs Nonfamily precip within-year	0.17 (-0.29, 0.97)	0.216
Pair_mixed temp between-year vs Multiple_family temp between-year	-0.28 (-0.75, 0.56)	0.812
Pair_mixed temp between-year vs Nonfamily temp between-year	0.1 (-0.62, 0.53)	0.956
Pair_mixed precip between-year vs Multiple_family precip between-year	0.17 (-0.73, 0.63)	0.996
Pair_mixed precip between-year vs Nonfamily precip between-year	0.24 (-0.25, 0.96)	0.312
Multiple_family temp vs Nonfamily temp	0.27 (-0.32, 0.64)	0.524
Multiple_family precip vs Nonfamily precip	0.14 (-0.53, 0.64)	0.838
Multiple_family temp within-year vs Nonfamily temp within-year	0.15 (-0.43, 0.66)	0.78
Multiple_family precip within-year vs Nonfamily precip within-year	0.48 (-0.15, 1.04)	0.128
Multiple_family temp between-year vs Nonfamily temp between-year	0.1 (-0.49, 0.71)	0.754
Multiple_family precip between-year vs Nonfamily precip between-year	0.37 (-0.36, 0.95)	0.338
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.3 (0.19, 0.4)	49.39 (31.79, 65.04)
Phylogeny temp within-year	0.45 (0.22, 0.61)	48.97 (21.86, 74.6)
Phylogeny temp between-year	0.46 (0.25, 0.67)	49.42 (25.71, 71.94)
Phylogeny precip	0.51 (0.22, 0.76)	48.89 (26.39, 72.5)
Phylogeny precip within-year	0.38 (0.25, 0.69)	49.21 (28.45, 73.84)
Phylogeny precip between-year	0.5 (0.22, 0.76)	48.86 (23.83, 76.91)
Residual temp	0.26 (0.19, 0.4)	50.61 (34.96, 68.21)
Residual temp within-year	0.43 (0.21, 0.61)	51.03 (25.4, 78.14)
Residual temp between-year	0.49 (0.24, 0.66)	50.58 (28.06, 74.29)
Residual precip	0.49 (0.22, 0.78)	51.11 (27.5, 73.61)
Residual precip within-year	0.53 (0.25, 0.69)	50.79 (26.16, 71.55)

Residual precip between-year	0.59 (0.21, 0.77)	51.14 (23.09, 76.17)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	-0.46 (-0.62, -0.13)	0.02
Phylogeny temp between-year : Phylogeny temp	-0.38 (-0.58, -0.06)	0.032
Phylogeny precip within-year : Phylogeny precip	0.61 (0.24, 0.78)	0.002
Phylogeny precip between-year : Phylogeny precip	0.83 (0.57, 0.88)	0.001
Phylogeny precip : Phylogeny temp	0.06 (-0.3, 0.35)	0.856
Phylogeny precip within-year : Phylogeny temp	0.28 (-0.11, 0.5)	0.186
Phylogeny precip between-year : Phylogeny temp	0.12 (-0.17, 0.49)	0.298
Phylogeny temp within-year : Phylogeny precip	-0.56 (-0.75, -0.2)	0.008
Phylogeny temp between-year : Phylogeny precip	-0.46 (-0.72, -0.11)	0.038
Residual temp within-year : Residual temp	-0.43 (-0.64, -0.15)	0.01
Residual temp between-year : Residual temp	-0.41 (-0.62, -0.12)	0.008
Residual precip within-year : Residual precip	0.61 (0.28, 0.78)	0.002
Residual precip between-year : Residual precip	0.82 (0.59, 0.89)	0.001
Residual precip : Residual temp	0.03 (-0.25, 0.4)	0.68
Residual precip within-year : Residual temp	0.27 (-0.06, 0.5)	0.122
Residual precip between-year : Residual temp	0.18 (-0.13, 0.48)	0.206
Residual temp within-year : Residual precip	-0.59 (-0.75, -0.19)	0.008
Residual temp between-year : Residual precip	-0.51 (-0.73, -0.13)	0.026

Supplementary Table 7: Differences in the environments of pair breeding species, cooperative species with pairs of breeders and cooperative species with multiple breeders.

Fixed Effects	**Posterior Mode (CI)**	**pMCMC**
Pair temp vs Coop pair temp	0.17 (-0.05, 0.4)	0.156
Pair temp vs Multiple temp	0.14 (-0.07, 0.43)	0.152
Pair precip vs Coop pair precip	0.32 (0.05, 0.62)	0.028
Pair precip vs Multiple precip	0.38 (0.05, 0.7)	0.038
Pair temp within-year vs Coop pair temp within-year	-0.04 (-0.33, 0.19)	0.562
Pair temp within-year vs Multiple temp within-year	0.19 (-0.14, 0.46)	0.36
Pair precip within-year vs Coop pair precip within-year	0.45 (0.23, 0.79)	0.001
Pair precip within-year vs Multiple precip within-year	0.38 (0.17, 0.77)	0.004
Pair temp between-year vs Coop pair temp between-year	-0.42 (-0.65, -0.1)	0.006
Pair temp between-year vs Multiple temp between-year	-0.19 (-0.47, 0.13)	0.31
Pair precip between-year vs Coop pair precip between-year	0.13 (-0.1, 0.48)	0.248
Pair precip between-year vs Multiple precip between-year	0.14 (-0.18, 0.48)	0.356
Coop pair temp vs Multiple temp	-0.04 (-0.33, 0.31)	0.902
Coop pair precip vs Multiple precip	-0.02 (-0.39, 0.46)	0.784
Coop pair temp within-year vs Multiple temp within-year	0.28 (-0.16, 0.6)	0.27
Coop pair precip within-year vs Multiple precip within-year	-0.05 (-0.48, 0.33)	0.732
Coop pair temp between-year vs Multiple temp between-year	0.16 (-0.14, 0.62)	0.278
Coop pair precip between-year vs Multiple precip between-year	-0.05 (-0.46, 0.39)	0.918
Random Effects	Posterior Mode (CI)	I2 % (CI)

