Cooperation facilitates the colonisation of harsh environments

Charlie K. Cornwallis[1*], Carlos A. Botero[2], Dustin R. Rubenstein[3], Philip A. Downing[4], Stuart A. West[4] & Ashleigh S. Griffin[4]

Affiliations:

[1]Department of Biology, Lund University, SE-223 62 Lund, Sweden.

[2]Department of Biology, Washington University, St Louis, MO 63130-4899, USA.

[3]Department of Ecology, Evolution and Environmental Biology and Center for Integrative Animal Behavior, Columbia University, NY 10027, USA.

[4]Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK.

Name and complete mailing address of the person to whom correspondence should be sent:

Charlie Cornwallis, Department of Biology, Lund University, SE-223 62 Lund, Sweden;

charlie.cornwallis@biol.lu.se

Animals living in harsh environments, where temperatures are hot and rainfall is unpredictable, are more likely to breed in cooperative groups. As a result, harsh environmental conditions have been accepted as a key factor explaining the evolution of cooperation. However, this is based on evidence that has not investigated the order of evolutionary events, so the inferred causality could be incorrect. We resolve this problem using phylogenetic analyses of 4707 bird species and found that causation was in the opposite direction to that previously assumed. Rather than harsh environments favouring cooperation, cooperative breeding has facilitated the colonisation of harsh environments. Cooperative breeding was, in fact, more likely to evolve from ancestors occupying relatively cool environmental niches with predictable rainfall, which had low levels of polyandry and hence high within-group relatedness. We also found that polyandry increased after cooperative breeders invaded harsh environments, suggesting that when helpers have limited options to breed independently, polyandry no longer destabilizes cooperation. This provides an explanation for the puzzling cases of polyandrous cooperative breeding birds. More generally, this illustrates how cooperation can play a key role in invading ecological niches, a pattern observed across all levels of biological organization from cells to animal societies.

Species breeding in cooperative groups are more commonly found living in hot and unpredictable environments (Fig. 1)[1–4]. This well documented relationship has long been taken as evidence for the intuitively satisfying idea that harsh environments favour the evolution of helping behaviour[2–6]. The theoretical argument is that in harsh environments individuals are better off helping others with whom they share genes, either because independent breeding is likely to fail[5,7,8], or because helpers provide greater benefits when environmental conditions are worse (e.g.[9,10]). This idea, often referred to as the 'ecological constraints hypothesis'[5,11], has been supported by a number of within-species studies

showing individuals are more likely to breed cooperatively when environmental factors limit independent breeding (e.g. [3,4,12–14]), and that helpers provide insurance against breeding failure during poor years, which are frequent in harsh environments (e.g.[9,10]).

The idea that environmental conditions drive the evolution of cooperative breeding could, however, be incorrect. An alternative explanation is that causation is in the opposite direction, with cooperative breeding allowing individuals to colonize and breed in harsher environments. Another potential explanation is that there is no causal relationship between environmental conditions and cooperative breeding, and that their association is instead explained by a third correlated variable[15]. For example, environmental conditions can influence rates of divorce and female polyandry, both of which determine within group relatedness[16,17]. Relatedness is important because cooperation is more likely to be favoured if it is directed towards relatives that share the genes for cooperation[18], termed kin selection[19]. In this case, cooperative breeding could occur more often in harsh environments simply because the environment determines rates of female polyandry and relatedness within families, rather than environmental conditions directly selecting for helping behaviour. These competing hypotheses have remained untested because reliably reconstructing the order of evolutionary events for more than two traits simultaneously is a major challenge and requires data on the all relevant variables for a large number of species[20].

Here we conducted an analysis across birds that allowed us to test the different competing explanations driving the relationship between cooperative breeding behaviour and environmental harshness. We collected data on the breeding system of 4707 species defining them as either cooperative ($n_{species}$=154) or noncooperative ($n_{species}$=4553) breeders depending on the presence of one or more non-breeding helpers at 10% or more of nests. This excludes communal breeders (e.g. purple swamphen, *Porphyrio porphyrio*, and greater

ani, *Crotophaga major*) and cooperative polygamists (e.g. Galapagos hawk, *Buteo galapagoensis,* and brown skua, *Catharacta lonnbergi*) where all adults in the group typically reproduce, since we are concerned with explaining cooperation where individuals forego their own reproduction. This dataset allowed us to identify the points at which transitions to and from cooperative breeding have occurred in birds. We combined these data with information on both the environmental conditions species experience (mean, variance and predictability[21] in temperature and rainfall) and levels of female polyandry ($n_{\text{cooperative species}}$=45, $n_{\text{noncooperative species}}$=263). The environmental variables were highly correlated and so we used phylogenetic principal component analyses to create indices of environmental variation (Table S1). The first principal component (environmental PC1) was strongly related to high mean temperature (factor loading = 0.76), low between-year variation in temperature (factor loading = -0.75), and high between-year variation in rainfall (factor loading = 0.69). For consistency with previous research, we refer to environmental PC1 as environmental harshness where high values indicate hot environments with variable rainfall (referred to as harsh) and low values represent cooler environments with lower variation in rainfall (referred to as benign)[16,22]. To tease apart the causality of the relationships between environmental conditions, cooperative breeding and polyandry we estimated phylogenetic correlations, ancestral states, and transition rates between variables using a combination of three phylogenetic techniques: multi-response Bayesian phylogenetic mixed models (BPMMs), reverse jump Markov chain Monte Carlo transition rate models (rj-MCMC), and phylogenetic path analysis.

Results

Our analyses confirm that cooperative breeding in birds is positively correlated with environmental harshness (Fig. 2 and Table S2: BPMM phylogenetic correlation (phylo *r*) = 0.40, credible interval (CI) =0.18 to 0.68, pMCMC = 0.001) and negatively correlated with

rates of polyandry (Table S2: phylo r = -0.34, CI = -0.53 to -0.03, pMCMC = 0.01). However, there was no apparent correlation between environmental conditions and rates of polyandry (Table S2: phylo r = 0.14, CI = -0.21 to 0.44, pMCMC = 0.22). We also found the same patterns using analyses that estimated the evolutionary transition rates between cooperative and noncooperative breeding, environmental conditions, and rates of polyandry, which indicated that cooperative breeding has coevolved with environmental conditions and rates of polyandry, but that polyandry and environmental conditions have evolved independently (rj-MCMC models of correlated versus independent evolution: cooperative breeding & environment, Bayes Factor (BF) = 11.12; cooperative breeding & polyandry, BF = 2.96; environment & polyandry: BF = 0.84, where a BF > 2 offers positive evidence, > 5 provides strong evidence, and >10 is very strong evidence). These analyses demonstrate that the association between cooperative breeding and environmental harshness is not simply a spurious relationship driven by female polyandry.

Next we examined the likely causality of the relationship between cooperative breeding and environmental traits by reconstructing the most likely environmental niches *prior* to cooperation evolving, and by examining transition rates to cooperative breeding from species with different environmental niches. We found no support for the hypothesis that living in harsh environments selects for cooperative breeding. The ancestral state reconstructions indicated that the ancestors of cooperative species occupied similar environmental niches to ancestors of noncooperative species (Fig. 3 and Table S3. BPMM: environment of ancestors of noncooperative species = 0.62, CI = -0.48 to 1.57; environment of ancestors of cooperative species = 0.58, CI = -0.85 to 1.89, difference pMCMC = 0.50). Examining transition rates, we found that the transition from noncooperative to cooperative breeding was higher in species occupying benign rather than harsh environmental niches, where benign and harsh were classified as < 70% and =>70% quartile of environmental PC1 respectively (see methods for

explanation and assessment of sensitivity to thresholds. Table S4. rjMCMC: benign conditions (mean ± SD) = 0.02 ± 0.005, percent of models where transition did not occur, which gives an indication of how likely the transition is to take place (Z) = 1.1%; harsh environments = 0.01 ± 0.02, Z = 44.7%). Importantly, our analyses were not hindered by an inability to reconstruct the environmental niches ancestors occupied, as there was a strong phylogenetic signature in environmental PC1, both when estimating this across all species (Table S2. BPMM: phylogenetic heritability = 71%, CI = 51% to 84%) and when estimating this separately for cooperative and noncooperative species (Table S5. BPMM: phylogenetic heritability for cooperative species = 68%, CI= 27 to 91%, phylogenetic heritability for noncooperative species = 84%, CI= 65 to 90%).

Although there was no support for harsh environmental conditions explaining the evolution of cooperative behaviour, we found strong support for the hypothesis that cooperative breeding facilitates the transition to living in harsh environments. The transition rate from living in benign environments to living in harsh environments was twice as high in cooperative as opposed to noncooperative breeders (Fig. 3 and Table S4. rjMCMC: cooperative breeders = 0.05 ± 0.03, Z = 2.7%; noncooperative species = 0.02 ± 0.01, Z = 1%). Furthermore, when we conducted a phylogenetic path analysis that tested alternative models of the relationships among cooperative breeding, environmental conditions and polyandry, we found that the best-supported model was one where transitions to cooperative breeding preceded transitions to living in harsh environments (Extended Data Fig. 1 and Table S6: best supported model C = 0.25, df = 2, P=0.88). Taken together our results strongly suggest that cooperative breeding facilitates living in harsh environments, and not that living in harsh environments favours cooperation (Fig. 3). What then explains the transition to cooperative breeding in birds?

Previous research on social insects[23], mammals[24] and birds[25] has suggested that monogamy or low levels of polyandry has played a key role in the evolution of complex social behaviour. Low levels of polyandry leads to high relatedness within family groups, which increases the kin-selected benefits of helping raise family members[26]. In support of this hypothesis and consistent with previous research, we found that the ancestors of cooperative species had significantly lower levels of polyandry than those of noncooperative species (Fig. 3 and Table S3. BPMM: noncooperative species = 0.20, CI = 0.07 to 0.55; cooperative species = 0.04, CI = 0.004 to 0.38, difference pMCMC = 0.03). Similarly to environmental PC1, ancestral levels of rates of polyandry could be estimated due to the high phylogenetic signature in this trait (Table S2: phylogenetic heritability = 77.12%, CI = 59.52 to 87.70%).

