Cooperation with nonfamily as a strategy for reproducing in variable climates in birds

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Abstract

Cooperative breeding is more common in extreme, variable environments, suggesting it may improve climate resilience. However, whether specific features of these systems evolved in response to particular environmental challenges remains unclear. Using phylogenetic analyses across birds, we test two predictions. First, cooperative breeding with unrelated individuals ('nonfamily') is an adaptation to environmental variability because groups form faster than multigenerational family groups. Second, species with larger groups can breed in more extreme environments. We found that nonfamily cooperation is more frequent, and groups are larger, in hot environments with variable precipitation, whereas family cooperation is more frequent in hot but stable environments, with group size varying independently of climate. Compared with closely related pair-breeders, both nonfamily and family cooperative breeders occupy broader, drier climatic niches. These results show that ecological associations with cooperative breeding depend on how groups form, and that nonfamily cooperation may help birds reproduce in areas with unpredictable precipitation.

Introduction

Extreme and variable climates constrain the ability of organisms to survive and reproduce[1,2], particularly for long-lived vertebrates, where environmental change can outpace genetic adaptation[3,4]. Cooperation can buffer individuals against adverse environmental conditions, leading to the expectation that cooperative breeding is a key strategy for coping with climatic challenges[5–9]. However, cooperative groups vary in how they are formed and maintained, 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[10–16].

Cooperative breeding groups can form and be maintained in different ways[15,17]. First, nonfamily members can 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[10,12,18–25]. Second, offspring can remain in their natal territory to help their parents raise siblings, resulting in multi-generational family groups[26,27]. Under these circumstances, individuals typically forego independent reproduction until breeding opportunities arise, either through breeder turnover or by dispersing to compete for vacant breeding positions[11–13,28,29].

The way groups are formed and maintained can also influence levels of relatedness[15], which may indirectly affect the climatic conditions that species can tolerate. For example, nonfamily groups can form relatively quickly in environments where high mortality erodes kinship among potential group members[11,21,23,24,30–33]. Nonfamily cooperative breeders are therefore expected to be more common in variable climatic regions where independent breeding is difficult and options for cooperating with kin are limited[34,35]. In contrast, family groups arise when kin associations are maintained across multiple generations through limited dispersal and low mortality rates, which are more likely in stable environments[26,27]. Family groups may also be able to colonise and persist in challenging environments because indirect fitness benefits allow helpers to pass on genes without reproducing themselves[13,36,37]. Foregoing reproduction allows individuals to devote more time to other activities, such as foraging and predator defence[38,39], which can be crucial to successfully raising offspring under adverse conditions[6].

Group size may also influence the environments species can occupy[40,41]. Larger groups benefit from economies of scale and division of labour, potentially enabling them to provision and protect offspring under more extreme conditions, while also being more robust to demographic changes that occur when environments shift[7,40,42,43]. Family and nonfamily cooperative breeders can differ markedly in group size: in nonfamily groups, reproductive competition among unrelated individuals can limit group size, whereas in family groups, helpers often forego reproduction to aid relatives, relaxing this constraint and potentially producing larger groups that inhabit more extreme environments[5,15,15,21]. However, it remains unclear whether group formation, maintenance, and size influence the climatic conditions species can tolerate[44–48]. This is primarily because the frequency of cooperation and group sizes of nonfamily and family breeders have not been analysed in relation to climate or formally compared with the climatic niches of phylogenetically matched pair-breeding species.

Here we test whether nonfamily and family cooperative breeders occupy distinct climatic niches, using a global dataset on birds and climate re-analysis data to characterise species' breeding-season environments (Supplementary Table 1; Supplementary Table 2). We first test whether variation in the frequency of cooperative breeding (% nests with 2+ adults) and group size are related to climate, and if this differs between nonfamily and family groups. Second, we test 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). The breeding systems of cooperative species were classified using data on the presence of cobreeders (pairs versus multiple breeders) and related and unrelated nonbreeding adults at

>10% of nests in the population (see Methods section 'Classification of breeding systems'. Table 2). Species were defined as nonfamily if groups had multiple co-breeding individuals (2+) without related nonbreeding individuals, and family if groups consisted of breeders assisted by one or more related nonbreeding helpers[15] (Table 2). We examined the sensitivity of our results to different classifications of cooperative breeding based on the numbers of breeders (pairs versus more than two breeders) and variation in the presence of related and unrelated helpers at different percentages of nests in populations (>0% versus >30% of nests). Data were analysed using multi-response (MR) Bayesian phylogenetic mixed models (BPMM) where climate variables (median, within-year variation and between-year variation in temperature and precipitation) were fitted as response variables to estimate phylogenetic correlations for nonfamily, family and pair breeding systems. By fitting climate variables as response variables in MR-BPMMs rather than as predictors in regression analysis, we avoid three key issues: (i) collinearity, as climate variables can be highly correlated; (ii) the assumption that species' climatic niches are independent of their phylogenetic history; and (iii) the assumption that climate causally affects cooperative breeding and not the reverse[49–52].

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 was significantly higher in environments with more variable precipitation across breeding seasons and higher average temperatures (Figure 2; Supplementary Fig. 3; variation in precipitation between years (95% credible interval, CI) = 0.34 (0.13, 0.5), pMCMC = 0.001; temperature = 0.28 (0.1, 0.45), pMCMC = 0.001; Supplementary Table 3). Similarly, nonfamily cooperative breeding groups were larger in hotter environments with more variable precipitation across breeding seasons (Figure 2; Supplementary Fig. 4; variation in precipitation between years (CI) = 0.97 (0, 2.36), pMCMC = 0.058; temperature (CI) = 1.44 (0.04, 2.39), pMCMC = 0.046; Supplementary Table 4).

In contrast, the frequency of family cooperative breeding increased in hotter, more stable environments (Figure 2; Supplementary Fig. 3; temperature (CI) 0.19 (0.03, 0.26), pMCMC = 0.012; variation in temperature between years (CI) -0.13 (-0.26, -0.02), pMCMC = 0.02; Supplementary Table 3). This is reflected by the concentration of family cooperative breeders around equatorial regions (Figure 1). Contrary to our findings for nonfamily cooperative breeders, the size of family groups was not related to any climate variables (Figure 2; Supplementary Fig. 4; Supplementary Table 4).

Cooperative breeders occupy drier environments than pair breeders

Nonfamily and family cooperative breeders inhabit drier environments than phylogenetically matched pair-breeding species (Figure 3 A; Supplementary Fig. 2; pair vs nonfamily precipitation (CI) = 0.42 (0.05, 0.81), pMCMC = 0.034; pair vs family precipitation (CI) = 0.28 (0.01, 0.58), pMCMC = 0.048; Table 1; Supplementary Table 5). These drier environments were further characterised by less variable precipitation during the breeding season, indicating cooperative breeders occupy consistently drier regions than pair breeders (Figure 3 B; pair vs nonfamily within-year variation in precipitation (CI) = 0.7 (0.3, 1.11), pMCMC = 0.001; pair vs family within-year variation in precipitation (CI) = 0.36 (0.12, 0.69), pMCMC = 0.004; Table 1; Supplementary Table 5). Family and nonfamily cooperative breeders also inhabited environments with similar mean temperatures but less variable temperatures than pair breeders (Figure 3 C,D; Table 1).

Cooperative breeders have weaker climatic constraints than pair breeders

The conditions species can cope with may depend on how climate variables covary. For example, it may be more challenging to reproduce in dry areas when temperatures are high, as limits to thermal tolerance may reduce the time animals can spend foraging[53]. In this scenario, precipitation and temperature will be negatively related, as species will only occur in dry areas under cooler conditions and hotter areas under wetter conditions. Such climatic constraints may be circumvented if cooperative breeding enables individuals to acquire sufficient resources to raise offspring while reducing their workloads[33]. In this case, cooperatively breeding species are expected to occupy hot, dry regions, weakening or even eliminating any cross-species correlation between precipitation and temperature.

We tested whether the correlations between climate variables differed between pair breeders, nonfamily and family cooperative breeders in two ways. First, we estimated phylogenetic covariance matrices of climate variables for each breeding system using MR-BPMMs (Figure 4). Second, we used eigenvector analysis to test if the overall structure of the climate covariance matrices differed between breeding systems. This approach identifies independent axes of climate variation (eigenvectors), where the amount of variation explained by each axis is given by its eigenvalue. If the leading eigenvector for one breeding system, such as pair breeders, has a larger eigenvalue than for other systems, such as nonfamily or family cooperative breeders, it suggests that these species occupy environments where climatic variation is concentrated along a single dominant axis (see Statistical analyses for more details).

Among the 15 possible phylogenetic correlations between climate variables, 12 were significant for pair breeders, whereas only four were significant for family cooperative breeders, and none were significant for nonfamily cooperative breeders (Figure 4). In particular, pair breeders occur in environments where precipitation is negatively correlated with temperature variation, both within and between years, which was not the case for nonfamily or family cooperative breeders (Figure 4 A-C; phylogenetic correlation between precipitation and temperature variation within-years (CI): pair = -0.59 (-0.69, -0.33), pMCMC = 0.001; nonfamily = -0.14 (-0.48, 0.4), pMCMC = 0.846; family = -0.27 (-0.58, 0.11), pMCMC = 0.236; Supplementary Table 6). Furthermore, across pair breeders the leading eigenvector explained significantly more variation compared to the leading eigenvector for nonfamily and family cooperative breeders (Figure 4 D).

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, which recovered qualitatively and quantitatively similar results (Supplementary Table 7). Together, these findings suggest that pair breeding is challenging in dry environments with low temperature variability and that cooperative breeding partially alleviates these constraints.

Sensitivity to breeding system classification

The group composition of family cooperative breeders varies. Some species have groups with a pair of breeders while others have multiple breeders (>2), and breeders can be assisted by family helpers or a mix of family and immigrant nonfamily helpers. Classifying species broadly as 'family' misses this variation, which may be important in determining the environments where species persist. Such variation does not occur in nonfamily cooperative breeders as they were defined as nonfamily individuals forming groups after dispersal from their natal territories.

We examined the sensitivity of our results to more detailed classifications of family cooperative breeding by defining species as pairs with family helpers ("Pair Family"), pairs with family and nonfamily helpers ("Pair Mixed") and multiple breeders with family helpers ("Multiple Family". Note that multiple breeders with nonfamily and family helpers is possible but did not occur in our dataset. Table 1; Table 2). Using these classifications, we repeated our analyses of the percentage of cooperative nests in populations, group size and differences between pair, nonfamily cooperative breeders and pair breeders (Table 1). In addition, we examined the sensitivity of our results to classifying species using different thresholds of the % of nests in populations where at least one family and nonfamily nonbreeder were present.

We found that the frequency of cooperation in populations increased with temperature in species where all helpers were family members, irrespective of the number of breeders (Table 1; Supplementary Table 10). Groups with multiple breeders were also in environments with more stable temperatures (Table 1; Supplementary Table 10). These results are largely consistent with our broad classification of family cooperative breeding (Figure 2). However, for groups with a mix of family and nonfamily helpers, the frequency of cooperation was not significantly related to temperature or precipitation (Table 1).

Consistent with our previous analyses, group sizes did not vary with climate across any of our more detailed classifications of family groups (Table 1; Supplementary Table 11). Furthermore, classifications made using >0% and >30% of nests in populations showed similar patterns to the >10% threshold, with pair breeders being in environments with higher precipitation and more variable precipitation than cooperative breeders (Table 1;Supplementary Table 8; Supplementary Table 9). There were, however, a number of results that became non-significant, for example, the difference in precipitation between pair breeders and nonfamily cooperative breeders and lower between-year temperature variation in family cooperative breeders (Table 1; Supplementary Fig. 5; Supplementary Table 8; Supplementary Table 9). In addition, only cooperative breeders where pairs were assisted by family helpers were in environments that significantly differed from pair breeders (Table 1). Differences in statistical significance were largely due to increased variation (wider CIs) around estimates, rather than differences in the direction or magnitude of the relationships, and in some cases sample sizes were much smaller (Table 1;Supplementary Fig. 5 ;Supplementary Table 8; Supplementary Table 9; Supplementary Table 12). It is therefore likely that differences across analyses are due to the power to detect effects rather than biological differences.

Table 1: Summary of the main analyses examining nonfamily cooperative breeding, family cooperative breeding and pair breeding in relation to climate (bolded analyses) and robustness tests assessing the sensitivity of results to breeding system classifications (unbolded analyses). Robustness tests included: (i) examining if variation within family groups in the number of breeders within groups ("Pair" versus more than two "Multiple") and whether helpers were all family ("Family") or a mix of family and nonfamily ("Mixed") was related to the percentage of cooperative nests within the population ("% Cooperative nests detailed") and group size ("Group size detailed"); (ii) comparing the climatic niches of species after reclassifying them according to presence of nonfamily and family nonbreeding individuals at >0% and >30% of nests, referred to as "0%" and "30%" respectively; (iii) comparing the climatic niches of species after reclassifying family groups according to the number of breeders within groups ("Pair" versus more than two "Multiple") and whether helpers were all family ("Family") or a mix of family and nonfamily ("Mixed"). Posterior modes with CIs are presented for significant relationships with blank cells indicating relationships were non-significant. Full details of analyses can be found in supplementary tables: Supplementary Table 3; Supplementary Table 10; Supplementary Table 4; Supplementary Table 11; Supplementary Table 5; Supplementary Table 8; Supplementary Table 9; and Supplementary Table 12.

Analysis	Comparison	Number of species	Precipitation	Precipitation within-year variation	Precipitation between-year variation	Temperature	Temperature within-year variation	Temperature between-year variation
% Cooperative nests	Nonfamily	37	0.17 (0.01, 0.39)	0.32 (0.11, 0.47)	0.34 (0.13, 0.5)	0.28 (0.1, 0.45)	-0.31 (-0.44, -0.09)	
	Family	125				0.19 (0.03, 0.26)		-0.13 (-0.26, -0.02)
% Cooperative nests detailed	Pair Family	65				0.15 (0.04, 0.35)		
	Pair Mixed	34						
	Multiple Family	26				0.19 (0.02, 0.56)	-0.41 (-0.65, -0.09)	
Group size	Nonfamily	35				1.44 (0.04, 2.39)		
	Family	119						
Group size detailed	Pair Family	60						
	Pair Mixed	33						
	Multiple Family	26						
Breeding system 10%	Pair vs Nonfamily	466 vs 27	0.42 (0.05, 0.81)	0.7 (0.3, 1.11)				

	Pair vs Family	466 vs 53	0.28 (0.01, 0.58)	0.36 (0.12, 0.69)	-0.27 (-0.58, -0.04)
	Nonfamily vs Family	53 vs 27			
Breeding system 0%	Pair vs Nonfamily	456 vs 39		0.5 (0.11, 0.75)	
	Pair vs Family[1]	456 vs 128	0.3 (0.08, 0.46)	0.34 (0.13, 0.51)	
	Nonfamily vs Family	128 vs 39			
Breeding system 30%	Pair vs Nonfamily	487 vs 21		0.47 (0.05, 0.93)	
	Pair vs Family	487 vs 35	0.4 (0.06, 0.75)	0.43 (0.08, 0.78)	
	Nonfamily vs Family	35 vs 21			
Breeding system detailed	Pair vs Pair Family	466 vs 23		0.71 (0.19, 1.06)	-0.46 (-0.85, -0.04)
	Pair vs Pair Mixed	466 vs 16			
	Pair vs Multiple Family	466 vs 14			
	Pair vs Nonfamily	466 vs 27	0.41 (0.05, 0.8)	0.67 (0.31, 1.11)	
	Pair Family vs Pair Mixed	23 vs 16			
	Pair Family vs Multiple Family	23 vs 14			
	Pair Family vs Nonfamily	23 vs 27			
	Pair Mixed vs Multiple Family	16 vs 14			
	Pair Mixed vs Nonfamily	16 vs 27			
	Multiple Family vs Nonfamily	14 vs 27			

[1]*No helpers indicates all individuals breed i.e. are nonfamily cooperative breeders*

Discussion

Our results show that cooperation with nonfamily is more common in hot climates with variable precipitation, conditions that are also associated with larger nonfamily groups. In contrast, cooperative breeding in family groups increases in 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.

Family and nonfamily cooperative breeding systems have evolved independently, with important consequences for the reproductive division of labour[15,17,37,55,56]. Our results suggest that this evolutionary distinction also extends to the ecological niches of species breeding in nonfamily versus family groups. In terrestrial vertebrates, cooperative breeding has been linked to high temperatures and variable rainfall, yet previous studies either examined only family groups or pooled family and nonfamily species[31,57–62]. Building on this work, we show that cooperative breeding in both nonfamily and family groups becomes more common with increasing temperature. Crucially, however, only nonfamily cooperative breeding is associated with greater precipitation variability, whereas family cooperative breeding shows the reverse pattern and is more prevalent in stable climates.

Multiple mechanisms may explain why nonfamily cooperative breeding is associated with more variable precipitation. First, fluctuating conditions can erode kin structure through increased dispersal, mortality, and reduced survival during extreme rainfall years[3,24,33,34,63–68], limiting opportunities for kin-based cooperation and creating vacancies for unrelated immigrants[5,23,26,27,69]. Consistent with this, our sensitivity analyses show that species with mixed family and nonfamily helpers had climatic associations distinct from exclusively family or nonfamily species (Table 1), suggesting that immigration and offspring retention are shaped by different ecological pressures. Second, nonfamily groups can form and dissolve quickly, allowing individuals to adjust cooperative behaviour in response to environmental change more readily than in family groups, which take longer to establish. For example, Taiwan yuhinas (Yuhina brunneiceps) increase cooperation with unrelated cobreeders when rainfall makes independent breeding harder[34], but groups can dissolve when conditions improve. Nonfamily cooperative breeding may therefore be favoured where variable conditions both erode kin structure and select for rapid group formation. Disentangling these processes requires tracking individual movement and group composition over time, underscoring the value of long-term longitudinal studies.