Phylogeny temp	0.29 (0.18, 0.38)	50.11 (33.21, 66.37)
Phylogeny temp within-year	0.41 (0.21, 0.6)	50.12 (24.38, 77.98)
Phylogeny temp between-year	0.39 (0.23, 0.67)	49.88 (27.5, 73.92)
Phylogeny precip	0.41 (0.23, 0.79)	50.3 (27.51, 73.49)
Phylogeny precip within-year	0.43 (0.23, 0.68)	49.89 (28.01, 74.79)
Phylogeny precip between-year	0.5 (0.21, 0.78)	49.94 (23.64, 77.13)
Residual temp	0.27 (0.19, 0.4)	49.89 (33.63, 66.79)
Residual temp within-year	0.44 (0.22, 0.61)	49.88 (22.02, 75.62)
Residual temp between-year	0.41 (0.24, 0.66)	50.12 (26.08, 72.5)
Residual precip	0.53 (0.23, 0.78)	49.7 (26.51, 72.49)
Residual precip within-year	0.46 (0.23, 0.68)	50.11 (25.21, 71.99)
Residual precip between-year	0.49 (0.23, 0.78)	50.06 (22.87, 76.36)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	-0.37 (-0.61, -0.14)	0.004
Phylogeny temp between-year : Phylogeny temp	-0.36 (-0.57, -0.05)	0.024
Phylogeny precip within-year : Phylogeny precip	0.65 (0.24, 0.76)	0.001
Phylogeny precip between-year : Phylogeny precip	0.81 (0.55, 0.88)	0.001
Phylogeny precip : Phylogeny temp	0.07 (-0.29, 0.37)	0.776
Phylogeny precip within-year : Phylogeny temp	0.18 (-0.09, 0.49)	0.16
Phylogeny precip between-year : Phylogeny temp	0.27 (-0.15, 0.47)	0.27
Phylogeny temp within-year : Phylogeny precip	-0.53 (-0.74, -0.17)	0.014
Phylogeny temp between-year : Phylogeny precip	-0.5 (-0.71, -0.08)	0.038
Residual temp within-year : Residual temp	-0.4 (-0.62, -0.12)	0.012
Residual temp between-year : Residual temp	-0.43 (-0.6, -0.09)	0.03

Residual precip within-year : Residual precip	0.59 (0.24, 0.77)	0.004
Residual precip between-year : Residual precip	0.8 (0.56, 0.89)	0.001
Residual precip : Residual temp	0.09 (-0.31, 0.35)	0.764
Residual precip within-year : Residual temp	0.2 (-0.07, 0.5)	0.194
Residual precip between-year : Residual temp	0.23 (-0.13, 0.48)	0.294
Residual temp within-year : Residual precip	-0.58 (-0.74, -0.17)	0.01
Residual temp between-year : Residual precip	-0.56 (-0.69, -0.07)	0.038

Supplementary Table 8: Differences in the environments of pair breeding species and cooperative breeding species with nonfamily, family, a mix of both nonfamily and family group members, or no helpers.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.14 (-0.16, 0.42)	0.436
Pair temp vs Mixed temp	0.08 (-0.19, 0.39)	0.506
Pair temp vs Nohelpers temp	0.23 (0.02, 0.55)	0.038
Pair precip vs Family precip	0.23 (-0.18, 0.56)	0.312
Pair precip vs Mixed precip	0.41 (0.06, 0.85)	0.016
Pair precip vs Nohelpers precip	0.49 (0.04, 0.72)	0.026
Pair temp within-year vs Family temp within-year	0.03 (-0.36, 0.35)	0.928
Pair temp within-year vs Mixed temp within-year	-0.09 (-0.37, 0.33)	0.828
Pair temp within-year vs Nohelpers temp within-year	0.03 (-0.22, 0.4)	0.71
Pair precip within-year vs Family precip within-year	0.47 (0.2, 0.87)	0.002
Pair precip within-year vs Mixed precip within-year	0.3 (-0.17, 0.61)	0.252
Pair precip within-year vs Nohelpers precip within-year	0.61 (0.27, 0.93)	0.001

Pair temp between-year vs Family temp between-year	-0.34 (-0.75, -0.03)	0.048
Pair temp between-year vs Mixed temp between-year	-0.17 (-0.59, 0.16)	0.286
Pair temp between-year vs Nohelpers temp between-year	-0.27 (-0.57, 0.08)	0.112
Pair precip between-year vs Family precip between-year	0.11 (-0.25, 0.48)	0.42
Pair precip between-year vs Mixed precip between-year	0.02 (-0.34, 0.44)	0.88
Pair precip between-year vs Nohelpers precip between-year	0.37 (-0.02, 0.66)	0.106
Family temp vs Mixed temp	-0.08 (-0.42, 0.4)	0.932
Family temp vs Nohelpers temp	0.25 (-0.22, 0.54)	0.422
Family precip vs Mixed precip	0.31 (-0.22, 0.86)	0.356
Family precip vs Nohelpers precip	0.19 (-0.31, 0.72)	0.452
Family temp within-year vs Mixed temp within-year	-0.01 (-0.53, 0.43)	0.824
Family temp within-year vs Nohelpers temp within-year	-0.03 (-0.4, 0.53)	0.85
Family precip within-year vs Mixed precip within-year	-0.27 (-0.8, 0.2)	0.254
Family precip within-year vs Nohelpers precip within-year	0.12 (-0.39, 0.53)	0.772
Family temp between-year vs Mixed temp between-year	0.12 (-0.38, 0.63)	0.548
Family temp between-year vs Nohelpers temp between-year	-0.06 (-0.34, 0.63)	0.672
Family precip between-year vs Mixed precip between-year	-0.1 (-0.66, 0.39)	0.63
Family precip between-year vs Nohelpers precip between-year	0.18 (-0.42, 0.57)	0.594
Mixed temp vs Nohelpers temp	0.11 (-0.21, 0.55)	0.39
Mixed precip vs Nohelpers precip	0 (-0.56, 0.44)	0.842
Mixed temp within-year vs Nohelpers temp within-year	0.02 (-0.34, 0.52)	0.666