There are however, a number of relatively polyandrous cooperative breeders (Fig. 2). For example, 70% of nests in Australian magpies, *Gymnorhina tibicen* (Table S13), and 40% of nests in western bluebirds, *Sialia Mexicana* (Table S13), contain chicks fathered by males outside the social group. There are at least two, non-mutually exclusive, explanations for why cooperative breeding persists in such polyandrous species. One possibility is that cooperative breeding may evolve from polyandrous species if they live in harsh environments. That is, if harsh environments restrict the opportunities for independent breeding, then individuals may be selected to stay and help, even if the breeding female is polyandrous. Another possibility is that cooperative breeders can become more polyandrous if they live in harsh environments where it is difficult for helpers to desert and breed on their own. Although both explanations are based upon similar reasoning, there is one key difference: the former hypothesis involves harsh environments facilitating the transition to cooperative breeding when species are polyandrous, whereas the latter hypothesis involves harsh environments '*trapping*' species as cooperative breeders.

We did not find consistent support for the hypothesis that harsh environments facilitate the evolution of cooperative breeding in polyandrous species. Our transition rate analysis indicated that evolution of cooperative breeding increased from 0.00 ± 0.00 (Z = 100%) in benign environments to 0.02 ± 0.01 (Z= 4%) in harsh environments (Table S4), suggesting that cooperative breeding can potentially evolve from polyandrous species when environmental conditions are harsh. However, if this hypothesis is true, then rates of polyandry should be positively associated with harsher environmental conditions in the ancestors of cooperative breeders. We tested this prediction by extending our BPMM models to estimate the correlation between environmental niches and rates of polyandry separately for each of the different transitions to cooperative breeding and found no support for this prediction (Table S7. BPMM phylogenetic correlation (phylo *r*) = -0.23, credible interval (CI) =-0.66 to 0.79, pMCMC = 0.49). Taken together these results suggest that, although possible, polyandrous species living in harsh environments do not tend to evolve into cooperative breeders.

In contrast, there was clear support for the prediction that rates of polyandry increase after species have become 'trapped' as cooperative breeders by harsh environments. We found that transitions from monogamy to polyandry in cooperative breeders were twice as high in harsh relative to benign environments (Fig. 4 and Table S4: rjMCMC harsh environments = 0.05 ± 0.03, Z = 2.5%: benign environments = 0.03 ± 0.03, Z = 2%). This result was not simply due to the effect of the environment on polyandrous behaviour as there was no difference across noncooperative species (Fig. 4 and Table S4: rjMCMC harsh environments = 0.05 ± 0.04, Z = 2.6%: benign environments = 0.05 ± 0.03, Z = 0%).

The result that harsh environments allow female cooperative breeders to evolve higher rates of polyandry was supported by a series of complementary analyses. We found that

polyandrous cooperative breeders inhabit harsher environments than monogamous cooperative breeders, whereas the rates of polyandry in noncooperative species were similar across environments (Fig. 4 and Table S8: BPMM, cooperation* polyandry = -0.31, CI = -0.61 to 0.05, pMCMC = 0.05). We then examined variation in the frequency of helping across cooperative species, as measured by the proportion of nests with helpers. We found that species that can cope with harsher environmental conditions had a significantly higher proportion of nests with helpers and higher rates of polyandry (Fig. 4 and Tables S8: BPMM, cooperation*polyandry = -2.37, CI = -3.40 to -1.14, pMCMC = 0.0002). Using quantile regression, which examines the effect of explanatory variables at different quantiles of the response variable, we found similar results: rates of helping behaviour and polyandry were most strongly and positively related to the upper quantiles of environmental PC1 (Fig. 4c, Extended Data Fig. 2, Table S9 and Table S10: quantile regression, 50^{th} percentile regression coefficient ± SE = 0.13 ± 0.17, P = 0.44, 95^{th} percentile regression coefficient ± SE = 0.98 ± 0.40, P = 0.02: see methods for details). This suggests that species with a higher frequency of helping can occupy the full range of environments, whereas when helping is rare, species are generally only found in benign environments (Fig. 4c). Additionally, it supports the idea that inhabiting harsh environments is associated with higher rates of polyandry (Fig. 4c). Overall, these results indicate that polyandrous cooperative breeders evolve from relatively monogamous cooperative breeders that live in harsh environments. This pattern echoes that observed in the eusocial insects where polyandry evolved following the development of sterile workers, most likely because sterile workers are unable to desert and reproduce themselves[23,26].

Within our dataset of 4707 species, cooperative breeding has also been lost approximately 82 times (range across 10 different maximum clade credibility trees = 54 to 116). One potential explanation for these losses of cooperation is that female polyandry has increased in species

that live in benign environments causing helpers to desert and breed alone. However, there was no clear evidence to explain why cooperation breaks down, either by jointly modelling the effects of polyandry and the environment using ancestral state reconstruction analyses (Table S11) or by estimating the transition rates from cooperative to independent breeding in harsh versus benign environments from monogamous and polyandrous ancestors (Table S4). One potential issue is that there is only data on female polyandry for species involved in just five out of the 82 losses. As a result, the breakdown of cooperative breeding across birds remains enigmatic for the moment, but our analyses pinpoint that in order to resolve this mystery, we need more data on cooperative species that are basal to noncooperative breeders, especially information on rates of polyandry and environmental niches (Table S12).

Discussion

Overall, our results overturn the accepted explanation for why cooperative breeding species tend to be found in harsher environments, namely that the benefits of helping are greater when environmental conditions are worse. Instead, our analyses suggest that cooperative breeding evolves from monogamous species in relatively benign environments (Fig. 2 & Fig. 5), which then enables species to colonize harsh environments (Fig. 3 & Fig. 5). More generally, our results illustrate how cooperation can influence evolution at a macro scale, by allowing species to colonise new environments. The idea that cooperation can aid pioneering into environments uninhabitable for individuals may occur at all levels of life. The formation of cooperative associations, such as biofilms, enable bacteria to survive in harsh environments and resist antibiotic attack[27]. The cooperative formation of multicellular organisms, with division of labour between cell types, has allowed exploitation of environments in numerous novel ways[28,29]. The evolution of sociality in insects and sponge-dwelling shrimps has allowed these diverse organisms to become keystone species in diverse habitats from jungles to oceans[1,30,31]. The acquisition of bacterial symbionts has facilitated the colonization of novel

niches, from sap feeding aphids to worms in deep-sea hydrothermal hot vents[32]. Together these results show how cooperation has played a key role in adaptive breakthroughs that have opened up new ecological niches.

Methods

1. Data collection

1.1 Data on breeding system. All species used in the analyses are listed in Table S13, which uses Latin names listed in the International Ornithological Congress (IOC) master list v2.3. We categorized species as cooperative or noncooperative across the phylogeny for which there was available data (Table S13: $n_{species}$ = 4707 of which 154 were cooperative). We collected data by starting with major reviews that have classified the breeding systems of birds[33,34] and then subsequently checked the primary literature to determine whether species classed as cooperative met our criteria. We classed species as cooperative when at least 10% of the nests in a population had at least one sexually mature, non-breeding helper, as we are concerned with explaining why individuals give up reproductive success to help others. In the vast majority of species these constituted retained natal offspring. We excluded species where sample sizes were not given or information was anecdotal.

Categorizing species as cooperative or noncooperative captures large differences and is analytically tractable, but inevitably misses the finer details of species characteristics. Therefore, to gain more precise information on the cooperative behaviour of species we searched for published data on the number of nests that were provisioned by pairs versus the number of nests assisted by helpers in populations ($n_{species}$=43). Where ever possible, we used estimates from the same study populations as those where extra-group paternity was measured (Table S14).

1.2 Data on polyandry. We collected data on female mating behaviour from published studies (see Cornwallis et. al 2010 for more details[25]). Two highly correlated statistics (Pearson's Correlation coefficient = 0.90, confidence interval = 0.88 to 0.92, N=304, t=36.55, P<0.0001) are frequently reported in parentage studies with respect to multiple paternity: (i) the percentage of chicks fathered by extra-pair/extra-group fathers; and (ii) the percentage of broods with one or more extra-pair/group chicks. We analysed data on the percentage of broods in the population containing extra-group offspring, which we refer to as 'polyandry' (in previously publications we have referred to this as promiscuity e.g.[25,35]). We chose the percentage of broods rather than the percentage of chicks with extra-group paternity as it is less susceptible to extreme values from individual nests providing a more robust estimate of population levels of female multiple mating. Moreover, we focused on extra-group paternity as we are concerned with behaviour that reduces relatedness between offspring and all individuals caring for offspring. Rates of within-group extra-pair paternity are extremely low in cooperative breeders when defined as 'species with one or more non-breeding adults helping to raise offspring' as helpers are typically retained natals[35]. In species without a pair bond, (e.g. lekking and parasitic species), we have used data on the proportion of nests containing offspring fathered by more than one male.

We compiled data on polyandry by updating the dataset published by Cornwallis et. al. 2010[25] to include recently published data (up to and including 15th October 2015). We searched for new studies on extra-group paternity data in birds by entering the following search terms into the web of science (WoS) keywords search "extra-pair paternity OR extra pair paternity OR extra-pair fertilisation OR extra pair fertilisation OR extra-pair fertilization OR extra pair fertilization OR extrapair", 2) title "parentage" AND topic "birds", 3) title "mating system" AND "birds", 4) all references that cite the following major reviews on extra-pair paternity in birds[36,37]. For several species there were multiple studies that measured polyandry and for

these we calculated the mean value of the studies weighted by sample size for use in subsequent analyses (Table S14). In some cases there were multiple studies presenting paternity data from the same study population over the same years. To avoid duplication we only used information from the paper with the largest sample size.