Group size also varied with climate, but only for nonfamily breeders. Reproductive competition among unrelated individuals may constrain nonfamily group size, such that groups expand only when environmental conditions sufficiently increase the benefits of cooperation[40,41]. For example, in nonfamily groups of the greater ani, Crotophaga major, 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[40]. In contrast, the consequences of living in different-sized family groups do not appear to be associated with climate in birds (e.g.[33,65,70]). Instead, the effect of group size on fitness in family groups may be determined by diminishing indirect fitness returns, capped by the reproductive output of the breeding female[11,71].

Although nonfamily and family cooperatively breeding species differ in the way they change with climate, both occupied broader climatic niches than pair-breeding species. In particular cooperative breeders were in more arid environments, which can be challenging for independent breeding because extended foraging periods are required to fledge offspring successfully, while also protecting them from thermal stress and predators[30,33,40,72,73]. Cooperation may enable individuals to overcome these challenges, especially where variation among group members in morphology or behaviour allows more efficient resource acquisition and defence against enemies[38,39,73,74]. In regions with extreme or variable climates, the mutual benefits of cooperating with nonkin and the indirect benefits of helping kin are therefore likely to be high[21], and may even be necessary for colonising and persisting in such environments[8,60,75,76]. Cooperative breeding may also be favoured in environments that are suitable for independent breeding when habitat saturation limits breeding opportunities[77]. Together, the combined ecological and demographic constraints on independent breeding may explain why cooperatively breeding species occupy a greater range of climates than pair breeders[30,77–79].

Extreme climatic conditions, where high temperatures are combined with periods of drought can lead to reproductive failure and even the collapse of entire communities[3,33,65,66]. Cooperative breeding is one way species may cope with such adverse climates[6,63,80]. 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[81]. However, recent work shows that variable environments do not always select for cooperative behaviour among relatives[16]. In line with this, our results show that family cooperative breeding is associated with hot, stable climates whereas 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 more common.

Methods

We collected data from published papers on group formation, relatedness among group members, presence of cobreeders, presence of nonbreeding adults assisting with offspring care, frequency of group breeding nests in populations, and group size to quantify variation across cooperative breeding systems. For each cooperative species, we selected the five most closely related pair-breeding species using phylogenetic information[82]. Five comparator species were chosen to provide a robust estimate of the climatic niche occupied by pair breeders at each phylogenetic position where cooperation has evolved. Results were qualitatively and quantitatively similar when down-sampling to one pair-breeding species per cooperative breeder (Supplementary Table 7). Pair-breeding species were initially identified using breeding system data from Cockburn 2006[83] and subsequently verified against current literature, including Birds of the World species accounts[84], to confirm that each species is pair-breeding. We extracted climate data (temperature and precipitation) for breeding and nonbreeding seasons from study sites and species ranges for 1979–2018 using the ERA5 global bioclimatic indicators dataset[85]. Data were analysed using the R package *MCMCglmm* to fit Bayesian phylogenetic mixed models[86].

Data collection

We used the species list of cooperative breeders and corresponding literature from Downing et al. 2020[15], 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. Because our data requirements are stringent (exact percentages of cooperative nests, helper relatedness), the resulting dataset may be biased towards well-studied species. However, our sensitivity analyses using relaxed classification criteria (see 'Classification of breeding systems') produced qualitatively similar results, suggesting that the findings are not driven by non-random sampling of species.

Breeding system data

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 help raise offspring (Table 2). 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 of avian breeding systems (Supplementary Table 1 and Supplementary Table 2)[15,20,60,83]. Data were compiled by two authors (CHW and PAD), with independent cross-checking of subsets by a third author (CKC). 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 'Sensitivity to breeding system classifications' 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 2: 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 only nonfamily helpers.

Classification of helpers and helper behaviour

Helpers were defined as adult nonbreeding 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. Although helping encompasses diverse behaviours (nest construction, incubation, provisioning, defence), we recorded only verified accounts of incubation and/or chick or fledgling provisioning. Studies including only 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 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.

Climate data

Information on temperature and precipitation was extracted from the ERA5 global bioclimatic indicators dataset[85]. 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. Before calculating summary statistics, precipitation values were converted to calendar-month totals (mm/month) using the number of days in each month.

ERA5 reanalysis data offers gap-free spatial and temporal coverage by integrating observational weather data from multiple sources (satellites, weather stations) into a model that accounts for climatic variable interactions, yielding highly reliable historical estimates[87]. Station-based precipitation data, such as CRU, which have been used in previous cooperative breeding studies[59,60,88], can be sensitive to gauge biases and local topography[89]. Reanalysis data is less impacted by anomalies in single sources of observational data[87,89,90].

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[91] and Handbook of Birds of the World[84]. 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[92]. 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 we 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 and precipitation calculated as the median of the standard deviation within years; and (iii) the between breeding season variation in temperature and precipitation calculated as the standard deviation of the yearly medians.

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.

Breeding seasons

Cooperative species with widespread distributions show variable breeding seasons across sites, so we used a two-step approach. 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 Birds of the World or Handbook of Birds of the World species accounts[84]. 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 across all references. For the breeding seasons of pair breeding species we used Birds of the World or Handbook of Birds of the World species accounts (Supplementary Table 2). When dated breeding records were sparse, we interpolated short gaps by coding one or two missing months between recorded breeding months as breeding months, unless the source indicated discontinuous breeding events. Breeding season data were used to select months from the climatic database to ensure conditions during breeding were examined.

Data compilation

Raw data on cooperative breeding species is presented in Supplementary Table 1 with references and details of where information in primary papers was obtained. Supplementary Table 1 contains multiple rows per species when multiple studies, populations, or years were available. Species data were summarized as follows: (i) cooperative and noncooperative nests were summed across years, studies, and populations; (ii) group size estimates were weighted-averaged; (iii) the percentage of nests with pair versus multiple (2+) breeders was calculated at >0%, 10%, and 30% thresholds; (iv) the percentage of nests with family and/or nonfamily members was calculated at the same thresholds. Datasets were compiled using the R script 'data_nonfam.R' and data on breeding seasons and climate data for all species, together with summarised information on cooperative breeders, is presented in Supplementary Table 2.

Statistical analyses

We conducted three sets of analyses using multi-response Bayesian phylogenetic mixed models (MR-BPMM) with the R package *MCMCglmm* for MCMC estimation[86]. First, we examined whether cooperative breeding frequency and group size relate to climate across nonfamily and family breeders. Second, we tested for climatic differences between cooperative and pair breeders. Third, we assessed whether the relationships between climate variables differ across breeding systems. 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' for convergence checks[93] 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 calculated 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[94,95].

Specific analyses

Cooperative breeding frequency and group size in relation to climate

We tested whether cooperative breeding frequency relates to climate using MR-BPMM with six climate response variables (median, within-year variation, and between-year variation for temperature and precipitation). The percentage of nests with more than two individuals (logit transformed) was fitted 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). Group size relationships with climate were examined using the same approach but substituting group size for cooperative nest percentage (model mod_groupsize).

Climate differences among breeding systems

We tested for climatic differences across breeding systems using MR-BPMM with six climate response variables and breeding system as a fixed effect. The "at.level" notation was used to estimate each climate variable at each breeding system level (model mod_bs10, Supplementary Table 5).

Climate covariance among breeding systems

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). To verify that differences in the covariance matrices between breeding systems were not due to different number of species (456 versus 39 nonfamily and 128 family), we re-ran this analysis on data where the number of pair breeding species was down-sampled to the same number of family cooperatively breeding species (Rcode model mod_climcorrsdown. Supplementary Table 7).

We analysed covariance matrix structure by calculating eigenvectors and eigenvalues for each posterior sample from model mod_climcorrs using the R function 'eigen'. The proportion of total eigenvalue variation for each eigenvector was calculated as (eigenvalue / sum of all eigenvalues) (Figure 4). Breeding systems were considered to differ in climatic niches when: (i) the 95% CI for the difference in proportion of eigenvalue variation between systems did not include zero, and (ii) fewer than 5% of iterations showed differences in the opposite direction.

Sensitivity to different breeding system classifications

The level of detail on cooperative breeding varied across species. The main analyses used a >10% nest threshold to assign species to 'multiple versus pair breeding' and 'presence of related nonbreeding individuals' categories for consistency with previous studies[15,60,83]. To assess the sensitivity of our results to excluding species without data on the exact percentages of nests with cobreeders and/or the presence of nonfamily and family members, 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 where there were 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). This is referred to as analyses using a >0% threshold of nests in a population. We also examined the sensitivity of our results to classifying species at a higher 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" whereas it would be reclassified at a >30% threshold as "pair family". We examined sensitivity to classification choices across three analyses: (i) detailed family group classifications (pair vs. multiple breeders; family vs. mixed helpers) and their relationships with cooperative breeding frequency and group size; (ii) species reclassification at >0% and >30% thresholds for family and nonfamily members; (iii) family groups reclassified by breeder number and helper type (family vs. mixed).

Data availability

All data and analysis results are available at the Open Science Framework project https://doi.org/10.17605/OSF.IO/QHVS5.

Code availability

All code required to reproduce the analyses is available at the Open Science Framework project https://doi.org/10.17605/OSF.IO/QHVS5.

Supplementary Information

Supplementary tables are provided as an Excel workbook SItables.xlsx produced by the code in 2_SI.qmd.

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Author contributions

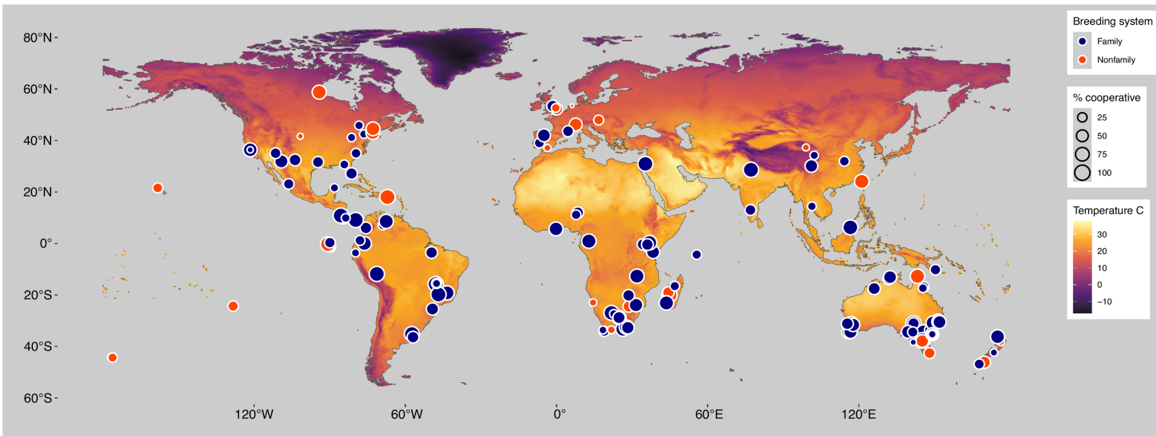
Conceptualization - CKC, EO, PD, ASG. Methodology: CKC, CHW, EO, PD. Investigation: CKC, CHW, EO. Visualization and analysis: CKC, EO. Funding acquisition: CKC, CHW. Project administration: CKC. Supervision: CKC. Writing – original draft: CKC. Writing – review & editing: CKC, CHW, EO, PD, ASG.

Competing interests

The authors declare no competing interests.

Figures

A



B

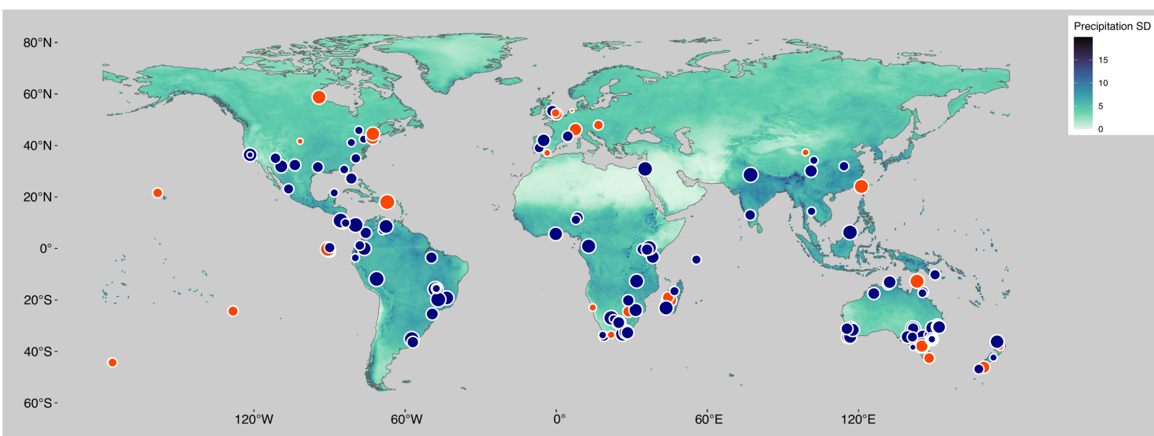


Fig. 1: The areas where family and nonfamily cooperative breeders occur in relation to (A) median temperature and (B) variation in precipitation across years. Points represent study sites, the colour of the circles represents the breeding system, and the size of the circle represents the % of cooperative nests in the population. Maps of all climatic variables with points labelled by species are presented in Supplementary Fig. 1. Median temperature is measured in centigrade and precipitation variation is shown as the square-root-transformed standard deviation of monthly precipitation (mm/month) across years.

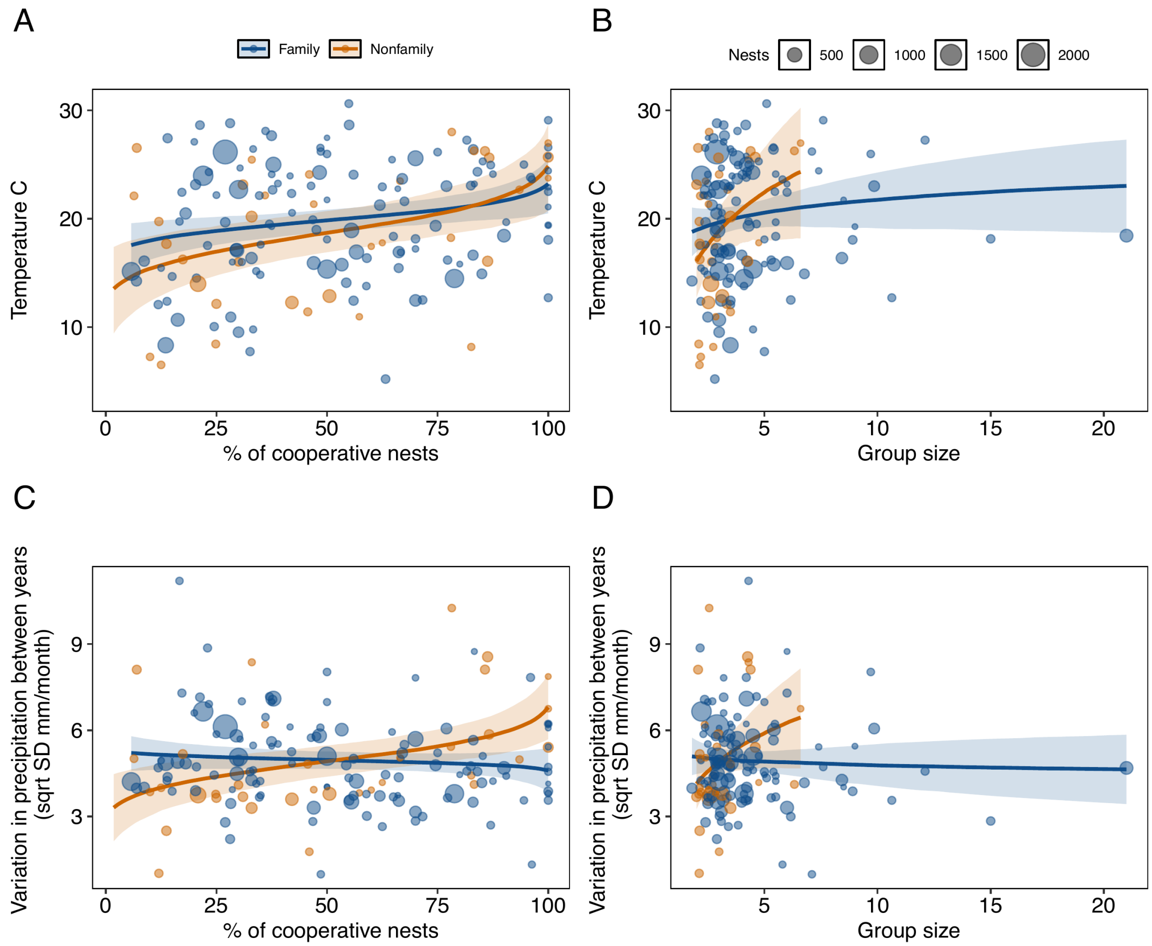


Fig. 2: Contrasting relationships between climate and the percentage of cooperative nests (>2 adults) and group sizes between family and nonfamily cooperative breeders. In nonfamily cooperative breeders, the percentage of cooperative nests and group sizes were greater in environments with higher temperatures (A-B) and variable precipitation across years (C-D). In family cooperative breeders, the percentage of cooperative nests only increased with median temperature (A) and group size was 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. Lines show posterior median fixed-effect predictions with shaded areas indicating 95% credible intervals from Bayesian phylogenetic mixed models. For relationships between all climatic variables and the % of cooperative nests and group sizes see Supplementary Fig. 3 and Supplementary Fig. 4. Median temperature is measured in centigrade and precipitation variation is measured as the square-root-transformed standard deviation of monthly precipitation (mm/month) across years.