Mixed precip within-year vs Nohelpers precip within-year	0.39 (-0.12, 0.85)	0.154
Mixed temp between-year vs Nohelpers temp between-year	0.08 (-0.53, 0.41)	0.86
Mixed precip between-year vs Nohelpers precip between-year	0.37 (-0.27, 0.73)	0.33
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.29 (0.19, 0.41)	50.12 (34.98, 68.95)
Phylogeny temp within-year	0.34 (0.21, 0.62)	48.92 (21.61, 75.09)
Phylogeny temp between-year	0.44 (0.22, 0.67)	49.59 (27.28, 75.45)
Phylogeny precip	0.39 (0.22, 0.77)	49.52 (24.99, 73.88)
Phylogeny precip within-year	0.41 (0.25, 0.72)	49.9 (26.05, 74.33)
Phylogeny precip between-year	0.41 (0.22, 0.76)	48.79 (23.04, 75.32)
Residual temp	0.3 (0.19, 0.39)	49.88 (31.05, 65.02)
Residual temp within-year	0.45 (0.21, 0.63)	51.08 (24.91, 78.39)
Residual temp between-year	0.46 (0.23, 0.68)	50.41 (24.55, 72.72)
Residual precip	0.48 (0.22, 0.78)	50.48 (26.12, 75.01)
Residual precip within-year	0.46 (0.22, 0.69)	50.1 (25.67, 73.95)
Residual precip between-year	0.49 (0.23, 0.79)	51.21 (24.68, 76.96)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	-0.37 (-0.63, -0.13)	0.014
Phylogeny temp between-year : Phylogeny temp	-0.37 (-0.57, -0.07)	0.028
Phylogeny precip within-year : Phylogeny precip	0.64 (0.2, 0.75)	0.002
Phylogeny precip between-year : Phylogeny precip	0.83 (0.56, 0.88)	0.001
Phylogeny precip : Phylogeny temp	0.03 (-0.31, 0.35)	0.822
Phylogeny precip within-year : Phylogeny temp	0.28 (-0.07, 0.5)	0.17
Phylogeny precip between-year : Phylogeny temp	0.21 (-0.13, 0.47)	0.276

Phylogeny temp within-year : Phylogeny precip	-0.64 (-0.76, -0.15)	0.008
Phylogeny temp between-year : Phylogeny precip	-0.55 (-0.7, -0.04)	0.056
Residual temp within-year : Residual temp	-0.45 (-0.6, -0.12)	0.008
Residual temp between-year : Residual temp	-0.38 (-0.59, -0.07)	0.03
Residual precip within-year : Residual precip	0.59 (0.25, 0.77)	0.004
Residual precip between-year : Residual precip	0.84 (0.6, 0.89)	0.001
Residual precip : Residual temp	0.08 (-0.28, 0.35)	0.756
Residual precip within-year : Residual temp	0.19 (-0.04, 0.53)	0.154
Residual precip between-year : Residual temp	0.28 (-0.12, 0.48)	0.24
Residual temp within-year : Residual precip	-0.6 (-0.73, -0.18)	0.008
Residual temp between-year : Residual precip	-0.55 (-0.72, -0.08)	0.044

Supplementary Table 9: Differences in the environments of pair breeders, nonfamily cooperative breeders and family cooperative breeders with classifications assigned without a threshold (>0%).

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.01 (-0.1, 0.19)	0.674
Pair temp vs Nonfamily temp	0.18 (-0.03, 0.45)	0.106
Pair precip vs Family precip	0.32 (0.07, 0.47)	0.006
Pair precip vs Nonfamily precip	0.14 (-0.12, 0.53)	0.254
Pair temp within-year vs Family temp within-year	0.09 (-0.08, 0.27)	0.352
Pair temp within-year vs Nonfamily temp within-year	0.25 (-0.1, 0.5)	0.186
Pair precip within-year vs Family precip within-year	0.29 (0.13, 0.52)	0.001

Pair precip within-year vs Nonfamily precip within-year	0.39 (0.07, 0.67)	0.018
Pair temp between-year vs Family temp between-year	-0.15 (-0.35, 0.02)	0.08
Pair temp between-year vs Nonfamily temp between-year	-0.12 (-0.42, 0.19)	0.598
Pair precip between-year vs Family precip between-year	0.13 (-0.05, 0.35)	0.182
Pair precip between-year vs Nonfamily precip between-year	0.05 (-0.29, 0.34)	0.92
Family temp vs Nonfamily temp	0.13 (-0.08, 0.46)	0.208
Family precip vs Nonfamily precip	-0.03 (-0.42, 0.29)	0.658
Family temp within-year vs Nonfamily temp within-year	0.12 (-0.21, 0.43)	0.46
Family precip within-year vs Nonfamily precip within-year	-0.09 (-0.27, 0.4)	0.728
Family temp between-year vs Nonfamily temp between-year	0.01 (-0.28, 0.4)	0.706
Family precip between-year vs Nonfamily precip between-year	-0.08 (-0.45, 0.25)	0.536
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.26 (0.2, 0.4)	52.5 (36.98, 70.22)
Phylogeny temp within-year	0.4 (0.2, 0.58)	52.15 (24.91, 78.61)
Phylogeny temp between-year	0.41 (0.25, 0.64)	50.77 (27.4, 73.43)
Phylogeny precip	0.56 (0.22, 0.76)	52.65 (27.37, 75.22)
Phylogeny precip within-year	0.53 (0.24, 0.69)	50.68 (27.91, 72.03)
Phylogeny precip between-year	0.63 (0.23, 0.78)	52.39 (25.02, 78.87)
Residual temp	0.28 (0.16, 0.36)	47.5 (29.78, 63.02)
Residual temp within-year	0.35 (0.2, 0.58)	47.85 (21.39, 75.09)
Residual temp between-year	0.34 (0.23, 0.62)	49.23 (26.57, 72.6)
Residual precip	0.3 (0.21, 0.75)	47.35 (24.78, 72.63)
Residual precip within-year	0.38 (0.22, 0.67)	49.32 (27.97, 72.09)
Residual precip between-year	0.45 (0.21, 0.76)	47.61 (21.13, 74.98)
Correlations	Posterior Mode (CI)	pMCMC