1.3 Data on the environment. For each study on paternity, we extracted the geographical coordinates and used these to extract climatic data for the population. Precipitation and temperature data were obtained from the University of East Anglia Climatic Research Unit's Time series data set, CRU-TS 3.21[38]. Mean and variances for each environmental parameter were computed annually and then averaged across years at each site. Predictability was measured via Colwell's P[21], an index that captures among-year variation in onset, intensity and duration of periodic phenomena ranging from 0 (completely unpredictable) to 1 (fully predictable). When multiple studies were available for a given species, environmental variables were first characterized locally and then averaged across sites for the species. Where paternity was measured in multiple populations, we extracted climate data for each population and used this to calculate an average for the species.

1.4 Phylogenetic trees

We used the complete phylogeny of birds ($N_{species}$ = 9993, 10,000 posterior tree samples) constructed by Jetz et al. 2012 available at www.birdtree.org with the Hackett backbone and pruned it to the 4707 species for which we had breeding data[39]. Out of the 308 species that we had complete data for all but 8 for were present in the genetically sequenced phylogeny available from Jetz et al. 2012.

We accounted for phylogenetic uncertainty in our analyses in two ways. First, for our Bayesian phylogenetic mixed models (BPMMs – see below for details) we used the 10,000

posterior tree samples to create 10 maximum clade credibility (MCC) consensus trees each constructed from 1000 different posterior samples using Tree Annotator v2.0.3[40]. We repeated each analysis 10 times, each time with a different tree and combined the posterior samples generated from each tree prior to parameter estimation. We used this approach for the BPMMs because at the time of analysing our data we were unaware of any techniques to resampling across a set of trees within a single analysis. Second, for our transition rate analysis using BayesTraits it was possible to take phylogenetic uncertainty into account by resampling each iteration from a posterior distribution of 1000 trees for the 4707 species in our dataset, therefore negating the need to create MCC trees.

Statistical Analyses

2. General approach

In this section we give details of: (i) how the analysis datasets were constructed; (ii) general model settings, model assessments and parameter estimation; and (iii) the six sets of analyses that were performed. Unless otherwise stated, all analyses were conducted in R v3.1.0[41]. All data figures were made in R.

2.1 Data set construction. Prior to the analyses we created an index of environmental conditions using a phylogenetic principle component (PCA) analysis from the mean, variance and Colwell's predictability estimates of temperature and precipitation. Separate phylogenetic PCAs were run for each of the 10 MCC trees and used to create 10 datasets that were then used in subsequent analyses. All explanatory variables were Z-transformed (mean centred with standard deviation = 1) prior to analyses. Where polyandry was used as an explanatory variable we square root arcsine transformed it before the analysis, as it is percentage data.

2.2 General model settings, model assessments and parameter estimation.

Bayesian phylogenetic models

We used the MCMCglmm package v2.20 to implement BPMMs with Markov chain Monte Carlo (MCMC) estimation[42]. We estimated the number of iterations, burnins and thinning intervals required for each analysis using the MCGIBBSIT package v1.1.0[43]. Each model was run for 6,000,000 iterations with a 1,000,000 burnin and chains sampled every1000 iterations unless otherwise specified. We examined the convergence of models by repeating each analysis three times and examining the correspondence between chains using the 'coda' package version 0.16-1[44] 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)[45]. Values substantially higher than 1.1 indicate chains with poor convergence properties. The PSR was less than 1.1 for all the parameter estimates presented. We modelled the probability of cooperative breeding as a binary trait with a logit link function, environmental PC1 and PC2 as Gaussian traits and polyandry as a binomial trait with logit link function (number of nests with extra-group chicks, number of nest without extra-group chicks).

The prior settings used for each analysis are specified in the Supplementary R code. For random effects we began prior selection by assessing model convergence using inverse-Wishart priors (V = 1, nu=0.002). If the mixing properties of the MCMC chain were poor, which was often the case for binary response traits, we examined two different parameter expanded priors (Fisher prior: V = 1, nu=1, alpha.mu = 0, alpha.V = 1000) and (χ^2 prior: V = 1, nu=1000, alpha.mu = 0, alpha.V = 1)[46]. For binary traits the residual variance cannot be identified and therefore we set the residual variance to 1, otherwise an inverse-Wishart prior was specified for residual variances (V = 1, nu=0.002). For fixed effects the default priors in

MCMCglmm (independent normal priors with zero mean and large variance (10^{10})) were used apart from in models with logit link functions (binary and binomial response variables). In these models we specified a fixed effect prior of mu = 0, V = $\sigma^2_{units}+\pi^{2/3}$, which is approximately flat on the probability scale when using logit link functions and improved the mixing properties of the fixed effect chains.

Parameter estimates from models are reported as the posterior modes with 95% lower (lower CI) and upper (upper CI) credible intervals (CIs). P values reported testing differences between levels (e.g cooperative versus non-cooperative breeders) are the number of iterations when one level is greater or less than the other level divided by the total number of iterations. P values reported for correlations (e.g. environmental conditions and the probability of being a cooperative breeder) are the number of iterations where the correlation is greater or less than 0 divided by the total number of iterations.

3. Specific Analyses

3.1 Testing if cooperative breeding, environmental conditions and polyandry are correlated over evolutionary time?

3.1.1 Estimating phylogenetic correlations using MCMCglmm

We used multi-response Bayesian phylogenetic mixed models (MR-BPMM) to estimate the phylogenetic and residual correlations between the probability of cooperative breeding, environmental PC1, environmental PC2 and rates of polyandry (Table S3). We removed the global intercept to allow trait specific intercepts to be estimated and fitted 4 x 4 unstructured phylogenetic and residual covariance matrices as random effects. Correlations between traits were calculated as covariance between traits *xy* / square root (variance in trait *x**variance in

406 trait *y*). Since cooperative breeding is a binary trait, the residual variance is not identifiable
407 and so it was not possible to estimate the residual correlations between cooperative breeding
408 and the other traits. We also estimated the amount of variation in each trait explained by
409 shared ancestry between species calculated as phylogenetic heritability (phylo H^2 =
410 (phylogenetic variance / residual + phylogenetic variance)*100) for environmental PC1,
411 environmental PC2 and polyandry, and the intraclass correlation coefficient (phylogenetic
412 variance / (phylogenetic variance + 1)+$\pi^{2/3}$) for cooperative breeding – an analogous measure
413 of the amount of variation explained by phylogenetic history appropriate for binary traits.
414
415 *3.1.2 Testing models of dependent versus independent evolution using BayesTraits*
416 We tested if models that allowed for coevolution between the probability of cooperative
417 breeding, environmental conditions, and polyandry better explained our data than models
418 that assumed independent evolution of each trait using the Multistate module with reverse
419 jump MCMC estimation implemented in BayesTraits v2[47]. We transformed environmental PC1
420 and polyandry into binary classifications as it is not possible to estimate transition rates using
421 continuous variables. We choose the 30th / 70th quantile boundary to split continuous
422 variables into binary traits as this captured large biological differences between species while
423 maintaining sample size in each combination of categories (number of cooperative species,
424 monogamy benign = 12, monogamy harsh = 9, polyandrous benign = 12, polyandrous harsh =
425 12. Number of noncooperative species monogamy benign = 48, monogamy harsh = 24,
426 polyandrous benign = 143, polyandrous harsh = 48). We examined the sensitivity of our
427 results to different thresholds (50th / 50th quantile boundary and 40th / 60th quantile
428 boundaries). The results from different thresholds were qualitatively similar supporting the
429 same conclusions (Table S4) and so we only presented the results from the 30th / 70th
430 quantile boundary.
431

We used the Multistate module in BayesTraits rather than the Discrete module, which is normally used to examine coevolutionary relationships as it only allows two traits to be modelled. We therefore coded the different combinations of the three traits as different states, for example, non-cooperative breeders living in benign environmental conditions with low rates of polyandry were classified as being in state 'A'. This resulted in eight different states which were used to construct a rate matrix that allowed transitions between the two states of each trait against the different backgrounds of the other traits leading to 24 different transition rates being estimated. All other possible transitions between states were restricted to 0 to prevent dual transitions (e.g. where there is a state change in two or more traits). The models of independent evolution, on the other hand, estimated transitions between the two states of each trait across the different levels of the two other traits. We used Bayes Factors (2 x (log-likelihood of complex model – log-likelihood of simple model)) to test the fit of an independent model of evolution against four alternative coevolutionary models: (i) all traits coevolve; (ii) cooperative breeding only coevolves with environmental conditions; (iii) cooperative breeding only coevolves with polyandry; and (iv) only polyandry and environmental conditions evolve (Table S4). It is commonly concluded that bayes factors over 2 offer positive evidence, those over 5 provides strong evidence, and those over 10 is very strong evidence[47].

We used hyper priors where values were drawn from a uniform distribution with a range 0 to 10 to seed the mean and variance of a exponential prior to reduce uncertainty over prior selection[47]. The prior settings were chosen according to the estimated range of transition rates obtained using analyses with maximum likelihood estimation. We also examined the sensitivity of our models to prior selection by running models with gamma priors seeded using hyper priors and recovered similar results. We only present the results from the models using exponential priors as the mixing properties of the MCMC from these models were better

than the other priors. We ran each model three times for a total of 6,000,000 iterations, a burnin of 1,000,000 iterations and sampled every 5000 iterations. Assessment of model convergence was carried out as described in section 2.2.

3.1.3 Estimating phylogenetic heritability of environmental PC1 for cooperative and noncooperative species separately using MCMCglmm

To accurately reconstruct the environmental conditions that the ancestors of cooperative and noncooperative species occupied, it is important that the environmental niches of cooperative and noncooperative species are equally conserved over evolutionary time. We examined this by quantifying the variation in environmental PC1 explained by phylogenetic history (phylogenetic heritability) separately for cooperative and noncooperative species using a BPMM. We fitted cooperative breeding as a fixed effect and removed the global intercept to allow separate means to be estimated for cooperative and noncooperative species. We fitted interactions between cooperative breeding and phylogenetic and residual variances as random effects using heterogeneous 2 x 2 covariance matrices where phylogenetic and residual variances are estimated separately for cooperative and noncooperative breeders and covariances are set to 0 (see Supplementary R code for more details).