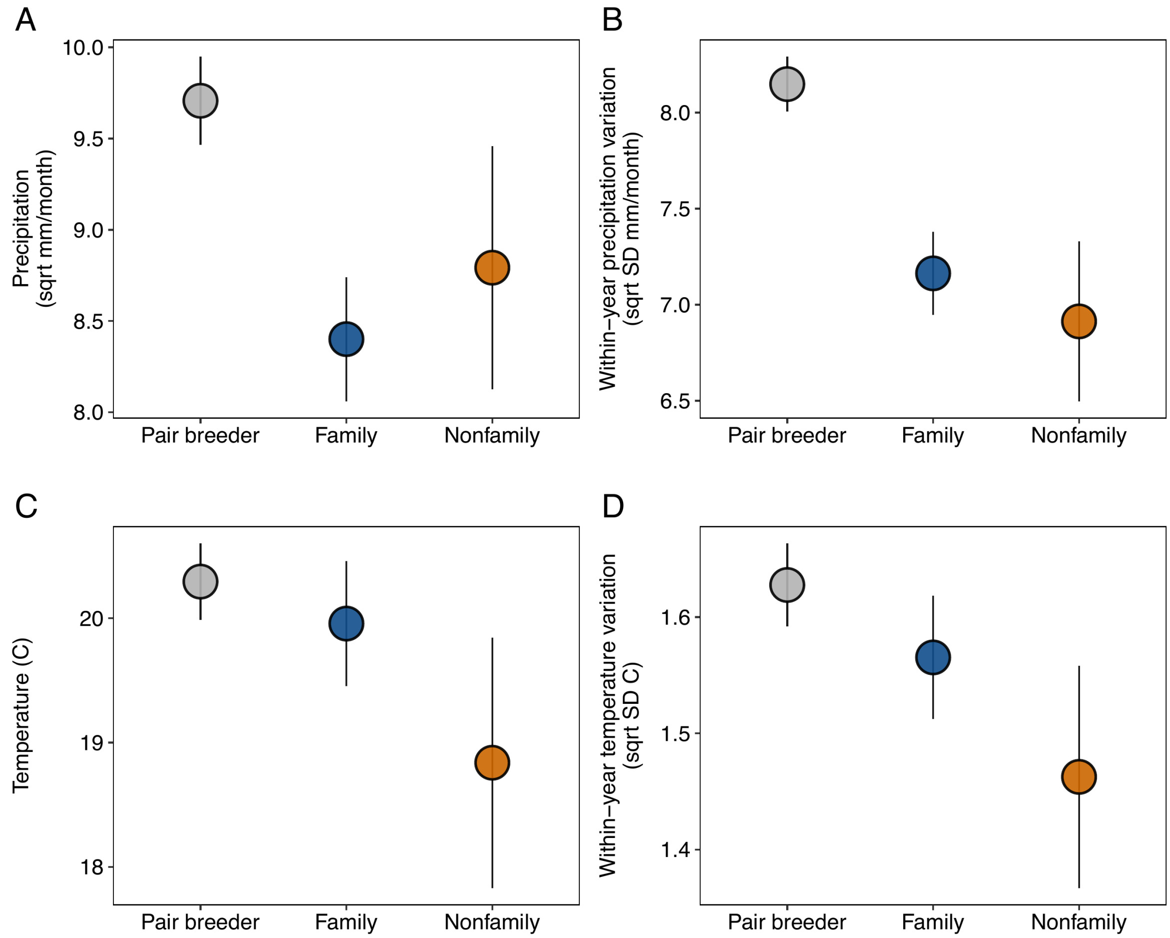


Fig. 3: The environments where nonfamily, family and pair-breeding species occur. Different breeding systems in relation to (A) square-root-transformed median monthly precipitation (mm/month), (B) within-year variation in precipitation (square-root-transformed SD mm/month), (C) median temperature (Centigrade) and (D) within-year variation in temperature (square-root-transformed SD Centigrade). Points and whiskers show means ± SEs across species within each breeding system. Nonfamily and family cooperative breeders were in environments with significantly less precipitation and lower within-year precipitation variation than closely related pair breeders, but occurred in environments with similar median temperatures and within-year temperature variation. For plots with more breeding system classifications that distinguish between species with multiple breeders and a combination of family and nonfamily members see Supplementary Fig. 5.

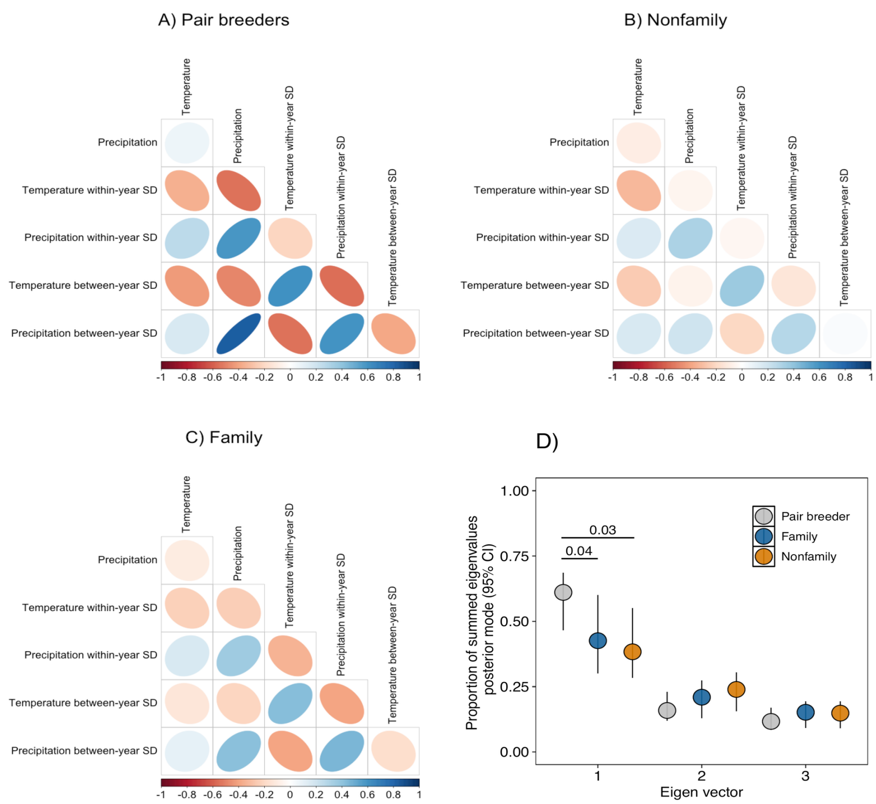


Fig. 4: Nonfamily and family cooperative breeders occupy a broader range of climates than pair breeding species. (A-C) The correlational structure of climate variables across the different breeding systems. Ellipses show the direction and strength of correlations (tighter ellipses represent stronger correlations) with more intense blue colours indicating stronger positive correlations and more intense red colours indicating stronger negative correlations. Temperature is measured in centigrade and precipitation variables are monthly totals or standard deviations in mm/month. D) The proportion of total eigenvalue variation (eigenvalue / sum of all eigenvalues) explained by each eigenvector across breeding systems. The leading eigenvector explained more variation than other eigenvalues across pair breeding species, indicating that more variation is aligned along a single axis of climatic variation than cooperative breeding species. Lines represent significant differences (95% CI of difference does not include 0) with pMCMC values (proportion of iterations greater or less than 0). Only the leading three eigenvectors are shown as the variation explained by eigenvectors four to six was less than 10% and were not significantly different between breeding systems.

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Supplementary Information

Cooperation with nonfamily as a strategy for reproducing in variable climates in birds

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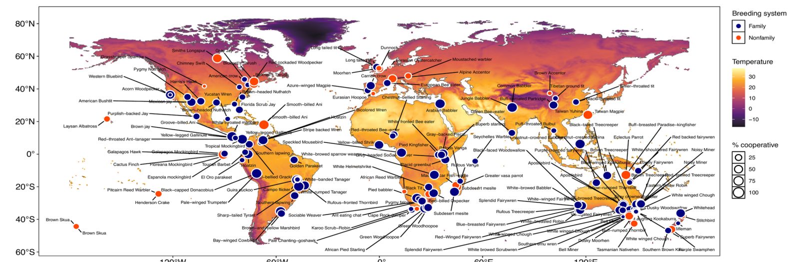
This file contains Supplementary Figures, Supplementary Tables, and session information. Supplementary tables are also provided as the Excel workbook SI/SItables.xlsx.

A



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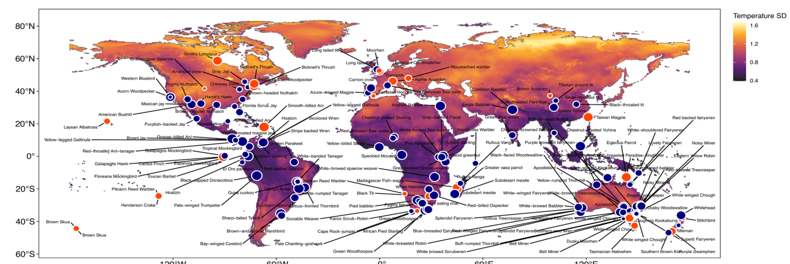

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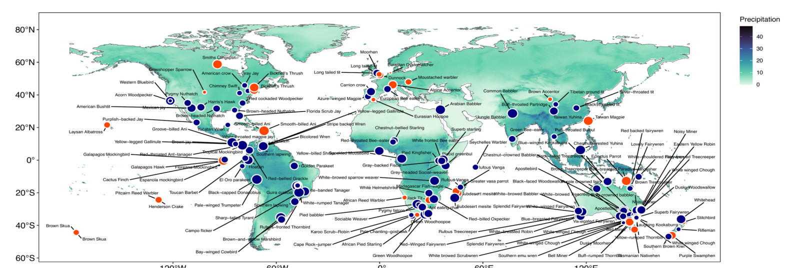

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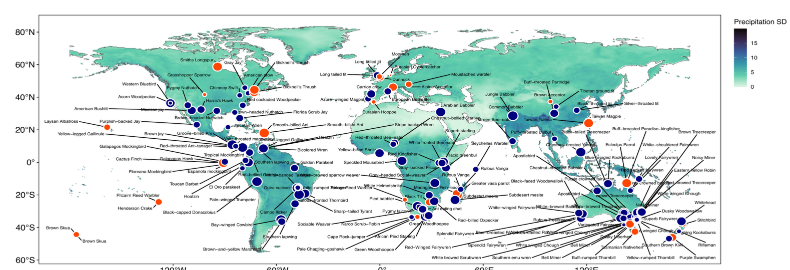
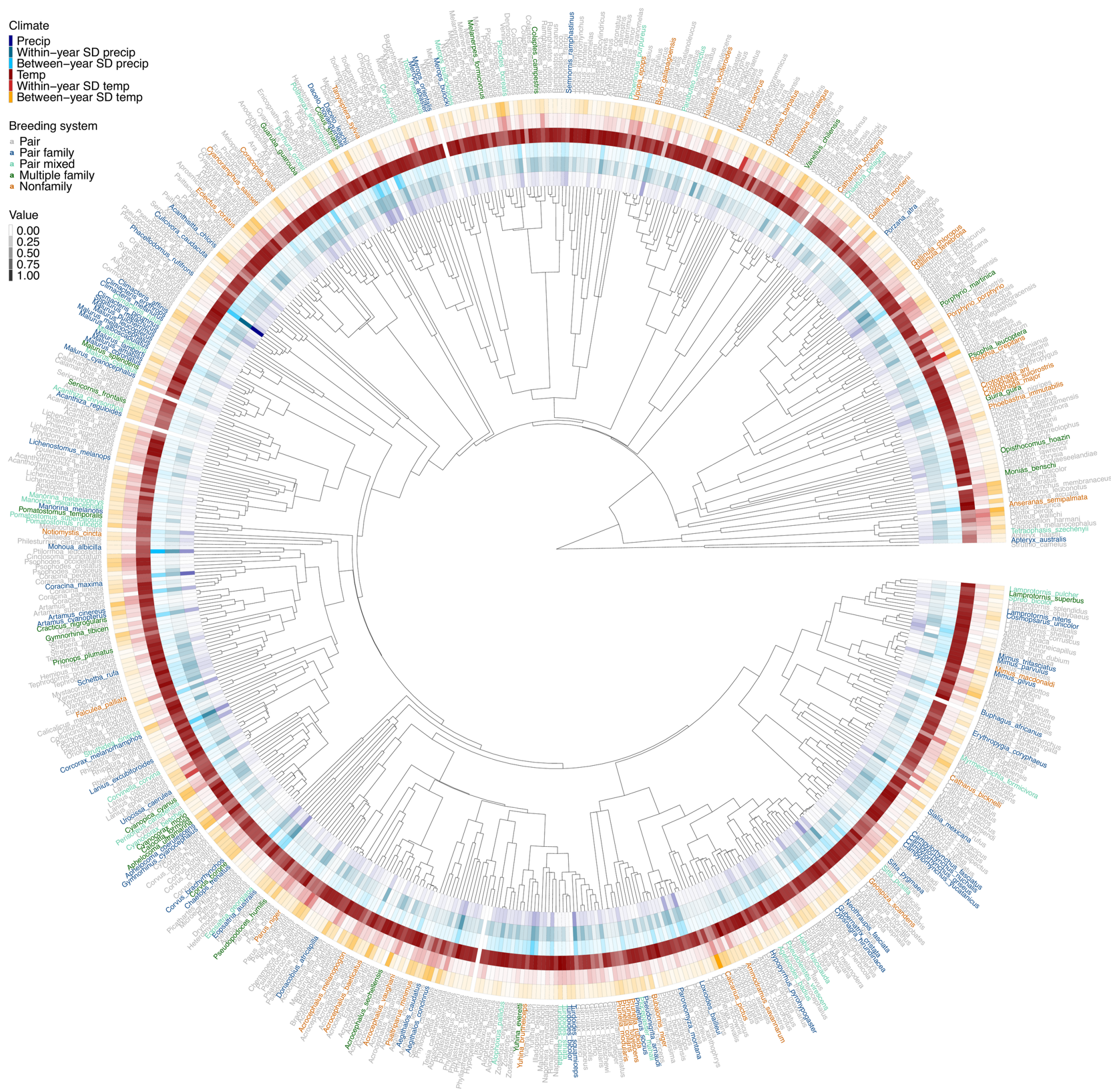
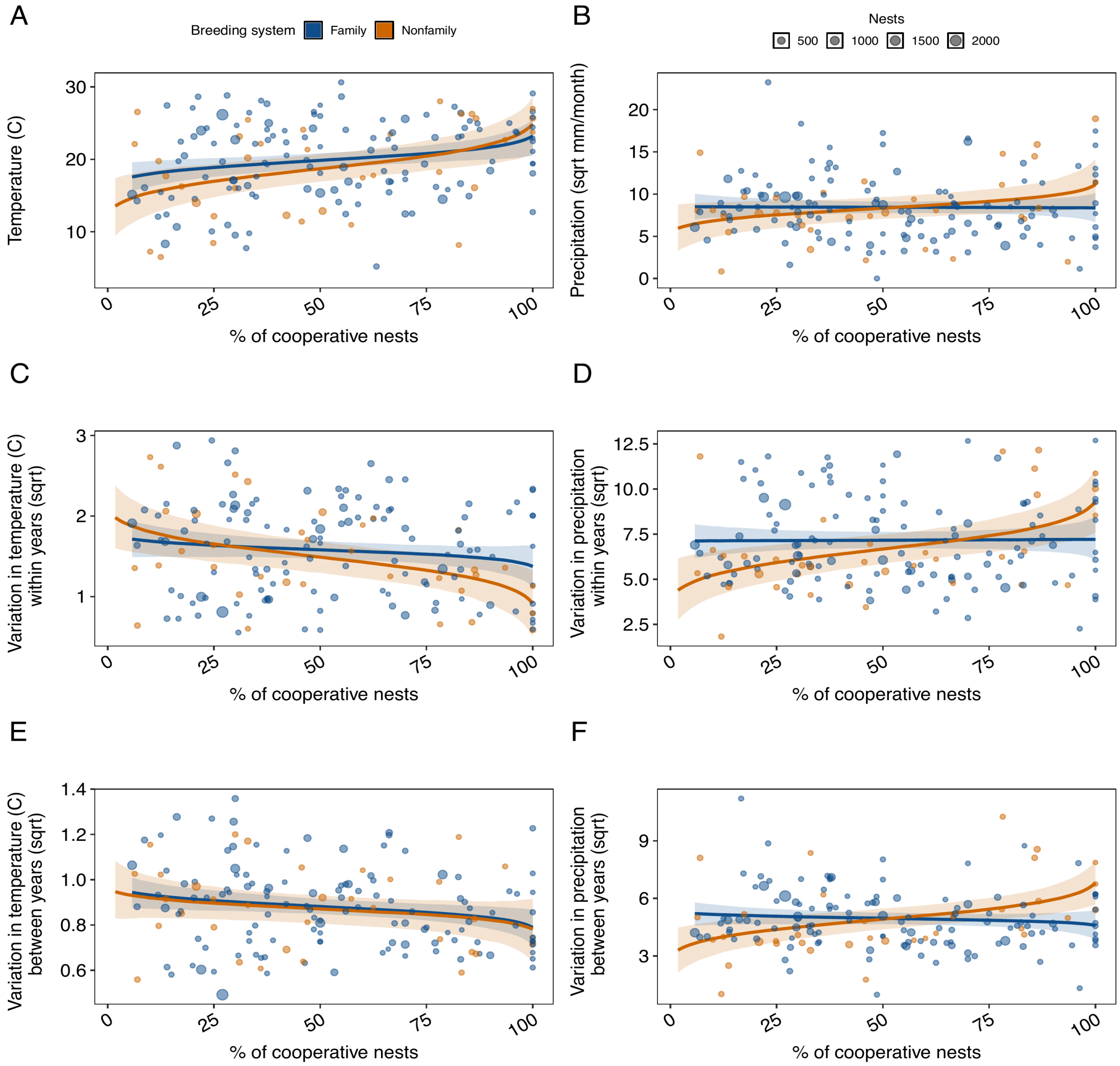