Phylogeny temp within-year : Phylogeny temp	-0.52 (-0.63, -0.2)	0.002
Phylogeny temp between-year : Phylogeny temp	-0.44 (-0.61, -0.16)	0.004
Phylogeny precip within-year : Phylogeny precip	0.69 (0.28, 0.78)	0.006
Phylogeny precip between-year : Phylogeny precip	0.82 (0.59, 0.89)	0.001
Phylogeny precip : Phylogeny temp	0.1 (-0.28, 0.37)	0.668
Phylogeny precip within-year : Phylogeny temp	0.34 (-0.03, 0.51)	0.088
Phylogeny precip between-year : Phylogeny temp	0.24 (-0.11, 0.47)	0.188
Phylogeny temp within-year : Phylogeny precip	-0.62 (-0.73, -0.19)	0.006
Phylogeny temp between-year : Phylogeny precip	-0.51 (-0.72, -0.1)	0.03
Residual temp within-year : Residual temp	-0.43 (-0.62, -0.14)	0.006
Residual temp between-year : Residual temp	-0.41 (-0.59, -0.07)	0.042
Residual precip within-year : Residual precip	0.6 (0.24, 0.78)	0.006
Residual precip between-year : Residual precip	0.82 (0.55, 0.88)	0.001
Residual precip : Residual temp	0.06 (-0.33, 0.37)	0.844
Residual precip within-year : Residual temp	0.28 (-0.08, 0.51)	0.164
Residual precip between-year : Residual temp	0.16 (-0.16, 0.47)	0.296
Residual temp within-year : Residual precip	-0.63 (-0.76, -0.19)	0.01
Residual temp between-year : Residual precip	-0.55 (-0.7, -0.05)	0.044

Supplementary Table 10: Differences in the environments of pair breeders, nonfamily cooperative breeders and family cooperative breeders with classifications assigned using a 30% nests threshold.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0 (-0.26, 0.29)	0.878
Pair temp vs Nonfamily temp	0.1 (-0.29, 0.4)	0.802
Pair precip vs Family precip	0.45 (0.08, 0.79)	0.026
Pair precip vs Nonfamily precip	0.39 (-0.08, 0.78)	0.136
Pair temp within-year vs Family temp within-year	-0.09 (-0.42, 0.2)	0.618
Pair temp within-year vs Nonfamily temp within-year	0.43 (-0.09, 0.69)	0.138
Pair precip within-year vs Family precip within-year	0.43 (0.08, 0.75)	0.012
Pair precip within-year vs Nonfamily precip within-year	0.31 (0.09, 0.88)	0.026
Pair temp between-year vs Family temp between-year	-0.37 (-0.62, 0.02)	0.056
Pair temp between-year vs Nonfamily temp between-year	-0.03 (-0.43, 0.41)	0.846
Pair precip between-year vs Family precip between-year	0.17 (-0.18, 0.53)	0.308
Pair precip between-year vs Nonfamily precip between-year	-0.02 (-0.4, 0.45)	0.918
Family temp vs Nonfamily temp	0.08 (-0.43, 0.42)	0.962
Family precip vs Nonfamily precip	-0.06 (-0.62, 0.5)	0.688
Family temp within-year vs Nonfamily temp within-year	0.44 (-0.09, 0.9)	0.138
Family precip within-year vs Nonfamily precip within-year	0.06 (-0.51, 0.53)	0.896
Family temp between-year vs Nonfamily temp between-year	0.35 (-0.24, 0.8)	0.296
Family precip between-year vs Nonfamily precip between-year	-0.36 (-0.72, 0.39)	0.534
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.31 (0.19, 0.41)	49.98 (35.11, 68.25)
Phylogeny temp within-year	0.35 (0.2, 0.6)	49.43 (22.78, 75.62)
Phylogeny temp between-year	0.43 (0.21, 0.64)	50.14 (26.95, 73.26)

Phylogeny precip	0.37 (0.24, 0.78)	49.39 (27.42, 74.7)
Phylogeny precip within-year	0.43 (0.23, 0.7)	49.7 (27.45, 73.78)
Phylogeny precip between-year	0.43 (0.21, 0.77)	49.48 (24.42, 78.22)
Residual temp	0.3 (0.2, 0.4)	50.02 (31.75, 64.89)
Residual temp within-year	0.39 (0.22, 0.61)	50.57 (24.38, 77.22)
Residual temp between-year	0.46 (0.24, 0.67)	49.86 (26.74, 73.05)
Residual precip	0.57 (0.24, 0.79)	50.61 (25.3, 72.58)
Residual precip within-year	0.5 (0.25, 0.71)	50.3 (26.22, 72.55)
Residual precip between-year	0.57 (0.22, 0.79)	50.52 (21.78, 75.58)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	-0.42 (-0.6, -0.12)	0.008
Phylogeny temp between-year : Phylogeny temp	-0.34 (-0.58, -0.09)	0.024
Phylogeny precip within-year : Phylogeny precip	0.63 (0.21, 0.77)	0.002
Phylogeny precip between-year : Phylogeny precip	0.84 (0.57, 0.89)	0.001
Phylogeny precip : Phylogeny temp	0.05 (-0.31, 0.38)	0.744
Phylogeny precip within-year : Phylogeny temp	0.26 (-0.05, 0.53)	0.142
Phylogeny precip between-year : Phylogeny temp	0.23 (-0.16, 0.47)	0.268
Phylogeny temp within-year : Phylogeny precip	-0.54 (-0.75, -0.17)	0.008
Phylogeny temp between-year : Phylogeny precip	-0.49 (-0.74, -0.09)	0.03
Residual temp within-year : Residual temp	-0.45 (-0.61, -0.12)	0.012
Residual temp between-year : Residual temp	-0.34 (-0.6, -0.08)	0.036
Residual precip within-year : Residual precip	0.63 (0.24, 0.78)	0.001
Residual precip between-year : Residual precip	0.82 (0.57, 0.88)	0.001

Residual precip : Residual temp	0.09 (-0.27, 0.4)	0.694
Residual precip within-year : Residual temp	0.32 (-0.07, 0.48)	0.138
Residual precip between-year : Residual temp	0.21 (-0.12, 0.49)	0.258
Residual temp within-year : Residual precip	-0.56 (-0.77, -0.19)	0.016
Residual temp between-year : Residual precip	-0.48 (-0.72, -0.09)	0.044