3.2 Examining the environmental conditions and levels of polyandry that preceded the evolution of cooperative breeding

3.2.1 Ancestral state reconstructions using MCMCglmm

We examined how the environmental conditions and levels of polyandry differed between ancestors of cooperative and noncooperative breeders using a two step approach: first, we reconstructed ancestral breeding states to predict transitions between cooperative and noncooperative breeding, and second, we tested whether transitions in breeding systems

484 differed in their estimated environmental conditions and levels of polyandry. We
485 reconstructed ancestral breeding states using a BPMM of the probability of cooperative
486 breeding as the response variable and a phylogenetic variance-covariance matrix fitted as a
487 random effect. Each model was run for 11,000,000 iterations with a 1,000,000 burnin and
488 chains sampled every1000 iterations. For each node in the phylogeny, this model produces a
489 posterior probability of being cooperative. We classified nodes as being cooperative if the
490 posterior probability was > 0.9 and non-cooperative if it was <0.1, otherwise nodes were
491 considered as unknown. This leads to nodes being classified in four ways: (i) noncooperative
492 node whose descendants are all noncooperative; (ii) noncooperative node with at least one
493 descendant that is cooperative; (iii) cooperative node whose descendants are all cooperative;
494 and (iv) cooperative node with at least one descendent that is noncooperative.
495
496 We entered the nodal classifications as an explanatory variable (4-level fixed factor) in a
497 multi-response BPMM with environmental PC1 and polyandry as the response traits and a
498 phylogenetic covariance matrix linked to ancestral nodes as a random effect (Table S3). We
499 removed the global intercept and fitted interactions between 'trait' and node classification to
500 estimate environmental conditions and polyandry preceding the origin (comparison of
501 classifications i versus ii), maintenance (comparison of classifications i versus iii) and loss of
502 cooperative breeding (comparison of classifications iii versus iv). To account for uncertainty
503 in our node classifications, we repeated the analysis 100 times, each time reclassifying nodes
504 by resampling from the posterior distribution of the probability of each node being
505 cooperative or non-cooperative from the original model used to reconstruct ancestral states
506 of cooperative breeding. We then combined posterior samples from across the 100 models
507 and from across the 10 different MCC trees to calculate parameter estimates. Each model was
508 run for 20,000 iterations with a burn-in of 10,000 iterations and thinning interval of 1000

samples, which across the resamplings and 10 different phylogenetic trees resulted in 10,000 posterior samples (10 trees x 100 resamplings x 10 samples per resampling).

3.2.2 Ancestral state reconstructions using MCMCglmm with transition specific covariance's between traits

The BPMM presented in section 3.2.1, fits a single phylogenetic covariance between environmental PC1 and polyandry that models the relationship between the environment and polyandry across all types of transitions in breeding system. As a result, it does not allow the possibility that the covariance between environmental PC1 and polyandry is different for different transitions. Theoretically, it is possible that cooperation may evolve from polyandrous ancestors when environmental conditions are harsh and independent breeding is constrained, as individuals have no other options of passing on their genes, but through helping. In contrast, in benign environments it is predicted that cooperation will only evolve from monogamous ancestors because if breeding females are polyandrous then the indirect fitness benefits will be low and potential helpers will desert to breed on their own. If true, then we would expect the phylogenetic correlation between environmental conditions and polyandry to be significantly higher across the ancestors of cooperative species (nodal classification ii) than ancestors that only gave rise to noncooperative descendents (nodal classification i). We tested this idea by extending the BPMM outlined in section 3.2.1 to include transition specific phylogenetic variances and covariances between traits using the *at.level* coding in *MCMCglmm* (see Supplementary R code for details). From these models we calculated whether the difference in the phylogenetic covariance between environmental PC1 and polyandry between transitions where cooperation evolved and those that involve noncooperative ancestors and descendents was significantly greater than 0 (phylo $COV_{env\ PC1,\ polyandry}$ at.level(Non-Coop) - phylo $COV_{env\ PC1,\ polyandry}$ at.level(Non-Non): Table S7). These models are extremely computer intensive. As a result we ran these models for 25,000

535 iterations per tree with a burn-in of 5,000 iterations and thinning interval of 200 creating
536 1000 posterior samples across the 10 different phylogenetic trees, which still resulted in all
537 convergence criteria being met (see section 2.2).
538
539 *3.2.3 Calculating evolutionary transition rates using BayesTraits*
540 We used the model in section 3.1.2 that allowed coevolutionary relationships between all
541 three traits to estimate the transition rates between states of cooperative breeding,
542 environmental conditions and polyandry. We examined whether transitions to cooperative
543 breeding differed according to benign and harsh environmental conditions, as well as in
544 relation to monogamy versus polyandry. We examined the likelihood of transitions occurring
545 by examining the proportion of models visited by the reverse jump MCMC algorithm where
546 the rates were assigned to zero (Table S7).
547
548 *3.2.4 Testing alternative evolutionary causal models using phylogenetic path analysis*
549 We used phylogenetic path analysis to examine alternative models of the causal relationships
550 between cooperative breeding, environmental PC1 and polyandry (fig. S1). The alternative
551 models we compared were constructed based on the correlations revealed by analysis in
552 section 3.1.1 and distinguish between the following possibilities: (i) variation in polyandry
553 predicts the probability of cooperative breeding which predicts the environments species
554 occupy; (ii) variation in the environment explains the probability of cooperative breeding that
555 in turn determines levels of polyandry; and (iii) cooperative breeding predicts the rates of
556 polyandry and the environment species inhabit (fig. S1). For these analyses, we treated the
557 probability of being a cooperative breeder as a Gaussian rather than a binary trait, as it has
558 been shown this results in more accurate parameter estimation (see [48] for justification for
559 treating this variable as continuous). We also did not include environment PC2 in these

models because there was no evidence from the analyses in section 3.1.1 that it influenced any of the other variables.

We use the methods described in [49] that integrate phylogenetic generalised least squares (PGLS) models, fitted using the R package 'Caper' v0.5.2[50], with the *d-sep* test outlined by Shipley[51] to identify the model that best explained our data. In brief, a causal model is proposed that specifies how the variables are related in terms of dependent (changes in A cause changes in B) and independent (A and B are conditionally independent given variable C) effects. Each conditional independency is then tested using PGLS models to estimate the probability that the partial regression coefficient is 0 while taking into account the non-independence of data arising due to shared ancestry between species. The probabilities associated with each conditional independency can then be combined using Fisher's *C* statistic, which follows a χ^2 distribution with degrees of freedom equal to 2*the number of tests conducted. Furthermore, the fit of different models to the data, including non-nested models (as long as the dataset is the same for all models) can be compared using an Information Theory approach based on Fisher's C statistic (CICc):

$$\text{CICc} = C + 2q \times n \,/\, (n - q - 1)$$

Where C is Fisher's *C* statistic, *n* is the sample size and *q* is the number of parameters used to build models plus the number of relationships linking the parameters. If the proposed causal model fits the data then P >0.05 for the *C* statistic and the model with the smallest CICc value represents the best candidate model out of the proposed set of models. For Frequentist analyses such as these there is, to our knowledge, no established way of integrating results obtained across different trees to take into account phylogenetic uncertainty. We therefore repeated our analyses across the 10 MCC trees and averaged p values and regression

586 coefficients across the 10 analyses (see [20] for discussion on averaging across phylogenetic
587 trees).
588
589 ***3.3 Testing if cooperation and polyandry predict the environments species inhabit***
590 *3.3.1 Calculating if the invasion of harsh environments is facilitated by cooperative breeding and*
591 *polyandry using BayesTraits*
592 We used the model in section 3.1.2 that allowed coevolutionary relationships between all
593 three traits to estimate the transition rates between states of cooperative breeding,
594 environmental conditions and polyandry. We examined whether transitions to harsh
595 environments differed between cooperative and noncooperative breeders and in relation to
596 monogamy versus polyandry. We again examined the likelihood of transitions occurring by
597 examining the proportion of models visited by the reverse jump MCMC algorithm where the
598 rates were assigned to zero (Table S4).
599
600 *3.3.2 Testing if cooperative breeding and rates of polyandry predict the environments species*
601 *inhabit using MCMCglmm*
602 We tested whether cooperative breeding and rates of polyandry were related to the
603 environmental niches species can occupy using a BPMM with a Gaussian error distribution.
604 We fitted environmental PC1 as the response variable, cooperative breeding (2-level factor:
605 cooperative versus noncooperative), rates of polyandry (covariate) and clade (2-level factor:
606 passerine versus nonpasserine) as fixed effects and a phylogenetic variance-covariance
607 matrix as a random effect. We included all interactions among fixed effects to test whether the
608 effect of cooperative breeding on the environments inhabited by cooperative and
609 noncooperative species differed according to rates of polyandry and between passerines and
610 nonpasserines. We included clade in this analysis because it has been suggested that the link
611 between cooperative breeding and ecology is different for passerines and nonpasserines[2].

612

613 ***3.4 Testing if the degree of cooperation (percent of nests with helpers) across cooperative***

614 ***breeders predicts the environments they inhabit and how polyandrous they are***

615 *3.4.1 Tests using quantile regression*

616 Examining the relationship between levels of cooperation and environmental conditions is
617 not straightforward as we expect that species with high levels of cooperation can occur in all
618 environments, whereas less cooperative species will only inhabit more benign environments.
619 Therefore we are interested in testing whether levels of cooperation determine the upper
620 environmental limit rather than the mean, which is typically estimated by regression
621 analyses. As a result we used quantile regression implemented in the R package 'quantreg'
622 v5.11[52], which splits the explanatory variable(s), in this case level of cooperation measured as
623 percent of nests with helpers and polyandry, into different quantiles and estimates regression
624 coefficients for each quantile. This procedure enables the change in regression coefficients
625 and their confidence intervals to be estimated across the whole range of an explanatory
626 variables (fig. S2). If the upper limit of the environmental PC1 species occupy depends upon
627 levels of cooperation then we expect that the relationship between environmental niche and
628 percent of cooperative nests will increase as data are restricted to higher quantiles of percent
629 of cooperative nests (fig. S2; Table S10). We also included polyandry and its interaction with
630 percent of cooperative nests in our quantile regression models to examine if polyandry
631 increases when constraints on independent breeding are expected to be greatest (species
632 occupy the most extreme environments and are obligately cooperative).