Supplementary Fig. 1: Geographic distribution of family and nonfamily cooperative breeders in relation to median temperature (C) (A), median precipitation (sqrt

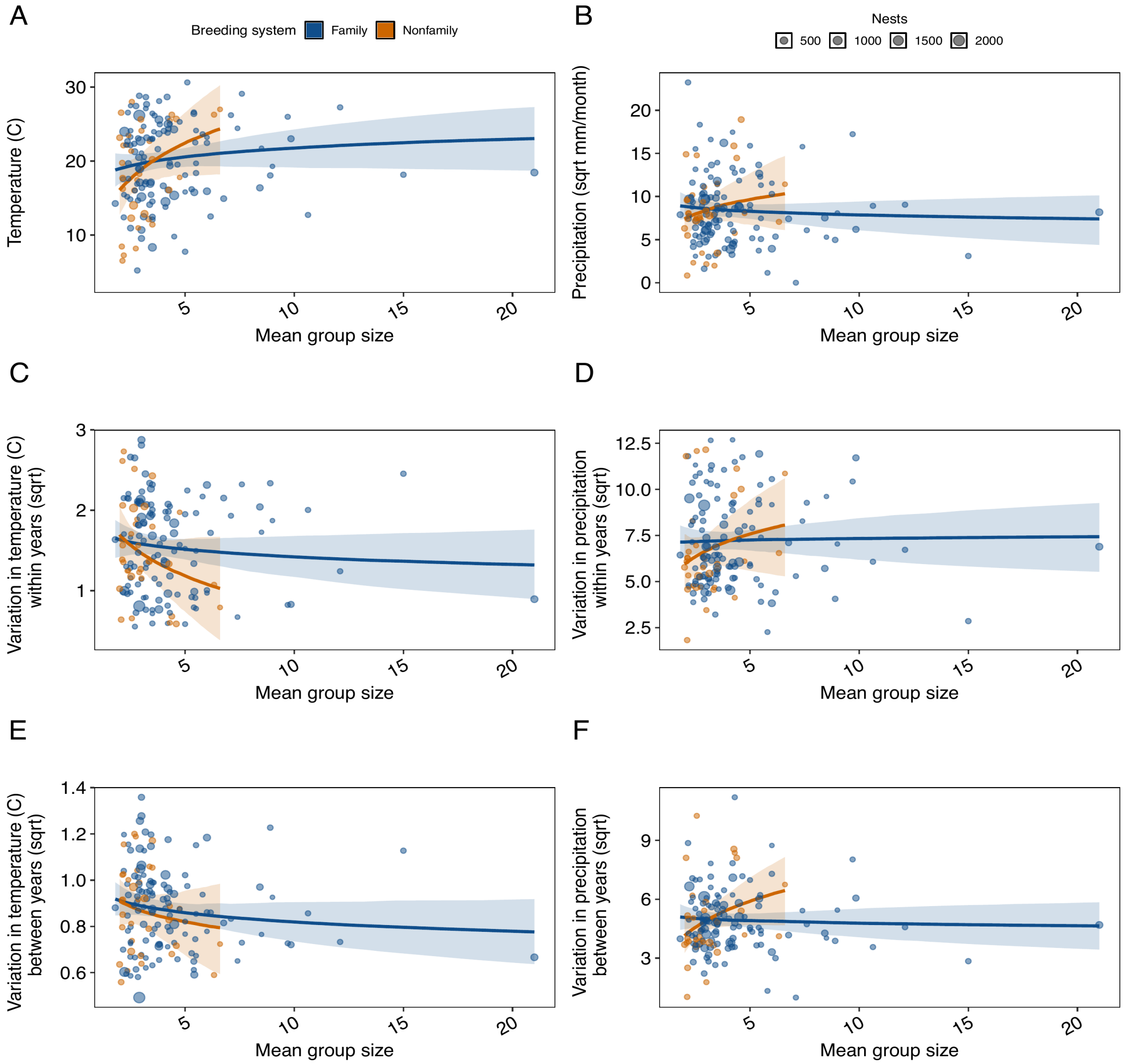
mm/month) (B), temperature variation across years (C), and precipitation variation across years (D). Variation in temperature and precipitation is calculated as the square-root-transformed standard deviation of yearly values from 1979 to 2018. Points represent study sites labelled by species common names. Circle color indicates breeding system, and circle size represents the percentage of cooperative nests in the population. Median temperature is measured in centigrade and precipitation variation is shown as the square-root-transformed standard deviation of monthly precipitation (mm/month) across years.



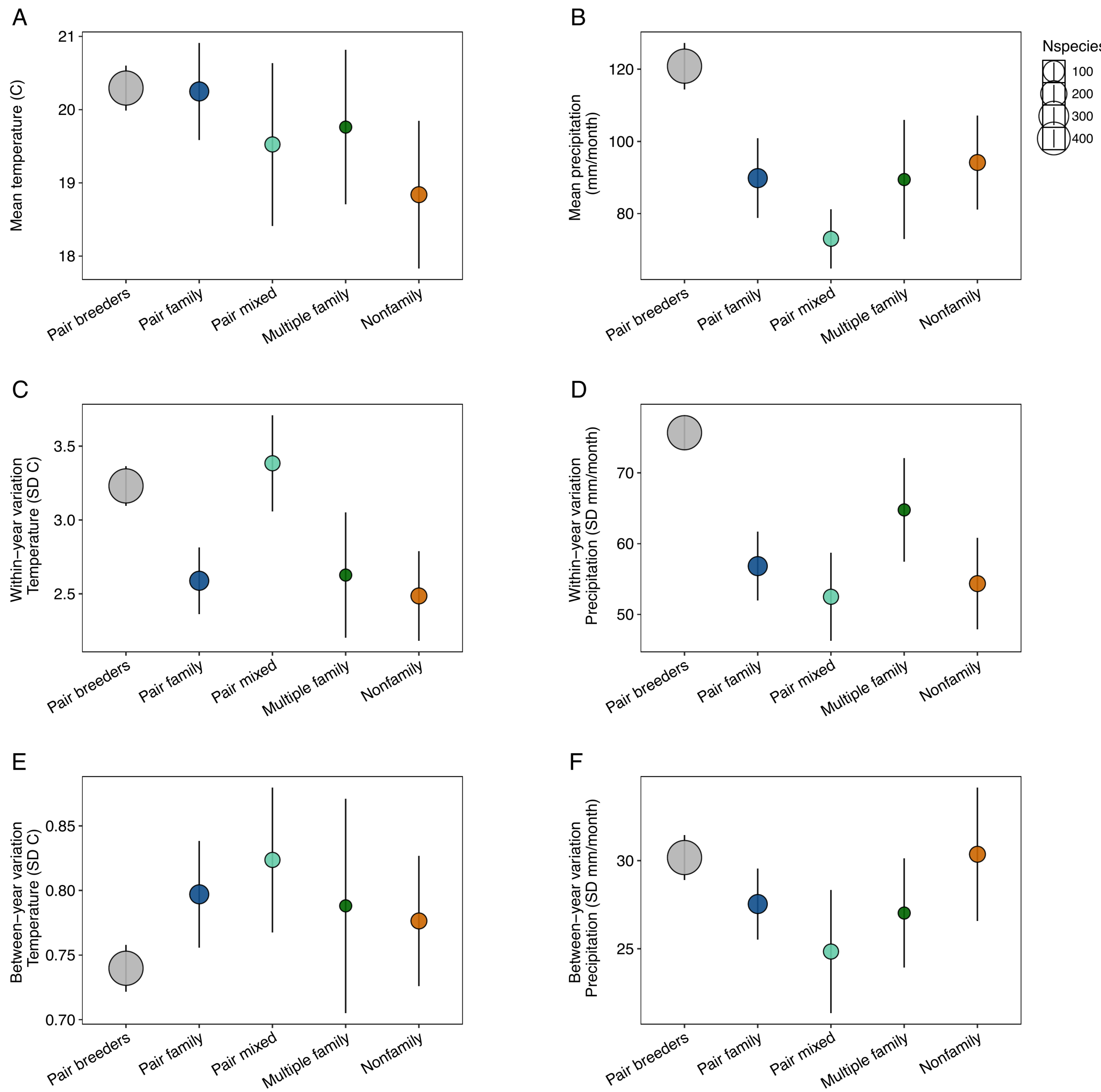
Supplementary Fig. 2: Phylogenetic distribution of cooperative breeding systems in relation to climatic variation. Tip label colors indicate different breeding systems. Color rings from inner to outer circle represent: median precipitation (dark blue), precipitation variation within breeding seasons (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 were restricted to months during which each species breeds.



Supplementary Fig. 3: Variation in the frequency of cooperation between nonfamily and family groups in relation to (A) median temperature, (B) median precipitation, (C) temperature variation within breeding seasons, (D) precipitation variation within breeding seasons, (E) temperature variation across breeding seasons, and (F) precipitation variation across breeding seasons. Climate data were restricted to months during which each species breeds. Lines show posterior median fixed-effect predictions with shaded areas indicating 95% credible intervals from Bayesian phylogenetic mixed models. Point size is proportional to the number of nests studied for each species.



Supplementary Fig. 4: Variation in group size in nonfamily and family groups in relation to (A) median temperature, (B) median precipitation, (C) temperature variation within breeding seasons, (D) precipitation variation within breeding seasons, (E) temperature variation across breeding seasons, and (F) precipitation variation across breeding seasons. Climate data were restricted to months during which each species breeds. Lines show posterior median fixed-effect predictions with shaded areas indicating 95% credible intervals from Bayesian phylogenetic mixed models. Point size is proportional to the number of nests studied for each species.



Supplementary Fig. 5: Comparison of environmental conditions among cooperative breeding species with different breeding structures and helper relatedness versus pair-breeding species. Mean values and standard errors are shown for different breeding systems, with circle size proportional to the number of species in each category.

Supplementary Tables

Data used for analyses

Supplementary Table 1: Data on cooperative breeding collected for each species used to derive species-level summaries for analysis. See file SItables.xlsx.

Supplementary Table 2: Species-level dataset used for analyses, combining breeding data derived from Supplementary Table 1 with ERA5 climate summaries from 1979-2018 for the breeding-season months listed. See file SItables.xlsx.

Results of analyses

Variation in response variables attributable to each random effect was quantified as the percentage of total random-effect variance on the latent data scale (I^2).

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

Fixed Effects	Posterior Mode (CI)	pMCMC
Family temp	0.05 (-0.17, 0.18)	-
Family precip	-0.03 (-0.19, 0.17)	-
Family temp within-year	0.08 (-0.1, 0.26)	-
Family precip within-year	-0.01 (-0.16, 0.21)	-
Family temp between-year	0.05 (-0.11, 0.25)	-
Family precip between-year	0.01 (-0.19, 0.17)	-
Nonfamily temp	-0.22 (-0.53, 0.12)	-
Nonfamily precip	-0.06 (-0.34, 0.32)	-
Nonfamily temp within-year	-0.11 (-0.39, 0.25)	-
Nonfamily precip within-year	-0.15 (-0.5, 0.16)	-
Nonfamily temp between-year	-0.01 (-0.36, 0.32)	-
Nonfamily precip between-year	-0.03 (-0.38, 0.28)	-
Family temp: coop frequency	0.19 (0.03, 0.26)	**0.012**

Family precip: coop frequency	-0.01 (-0.13, 0.11)	0.924
Family temp within-year: coop frequency	-0.06 (-0.2, 0.02)	0.14
Family precip within-year: coop frequency	-0.01 (-0.11, 0.13)	0.914
Family temp between-year: coop frequency	-0.13 (-0.26, -0.02)	**0.02**
Family precip between-year: coop frequency	-0.09 (-0.18, 0.07)	0.324
Nonfamily temp: coop frequency	0.28 (0.1, 0.45)	**0.001**
Nonfamily precip: coop frequency	0.17 (0.01, 0.39)	**0.042**
Nonfamily temp within-year: coop frequency	-0.31 (-0.44, -0.09)	**0.002**
Nonfamily precip within-year: coop frequency	0.32 (0.11, 0.47)	**0.001**
Nonfamily temp between-year: coop frequency	-0.12 (-0.33, 0.04)	0.124
Nonfamily precip between-year: coop frequency	0.34 (0.13, 0.5)	**0.001**
Random Effects	**Posterior Mode (CI)**	**I2 % (CI)**
Phylogeny temp	0.55 (0.27, 0.8)	56.42 (29.61, 73.49)
Phylogeny temp within-year	0.52 (0.26, 0.86)	59.47 (26.8, 77.44)
Phylogeny temp between-year	0.49 (0.26, 0.85)	50.85 (27.3, 75.88)
Phylogeny precip	0.56 (0.26, 0.91)	44.6 (26.8, 78.24)
Phylogeny precip within-year	0.45 (0.26, 0.9)	45.44 (25.76, 71.24)
Phylogeny precip between-year	0.53 (0.26, 0.89)	56.8 (25.2, 77.74)
Residual temp	0.51 (0.26, 0.77)	43.58 (26.51, 70.39)
Residual temp within-year	0.5 (0.26, 0.83)	40.53 (22.56, 73.2)
Residual temp between-year	0.55 (0.29, 0.84)	49.15 (24.12, 72.7)
Residual precip	0.64 (0.26, 0.88)	55.4 (21.76, 73.2)
Residual precip within-year	0.56 (0.22, 0.83)	54.56 (28.76, 74.24)
Residual precip between-year	0.46 (0.23, 0.83)	43.2 (22.26, 74.8)
Correlations	**Posterior Mode (CI)**	**pMCMC**

Phylogeny temp within-year : Phylogeny temp	0.08 (-0.37, 0.41)	0.874
Phylogeny temp between-year : Phylogeny temp	-0.6 (-0.75, -0.2)	**0.008**
Phylogeny precip : Phylogeny temp	0.39 (-0.02, 0.64)	0.11
Phylogeny precip within-year : Phylogeny temp	-0.43 (-0.67, -0.06)	**0.034**
Phylogeny precip between-year : Phylogeny temp	0.24 (-0.12, 0.58)	0.188
Phylogeny temp between-year : Phylogeny temp within-year	-0.52 (-0.73, -0.06)	0.052
Phylogeny precip : Phylogeny temp within-year	0.64 (0.26, 0.8)	**0.002**
Phylogeny precip within-year : Phylogeny temp within-year	-0.37 (-0.67, 0)	0.076
Phylogeny precip between-year : Phylogeny temp within-year	0.65 (0.34, 0.82)	**0.001**
Phylogeny precip : Phylogeny temp between-year	-0.46 (-0.72, -0.05)	**0.04**
Phylogeny precip within-year : Phylogeny temp between-year	0.72 (0.39, 0.84)	**0.001**
Phylogeny precip between-year : Phylogeny temp between-year	-0.68 (-0.77, -0.19)	**0.004**
Phylogeny precip within-year : Phylogeny precip	-0.6 (-0.75, -0.15)	**0.016**
Phylogeny precip between-year : Phylogeny precip	0.73 (0.35, 0.82)	**0.002**
Phylogeny precip between-year : Phylogeny precip within-year	-0.41 (-0.63, 0.1)	0.166
Residual temp within-year : Residual temp	0.05 (-0.4, 0.43)	0.968
Residual temp between-year : Residual temp	-0.41 (-0.68, -0.04)	**0.03**
Residual precip : Residual temp	0.3 (-0.08, 0.62)	0.162
Residual precip within-year : Residual temp	-0.4 (-0.64, 0)	0.09
Residual precip between-year : Residual temp	0.26 (-0.18, 0.58)	0.266

Residual temp between-year : Residual temp within-year	-0.41 (-0.71, -0.03)	0.054
Residual precip : Residual temp within-year	0.61 (0.24, 0.79)	**0.004**
Residual precip within-year : Residual temp within-year	-0.37 (-0.69, 0.02)	0.1
Residual precip between-year : Residual temp within-year	0.62 (0.28, 0.82)	**0.001**
Residual precip : Residual temp between-year	-0.45 (-0.67, 0.05)	0.118
Residual precip within-year : Residual temp between-year	0.7 (0.43, 0.84)	**0.001**
Residual precip between-year : Residual temp between-year	-0.54 (-0.73, -0.03)	0.05
Residual precip within-year : Residual precip	-0.54 (-0.68, -0.05)	0.05
Residual precip between-year : Residual precip	0.69 (0.3, 0.82)	**0.001**
Residual precip between-year : Residual precip within-year	-0.37 (-0.6, 0.19)	0.314