Supplementary Table 11: Examining the correlations between climate variables across different breeding systems.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.1 (-0.13, 0.32)	0.386
Pair temp vs Nonfamily temp	0.19 (-0.16, 0.6)	0.24
Pair precip vs Family precip	0.3 (0.05, 0.58)	0.026
Pair precip vs Nonfamily precip	0.5 (0.05, 0.83)	0.036
Pair temp within-year vs Family temp within-year	-0.07 (-0.26, 0.24)	0.962
Pair temp within-year vs Nonfamily temp within-year	0.04 (-0.2, 0.51)	0.414
Pair precip within-year vs Family precip within-year	0.39 (0.11, 0.64)	0.01
Pair precip within-year vs Nonfamily precip within-year	0.74 (0.28, 1.02)	0.001
Pair temp between-year vs Family temp between-year	-0.29 (-0.55, -0.02)	0.058
Pair temp between-year vs Nonfamily temp between-year	-0.05 (-0.52, 0.3)	0.52
Pair precip between-year vs Family precip between-year	0.04 (-0.19, 0.36)	0.57
Pair precip between-year vs Nonfamily precip between-year	0.38 (-0.09, 0.71)	0.164
Family temp vs Nonfamily temp	0.29 (-0.36, 0.5)	0.514
Family precip vs Nonfamily precip	0.18 (-0.35, 0.55)	0.576

Family temp within-year vs Nonfamily temp within-year	0.19 (-0.26, 0.57)	0.454
Family precip within-year vs Nonfamily precip within-year	0.32 (-0.2, 0.69)	0.258
Family temp between-year vs Nonfamily temp between-year	0.17 (-0.36, 0.6)	0.552
Family precip between-year vs Nonfamily precip between-year	0.25 (-0.28, 0.7)	0.326
Random Effects	Posterior Mode (CI)	I2 % (CI)
Pair Phylogeny temp	0.3 (0.22, 0.43)	20.82 (12.86, 28.93)
Pair Phylogeny temp within-year	0.54 (0.36, 0.71)	31.18 (18.68, 42.8)
Pair Phylogeny temp between-year	0.49 (0.32, 0.7)	30.85 (18.83, 39.96)
Pair Phylogeny precip	0.65 (0.38, 0.88)	27.89 (16.59, 37.97)
Pair Phylogeny precip within-year	0.58 (0.36, 0.79)	24.25 (14.04, 33.57)
Pair Phylogeny precip between-year	0.61 (0.4, 0.87)	28.18 (17.01, 39.13)
Family Phylogeny temp	0.32 (0.22, 0.6)	24.54 (13.24, 34.89)
Family Phylogeny temp within-year	0.29 (0.19, 0.6)	20.77 (11.74, 30.5)
Family Phylogeny temp between-year	0.41 (0.22, 0.78)	21.24 (11.66, 32)
Family Phylogeny precip	0.4 (0.21, 0.69)	23.5 (12.1, 34.82)
Family Phylogeny precip within-year	0.46 (0.22, 0.78)	23.52 (12.52, 34.92)
Family Phylogeny precip between-year	0.44 (0.24, 0.81)	21.77 (11.77, 33.35)
Nonfamily Phylogeny temp	0.57 (0.26, 1.1)	37.87 (21.93, 54.56)
Nonfamily Phylogeny temp within-year	0.44 (0.19, 0.96)	28.87 (16.59, 45.66)
Nonfamily Phylogeny temp between-year	0.77 (0.32, 1.33)	30.19 (16.84, 46.24)
Nonfamily Phylogeny precip	0.54 (0.22, 1.08)	28.18 (14.33, 42.22)
Nonfamily Phylogeny precip within-year	0.44 (0.24, 1.02)	33.42 (18.22, 49.49)
Nonfamily Phylogeny precip between-year	0.46 (0.27, 1.26)	31.32 (18.93, 48.66)
Residual temp	0.25 (0.18, 0.37)	16.77 (8.86, 24.83)
Residual temp within-year	0.26 (0.17, 0.46)	19.19 (8.13, 31.2)
Residual temp between-year	0.34 (0.21, 0.57)	17.72 (8.87, 28.54)

Residual precip	0.41 (0.2, 0.6)	20.43 (9.2, 32.16)
Residual precip within-year	0.42 (0.23, 0.61)	18.81 (8.7, 29.32)
Residual precip between-year	0.37 (0.21, 0.62)	18.72 (7.84, 31.03)
Correlations	Posterior Mode (CI)	pMCMC
Pair Phylogeny temp within-year : Pair Phylogeny temp	-0.38 (-0.61, -0.21)	0.001
Pair Phylogeny temp between-year : Pair Phylogeny temp	-0.32 (-0.56, -0.13)	0.002
Pair Phylogeny precip within-year : Pair Phylogeny precip	0.57 (0.34, 0.73)	0.001
Pair Phylogeny precip between-year : Pair Phylogeny precip	0.85 (0.74, 0.9)	0.001
Pair Phylogeny precip : Pair Phylogeny temp	0.12 (-0.18, 0.32)	0.598
Pair Phylogeny precip within-year : Pair Phylogeny temp	0.21 (-0.1, 0.41)	0.164
Pair Phylogeny precip between-year : Pair Phylogeny temp	0.19 (-0.11, 0.4)	0.188
Pair Phylogeny temp within-year : Pair Phylogeny precip	-0.56 (-0.71, -0.37)	0.001
Pair Phylogeny temp between-year : Pair Phylogeny precip	-0.54 (-0.67, -0.26)	0.002
Pair Phylogeny precip within-year : Pair Phylogeny temp within-year	-0.24 (-0.45, 0.04)	0.116
Pair Phylogeny precip between-year : Pair Phylogeny temp between-year	-0.44 (-0.63, -0.15)	0.018
Family Phylogeny temp within-year : Family Phylogeny temp	-0.18 (-0.51, 0.16)	0.26
Family Phylogeny temp between-year : Family Phylogeny temp	-0.16 (-0.48, 0.24)	0.518
Family Phylogeny precip within-year : Family Phylogeny precip	0.34 (-0.05, 0.65)	0.086
Family Phylogeny precip between-year : Family Phylogeny precip	0.44 (0.06, 0.72)	0.042
Family Phylogeny precip : Family Phylogeny temp	-0.19 (-0.45, 0.27)	0.624
Family Phylogeny precip within-year : Family Phylogeny temp	0.29 (-0.22, 0.5)	0.376