633

634 *3.4.2 Tests using MCMCglmm*

635 An important limitation of the currently available programs for performing quantile
636 regression is that they do not allow modelling of phylogenetic relationships between species.
637 We therefore verified our results from the quantile regression analysis by converting our

continuous explanatory variables into categories (obligate (> 90% nests have helpers) versus facultative (<=90% of nests with helpers) cooperative breeders, and monogamous (<=30% quantile of extra-group paternity) versus polyandrous (>30% quantile of extra-group paternity)) and performing a BPMM with environmental PC1 as the response variable, cooperative breeding and polyandry as 2-level fixed factors and a phylogenetic variance-covariance matrix as a random effect. We once again tested if cooperative breeding allows species to occupy more extreme environments, and if this in turn relaxed constraints on female mating behavior, because it makes independent breeding more difficult, by fitting an interaction between cooperation and polyandry.

3.4.3 Testing if increases in female polyandry in cooperative breeders are higher in harsh versus benign environments using BayesTraits

We extracted the estimated transition rates from monogamy to polyandry for cooperative breeders in benign versus harsh environments from the model in section 3.1.2 that allowed coevolutionary relationships between all traits. We examined the likelihood of transitions occurring by examining the proportion of models visited by the reverse jump MCMC algorithm where the rates were assigned to zero (Table S4).

3.5 Testing if the breakdown of cooperation is explained by increases in polyandry when environmental conditions are benign

3.5.1 Estimating the environmental conditions and levels of polyandry in cooperative species with noncooperative descendants using MCMCglmm

The analysis presented in section 3.2.1 allows environmental conditions and rates of polyandry to be compared between cooperative ancestors that only have cooperative descendants (maintenance of cooperation, nodal classification iii) and those that have

664 noncooperative descendants (breakdown of cooperation, nodal classification iv). We found no
665 evidence that the breakdown of cooperation was associated with differences in estimated
666 environmental conditions or rates of polyandry (Table S3). However, in the BPMM used in
667 section 3.2.1, a single phylogenetic variance was fitted for each trait and only a single
668 covariance for each trait combination (e.g. environmental PC1: polyandry). This does not
669 allow for the possibility that the covariance between traits is different between the
670 maintenance of cooperation and the breakdown of cooperation. This is particularly important
671 in this context because we predict that cooperation will breakdown when polyandry is high
672 (low *r*) and environmental conditions are benign (low *b:c*). We predicted that this would be
673 reflected in the phylogenetic covariance between polyandry and environmental PC1 being
674 significantly more positive when cooperation is maintained (nodal classification iii) versus
675 when cooperation is lost (nodal classification iv).
676
677 We used the models specified in section 3.2.2 to calculate the differences in phylogenetic
678 covariance between environmental PC1 and polyandry between transitions where
679 cooperation was maintained and where cooperation was lost (phylo $COV_{env\ PC1,\ polyandry}$
680 at.level(Coop-Coop) - phylo $COV_{env\ PC1,\ polyandry}$ at.level(Coop-Non-coop: Table S11).
681
682 *3.5.2 Estimating the rate of breakdown of cooperative breeding in relation to different*
683 *environmental conditions and levels of polyandry using BayesTraits*
684 We examined the rates of breakdown of cooperative breeding in relation to rates of polyandry
685 and environmental conditions using the model described in section 3.1.2 that allowed
686 coevolutionary relationships between all traits. We examined the likelihood of transitions
687 occurring by examining the proportion of models visited by the reverse jump MCMC
688 algorithm where the rates were assigned to zero (Table S4).
689

Code availability

The R code used to conduct analyses is supplied as a supplementary file.

Data availability

All data generated or analysed during this study are included in this published article (and its supplementary information files).

References

1. Wilson, E. O. *The Insect Societies* (Cambridge Univ. Press, 1971).

2. Jetz, W. & Rubenstein, D. R. Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* **21,** 72–78 (2011).

3. Koenig, W. D. & Dickinson, J. L. *Cooperative Breeding in Vertebrates*. (Cambridge Univ. Press, 2016).

4. Rubenstein, D. R. & Lovette, I. J. Temporal Environmental Variability Drives the Evolution of Cooperative Breeding in Birds. *Curr. Biol.* **17,** 1414–1419 (2007).

5. Emlen, S. T. The Evolution of Helping. I. An Ecological Constraints Model. *Am. Nat.* **119,** 29–39 (1982).

6. Arnold, K. E. & Owens, I. P. F. Cooperative breeding in birds: the role of ecology. *Behav. Ecol.* **10,** 465–471 (1999).

7. Pen, I. & Weissing, F. J. Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. *Proc. R. Soc. Lond. B* **267,** 2411–2418 (2000).

8. Mcleod, D. V & Wild, G. The relationship between ecology and the optimal helping

strategy in cooperative breeders. *J. Theor. Biol.* **354,** 25–34 (2014).

9. Covas, R., Du Plessis, M. A. & Doutrelant, C. Helpers in colonial cooperatively breeding sociable weavers Philetairus socius contribute to buffer the effects of adverse breeding conditions. *Behav. Ecol. Sociobiol.* **63,** 103–112 (2008).

10. Rubenstein, D. R. Spatiotemporal environmental variation , risk aversion , and the evolution of cooperative breeding as a bet-hedging strategy. *Proc. Natl. Acad. Sci. USA* **108,** 10816-10822 (2011).

11. Hatchwell, B. J. & Komdeur, J. Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim. Behav.* **59,** 1079–1086 (2000).

12. Pruett-Jones, S. G. & Lewis, M. J. Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature* **348,** 541–542 (1990).

13. Komdeur, J. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* **358,** 493–495 (1992).

14. Bergmüller, R., Heg, D. & Taborsky, M. Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. *Proc. R. Soc. Lond. B* **272,** 325–31 (2005).

15. Dillard, J. R. & Westneat, D. F. Disentangling the Correlated Evolution of Monogamy and Cooperation. *Trends Ecol. Evol.* **31,** 503–513 (2016).

16. Botero, C. A. & Rubenstein, D. R. Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. *PLoS One* **7,** e32311 (2012).

17. Culina, A., Radersma, R. & Sheldon, B. C. Trading up: The fitness consequences of divorce in monogamous birds. *Biol. Rev.* **90,** 1015–1034 (2015).

18. Hamilton, W. D. The genetical evolution of social behaviour. I & II. *J. Theor. Biol.* **7,** 1–16 (1964).

19. Maynard-Smith, J. Group Selection and Kin Selection. *Nature* **201,** 1145–1147 (1964).

20. Garamszegi, L. Z. *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*. (Springer, 2014).

21. Colwell, R. K., Ecology, S., Summer, N. L. & Colwell, R. K. Predictability , Constancy , and Contingency of Periodic Phenomena. *Ecology* **55,** 1148–1153 (1974).

22. Botero, C. A., Dor, R., McCain, C. M. & Safran, R. J. Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. *Mol. Ecol.* **23,** 259–268 (2014).

23. Hughes, W. O. H., Oldroyd, B. P., Beekman, M. & Ratnieks, F. L. W. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* **320,** 1213–6 (2008).

24. Lukas, D. & Clutton-Brock, T. Cooperative breeding and monogamy in mammalian societies. *Proc. R. Soc. Lond. B* **279,** 2151–6 (2012).

25. Cornwallis, C. K., West, S. A., Davis, K. E. & Griffin, A. S. Promiscuity and the evolutionary transition to complex societies. *Nature* **466,** 969–972 (2010).

26. Boomsma, J. J. Kin Selection versus Sexual Selection: Why the Ends Do Not Meet. *Curr. Biol.* **17,** 673–683 (2007).

27. Hall-Stoodley, L., Costerton, J. W. & Stoodley, P. Bacterial biofilms: from the natural environment to infectious diseases. *Nat. Rev. Microbiol.* **2,** 95–108 (2004).

28. Maynard-Smith, J. & Szathmary, E. *The Major Transitions in Evolution.* (Oxford Univ. Press, 1995).

29. Bourke, A. F. G. *Principles of Social Evolution*. (Oxford Univ. Press, 2011).

30. Duffy, J. E. & Macdonald, K. S. Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis. *Proc. R. Soc. Lond. B* **277,** 575–84 (2010).

31. Sun, S. J. *et al.* Climate-mediated cooperation promotes niche expansion in burying beetles. *Elife* **2014,** 1–15 (2014).

32. Archibald, J. *One Plus One Equals One: Symbiosis and the Evolution of Complex Life*. (Oxford Univ. Press, 2014).

33. Cockburn, A. Prevalence of different modes of parental care in birds. *Proc. R. Soc. Lond. B* **273,** 1375–1383 (2006).

34. Riehl, C. Evolutionary routes to non-kin cooperative breeding in birds Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R. Soc. Lond. B* **280,** 1830-1833 (2013).

35. Downing, P. A., Cornwallis, C. K., Griffin, A. S. & Griffin, A. S. Sex , long life and the evolutionary transition to cooperative breeding in birds. *Proc. R. Soc. Lond. B* **282,** 1–7 (2015).

36. Griffith, S. C., Owens, I. P. F. & Thuman, K. A. Extra pair paternity in birds: A review of interspecific variation and adaptive function. *Mol. Ecol.* **11,** 2195–2212 (2002).

37. Spottiswoode, C. & Møller, A. P. Extrapair paternity, migration, and breeding synchrony in birds. *Behav. Ecol.* **15,** 41–57 (2004).