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

Fixed Effects	Posterior Mode (CI)	pMCMC
Family temp	-0.22 (-0.95, 0.26)	-
Family precip	0.34 (-0.39, 0.87)	-
Family temp within-year	0.42 (-0.31, 0.94)	-
Family precip within-year	-0.06 (-0.6, 0.62)	-
Family temp between-year	0.51 (-0.16, 1.11)	-
Family precip between-year	0.14 (-0.4, 0.81)	-
Nonfamily temp	-1.41 (-2.73, -0.05)	-
Nonfamily precip	-0.88 (-2.1, 0.56)	-
Nonfamily temp within-year	0.8 (-0.33, 2.28)	-

Nonfamily precip within-year	-0.86 (-2.34, 0.32)	-
Nonfamily temp between-year	0.53 (-0.66, 1.9)	-
Nonfamily precip between-year	-1.32 (-2.52, 0.06)	-
Family temp: group size	0.25 (-0.09, 0.76)	0.194
Family precip: group size	-0.12 (-0.6, 0.25)	0.502
Family temp within-year: group size	-0.35 (-0.68, 0.17)	0.314
Family precip within-year: group size	0.04 (-0.36, 0.52)	0.78
Family temp between-year: group size	-0.38 (-0.78, 0.11)	0.14
Family precip between-year: group size	-0.11 (-0.57, 0.28)	0.59
Nonfamily temp: group size	1.44 (0.04, 2.39)	**0.046**
Nonfamily precip: group size	0.71 (-0.59, 1.9)	0.304
Nonfamily temp within-year: group size	-0.79 (-2.11, 0.23)	0.134
Nonfamily precip within-year: group size	0.76 (-0.41, 2.03)	0.25
Nonfamily temp between-year: group size	-0.29 (-1.67, 0.7)	0.376
Nonfamily precip between-year: group size	0.97 (0, 2.36)	0.058
Random Effects	**Posterior Mode (CI)**	**I2 % (CI)**
Phylogeny temp	0.64 (0.34, 0.92)	59.03 (31.98, 77.09)
Phylogeny temp within-year	0.53 (0.27, 0.89)	55.12 (26.64, 76.45)
Phylogeny temp between-year	0.48 (0.26, 0.87)	51.33 (26.36, 76.2)
Phylogeny precip	0.53 (0.27, 0.92)	58.38 (22.81, 75.76)
Phylogeny precip within-year	0.65 (0.26, 0.95)	58.65 (27.64, 73.32)
Phylogeny precip between-year	0.45 (0.25, 0.88)	45.4 (25.74, 76.28)
Residual temp	0.49 (0.23, 0.76)	40.97 (22.91, 68.02)
Residual temp within-year	0.5 (0.24, 0.85)	44.88 (23.55, 73.36)
Residual temp between-year	0.39 (0.29, 0.85)	48.67 (23.8, 73.64)
Residual precip	0.5 (0.26, 0.92)	41.62 (24.24, 77.19)
Residual precip within-year	0.44 (0.25, 0.92)	41.35 (26.68, 72.36)
Residual precip between-year	0.47 (0.24, 0.87)	54.6 (23.72, 74.26)

Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	0.02 (-0.44, 0.38)	0.836
Phylogeny temp between-year : Phylogeny temp	-0.59 (-0.72, -0.15)	**0.008**
Phylogeny precip : Phylogeny temp	0.4 (-0.07, 0.66)	0.124
Phylogeny precip within-year : Phylogeny temp	-0.51 (-0.71, -0.11)	**0.028**
Phylogeny precip between-year : Phylogeny temp	0.37 (-0.16, 0.62)	0.26
Phylogeny temp between-year : Phylogeny temp within-year	-0.51 (-0.7, -0.02)	0.054
Phylogeny precip : Phylogeny temp within-year	0.72 (0.3, 0.81)	**0.002**
Phylogeny precip within-year : Phylogeny temp within-year	-0.52 (-0.68, 0.03)	0.12
Phylogeny precip between-year : Phylogeny temp within-year	0.65 (0.33, 0.81)	**0.002**
Phylogeny precip : Phylogeny temp between-year	-0.55 (-0.77, -0.07)	**0.048**
Phylogeny precip within-year : Phylogeny temp between-year	0.66 (0.37, 0.83)	**0.002**
Phylogeny precip between-year : Phylogeny temp between-year	-0.57 (-0.78, -0.14)	**0.014**
Phylogeny precip within-year : Phylogeny precip	-0.56 (-0.76, -0.11)	**0.028**
Phylogeny precip between-year : Phylogeny precip	0.68 (0.32, 0.83)	**0.001**
Phylogeny precip between-year : Phylogeny precip within-year	-0.31 (-0.66, 0.15)	0.23
Residual temp within-year : Residual temp	0.04 (-0.43, 0.41)	0.932
Residual temp between-year : Residual temp	-0.38 (-0.71, -0.02)	0.074
Residual precip : Residual temp	0.39 (-0.1, 0.67)	0.21
Residual precip within-year : Residual temp	-0.33 (-0.61, 0.11)	0.146

Residual precip between-year : Residual temp	0.38 (-0.23, 0.58)	0.338
Residual temp between-year : Residual temp within-year	-0.44 (-0.73, -0.06)	0.056
Residual precip : Residual temp within-year	0.64 (0.25, 0.8)	**0.006**
Residual precip within-year : Residual temp within-year	-0.46 (-0.68, 0.01)	0.086
Residual precip between-year : Residual temp within-year	0.68 (0.33, 0.84)	**0.001**
Residual precip : Residual temp between-year	-0.54 (-0.72, 0)	0.084
Residual precip within-year : Residual temp between-year	0.69 (0.41, 0.83)	**0.001**
Residual precip between-year : Residual temp between-year	-0.49 (-0.74, -0.09)	**0.034**
Residual precip within-year : Residual precip	-0.6 (-0.7, -0.05)	**0.046**
Residual precip between-year : Residual precip	0.7 (0.3, 0.83)	**0.001**
Residual precip between-year : Residual precip within-year	-0.33 (-0.64, 0.15)	0.29

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Supplementary Table 5: Environmental differences among pair-breeding, family cooperative breeding, and nonfamily cooperative breeding species.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.11 (-0.14, 0.31)	0.358
Pair temp vs Nonfamily temp	0.23 (-0.12, 0.47)	0.222
Pair precip vs Family precip	0.28 (0.01, 0.58)	**0.048**
Pair precip vs Nonfamily precip	0.42 (0.05, 0.81)	**0.034**
Pair temp within-year vs Family temp within-year	0.01 (-0.34, 0.19)	0.836
Pair temp within-year vs Nonfamily temp within-year	0.09 (-0.23, 0.47)	0.42

Pair precip within-year vs Family precip within-year	0.36 (0.12, 0.69)	**0.004**
Pair precip within-year vs Nonfamily precip within-year	0.7 (0.3, 1.11)	**0.001**
Pair temp between-year vs Family temp between-year	-0.27 (-0.58, -0.04)	**0.018**
Pair temp between-year vs Nonfamily temp between-year	-0.22 (-0.53, 0.17)	0.326
Pair precip between-year vs Family precip between-year	-0.03 (-0.27, 0.31)	0.776
Pair precip between-year vs Nonfamily precip between-year	0.24 (-0.08, 0.7)	0.126
Family temp vs Nonfamily temp	0.04 (-0.28, 0.42)	0.654
Family precip vs Nonfamily precip	0.17 (-0.26, 0.61)	0.528
Family temp within-year vs Nonfamily temp within-year	0.17 (-0.23, 0.61)	0.412
Family precip within-year vs Nonfamily precip within-year	0.3 (-0.18, 0.77)	0.248
Family temp between-year vs Nonfamily temp between-year	0.07 (-0.35, 0.54)	0.558
Family precip between-year vs Nonfamily precip between-year	0.15 (-0.17, 0.72)	0.282
Random Effects	**Posterior Mode (CI)**	**I2 % (CI)**
Phylogeny temp	0.33 (0.2, 0.41)	47.73 (32.59, 66.63)
Phylogeny temp within-year	0.41 (0.24, 0.65)	57.42 (22.64, 76.87)
Phylogeny temp between-year	0.41 (0.23, 0.67)	45.71 (26.04, 71.24)
Phylogeny precip	0.56 (0.21, 0.78)	42 (24.81, 75.6)
Phylogeny precip within-year	0.46 (0.24, 0.77)	50.64 (27.64, 76.22)
Phylogeny precip between-year	0.47 (0.23, 0.78)	38.95 (23.14, 75.42)
Residual temp	0.31 (0.18, 0.41)	52.27 (33.37, 67.41)
Residual temp within-year	0.48 (0.23, 0.65)	42.58 (23.13, 77.36)
Residual temp between-year	0.42 (0.21, 0.66)	54.29 (28.76, 73.96)
Residual precip	0.43 (0.21, 0.78)	58 (24.4, 75.19)
Residual precip within-year	0.53 (0.25, 0.8)	49.36 (23.78, 72.36)

Residual precip between-year	0.56 (0.22, 0.78)	61.05 (24.58, 76.86)
Correlations	**Posterior Mode (CI)**	**pMCMC**
Phylogeny temp within-year : Phylogeny temp	0.1 (-0.34, 0.36)	0.78
Phylogeny temp between-year : Phylogeny temp	-0.38 (-0.58, -0.07)	**0.014**
Phylogeny precip : Phylogeny temp	0.24 (-0.03, 0.55)	0.112
Phylogeny precip within-year : Phylogeny temp	-0.42 (-0.63, -0.14)	**0.018**
Phylogeny precip between-year : Phylogeny temp	0.16 (-0.15, 0.48)	0.376
Phylogeny temp between-year : Phylogeny temp within-year	-0.63 (-0.74, -0.17)	**0.016**
Phylogeny precip : Phylogeny temp within-year	0.62 (0.24, 0.77)	**0.001**
Phylogeny precip within-year : Phylogeny temp within-year	-0.52 (-0.68, -0.05)	**0.036**
Phylogeny precip between-year : Phylogeny temp within-year	0.81 (0.57, 0.87)	**0.001**
Phylogeny precip : Phylogeny temp between-year	-0.4 (-0.57, 0.17)	0.272
Phylogeny precip within-year : Phylogeny temp between-year	0.62 (0.33, 0.79)	**0.001**
Phylogeny precip between-year : Phylogeny temp between-year	-0.59 (-0.75, -0.2)	**0.006**
Phylogeny precip within-year : Phylogeny precip	-0.62 (-0.74, -0.21)	**0.004**
Phylogeny precip between-year : Phylogeny precip	0.61 (0.3, 0.81)	**0.002**
Phylogeny precip between-year : Phylogeny precip within-year	-0.5 (-0.64, 0.07)	0.146
Residual temp within-year : Residual temp	0.07 (-0.3, 0.4)	0.768
Residual temp between-year : Residual temp	-0.42 (-0.61, -0.11)	**0.014**
Residual precip : Residual temp	0.37 (-0.05, 0.52)	0.104
Residual precip within-year : Residual temp	-0.45 (-0.63, -0.13)	**0.02**

Residual precip between-year : Residual temp	0.2 (-0.17, 0.46)	0.344
Residual temp between-year : Residual temp within-year	-0.55 (-0.72, -0.12)	**0.014**
Residual precip : Residual temp within-year	0.64 (0.27, 0.8)	**0.006**
Residual precip within-year : Residual temp within-year	-0.47 (-0.72, -0.05)	0.06
Residual precip between-year : Residual temp within-year	0.83 (0.57, 0.88)	**0.001**
Residual precip : Residual temp between-year	-0.4 (-0.59, 0.15)	0.28
Residual precip within-year : Residual temp between-year	0.62 (0.33, 0.78)	**0.001**
Residual precip between-year : Residual temp between-year	-0.61 (-0.76, -0.18)	**0.012**
Residual precip within-year : Residual precip	-0.63 (-0.75, -0.22)	**0.001**
Residual precip between-year : Residual precip	0.67 (0.3, 0.81)	**0.004**
Residual precip between-year : Residual precip within-year	-0.4 (-0.65, 0.11)	0.178

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Supplementary Table 6: Correlations between climate variables across different breeding systems.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.1 (-0.11, 0.34)	0.324
Pair temp vs Nonfamily temp	0.26 (-0.15, 0.56)	0.274
Pair precip vs Family precip	0.23 (0.04, 0.58)	**0.034**
Pair precip vs Nonfamily precip	0.5 (0.09, 0.88)	**0.03**
Pair temp within-year vs Family temp within-year	-0.04 (-0.28, 0.21)	0.814
Pair temp within-year vs Nonfamily temp within-year	0.14 (-0.24, 0.51)	0.414

Pair precip within-year vs Family precip within-year	0.37 (0.15, 0.68)	**0.002**
Pair precip within-year vs Nonfamily precip within-year	0.69 (0.33, 1.05)	**0.001**
Pair temp between-year vs Family temp between-year	-0.27 (-0.6, -0.07)	**0.026**
Pair temp between-year vs Nonfamily temp between-year	-0.17 (-0.6, 0.2)	0.34
Pair precip between-year vs Family precip between-year	0.01 (-0.23, 0.31)	0.75
Pair precip between-year vs Nonfamily precip between-year	0.34 (-0.08, 0.74)	0.152
Family temp vs Nonfamily temp	0.04 (-0.3, 0.48)	0.676
Family precip vs Nonfamily precip	0.05 (-0.31, 0.61)	0.488
Family temp within-year vs Nonfamily temp within-year	0.17 (-0.29, 0.59)	0.384
Family precip within-year vs Nonfamily precip within-year	0.22 (-0.13, 0.76)	0.236
Family temp between-year vs Nonfamily temp between-year	0.05 (-0.32, 0.6)	0.616
Family precip between-year vs Nonfamily precip between-year	0.35 (-0.21, 0.72)	0.294
Random Effects	**Posterior Mode (CI)**	**I2 % (CI)**
Pair Phylogeny temp	0.37 (0.23, 0.45)	20.76 (12.92, 28.78)
Pair Phylogeny precip	0.72 (0.43, 0.94)	31.92 (19.08, 44.04)
Pair Phylogeny temp within-year	0.61 (0.4, 0.78)	28.76 (21.38, 42.38)
Pair Phylogeny precip within-year	0.63 (0.39, 0.88)	31.01 (18.84, 41.6)
Pair Phylogeny temp between-year	0.56 (0.32, 0.74)	23.55 (15.12, 34.8)
Pair Phylogeny precip between-year	0.65 (0.42, 0.93)	28.91 (18.13, 40.28)
Family Phylogeny temp	0.41 (0.23, 0.63)	25.75 (14.82, 37.1)
Family Phylogeny precip	0.39 (0.24, 0.74)	19.57 (11.01, 31.16)
Family Phylogeny temp within-year	0.35 (0.19, 0.63)	20.53 (11.11, 31.58)
Family Phylogeny precip within-year	0.48 (0.24, 0.85)	21.89 (13.32, 37.3)
Family Phylogeny temp between-year	0.49 (0.25, 0.81)	22.41 (12.42, 34.39)

Family Phylogeny precip between-year	0.37 (0.22, 0.82)	21.53 (11.15, 32.92)
Nonfamily Phylogeny temp	0.56 (0.25, 1)	34.22 (21.2, 51.45)
Nonfamily Phylogeny precip	0.55 (0.25, 1.06)	29.97 (15.26, 43.18)
Nonfamily Phylogeny temp within-year	0.52 (0.24, 0.97)	30.95 (16.48, 43.7)
Nonfamily Phylogeny precip within-year	0.56 (0.27, 1.08)	27.94 (13.9, 40.97)
Nonfamily Phylogeny temp between-year	0.54 (0.3, 1.24)	30.11 (17.84, 49.18)
Nonfamily Phylogeny precip between-year	0.6 (0.3, 1.26)	27.25 (17.67, 46.56)
Residual Phylogeny temp	0.28 (0.18, 0.37)	16.64 (9.84, 26.38)
Residual Phylogeny precip	0.4 (0.2, 0.61)	17.5 (8.67, 30.72)
Residual Phylogeny temp within-year	0.3 (0.19, 0.5)	15.68 (8.26, 28.62)
Residual Phylogeny precip within-year	0.36 (0.2, 0.64)	17.73 (8.92, 33.41)
Residual Phylogeny temp between-year	0.35 (0.21, 0.57)	17.85 (8.22, 29.11)
Residual Phylogeny precip between-year	0.39 (0.2, 0.62)	17.1 (7.58, 30.1)
Correlations	**Posterior Mode (CI)**	**pMCMC**
Pair Phylogeny precip : Pair Phylogeny temp	0.12 (-0.21, 0.32)	0.54
Pair Phylogeny temp within-year : Pair Phylogeny temp	-0.4 (-0.55, -0.13)	**0.004**
Pair Phylogeny precip within-year : Pair Phylogeny temp	0.29 (0, 0.47)	**0.048**
Pair Phylogeny temp between-year : Pair Phylogeny temp	-0.44 (-0.62, -0.19)	**0.006**
Pair Phylogeny precip between-year : Pair Phylogeny temp	0.13 (-0.1, 0.41)	0.232
Pair Phylogeny temp within-year : Pair Phylogeny precip	-0.59 (-0.69, -0.33)	**0.001**
Pair Phylogeny precip within-year : Pair Phylogeny precip	0.63 (0.38, 0.74)	**0.001**
Pair Phylogeny temp between-year : Pair Phylogeny precip	-0.51 (-0.67, -0.25)	**0.002**
Pair Phylogeny precip between-year : Pair Phylogeny precip	0.83 (0.73, 0.9)	**0.001**