Family Phylogeny precip between-year : Family Phylogeny temp	0.1 (-0.26, 0.45)	0.574
Family Phylogeny temp within-year : Family Phylogeny precip	-0.18 (-0.56, 0.17)	0.248
Family Phylogeny temp between-year : Family Phylogeny precip	-0.26 (-0.58, 0.14)	0.294
Family Phylogeny precip within-year : Family Phylogeny temp within-year	-0.31 (-0.67, 0.03)	0.096
Family Phylogeny precip between-year : Family Phylogeny temp between-year	-0.07 (-0.54, 0.24)	0.43
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny temp	-0.29 (-0.67, 0.13)	0.158
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny temp	-0.22 (-0.65, 0.21)	0.294
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny precip	0.39 (-0.13, 0.7)	0.19
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny precip	0.15 (-0.25, 0.63)	0.376
Nonfamily Phylogeny precip : Nonfamily Phylogeny temp	-0.07 (-0.53, 0.34)	0.788
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp	0.22 (-0.31, 0.58)	0.484
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp	0.09 (-0.25, 0.62)	0.39
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny precip	-0.14 (-0.5, 0.41)	0.754
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny precip	-0.06 (-0.55, 0.35)	0.704
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp within-year	0.02 (-0.52, 0.4)	0.852
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp between-year	-0.1 (-0.49, 0.42)	0.914
Residual temp within-year : Residual temp	-0.46 (-0.62, -0.16)	0.004
Residual temp between-year : Residual temp	-0.43 (-0.6, -0.11)	0.014
Residual precip within-year : Residual precip	0.62 (0.34, 0.79)	0.002

Residual precip between-year : Residual precip	0.77 (0.58, 0.86)	0.001
Residual precip : Residual temp	0.05 (-0.24, 0.36)	0.728
Residual precip within-year : Residual temp	0.32 (0, 0.53)	0.072
Residual precip between-year : Residual temp	0.24 (-0.1, 0.48)	0.192
Residual temp within-year : Residual precip	-0.35 (-0.63, -0.01)	0.046
Residual temp between-year : Residual precip	-0.33 (-0.65, -0.02)	0.074
Residual precip within-year : Residual temp within-year	-0.43 (-0.6, -0.01)	0.046
Residual precip between-year : Residual temp between-year	-0.35 (-0.63, -0.02)	0.074
Correlation comparions	Estimates	pMCMC
Pair Phylogeny precip : Pair Phylogeny temp vs Family Phylogeny precip : Family Phylogeny temp	0.25 (-0.27, 0.58)	0.456
Pair Phylogeny precip : Pair Phylogeny temp vs Nonfamily Phylogeny precip : Nonfamily Phylogeny temp	0.21 (-0.33, 0.66)	0.616
Pair Phylogeny precip within-year : Pair Phylogeny temp vs Family Phylogeny precip within-year : Family Phylogeny temp	0.13 (-0.4, 0.45)	0.922
Pair Phylogeny precip within-year : Pair Phylogeny temp vs Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp	-0.08 (-0.48, 0.53)	0.982
Pair Phylogeny precip between-year : Pair Phylogeny temp vs Family Phylogeny precip between-year : Family Phylogeny temp	0.02 (-0.31, 0.5)	0.76
Pair Phylogeny precip between-year : Pair Phylogeny temp vs Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp	0.04 (-0.5, 0.46)	0.942
Pair Phylogeny temp within-year : Pair Phylogeny precip vs Family Phylogeny temp within-year : Family Phylogeny precip	-0.2 (-0.74, 0.03)	0.074

Pair Phylogeny temp within-year : Pair Phylogeny precip vs Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny precip	-0.4 (-0.98, -0.02)	0.038
Pair Phylogeny temp between-year : Pair Phylogeny precip vs Family Phylogeny temp between-year : Family Phylogeny precip	-0.34 (-0.65, 0.12)	0.156
Pair Phylogeny temp between-year : Pair Phylogeny precip vs Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny precip	-0.55 (-0.91, 0.06)	0.096
Pair Phylogeny precip within-year : Pair Phylogeny temp within-year vs Family Phylogeny precip within-year : Family Phylogeny temp within-year	0.07 (-0.38, 0.41)	0.588
Pair Phylogeny precip within-year : Pair Phylogeny temp within-year vs Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp within-year	-0.32 (-0.64, 0.38)	0.514
Pair Phylogeny precip between-year : Pair Phylogeny temp between-year vs Family Phylogeny precip between-year : Family Phylogeny temp between-year	-0.18 (-0.66, 0.17)	0.226
Pair Phylogeny precip between-year : Pair Phylogeny temp between-year vs Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp between-year	-0.39 (-0.83, 0.2)	0.16
Family Phylogeny precip : Family Phylogeny temp vs Nonfamily Phylogeny precip : Nonfamily Phylogeny temp	-0.17 (-0.55, 0.55)	0.88
Family Phylogeny precip within-year : Family Phylogeny temp vs Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp	-0.05 (-0.52, 0.62)	0.992
Family Phylogeny precip between-year : Family Phylogeny temp vs Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp	-0.14 (-0.6, 0.49)	0.746
Family Phylogeny temp within-year : Family Phylogeny precip vs Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny precip	-0.2 (-0.68, 0.47)	0.648
Family Phylogeny temp between-year : Family Phylogeny precip vs Nonfamily	0.07 (-0.7, 0.47)	0.712

Phylogeny temp between-year : Nonfamily Phylogeny precip		
Family Phylogeny precip within-year : Family Phylogeny temp within-year vs Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp within-year	-0.27 (-0.81, 0.33)	0.396
Family Phylogeny precip between-year : Family Phylogeny temp between-year vs Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp between-year	-0.04 (-0.71, 0.46)	0.668