38. Harris, I., Jones, P. D., Osborn, T. J. & Lister, D. H. Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *Int. J. Climatol.* **34,** 623–642

(2014).

39. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491,** 444–448 (2012).

40. Drummond, A. J., Suchard, M. A., Xie, D. & Rambaut, A. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* **29,** 1969–1973 (2012).

41. R Development Core Team, R. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing 2015).

42. Hadfield, J. D. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* **33,** 1–22 (2010).

43. Warnes, G. R. & Burrows, R. Warnes and Raftery's MCGibbsit MCMC diagnostic. *See https//cran.r-project.org/web/packages/mcgibbsit/*

44. Plummer, M., Best, N., Cowles, K. & Vines, K. CODA: convergence diagnosis and output analysis for MCMC. *R News* **6,** 7–11 (2006).

45. Gelman, A. & Rubin, D. B. Inference from Iterative Simulation Using Multiple Sequences. *Stat. Sci.* **7,** 457–511 (1992).

46. de Villemereuil, P., Gimenez, O. & Doligez, B. Comparing parent-offspring regression with frequentist and Bayesian animal models to estimate heritability in wild populations: a simulation study for Gaussian and binary traits. *Methods Ecol. Evol.* **4,** 260–275 (2013).

47. Pagel, M. & Meade, A. Bayesian Analysis of Correlated Evolution of Discrete Characters by Reversible-Jump Markov Chain Monte Carlo. *Am. Nat.* **167,** 808–825 (2006).

48. Ives, A. R. & Garland, T. J. in *Modern Phylogenetic Comparative Methods and Their*

Application in Evolutionary Biology (ed. Garamszegi, L. Z.) 231–262 (Springer, 2014).

49. Hardenberg, A. von & Gonzalez-Voyer, A. Disentangling evolutionary cause-effect relationships with phylogenetic confirmatory path analysis. *Evolution* **67,** 378–387 (2013).

50. Orme, C. D. L. *et al.* CAPER: Comparative Analyses of Phylogenetics and Evolution in R. *Methods Ecol. Evol.* **3,** 145–151 (2012).

51. Shipley, B. Cause and Correlation in Biology: *A User's Guide to Path Analysis, Structural Equations and Causal Inference* (Cambridge Univ. Press 2002).

52. Koenker, R. Quantile regression in R: A Vignette. *Online* **15,** 1–21 (2011).

Acknowledgements

We thank the Swedish Research Council (VR), the Knut and Alice Wallenberg foundation, the Royal Society, the US National Science Foundation (IOS-1121435, IOS-1257530, IOS-1439985) and the European Research Council for funding and Shen-Feng Shen for comments. The authors declare no conflict of interests.

Author Information

CKC, SA, DRR and ASG conceived the study, CKC analysed the data, CAB and PD contributed materials and all authors contributed substantially to writing the paper.

Competing financial interests

The authors declare no competing financial interests.

Figure legends

Figure 1: Where do cooperative animals live? Animals living in harsh environments are more likely to breed cooperatively. For example, **(a)** honeypot ants, *Myrmecocystus spp,*[1] (Photo by Smithsonian Institution-NMNH-Insect Zoo) **(b)** meerkats, *Suricata suricatta (*Photo by AS Griffin*)*, **(c)** snapping shrimp, *Synalpheus regalis,*[30] (Photo by JE Duffy) and **(d)** superb starlings, *Lamprotomis superbus,*[4] (Photo by DR Rubenstein) are all able to inhabit environments where independent breeding is difficult. However, whether the environment selects for cooperative breeding or cooperative breeding facilitates the colonization of such harsh environments remains unknown.

Fig. 2: Cooperative breeding and the association with harsh environments and low levels of polyandry. (a) Cooperative breeders occur in environments that are hotter with more variable rainfall (higher values of PC1 indicate higher mean temperatures, factor loading = 0.76, and greater between-year variance in rainfall, factor loading = 0.69: BPMM $n_{cooperative}$=45, $n_{noncooperative}$=263, pMCMC = 0.001). Twenty eight percent of species are cooperative in harsh environments (environmental PC1 > 70% quantile), whereas only 7% are in benign environments (environmental PC1 <= 70% quantile), equating to a four-fold difference. **(b)** In noncooperative species, three times the number of nests have polyandrous females relative to cooperative species (pMCMC = 0.01). Small dots represent species averages, large dots with error bars represent mean ± 95% confidence intervals.

Fig. 3: Cooperation and the invasion of harsh environments. (a) The phylogenetic distribution of the transitions to cooperative breeding (red circles, $n_{species}$=154) and their relationship to environmental conditions (black circles, larger size = harsher environment) and polyandry (gray circles, larger size = higher levels of polyandry). Red branches are estimated transitions to cooperative breeding. **(b)** Estimated environmental niches occupied

by noncooperative ancestors to cooperative and noncooperative descendents (number of transitions from noncooperative to cooperative breeders: range across 10 MCC trees 52 to 122. Number of transitions from noncooperative to noncooperative breeders: range across 10 MCC trees = 7476 to 8794; difference between environments pMCMC = 0.49). Dots represent mean ± 95% confidence intervals. **(c)** Estimated levels of polyandry of the noncooperative ancestors to cooperative and noncooperative descendents (difference in levels of polyandry pMCMC = 0.03). **(d)** The evolutionary transition rates from benign to harsh environmental niches from monogamous (blue) and polyandrous (black) cooperative and noncoooperative species estimated using BayesTraits rjMCMC. Plots in (B) and (C) were drawn using the posterior samples of the BPMMs, and (D) from the posterior samples from the BayesTraits RJ-MCMC analysis. Dots represent mean ± 95% confidence intervals.

Fig. 4: The release of constraints on female polyandry in harsh environments. (a) The transition rate from monogamy to polyandry was higher in cooperative species living in harsh environments (brown) than benign environments (green), but did not differ across noncooperative species. Plots were drawn using the posterior samples from the BayesTraits RJ-MCMC analysis. Dots represent mean ± 95% confidence intervals. **(b)** Cooperative breeders living in harsh environments tend to be more polyandrous than cooperative species occupying more benign environments (red, $n_{species}$=45). In contrast, there was no relationship between environmental conditions and polyandry across noncooperative breeders (gray, $n_{species}$=263. Cooperation*polyandry pMCMC = 0.05). Dots represent species averages and fitted lines are mean regression slopes with 95% confidence intervals. **(c)** Species with a higher percentage of nests with a least one helper inhabited harsher environments and were more polyandrous (black) than species living in benign environments that were more monogamous (blue. $N_{species}$=43 split into polyandrous and monogamous for graphical

purposes only). Dots represent species averages. Fitted lines are from 90th percentile quantile regressions with 95% confidence intervals.

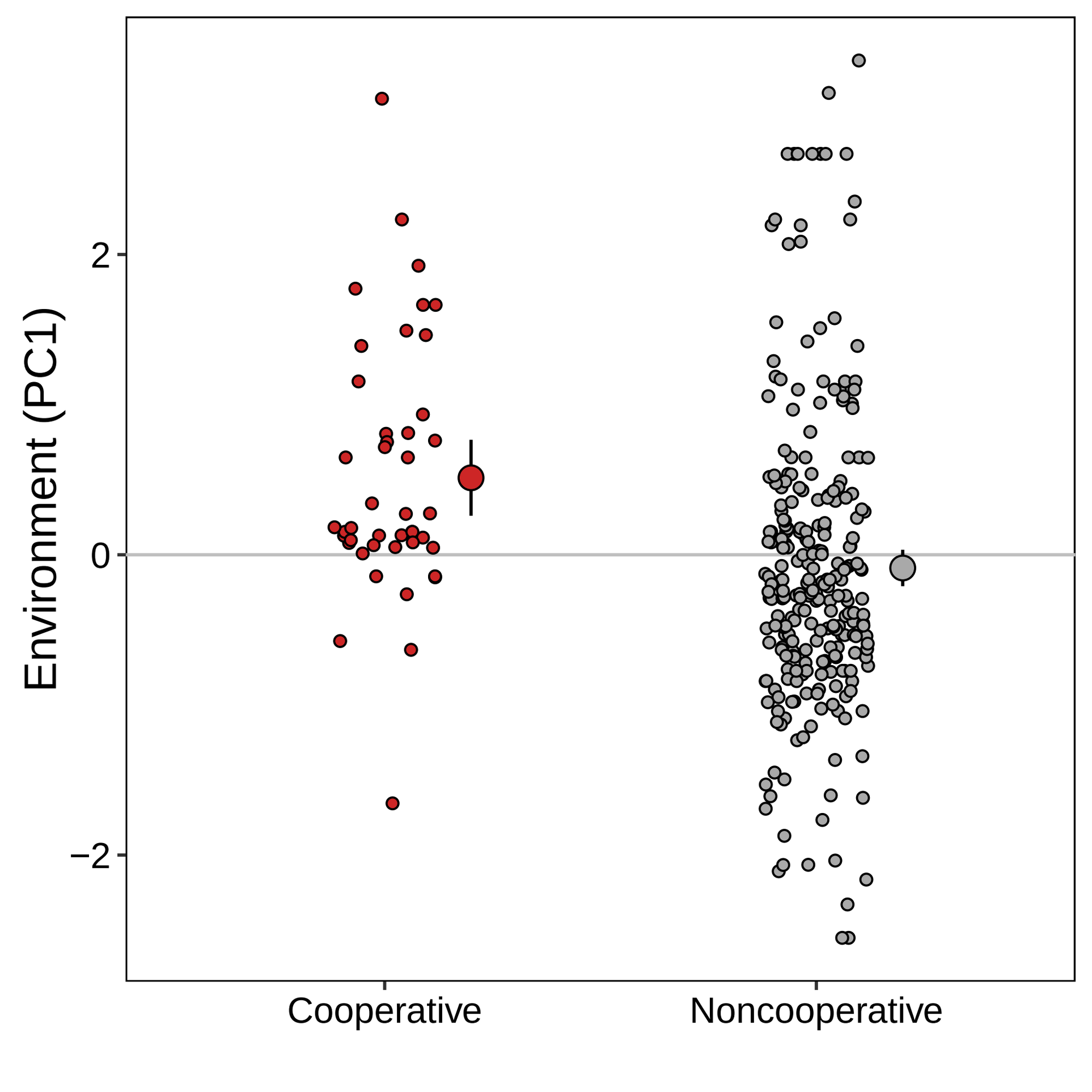
Fig. 5: Evolutionary transitions between cooperative breeding and environmental niches. Cooperative breeding is more likely to evolve in species occupying benign environment niches, which subsequently facilitates the invasion of hot environments with variable rainfall. Width of arrows indicate transition rates estimated using RJ-MCMC implemented in BayesTraits (Picture credits: Left St Strake, Right: CK Cornwallis).