Pair Phylogeny precip within-year : Pair Phylogeny temp within-year	-0.24 (-0.44, 0.08)	0.152
Pair Phylogeny temp between-year : Pair Phylogeny temp within-year	0.6 (0.43, 0.74)	**0.001**
Pair Phylogeny precip between-year : Pair Phylogeny temp within-year	-0.6 (-0.72, -0.36)	**0.001**
Pair Phylogeny temp between-year : Pair Phylogeny precip within-year	-0.58 (-0.71, -0.34)	**0.001**
Pair Phylogeny precip between-year : Pair Phylogeny precip within-year	0.64 (0.4, 0.75)	**0.001**
Pair Phylogeny precip between-year : Pair Phylogeny temp between-year	-0.36 (-0.62, -0.13)	**0.018**
Family Phylogeny precip : Family Phylogeny temp	-0.2 (-0.43, 0.27)	0.572
Family Phylogeny temp within-year : Family Phylogeny temp	-0.31 (-0.55, 0.12)	0.21
Family Phylogeny precip within-year : Family Phylogeny temp	0.17 (-0.19, 0.54)	0.428
Family Phylogeny temp between-year : Family Phylogeny temp	-0.17 (-0.45, 0.23)	0.492
Family Phylogeny precip between-year : Family Phylogeny temp	0.08 (-0.23, 0.46)	0.606
Family Phylogeny temp within-year : Family Phylogeny precip	-0.27 (-0.58, 0.11)	0.236
Family Phylogeny precip within-year : Family Phylogeny precip	0.37 (-0.04, 0.66)	0.086
Family Phylogeny temp between-year : Family Phylogeny precip	-0.24 (-0.57, 0.15)	0.306
Family Phylogeny precip between-year : Family Phylogeny precip	0.45 (0.06, 0.69)	**0.038**
Family Phylogeny precip within-year : Family Phylogeny temp within-year	-0.37 (-0.65, 0.04)	0.096
Family Phylogeny temp between-year : Family Phylogeny temp within-year	0.42 (0.08, 0.69)	**0.018**
Family Phylogeny precip between-year : Family Phylogeny temp within-year	-0.4 (-0.67, -0.04)	**0.03**
Family Phylogeny temp between-year : Family Phylogeny precip within-year	-0.45 (-0.68, -0.03)	0.052

Family Phylogeny precip between-year : Family Phylogeny precip within-year	0.4 (0.09, 0.75)	**0.028**
Family Phylogeny precip between-year : Family Phylogeny temp between-year	-0.05 (-0.56, 0.23)	0.43
Nonfamily Phylogeny precip : Nonfamily Phylogeny temp	0 (-0.55, 0.36)	0.72
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny temp	-0.3 (-0.68, 0.1)	0.162
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp	0.19 (-0.31, 0.59)	0.53
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny temp	-0.31 (-0.65, 0.2)	0.302
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp	0.16 (-0.25, 0.63)	0.462
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny precip	-0.14 (-0.48, 0.4)	0.846
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny precip	0.41 (-0.15, 0.7)	0.21
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny precip	-0.03 (-0.5, 0.41)	0.844
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny precip	0.15 (-0.29, 0.6)	0.432
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp within-year	-0.03 (-0.5, 0.39)	0.834
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny temp within-year	0.45 (-0.04, 0.74)	0.134
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp within-year	-0.29 (-0.64, 0.25)	0.39
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny precip within-year	-0.21 (-0.57, 0.35)	0.622
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny precip within-year	0.37 (-0.22, 0.65)	0.232
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp between-year	0.04 (-0.46, 0.46)	0.926

Supplementary Table 7: Reanalysis of climate correlations with downsampling to verify that the greater number of pair-breeding species does not affect results.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	-0.04 (-0.28, 0.36)	0.95
Pair temp vs Nonfamily temp	0.14 (-0.34, 0.48)	0.63
Pair precip vs Family precip	0.18 (-0.11, 0.57)	0.148
Pair precip vs Nonfamily precip	0.46 (-0.05, 0.82)	0.06
Pair temp within-year vs Family temp within-year	-0.04 (-0.3, 0.33)	0.996
Pair temp within-year vs Nonfamily temp within-year	0.21 (-0.29, 0.61)	0.418
Pair precip within-year vs Family precip within-year	0.56 (0.13, 0.86)	**0.01**
Pair precip within-year vs Nonfamily precip within-year	0.67 (0.37, 1.28)	**0.002**
Pair temp between-year vs Family temp between-year	-0.41 (-0.74, 0.01)	0.052
Pair temp between-year vs Nonfamily temp between-year	-0.2 (-0.73, 0.2)	0.314
Pair precip between-year vs Family precip between-year	0.09 (-0.31, 0.41)	0.834
Pair precip between-year vs Nonfamily precip between-year	0.3 (-0.15, 0.8)	0.228
Family temp vs Nonfamily temp	0.18 (-0.34, 0.53)	0.704
Family precip vs Nonfamily precip	0.21 (-0.24, 0.61)	0.474
Family temp within-year vs Nonfamily temp within-year	0.26 (-0.28, 0.55)	0.426
Family precip within-year vs Nonfamily precip within-year	0.22 (-0.2, 0.73)	0.276
Family temp between-year vs Nonfamily temp between-year	0.13 (-0.35, 0.61)	0.558
Family precip between-year vs Nonfamily precip between-year	0.16 (-0.19, 0.73)	0.276
Random Effects	**Posterior Mode (CI)**	**I2 % (CI)**

Pair Phylogeny temp	0.4 (0.28, 0.73)	27.48 (15.46, 38.64)
Pair Phylogeny precip	0.59 (0.29, 0.91)	25.85 (14.84, 40.79)
Pair Phylogeny temp within-year	0.49 (0.27, 0.88)	29.3 (16.43, 42.56)
Pair Phylogeny precip within-year	0.69 (0.29, 1.09)	27.64 (15.55, 43.98)
Pair Phylogeny temp between-year	0.62 (0.3, 1.02)	24.35 (13.82, 40.98)
Pair Phylogeny precip between-year	0.46 (0.31, 1.02)	27.12 (14.6, 41.3)
Family Phylogeny temp	0.4 (0.2, 0.63)	19.56 (12.37, 33.25)
Family Phylogeny precip	0.39 (0.23, 0.77)	21.31 (11.57, 34.6)
Family Phylogeny temp within-year	0.34 (0.19, 0.62)	20.05 (12.44, 32.69)
Family Phylogeny precip within-year	0.45 (0.21, 0.84)	21.82 (11.82, 35.77)
Family Phylogeny temp between-year	0.46 (0.25, 0.8)	17.66 (11.42, 33.7)
Family Phylogeny precip between-year	0.43 (0.23, 0.82)	23.69 (11.44, 35.05)
Nonfamily Phylogeny temp	0.44 (0.25, 1.03)	32.2 (17.75, 49.28)
Nonfamily Phylogeny precip	0.54 (0.22, 1.14)	32.49 (16.84, 48)
Nonfamily Phylogeny temp within-year	0.47 (0.23, 0.98)	30.39 (16.91, 46.59)
Nonfamily Phylogeny precip within-year	0.48 (0.26, 1.07)	25.32 (14.22, 42.13)
Nonfamily Phylogeny temp between-year	0.67 (0.29, 1.3)	32.8 (17.06, 48.06)
Nonfamily Phylogeny precip between-year	0.53 (0.28, 1.27)	31.6 (15.5, 47.69)
Residual Phylogeny temp	0.3 (0.18, 0.44)	16.17 (8.96, 26.52)
Residual Phylogeny precip	0.35 (0.21, 0.58)	19.53 (8.73, 30.69)
Residual Phylogeny temp within-year	0.34 (0.19, 0.51)	16.68 (8.91, 29.79)
Residual Phylogeny precip within-year	0.37 (0.23, 0.69)	20.32 (9.09, 33.05)
Residual Phylogeny temp between-year	0.4 (0.24, 0.64)	17.9 (10.02, 31.62)
Residual Phylogeny precip between-year	0.37 (0.23, 0.65)	16.7 (9.17, 31.85)
Correlations	**Posterior Mode (CI)**	**pMCMC**
Pair Phylogeny precip : Pair Phylogeny temp	0.22 (-0.26, 0.48)	0.518

Pair Phylogeny temp within-year : Pair Phylogeny temp	-0.35 (-0.62, 0.03)	0.088
Pair Phylogeny precip within-year : Pair Phylogeny temp	0.31 (-0.13, 0.57)	0.182
Pair Phylogeny temp between-year : Pair Phylogeny temp	-0.46 (-0.67, -0.03)	0.058
Pair Phylogeny precip between-year : Pair Phylogeny temp	0.26 (-0.14, 0.56)	0.278
Pair Phylogeny temp within-year : Pair Phylogeny precip	-0.45 (-0.7, -0.08)	**0.01**
Pair Phylogeny precip within-year : Pair Phylogeny precip	0.52 (0.15, 0.75)	**0.01**
Pair Phylogeny temp between-year : Pair Phylogeny precip	-0.46 (-0.71, -0.06)	**0.042**
Pair Phylogeny precip between-year : Pair Phylogeny precip	0.7 (0.41, 0.84)	**0.001**
Pair Phylogeny precip within-year : Pair Phylogeny temp within-year	-0.34 (-0.62, 0.09)	0.16
Pair Phylogeny temp between-year : Pair Phylogeny temp within-year	0.55 (0.26, 0.78)	**0.004**
Pair Phylogeny precip between-year : Pair Phylogeny temp within-year	-0.51 (-0.72, -0.1)	**0.028**
Pair Phylogeny temp between-year : Pair Phylogeny precip within-year	-0.6 (-0.76, -0.18)	**0.016**
Pair Phylogeny precip between-year : Pair Phylogeny precip within-year	0.59 (0.19, 0.79)	**0.012**
Pair Phylogeny precip between-year : Pair Phylogeny temp between-year	-0.43 (-0.7, -0.01)	0.074
Family Phylogeny precip : Family Phylogeny temp	-0.07 (-0.44, 0.3)	0.612
Family Phylogeny temp within-year : Family Phylogeny temp	-0.24 (-0.56, 0.14)	0.246
Family Phylogeny precip within-year : Family Phylogeny temp	0.21 (-0.22, 0.5)	0.446
Family Phylogeny temp between-year : Family Phylogeny temp	-0.23 (-0.45, 0.25)	0.496
Family Phylogeny precip between-year : Family Phylogeny temp	0 (-0.3, 0.44)	0.688

Family Phylogeny temp within-year : Family Phylogeny precip	-0.29 (-0.57, 0.18)	0.27
Family Phylogeny precip within-year : Family Phylogeny precip	0.45 (-0.04, 0.65)	0.088
Family Phylogeny temp between-year : Family Phylogeny precip	-0.19 (-0.59, 0.18)	0.326
Family Phylogeny precip between-year : Family Phylogeny precip	0.46 (0.07, 0.72)	0.054
Family Phylogeny precip within-year : Family Phylogeny temp within-year	-0.38 (-0.65, 0.08)	0.118
Family Phylogeny temp between-year : Family Phylogeny temp within-year	0.54 (0.05, 0.68)	**0.04**
Family Phylogeny precip between-year : Family Phylogeny temp within-year	-0.48 (-0.67, -0.01)	0.056
Family Phylogeny temp between-year : Family Phylogeny precip within-year	-0.46 (-0.67, 0.03)	0.08
Family Phylogeny precip between-year : Family Phylogeny precip within-year	0.41 (0.09, 0.74)	**0.038**
Family Phylogeny precip between-year : Family Phylogeny temp between-year	-0.33 (-0.51, 0.26)	0.442
Nonfamily Phylogeny precip : Nonfamily Phylogeny temp	-0.07 (-0.52, 0.38)	0.7
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny temp	-0.28 (-0.68, 0.11)	0.194
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp	0.24 (-0.37, 0.55)	0.584
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny temp	-0.24 (-0.64, 0.16)	0.314
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp	0.22 (-0.3, 0.61)	0.558
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny precip	-0.13 (-0.5, 0.38)	0.798
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny precip	0.45 (-0.14, 0.68)	0.18
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny precip	-0.11 (-0.52, 0.37)	0.754
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny precip	0.17 (-0.22, 0.68)	0.394

Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp within-year	-0.15 (-0.5, 0.42)	0.834
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny temp within-year	0.47 (-0.06, 0.71)	0.122
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp within-year	-0.28 (-0.61, 0.28)	0.484
Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny precip within-year	-0.14 (-0.58, 0.34)	0.654
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny precip within-year	0.34 (-0.18, 0.66)	0.262
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp between-year	-0.01 (-0.45, 0.47)	0.938

Supplementary Table 8: Environmental differences among pair-breeding, nonfamily cooperative breeding, and family cooperative breeding species with classifications assigned without a threshold (>0%).

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.02 (-0.12, 0.17)	0.63
Pair temp vs Nonfamily temp	0.14 (-0.06, 0.42)	0.15
Pair precip vs Family precip	0.3 (0.08, 0.46)	**0.01**
Pair precip vs Nonfamily precip	0.17 (-0.15, 0.48)	0.286
Pair temp within-year vs Family temp within-year	0.08 (-0.1, 0.25)	0.37
Pair temp within-year vs Nonfamily temp within-year	0.21 (-0.09, 0.51)	0.186
Pair precip within-year vs Family precip within-year	0.34 (0.13, 0.51)	**0.002**
Pair precip within-year vs Nonfamily precip within-year	0.5 (0.11, 0.75)	**0.01**
Pair temp between-year vs Family temp between-year	-0.16 (-0.35, -0.01)	**0.036**

Pair temp between-year vs Nonfamily temp between-year	-0.06 (-0.46, 0.15)	0.41
Pair precip between-year vs Family precip between-year	0.1 (-0.13, 0.27)	0.394
Pair precip between-year vs Nonfamily precip between-year	-0.12 (-0.35, 0.29)	0.976
Family temp vs Nonfamily temp	0.12 (-0.12, 0.43)	0.3
Family precip vs Nonfamily precip	-0.1 (-0.45, 0.23)	0.632
Family temp within-year vs Nonfamily temp within-year	0.18 (-0.23, 0.44)	0.432
Family precip within-year vs Nonfamily precip within-year	0.01 (-0.26, 0.44)	0.632
Family temp between-year vs Nonfamily temp between-year	0.03 (-0.28, 0.38)	0.722
Family precip between-year vs Nonfamily precip between-year	-0.11 (-0.44, 0.24)	0.596
Random Effects	**Posterior Mode (CI)**	**I2 % (CI)**
Phylogeny temp	0.28 (0.19, 0.41)	46.42 (33.04, 68.73)
Phylogeny temp within-year	0.45 (0.25, 0.62)	52.21 (22.71, 78.02)
Phylogeny temp between-year	0.5 (0.22, 0.63)	43.77 (29.02, 72.43)
Phylogeny precip	0.41 (0.2, 0.76)	46.71 (26.24, 77.33)
Phylogeny precip within-year	0.41 (0.24, 0.75)	51.8 (25.02, 70.94)
Phylogeny precip between-year	0.44 (0.23, 0.78)	45.1 (23.16, 78.32)
Residual temp	0.27 (0.18, 0.39)	53.58 (31.27, 66.96)
Residual temp within-year	0.49 (0.24, 0.63)	47.79 (21.98, 77.29)
Residual temp between-year	0.4 (0.25, 0.66)	56.23 (27.57, 70.98)
Residual precip	0.49 (0.18, 0.73)	53.29 (22.67, 73.76)
Residual precip within-year	0.42 (0.21, 0.74)	48.2 (29.06, 74.98)
Residual precip between-year	0.53 (0.21, 0.77)	54.9 (21.68, 76.84)
Correlations	**Posterior Mode (CI)**	**pMCMC**
Phylogeny temp within-year : Phylogeny temp	0.07 (-0.31, 0.36)	0.678
Phylogeny temp between-year : Phylogeny temp	-0.43 (-0.62, -0.11)	**0.014**

Phylogeny precip : Phylogeny temp	0.31 (-0.04, 0.54)	0.098
Phylogeny precip within-year : Phylogeny temp	-0.44 (-0.63, -0.15)	**0.01**
Phylogeny precip between-year : Phylogeny temp	0.25 (-0.15, 0.46)	0.28
Phylogeny temp between-year : Phylogeny temp within-year	-0.58 (-0.74, -0.2)	**0.012**
Phylogeny precip : Phylogeny temp within-year	0.73 (0.29, 0.8)	**0.002**
Phylogeny precip within-year : Phylogeny temp within-year	-0.54 (-0.7, -0.04)	0.052
Phylogeny precip between-year : Phylogeny temp within-year	0.84 (0.57, 0.88)	**0.001**
Phylogeny precip : Phylogeny temp between-year	-0.44 (-0.59, 0.14)	0.196
Phylogeny precip within-year : Phylogeny temp between-year	0.66 (0.36, 0.78)	**0.001**
Phylogeny precip between-year : Phylogeny temp between-year	-0.63 (-0.78, -0.24)	**0.012**
Phylogeny precip within-year : Phylogeny precip	-0.58 (-0.77, -0.24)	**0.004**
Phylogeny precip between-year : Phylogeny precip	0.69 (0.28, 0.79)	**0.001**
Phylogeny precip between-year : Phylogeny precip within-year	-0.41 (-0.66, 0.07)	0.14
Residual temp within-year : Residual temp	0.12 (-0.33, 0.35)	0.78
Residual temp between-year : Residual temp	-0.37 (-0.59, -0.08)	**0.02**
Residual precip : Residual temp	0.32 (-0.05, 0.53)	0.098
Residual precip within-year : Residual temp	-0.36 (-0.63, -0.14)	**0.024**
Residual precip between-year : Residual temp	0.22 (-0.17, 0.47)	0.362
Residual temp between-year : Residual temp within-year	-0.58 (-0.75, -0.17)	**0.008**
Residual precip : Residual temp within-year	0.69 (0.24, 0.79)	**0.004**