Supplementary Table 12: Reanalysis of model mod_climcorrs but with down sampling to check greater number of pair species does not alter results.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.07 (-0.19, 0.34)	0.62
Pair temp vs Nonfamily temp	0.2 (-0.19, 0.58)	0.33
Pair precip vs Family precip	0.33 (0.04, 0.64)	0.01
Pair precip vs Nonfamily precip	0.46 (0.08, 0.91)	0.018
Pair temp within-year vs Family temp within-year	-0.08 (-0.35, 0.2)	0.672
Pair temp within-year vs Nonfamily temp within-year	0.06 (-0.32, 0.47)	0.628
Pair precip within-year vs Family precip within-year	0.41 (0.14, 0.78)	0.016
Pair precip within-year vs Nonfamily precip within-year	0.7 (0.29, 1.1)	0.002
Pair temp between-year vs Family temp between-year	-0.36 (-0.67, -0.05)	0.03
Pair temp between-year vs Nonfamily temp between-year	-0.29 (-0.67, 0.18)	0.28
Pair precip between-year vs Family precip between-year	0.19 (-0.16, 0.46)	0.334
Pair precip between-year vs Nonfamily precip between-year	0.41 (-0.05, 0.81)	0.078
Family temp vs Nonfamily temp	0.12 (-0.3, 0.53)	0.56
Family precip vs Nonfamily precip	0.24 (-0.29, 0.6)	0.534

Family temp within-year vs Nonfamily temp within-year	0.16 (-0.28, 0.56)	0.484
Family precip within-year vs Nonfamily precip within-year	0.3 (-0.16, 0.73)	0.228
Family temp between-year vs Nonfamily temp between-year	0.03 (-0.4, 0.57)	0.632
Family precip between-year vs Nonfamily precip between-year	0.09 (-0.2, 0.71)	0.336
Random Effects	Posterior Mode (CI)	I2 % (CI)
Pair Phylogeny temp	0.36 (0.25, 0.57)	23.46 (13.73, 33.12)
Pair Phylogeny temp within-year	0.55 (0.35, 0.85)	27.42 (15.96, 39.47)
Pair Phylogeny temp between-year	0.46 (0.26, 0.73)	32.6 (21.66, 46.27)
Pair Phylogeny precip	0.59 (0.3, 0.83)	31.46 (18.33, 44.58)
Pair Phylogeny precip within-year	0.72 (0.38, 1.02)	23.39 (13.35, 34.06)
Pair Phylogeny precip between-year	0.62 (0.32, 0.91)	27.97 (14.97, 39.26)
Family Phylogeny temp	0.35 (0.22, 0.63)	23.4 (13.48, 35.08)
Family Phylogeny temp within-year	0.31 (0.19, 0.6)	22.7 (12.66, 34.28)
Family Phylogeny temp between-year	0.53 (0.26, 0.8)	20.16 (10.95, 30.37)
Family Phylogeny precip	0.38 (0.23, 0.74)	21.4 (10.99, 32.46)
Family Phylogeny precip within-year	0.41 (0.22, 0.77)	24.14 (13.64, 36.41)
Family Phylogeny precip between-year	0.45 (0.24, 0.8)	21.61 (11.55, 32.94)
Nonfamily Phylogeny temp	0.54 (0.3, 1.09)	35.59 (20.83, 51.27)
Nonfamily Phylogeny temp within-year	0.43 (0.26, 0.96)	31.39 (17.07, 46.46)
Nonfamily Phylogeny temp between-year	0.54 (0.31, 1.29)	29.35 (16.77, 44.18)
Nonfamily Phylogeny precip	0.53 (0.27, 1.17)	26.61 (13.03, 41.49)
Nonfamily Phylogeny precip within-year	0.54 (0.26, 1.11)	33.77 (19.83, 51.8)
Nonfamily Phylogeny precip between-year	0.6 (0.29, 1.25)	30.91 (17.28, 46.47)
Residual temp	0.29 (0.17, 0.41)	17.55 (9.89, 27.15)
Residual temp within-year	0.36 (0.19, 0.5)	18.5 (8.83, 29.14)
Residual temp between-year	0.38 (0.21, 0.55)	17.88 (8.18, 27.02)

Residual precip	0.36 (0.19, 0.53)	20.53 (9.79, 33.26)
Residual precip within-year	0.43 (0.23, 0.65)	18.7 (7.78, 28.61)
Residual precip between-year	0.37 (0.22, 0.65)	19.5 (8.63, 31.77)
Correlations	Posterior Mode (CI)	pMCMC
Pair Phylogeny temp within-year : Pair Phylogeny temp	-0.35 (-0.6, -0.1)	0.028
Pair Phylogeny temp between-year : Pair Phylogeny temp	-0.31 (-0.6, -0.05)	0.032
Pair Phylogeny precip within-year : Pair Phylogeny precip	0.42 (0, 0.61)	0.07
Pair Phylogeny precip between-year : Pair Phylogeny precip	0.78 (0.59, 0.88)	0.001
Pair Phylogeny precip : Pair Phylogeny temp	0.1 (-0.23, 0.4)	0.536
Pair Phylogeny precip within-year : Pair Phylogeny temp	0.16 (-0.12, 0.46)	0.266
Pair Phylogeny precip between-year : Pair Phylogeny temp	0.23 (-0.11, 0.5)	0.186
Pair Phylogeny temp within-year : Pair Phylogeny precip	-0.51 (-0.73, -0.29)	0.004
Pair Phylogeny temp between-year : Pair Phylogeny precip	-0.53 (-0.71, -0.18)	0.01
Pair Phylogeny precip within-year : Pair Phylogeny temp within-year	-0.12 (-0.34, 0.32)	0.77
Pair Phylogeny precip between-year : Pair Phylogeny temp between-year	-0.5 (-0.72, -0.13)	0.028
Family Phylogeny temp within-year : Family Phylogeny temp	-0.23 (-0.59, 0.11)	0.24
Family Phylogeny temp between-year : Family Phylogeny temp	-0.18 (-0.46, 0.22)	0.506
Family Phylogeny precip within-year : Family Phylogeny precip	0.29 (-0.03, 0.66)	0.08
Family Phylogeny precip between-year : Family Phylogeny precip	0.47 (0.05, 0.68)	0.038
Family Phylogeny precip : Family Phylogeny temp	-0.17 (-0.48, 0.28)	0.66
Family Phylogeny precip within-year : Family Phylogeny temp	0.16 (-0.21, 0.52)	0.404