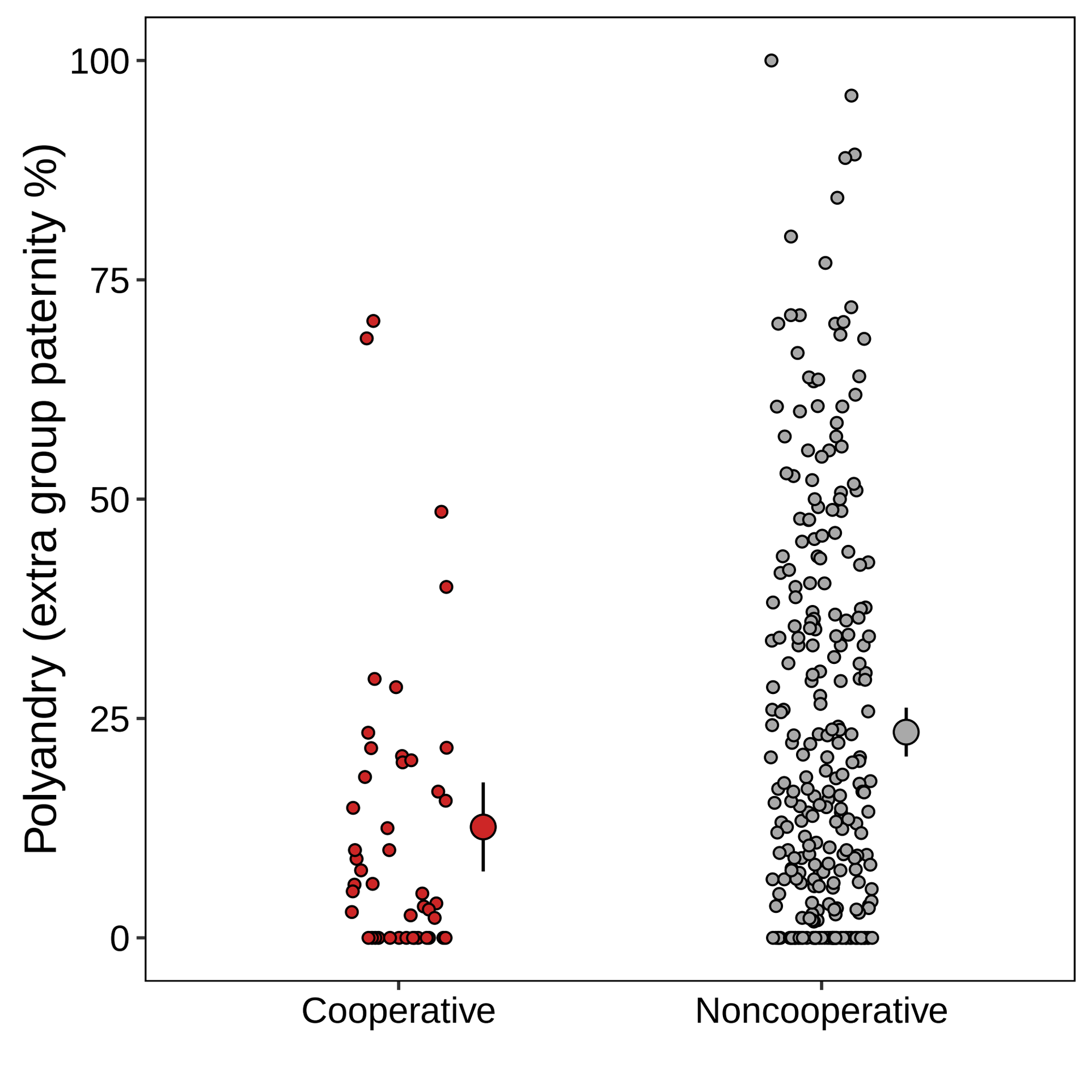

a

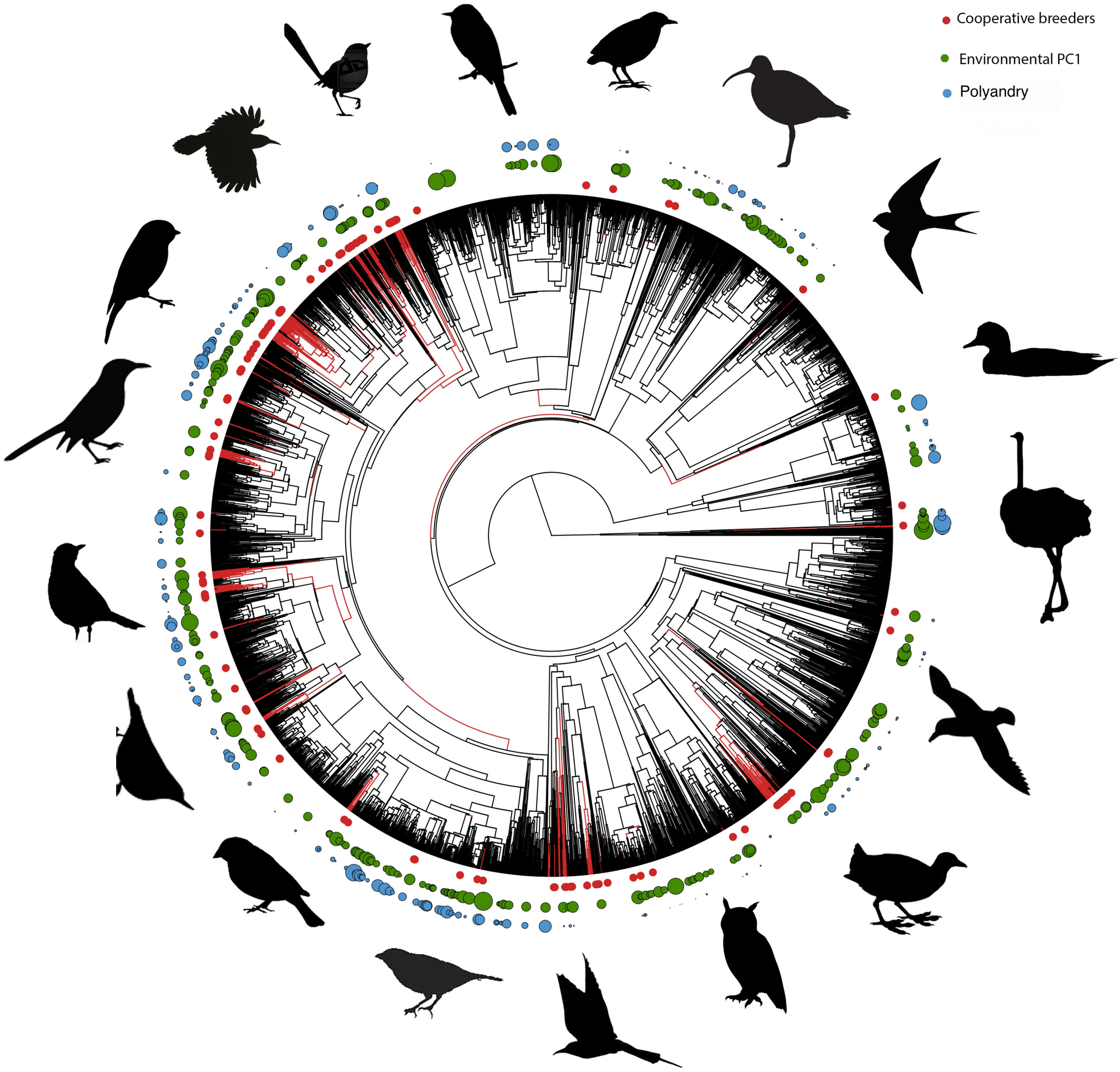

b

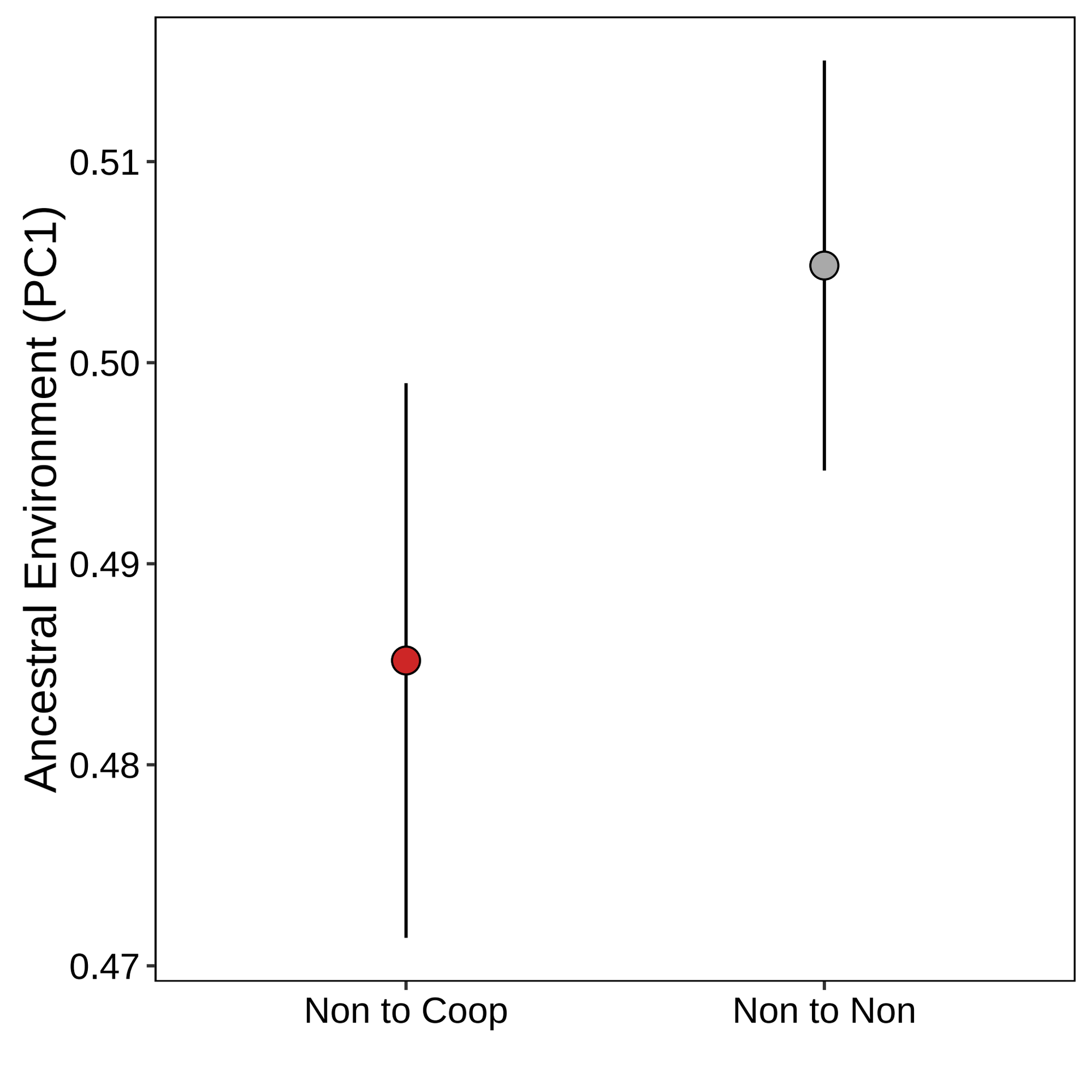

c