Residual precip within-year : Residual temp within-year	-0.54 (-0.71, -0.07)	**0.042**
Residual precip between-year : Residual temp within-year	0.8 (0.56, 0.89)	**0.001**
Residual precip : Residual temp between-year	-0.25 (-0.57, 0.17)	0.274
Residual precip within-year : Residual temp between-year	0.67 (0.39, 0.77)	**0.001**
Residual precip between-year : Residual temp between-year	-0.6 (-0.72, -0.16)	**0.01**
Residual precip within-year : Residual precip	-0.59 (-0.74, -0.19)	**0.004**
Residual precip between-year : Residual precip	0.69 (0.27, 0.79)	**0.002**
Residual precip between-year : Residual precip within-year	-0.43 (-0.65, 0.09)	0.184

Supplementary Table 9: Environmental differences among pair-breeding, nonfamily cooperative breeding, and family cooperative breeding species with classifications assigned using a 30% nests threshold.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.1 (-0.23, 0.3)	0.804
Pair temp vs Nonfamily temp	0 (-0.37, 0.32)	0.974
Pair precip vs Family precip	0.4 (0.06, 0.75)	**0.028**
Pair precip vs Nonfamily precip	0.36 (-0.06, 0.79)	0.126
Pair temp within-year vs Family temp within-year	-0.17 (-0.36, 0.23)	0.61
Pair temp within-year vs Nonfamily temp within-year	0.32 (-0.14, 0.68)	0.204
Pair precip within-year vs Family precip within-year	0.43 (0.08, 0.78)	**0.016**
Pair precip within-year vs Nonfamily precip within-year	0.47 (0.05, 0.93)	**0.026**
Pair temp between-year vs Family temp between-year	-0.29 (-0.66, -0.03)	**0.032**

Pair temp between-year vs Nonfamily temp between-year	-0.15 (-0.56, 0.25)	0.628
Pair precip between-year vs Family precip between-year	0.07 (-0.23, 0.49)	0.41
Pair precip between-year vs Nonfamily precip between-year	-0.02 (-0.38, 0.47)	0.87
Family temp vs Nonfamily temp	-0.06 (-0.45, 0.39)	0.908
Family precip vs Nonfamily precip	-0.09 (-0.57, 0.51)	0.856
Family temp within-year vs Nonfamily temp within-year	0.42 (-0.15, 0.85)	0.158
Family precip within-year vs Nonfamily precip within-year	-0.01 (-0.6, 0.5)	0.898
Family temp between-year vs Nonfamily temp between-year	0.29 (-0.3, 0.72)	0.35
Family precip between-year vs Nonfamily precip between-year	-0.04 (-0.62, 0.44)	0.692
Random Effects	**Posterior Mode (CI)**	**I2 % (CI)**
Phylogeny temp	0.32 (0.19, 0.41)	47.32 (33.5, 68.27)
Phylogeny temp within-year	0.49 (0.25, 0.67)	43.49 (23.32, 77.76)
Phylogeny temp between-year	0.4 (0.22, 0.66)	57.19 (28.38, 73.74)
Phylogeny precip	0.47 (0.22, 0.8)	46.01 (26.44, 74.64)
Phylogeny precip within-year	0.55 (0.27, 0.78)	45.97 (28.97, 74.58)
Phylogeny precip between-year	0.55 (0.24, 0.82)	55.71 (22.49, 76.72)
Residual temp	0.32 (0.2, 0.41)	52.68 (31.73, 66.5)
Residual temp within-year	0.39 (0.22, 0.64)	56.51 (22.24, 76.68)
Residual temp between-year	0.47 (0.23, 0.65)	42.81 (26.26, 71.62)
Residual precip	0.43 (0.22, 0.8)	53.99 (25.36, 73.56)
Residual precip within-year	0.41 (0.25, 0.78)	54.03 (25.42, 71.03)
Residual precip between-year	0.43 (0.24, 0.81)	44.29 (23.28, 77.51)
Correlations	**Posterior Mode (CI)**	**pMCMC**
Phylogeny temp within-year : Phylogeny temp	0.15 (-0.29, 0.38)	0.66
Phylogeny temp between-year : Phylogeny temp	-0.39 (-0.59, -0.08)	**0.016**

Phylogeny precip : Phylogeny temp	0.4 (-0.03, 0.54)	0.086
Phylogeny precip within-year : Phylogeny temp	-0.42 (-0.62, -0.13)	**0.012**
Phylogeny precip between-year : Phylogeny temp	0.25 (-0.15, 0.52)	0.264
Phylogeny temp between-year : Phylogeny temp within-year	-0.6 (-0.73, -0.16)	**0.016**
Phylogeny precip : Phylogeny temp within-year	0.66 (0.26, 0.79)	**0.008**
Phylogeny precip within-year : Phylogeny temp within-year	-0.55 (-0.7, -0.05)	**0.044**
Phylogeny precip between-year : Phylogeny temp within-year	0.83 (0.58, 0.89)	**0.001**
Phylogeny precip : Phylogeny temp between-year	-0.35 (-0.57, 0.19)	0.254
Phylogeny precip within-year : Phylogeny temp between-year	0.64 (0.36, 0.8)	**0.001**
Phylogeny precip between-year : Phylogeny temp between-year	-0.64 (-0.73, -0.2)	**0.006**
Phylogeny precip within-year : Phylogeny precip	-0.63 (-0.75, -0.24)	**0.006**
Phylogeny precip between-year : Phylogeny precip	0.67 (0.29, 0.79)	**0.006**
Phylogeny precip between-year : Phylogeny precip within-year	-0.47 (-0.64, 0.07)	0.156
Residual temp within-year : Residual temp	0.04 (-0.31, 0.36)	0.736
Residual temp between-year : Residual temp	-0.37 (-0.6, -0.07)	**0.04**
Residual precip : Residual temp	0.36 (-0.03, 0.54)	0.098
Residual precip within-year : Residual temp	-0.4 (-0.6, -0.12)	**0.022**
Residual precip between-year : Residual temp	0.29 (-0.2, 0.45)	0.354
Residual temp between-year : Residual temp within-year	-0.57 (-0.73, -0.16)	**0.016**
Residual precip : Residual temp within-year	0.67 (0.26, 0.78)	**0.002**

Residual precip within-year : Residual temp within-year	-0.48 (-0.69, -0.05)	**0.042**
Residual precip between-year : Residual temp within-year	0.82 (0.56, 0.88)	**0.001**
Residual precip : Residual temp between-year	-0.36 (-0.55, 0.19)	0.29
Residual precip within-year : Residual temp between-year	0.63 (0.32, 0.77)	**0.004**
Residual precip between-year : Residual temp between-year	-0.53 (-0.74, -0.2)	**0.012**
Residual precip within-year : Residual precip	-0.57 (-0.75, -0.22)	**0.004**
Residual precip between-year : Residual precip	0.65 (0.28, 0.77)	**0.001**
Residual precip between-year : Residual precip within-year	-0.47 (-0.64, 0.07)	0.142

Supplementary Table 10: Variation in the frequency of cooperative breeding (% nests with group breeding, logit transformed) in groups with a breeding pair versus multiple breeders (2+) and with only family helpers versus a mix of family and nonfamily helpers in relation to climate.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair Family temp	0.08 (-0.17, 0.34)	-
Pair Family precip	-0.06 (-0.23, 0.31)	-
Pair Family temp within-year	-0.05 (-0.3, 0.22)	-
Pair Family precip within-year	-0.01 (-0.27, 0.24)	-
Pair Family temp between-year	0.02 (-0.23, 0.31)	-
Pair Family precip between-year	0.01 (-0.21, 0.27)	-
Pair Mixed temp	-0.07 (-0.46, 0.3)	-
Pair Mixed precip	-0.12 (-0.43, 0.33)	-
Pair Mixed temp within-year	0.31 (-0.05, 0.68)	-
Pair Mixed precip within-year	0.01 (-0.39, 0.36)	-

Pair Mixed temp between-year	0.2 (-0.24, 0.53)	**-**
Pair Mixed precip between-year	0.01 (-0.44, 0.28)	**-**
Multiple Family temp	-0.14 (-0.56, 0.3)	**-**
Multiple Family precip	-0.18 (-0.47, 0.42)	**-**
Multiple Family temp within-year	0.09 (-0.21, 0.65)	**-**
Multiple Family precip within-year	0.12 (-0.26, 0.65)	**-**
Multiple Family temp between-year	0.25 (-0.29, 0.62)	**-**
Multiple Family precip between-year	0.07 (-0.39, 0.46)	**-**
Pair Family temp: coop frequency	0.15 (0.04, 0.35)	**0.022**
Pair Family precip: coop frequency	0 (-0.13, 0.2)	0.584
Pair Family temp within-year: coop frequency	-0.09 (-0.27, 0.04)	0.186
Pair Family precip within-year: coop frequency	0.02 (-0.16, 0.17)	0.858
Pair Family temp between-year: coop frequency	-0.12 (-0.3, 0.03)	0.146
Pair Family precip between-year: coop frequency	-0.02 (-0.16, 0.16)	0.888
Pair Mixed temp: coop frequency	0 (-0.23, 0.29)	0.844
Pair Mixed precip: coop frequency	-0.13 (-0.42, 0.09)	0.196
Pair Mixed temp within-year: coop frequency	0.13 (-0.14, 0.36)	0.366
Pair Mixed precip within-year: coop frequency	-0.14 (-0.4, 0.11)	0.264
Pair Mixed temp between-year: coop frequency	-0.02 (-0.31, 0.2)	0.626
Pair Mixed precip between-year: coop frequency	-0.18 (-0.46, 0.02)	0.062
Multiple Family temp: coop frequency	0.19 (0.02, 0.56)	**0.032**
Multiple Family precip: coop frequency	0.03 (-0.23, 0.33)	0.662
Multiple Family temp within-year: coop frequency	-0.41 (-0.65, -0.09)	**0.012**
Multiple Family precip within-year: coop frequency	0.13 (-0.15, 0.4)	0.382

Multiple Family temp between-year: coop frequency	-0.25 (-0.62, -0.03)	**0.044**
Multiple Family precip between-year: coop frequency	-0.06 (-0.25, 0.3)	1
Random Effects	**Posterior Mode (CI)**	**I2 % (CI)**
Phylogeny temp	0.52 (0.28, 0.81)	49.95 (31.33, 73.29)
Phylogeny temp within-year	0.53 (0.26, 0.9)	46.9 (26.26, 75.85)
Phylogeny temp between-year	0.62 (0.27, 0.93)	48.94 (25.98, 77.38)
Phylogeny precip	0.7 (0.28, 0.95)	61.26 (25.57, 77.87)
Phylogeny precip within-year	0.43 (0.26, 0.95)	53.84 (26.1, 73.65)
Phylogeny precip between-year	0.48 (0.27, 0.85)	57.03 (26.47, 77.44)
Residual temp	0.46 (0.24, 0.76)	50.05 (26.71, 68.67)
Residual temp within-year	0.51 (0.22, 0.84)	53.1 (24.15, 73.74)
Residual temp between-year	0.48 (0.26, 0.91)	51.06 (22.62, 74.02)
Residual precip	0.42 (0.26, 0.94)	38.74 (22.13, 74.43)
Residual precip within-year	0.44 (0.24, 0.91)	46.16 (26.35, 73.9)
Residual precip between-year	0.39 (0.23, 0.84)	42.97 (22.56, 73.53)
Correlations	**Posterior Mode (CI)**	**pMCMC**
Phylogeny temp within-year : Phylogeny temp	0.07 (-0.36, 0.44)	0.854
Phylogeny temp between-year : Phylogeny temp	-0.43 (-0.71, -0.08)	**0.036**
Phylogeny precip : Phylogeny temp	0.44 (-0.07, 0.63)	0.112
Phylogeny precip within-year : Phylogeny temp	-0.46 (-0.66, -0.01)	0.068
Phylogeny precip between-year : Phylogeny temp	0.16 (-0.21, 0.54)	0.324
Phylogeny temp between-year : Phylogeny temp within-year	-0.48 (-0.74, -0.08)	**0.032**
Phylogeny precip : Phylogeny temp within-year	0.71 (0.24, 0.79)	**0.004**
Phylogeny precip within-year : Phylogeny temp within-year	-0.46 (-0.66, 0.07)	0.104

Phylogeny precip between-year : Phylogeny temp within-year	0.66 (0.35, 0.81)	**0.001**
Phylogeny precip : Phylogeny temp between-year	-0.56 (-0.74, -0.06)	**0.038**
Phylogeny precip within-year : Phylogeny temp between-year	0.71 (0.37, 0.83)	**0.002**
Phylogeny precip between-year : Phylogeny temp between-year	-0.61 (-0.77, -0.16)	**0.014**
Phylogeny precip within-year : Phylogeny precip	-0.59 (-0.78, -0.14)	**0.016**
Phylogeny precip between-year : Phylogeny precip	0.71 (0.31, 0.81)	**0.001**
Phylogeny precip between-year : Phylogeny precip within-year	-0.34 (-0.67, 0.09)	0.16
Residual temp within-year : Residual temp	0.07 (-0.43, 0.4)	0.936
Residual temp between-year : Residual temp	-0.39 (-0.66, 0.04)	0.114
Residual precip : Residual temp	0.29 (-0.12, 0.61)	0.236
Residual precip within-year : Residual temp	-0.31 (-0.63, 0.11)	0.214
Residual precip between-year : Residual temp	0.09 (-0.23, 0.57)	0.416
Residual temp between-year : Residual temp within-year	-0.58 (-0.73, -0.03)	0.056
Residual precip : Residual temp within-year	0.67 (0.17, 0.79)	**0.012**
Residual precip within-year : Residual temp within-year	-0.46 (-0.67, 0.07)	0.132
Residual precip between-year : Residual temp within-year	0.63 (0.28, 0.81)	**0.006**
Residual precip : Residual temp between-year	-0.44 (-0.74, 0.02)	0.108
Residual precip within-year : Residual temp between-year	0.67 (0.36, 0.84)	**0.001**
Residual precip between-year : Residual temp between-year	-0.53 (-0.76, -0.09)	**0.036**
Residual precip within-year : Residual precip	-0.47 (-0.71, 0.01)	0.088

Residual precip between-year : Residual precip	0.65 (0.29, 0.82)	**0.001**
Residual precip between-year : Residual precip within-year	-0.34 (-0.63, 0.17)	0.312

Supplementary Table 11: Variation in the size of groups (log transformed) with a breeding pair versus multiple breeders (2+) and with only family helpers versus a mix of family and nonfamily helpers in relation to climate.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair Family temp	-0.32 (-1.37, 0.68)	-
Pair Family precip	0.45 (-0.66, 1.53)	-
Pair Family temp within-year	0.2 (-0.86, 1.19)	-
Pair Family precip within-year	0.2 (-0.88, 1.16)	-
Pair Family temp between-year	-0.14 (-1.09, 0.98)	-
Pair Family precip between-year	0.26 (-0.92, 1.08)	-
Pair Mixed temp	-0.76 (-2.14, 0.47)	-
Pair Mixed precip	0.32 (-0.86, 1.76)	-
Pair Mixed temp within-year	0.64 (-0.62, 1.85)	-
Pair Mixed precip within-year	-0.28 (-1.26, 1.33)	-
Pair Mixed temp between-year	0.87 (-0.51, 2.26)	-
Pair Mixed precip between-year	0.4 (-0.78, 1.61)	-
Multiple Family temp	-0.09 (-1.45, 0.99)	-
Multiple Family precip	-0.59 (-1.58, 1.12)	-
Multiple Family temp within-year	0.49 (-0.49, 2.09)	-
Multiple Family precip within-year	-0.3 (-1.22, 1.4)	-
Multiple Family temp between-year	1 (-0.29, 2.41)	-
Multiple Family precip between-year	0.14 (-1.48, 1.07)	-
Pair Family temp: group size	0.37 (-0.48, 1.07)	0.464
Pair Family precip: group size	-0.41 (-1.09, 0.58)	0.5

Pair Family temp within-year: group size	-0.3 (-1.04, 0.55)	0.52
Pair Family precip within-year: group size	-0.04 (-0.95, 0.7)	0.818
Pair Family temp between-year: group size	0.31 (-0.72, 0.86)	0.854
Pair Family precip between-year: group size	-0.19 (-0.73, 0.8)	0.952
Pair Mixed temp: group size	0.45 (-0.34, 1.35)	0.204
Pair Mixed precip: group size	-0.38 (-1.34, 0.41)	0.382
Pair Mixed temp within-year: group size	-0.18 (-0.93, 0.7)	0.72
Pair Mixed precip within-year: group size	0.13 (-0.98, 0.72)	0.85
Pair Mixed temp between-year: group size	-0.57 (-1.45, 0.35)	0.294
Pair Mixed precip between-year: group size	-0.39 (-1.18, 0.37)	0.322
Multiple Family temp: group size	0.26 (-0.47, 1.01)	0.472
Multiple Family precip: group size	0.16 (-0.66, 0.94)	0.756
Multiple Family temp within-year: group size	-0.58 (-1.23, 0.31)	0.196
Multiple Family precip within-year: group size	0.27 (-0.63, 0.9)	0.706
Multiple Family temp between-year: group size	-0.61 (-1.35, 0.2)	0.112
Multiple Family precip between-year: group size	0.08 (-0.61, 0.89)	0.788
Random Effects	**Posterior Mode (CI)**	**I2 % (CI)**
Phylogeny temp	0.59 (0.3, 0.93)	58.63 (30.18, 74.58)
Phylogeny temp within-year	0.58 (0.26, 0.95)	44.45 (27.18, 79.37)
Phylogeny temp between-year	0.62 (0.28, 0.98)	43.25 (25, 76.93)
Phylogeny precip	0.62 (0.29, 1.05)	66.27 (24.55, 79.28)
Phylogeny precip within-year	0.67 (0.2, 0.97)	55.36 (26, 74.88)
Phylogeny precip between-year	0.44 (0.24, 0.89)	61.45 (25.59, 78.83)
Residual temp	0.43 (0.26, 0.82)	41.37 (25.42, 69.82)