Family Phylogeny precip between-year : Family Phylogeny temp	0.11 (-0.3, 0.44)	0.618
Family Phylogeny temp within-year : Family Phylogeny precip	-0.25 (-0.56, 0.15)	0.254
Family Phylogeny temp between-year : Family Phylogeny precip	-0.2 (-0.55, 0.17)	0.276
Family Phylogeny precip within-year : Family Phylogeny temp within-year	-0.34 (-0.69, 0.02)	0.122
Family Phylogeny precip between-year : Family Phylogeny temp between-year	-0.24 (-0.51, 0.26)	0.486
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny temp	-0.43 (-0.66, 0.15)	0.21
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny temp	-0.33 (-0.64, 0.19)	0.32
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny precip	0.34 (-0.11, 0.71)	0.168
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny precip	0.24 (-0.23, 0.62)	0.366
Nonfamily Phylogeny precip : Nonfamily Phylogeny temp	-0.08 (-0.49, 0.43)	0.752
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp	0.3 (-0.28, 0.62)	0.566
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp	0.34 (-0.29, 0.59)	0.464
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny precip	-0.14 (-0.49, 0.4)	0.756
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny precip	-0.17 (-0.52, 0.35)	0.752
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp within-year	-0.01 (-0.49, 0.38)	0.844
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp between-year	0.08 (-0.52, 0.42)	0.978
Residual temp within-year : Residual temp	-0.36 (-0.62, -0.09)	0.014
Residual temp between-year : Residual temp	-0.33 (-0.61, -0.07)	0.026
Residual precip within-year : Residual precip	0.55 (0.23, 0.73)	0.004

Residual precip between-year : Residual precip	0.73 (0.45, 0.81)	0.001
Residual precip : Residual temp	0.03 (-0.18, 0.46)	0.592
Residual precip within-year : Residual temp	0.34 (0, 0.56)	0.066
Residual precip between-year : Residual temp	0.23 (-0.05, 0.52)	0.156
Residual temp within-year : Residual precip	-0.46 (-0.74, -0.04)	0.04
Residual temp between-year : Residual precip	-0.47 (-0.75, -0.07)	0.036
Residual precip within-year : Residual temp within-year	-0.47 (-0.64, -0.04)	0.04
Residual precip between-year : Residual temp between-year	-0.42 (-0.68, -0.09)	0.036
Correlation comparions	Estimates	pMCMC
Pair Phylogeny precip : Pair Phylogeny temp vs Family Phylogeny precip : Family Phylogeny temp	0.25 (-0.29, 0.64)	0.436
Pair Phylogeny precip : Pair Phylogeny temp vs Nonfamily Phylogeny precip : Nonfamily Phylogeny temp	0.11 (-0.39, 0.7)	0.52
Pair Phylogeny precip within-year : Pair Phylogeny temp vs Family Phylogeny precip within-year : Family Phylogeny temp	-0.11 (-0.41, 0.49)	0.99
Pair Phylogeny precip within-year : Pair Phylogeny temp vs Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp	0 (-0.48, 0.58)	0.944
Pair Phylogeny precip between-year : Pair Phylogeny temp vs Family Phylogeny precip between-year : Family Phylogeny temp	0.08 (-0.31, 0.59)	0.644
Pair Phylogeny precip between-year : Pair Phylogeny temp vs Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp	-0.06 (-0.46, 0.59)	0.93
Pair Phylogeny temp within-year : Pair Phylogeny precip vs Family Phylogeny temp within-year : Family Phylogeny precip	-0.33 (-0.69, 0.09)	0.156

Pair Phylogeny temp within-year : Pair Phylogeny precip vs Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny precip	-0.35 (-0.99, -0.01)	0.064
Pair Phylogeny temp between-year : Pair Phylogeny precip vs Family Phylogeny temp between-year : Family Phylogeny precip	-0.2 (-0.68, 0.14)	0.204
Pair Phylogeny temp between-year : Pair Phylogeny precip vs Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny precip	-0.44 (-0.9, 0.11)	0.118
Pair Phylogeny precip within-year : Pair Phylogeny temp within-year vs Family Phylogeny precip within-year : Family Phylogeny temp within-year	0.21 (-0.16, 0.7)	0.224
Pair Phylogeny precip within-year : Pair Phylogeny temp within-year vs Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp within-year	-0.07 (-0.57, 0.51)	0.982
Pair Phylogeny precip between-year : Pair Phylogeny temp between-year vs Family Phylogeny precip between-year : Family Phylogeny temp between-year	-0.23 (-0.71, 0.16)	0.202
Pair Phylogeny precip between-year : Pair Phylogeny temp between-year vs Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp between-year	-0.44 (-0.98, 0.07)	0.1
Family Phylogeny precip : Family Phylogeny temp vs Nonfamily Phylogeny precip : Nonfamily Phylogeny temp	0.15 (-0.61, 0.58)	0.932
Family Phylogeny precip within-year : Family Phylogeny temp vs Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp	0.05 (-0.56, 0.57)	0.946
Family Phylogeny precip between-year : Family Phylogeny temp vs Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp	-0.14 (-0.64, 0.48)	0.758
Family Phylogeny temp within-year : Family Phylogeny precip vs Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny precip	-0.23 (-0.72, 0.42)	0.632
Family Phylogeny temp between-year : Family Phylogeny precip vs Nonfamily	-0.17 (-0.7, 0.44)	0.698

Phylogeny temp between-year : Nonfamily Phylogeny precip			
Family Phylogeny precip within-year : Family Phylogeny temp within-year vs Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp within-year	-0.42 (-0.9, 0.24)	0.354	
Family Phylogeny precip between-year : Family Phylogeny temp between-year vs Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp between-year	-0.11 (-0.68, 0.48)	0.642	

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