Residual temp within-year	0.44 (0.24, 0.9)	55.55 (20.63, 72.82)
Residual temp between-year	0.53 (0.27, 0.9)	56.75 (23.07, 75)
Residual precip	0.51 (0.24, 0.95)	33.73 (20.72, 75.45)
Residual precip within-year	0.48 (0.22, 0.96)	44.64 (25.12, 74)
Residual precip between-year	0.4 (0.19, 0.82)	38.55 (21.17, 74.41)
Correlations	**Posterior Mode (CI)**	**pMCMC**
Phylogeny temp within-year : Phylogeny temp	0.03 (-0.39, 0.45)	0.824
Phylogeny temp between-year : Phylogeny temp	-0.34 (-0.68, -0.07)	**0.02**
Phylogeny precip : Phylogeny temp	0.39 (-0.04, 0.66)	0.102
Phylogeny precip within-year : Phylogeny temp	-0.38 (-0.67, 0.02)	0.08
Phylogeny precip between-year : Phylogeny temp	0.31 (-0.19, 0.58)	0.332
Phylogeny temp between-year : Phylogeny temp within-year	-0.5 (-0.75, -0.07)	**0.044**
Phylogeny precip : Phylogeny temp within-year	0.65 (0.19, 0.8)	**0.022**
Phylogeny precip within-year : Phylogeny temp within-year	-0.47 (-0.68, 0.07)	0.112
Phylogeny precip between-year : Phylogeny temp within-year	0.67 (0.32, 0.83)	**0.004**
Phylogeny precip : Phylogeny temp between-year	-0.59 (-0.75, -0.06)	**0.04**
Phylogeny precip within-year : Phylogeny temp between-year	0.73 (0.35, 0.85)	**0.001**
Phylogeny precip between-year : Phylogeny temp between-year	-0.57 (-0.77, -0.1)	**0.02**
Phylogeny precip within-year : Phylogeny precip	-0.58 (-0.77, -0.08)	**0.048**
Phylogeny precip between-year : Phylogeny precip	0.68 (0.28, 0.84)	**0.002**
Phylogeny precip between-year : Phylogeny precip within-year	-0.44 (-0.66, 0.15)	0.204
Residual temp within-year : Residual temp	0.1 (-0.46, 0.37)	0.99

Residual temp between-year : Residual temp	-0.43 (-0.65, 0.09)	0.158
Residual precip : Residual temp	0.31 (-0.13, 0.63)	0.236
Residual precip within-year : Residual temp	-0.29 (-0.56, 0.19)	0.24
Residual precip between-year : Residual temp	0.21 (-0.24, 0.57)	0.472
Residual temp between-year : Residual temp within-year	-0.5 (-0.72, -0.02)	**0.048**
Residual precip : Residual temp within-year	0.59 (0.16, 0.79)	**0.01**
Residual precip within-year : Residual temp within-year	-0.35 (-0.67, 0.06)	0.134
Residual precip between-year : Residual temp within-year	0.69 (0.3, 0.83)	**0.002**
Residual precip : Residual temp between-year	-0.49 (-0.74, 0.02)	0.11
Residual precip within-year : Residual temp between-year	0.66 (0.31, 0.82)	**0.002**
Residual precip between-year : Residual temp between-year	-0.59 (-0.72, -0.05)	**0.046**
Residual precip within-year : Residual precip	-0.52 (-0.75, -0.05)	0.064
Residual precip between-year : Residual precip	0.65 (0.28, 0.83)	**0.001**
Residual precip between-year : Residual precip within-year	-0.33 (-0.64, 0.21)	0.332

Supplementary Table 12: 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	0.16 (-0.17, 0.46)	0.454
Pair temp vs Pair_mixed temp	0.18 (-0.26, 0.49)	0.522
Pair temp vs Multiple_family temp	-0.02 (-0.35, 0.48)	0.81

Pair temp vs Nonfamily temp	0.24 (-0.1, 0.52)	0.228
Pair precip vs Pair_family precip	0.19 (-0.24, 0.63)	0.356
Pair precip vs Pair_mixed precip	0.4 (-0.13, 0.88)	0.172
Pair precip vs Multiple_family precip	0.49 (-0.14, 0.87)	0.162
Pair precip vs Nonfamily precip	0.41 (0.05, 0.8)	**0.024**
Pair temp within-year vs Pair_family temp within-year	-0.02 (-0.42, 0.36)	0.682
Pair temp within-year vs Pair_mixed temp within-year	-0.07 (-0.51, 0.38)	0.786
Pair temp within-year vs Multiple_family temp within-year	0.12 (-0.46, 0.55)	0.832
Pair temp within-year vs Nonfamily temp within-year	0.15 (-0.21, 0.49)	0.436
Pair precip within-year vs Pair_family precip within-year	0.71 (0.19, 1.06)	**0.004**
Pair precip within-year vs Pair_mixed precip within-year	0.22 (-0.26, 0.78)	0.31
Pair precip within-year vs Multiple_family precip within-year	0.14 (-0.35, 0.65)	0.548
Pair precip within-year vs Nonfamily precip within-year	0.67 (0.31, 1.11)	**0.001**
Pair temp between-year vs Pair_family temp between-year	-0.46 (-0.85, -0.04)	**0.02**
Pair temp between-year vs Pair_mixed temp between-year	-0.16 (-0.62, 0.27)	0.46
Pair temp between-year vs Multiple_family temp between-year	-0.29 (-0.79, 0.19)	0.296
Pair temp between-year vs Nonfamily temp between-year	-0.21 (-0.52, 0.2)	0.332
Pair precip between-year vs Pair_family precip between-year	0.17 (-0.26, 0.58)	0.502
Pair precip between-year vs Pair_mixed precip between-year	-0.07 (-0.54, 0.45)	0.87
Pair precip between-year vs Multiple_family precip between-year	0.05 (-0.55, 0.5)	0.96
Pair precip between-year vs Nonfamily precip between-year	0.27 (-0.08, 0.68)	0.126

Pair_family temp vs Pair_mixed temp	0.02 (-0.46, 0.55)	0.968
Pair_family temp vs Multiple_family temp	0.04 (-0.6, 0.45)	0.79
Pair_family temp vs Nonfamily temp	0.02 (-0.38, 0.49)	0.76
Pair_family precip vs Pair_mixed precip	0.01 (-0.46, 0.82)	0.612
Pair_family precip vs Multiple_family precip	0.33 (-0.53, 0.77)	0.582
Pair_family precip vs Nonfamily precip	0.3 (-0.33, 0.76)	0.434
Pair_family temp within-year vs Pair_mixed temp within-year	-0.05 (-0.6, 0.57)	0.998
Pair_family temp within-year vs Multiple_family temp within-year	0.03 (-0.5, 0.73)	0.664
Pair_family temp within-year vs Nonfamily temp within-year	0.15 (-0.35, 0.68)	0.412
Pair_family precip within-year vs Pair_mixed precip within-year	-0.24 (-1.06, 0.27)	0.258
Pair_family precip within-year vs Multiple_family precip within-year	-0.46 (-1.14, 0.11)	0.162
Pair_family precip within-year vs Nonfamily precip within-year	0.05 (-0.52, 0.62)	0.87
Pair_family temp between-year vs Pair_mixed temp between-year	0.17 (-0.23, 0.95)	0.32
Pair_family temp between-year vs Multiple_family temp between-year	0.22 (-0.36, 0.85)	0.532
Pair_family temp between-year vs Nonfamily temp between-year	0.36 (-0.26, 0.76)	0.308
Pair_family precip between-year vs Pair_mixed precip between-year	-0.07 (-0.79, 0.49)	0.582
Pair_family precip between-year vs Multiple_family precip between-year	-0.34 (-0.87, 0.42)	0.638
Pair_family precip between-year vs Nonfamily precip between-year	0.15 (-0.38, 0.67)	0.532
Pair_mixed temp vs Multiple_family temp	0.14 (-0.66, 0.46)	0.828
Pair_mixed temp vs Nonfamily temp	0.1 (-0.39, 0.57)	0.778
Pair_mixed precip vs Multiple_family precip	0.04 (-0.66, 0.79)	0.918

Pair_mixed precip vs Nonfamily precip	-0.08 (-0.53, 0.73)	0.812
Pair_mixed temp within-year vs Multiple_family temp within-year	0.17 (-0.52, 0.81)	0.738
Pair_mixed temp within-year vs Nonfamily temp within-year	0.23 (-0.35, 0.75)	0.454
Pair_mixed precip within-year vs Multiple_family precip within-year	-0.04 (-0.81, 0.62)	0.778
Pair_mixed precip within-year vs Nonfamily precip within-year	0.51 (-0.31, 1.03)	0.23
Pair_mixed temp between-year vs Multiple_family temp between-year	-0.19 (-0.77, 0.55)	0.772
Pair_mixed temp between-year vs Nonfamily temp between-year	-0.07 (-0.58, 0.59)	0.948
Pair_mixed precip between-year vs Multiple_family precip between-year	-0.09 (-0.7, 0.73)	0.95
Pair_mixed precip between-year vs Nonfamily precip between-year	0.3 (-0.27, 0.96)	0.262
Multiple_family temp vs Nonfamily temp	0.16 (-0.35, 0.65)	0.584
Multiple_family precip vs Nonfamily precip	0.05 (-0.56, 0.68)	0.876
Multiple_family temp within-year vs Nonfamily temp within-year	-0.12 (-0.53, 0.64)	0.786
Multiple_family precip within-year vs Nonfamily precip within-year	0.38 (-0.08, 1.22)	0.102
Multiple_family temp between-year vs Nonfamily temp between-year	0.14 (-0.51, 0.66)	0.82
Multiple_family precip between-year vs Nonfamily precip between-year	0.35 (-0.37, 0.89)	0.34
Random Effects	**Posterior Mode (CI)**	**I2 % (CI)**
Phylogeny temp	0.27 (0.2, 0.42)	47.52 (32.75, 66.63)
Phylogeny temp within-year	0.5 (0.24, 0.65)	54.94 (22.92, 74.78)
Phylogeny temp between-year	0.42 (0.23, 0.67)	49.76 (28.29, 72.86)
Phylogeny precip	0.61 (0.22, 0.77)	44.09 (23.96, 72.73)
Phylogeny precip within-year	0.63 (0.24, 0.76)	51.42 (26.75, 73.98)
Phylogeny precip between-year	0.57 (0.23, 0.76)	53.45 (24, 75.49)
Residual temp	0.31 (0.2, 0.42)	52.48 (33.37, 67.25)

Residual temp within-year	0.37 (0.25, 0.65)	45.06 (25.22, 77.08)
Residual temp between-year	0.45 (0.23, 0.67)	50.24 (27.14, 71.71)
Residual precip	0.46 (0.24, 0.79)	55.91 (27.27, 76.04)
Residual precip within-year	0.53 (0.27, 0.79)	48.58 (26.02, 73.25)
Residual precip between-year	0.44 (0.22, 0.77)	46.55 (24.51, 76)
Correlations	**Posterior Mode (CI)**	**pMCMC**
Phylogeny temp within-year : Phylogeny temp	0.17 (-0.34, 0.36)	0.786
Phylogeny temp between-year : Phylogeny temp	-0.45 (-0.58, -0.07)	**0.016**
Phylogeny precip : Phylogeny temp	0.29 (-0.03, 0.6)	0.12
Phylogeny precip within-year : Phylogeny temp	-0.45 (-0.62, -0.14)	**0.008**
Phylogeny precip between-year : Phylogeny temp	0.18 (-0.19, 0.47)	0.36
Phylogeny temp between-year : Phylogeny temp within-year	-0.61 (-0.75, -0.17)	**0.016**
Phylogeny precip : Phylogeny temp within-year	0.67 (0.25, 0.79)	**0.002**
Phylogeny precip within-year : Phylogeny temp within-year	-0.55 (-0.68, -0.04)	**0.046**
Phylogeny precip between-year : Phylogeny temp within-year	0.83 (0.57, 0.88)	**0.001**
Phylogeny precip : Phylogeny temp between-year	-0.37 (-0.61, 0.14)	0.264
Phylogeny precip within-year : Phylogeny temp between-year	0.66 (0.35, 0.78)	**0.001**
Phylogeny precip between-year : Phylogeny temp between-year	-0.64 (-0.76, -0.2)	**0.006**
Phylogeny precip within-year : Phylogeny precip	-0.6 (-0.75, -0.21)	**0.002**
Phylogeny precip between-year : Phylogeny precip	0.7 (0.3, 0.8)	**0.001**
Phylogeny precip between-year : Phylogeny precip within-year	-0.4 (-0.62, 0.11)	0.198
Residual temp within-year : Residual temp	0.1 (-0.31, 0.37)	0.762

Residual temp between-year : Residual temp	-0.38 (-0.62, -0.09)	**0.032**
Residual precip : Residual temp	0.31 (-0.06, 0.55)	0.124
Residual precip within-year : Residual temp	-0.41 (-0.61, -0.09)	**0.012**
Residual precip between-year : Residual temp	0.17 (-0.19, 0.46)	0.318
Residual temp between-year : Residual temp within-year	-0.54 (-0.73, -0.19)	**0.008**
Residual precip : Residual temp within-year	0.62 (0.28, 0.79)	**0.006**
Residual precip within-year : Residual temp within-year	-0.44 (-0.7, -0.08)	**0.032**
Residual precip between-year : Residual temp within-year	0.82 (0.57, 0.88)	**0.001**
Residual precip : Residual temp between-year	-0.37 (-0.56, 0.19)	0.246
Residual precip within-year : Residual temp between-year	0.67 (0.33, 0.79)	**0.001**
Residual precip between-year : Residual temp between-year	-0.59 (-0.74, -0.2)	**0.004**
Residual precip within-year : Residual precip	-0.62 (-0.75, -0.25)	**0.001**
Residual precip between-year : Residual precip	0.67 (0.3, 0.81)	**0.01**
Residual precip between-year : Residual precip within-year	-0.45 (-0.63, 0.07)	0.142

Session information

```
R version 4.5.1 (2025-06-13)
Platform: aarch64-apple-darwin20
Running under: macOS Tahoe 26.5.1

Matrix products: default
BLAS:   /Library/Frameworks/R.framework/Versions/4.5-arm64/Resources/lib/libRblas.0.dylib
LAPACK: /Library/Frameworks/R.framework/Versions/4.5-arm64/Resources/lib/libRlapack.dyl
```

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ib;  LAPACK version 3.12.1

locale:
[1] C.UTF-8/C.UTF-8/C.UTF-8/C/C.UTF-8/C.UTF-8

time zone: Europe/Stockholm
tzcode source: internal

attached base packages:
[1] stats     graphics  grDevices utils     datasets  methods   base

other attached packages:
 [1] corpcor_1.6.10     kableExtra_1.4.0   ggrepel_0.9.8      officer_0.7.4
 [5] flextable_0.9.11   GGally_2.4.0       corrplot_0.95      magick_2.9.1
 [9] TreeTools_2.3.0    ggnewscale_0.5.2   ggtreeExtra_1.18.1 treeio_1.32.0
[13] ggtree_3.16.3      tidytree_0.4.7     psych_2.6.3        ggsci_5.0.0
[17] stringdist_0.9.17  openxlsx_4.2.8.1   car_3.1-5          carData_3.0-6
[21] cowplot_1.2.0      MCMCglmm_2.36      ape_5.8-1          coda_0.19-4.1
[25] Matrix_1.7-5       lubridate_1.9.5    forcats_1.0.1      stringr_1.6.0
[29] purrr_1.2.2        readr_2.2.0        tidyr_1.3.2        tibble_3.3.1
[33] ggplot2_4.0.3      tidyverse_2.0.0    dplyr_1.2.1

loaded via a namespace (and not attached):
 [1] DBI_1.3.0              Rdpack_2.6.6           mnormt_2.1.2
 [4] rlang_1.2.0            magrittr_2.0.5         otel_0.2.0
 [7] e1071_1.7-17           compiler_4.5.1         png_0.1-9
[10] systemfonts_1.3.2      vctrs_0.7.3            pkgconfig_2.0.3
[13] fastmap_1.2.0          labeling_0.4.3         rmarkdown_2.31
[16] tzdb_0.5.0             ragg_1.5.2             bit_4.6.0
[19] xfun_0.57              aplot_0.2.9            jsonlite_2.0.0
[22] uuid_1.2-2             parallel_4.5.1         R6_2.6.1
[25] stringi_1.8.7          RColorBrewer_1.1-3     Rcpp_1.1.1-1.1
[28] knitr_1.51             pacman_0.5.1           timechange_0.4.0
[31] tidyselect_1.2.1       rstudioapi_0.18.0      dichromat_2.0-0.1
[34] abind_1.4-8            yaml_2.3.12            qpdf_1.4.1
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[79] yulab.utils_0.2.4     digest_0.6.39         fontquiver_0.2.1
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```