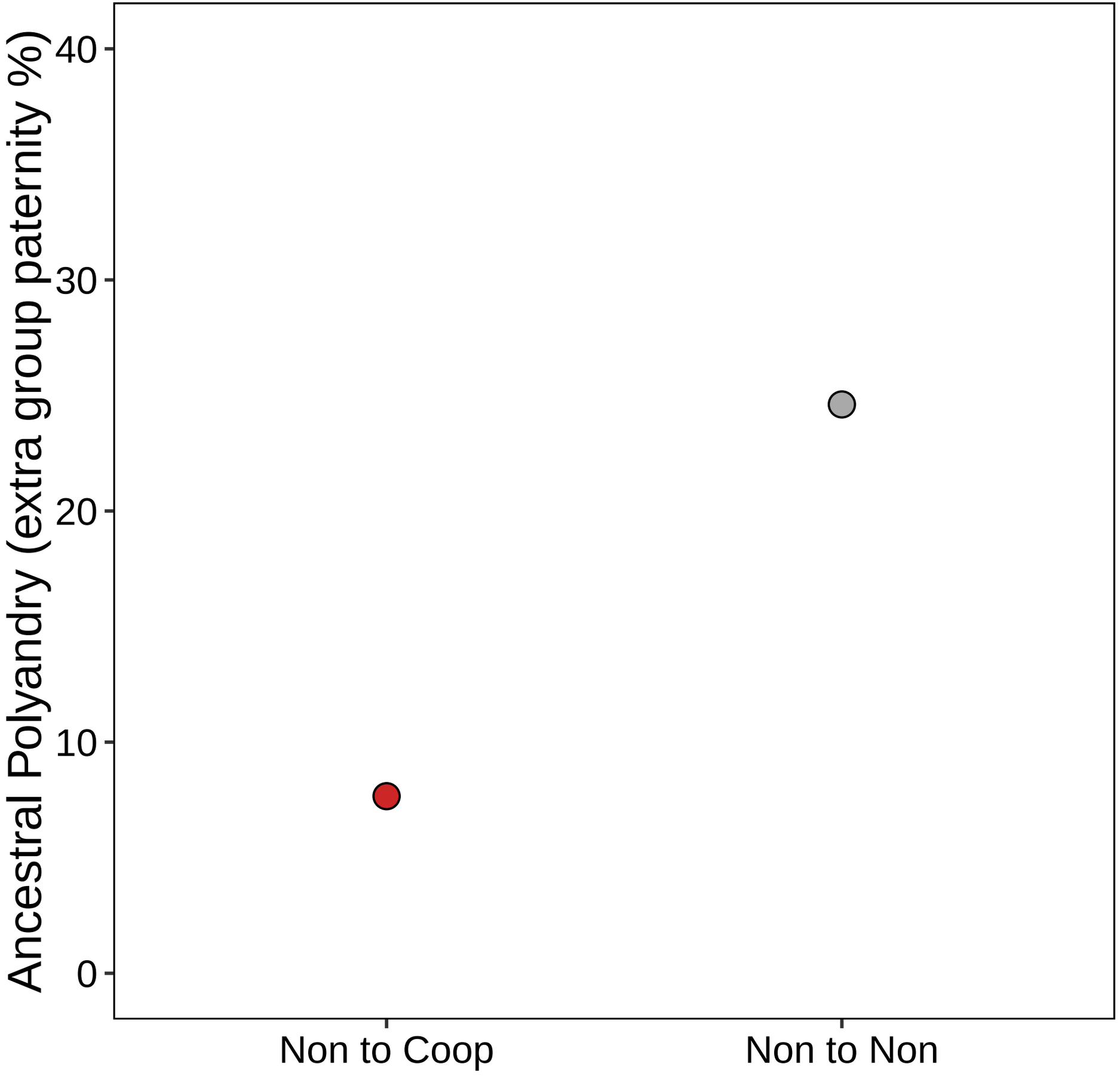

d

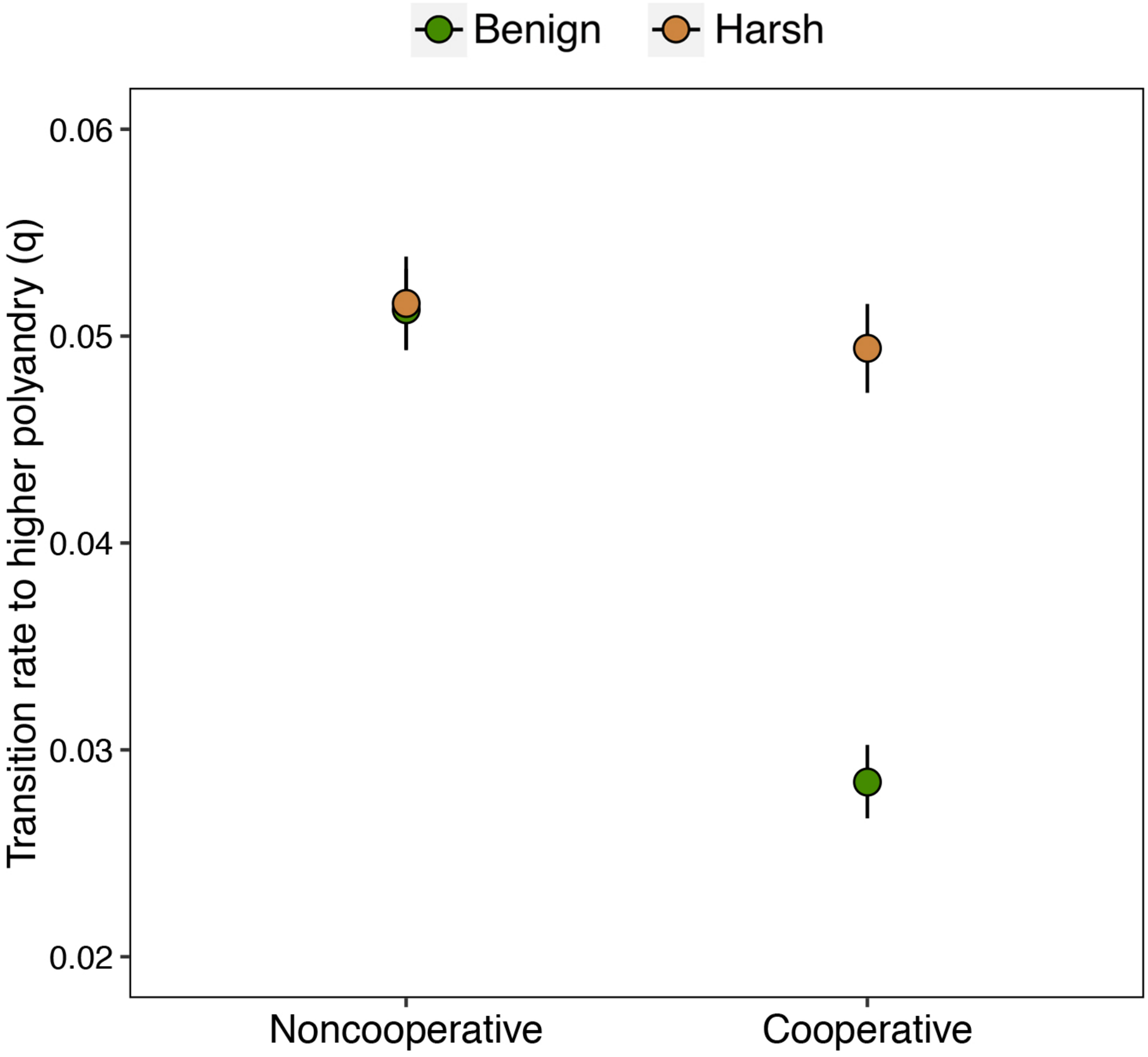

Environment (PC1)
2
0
−2
Cooperative
Noncooperative

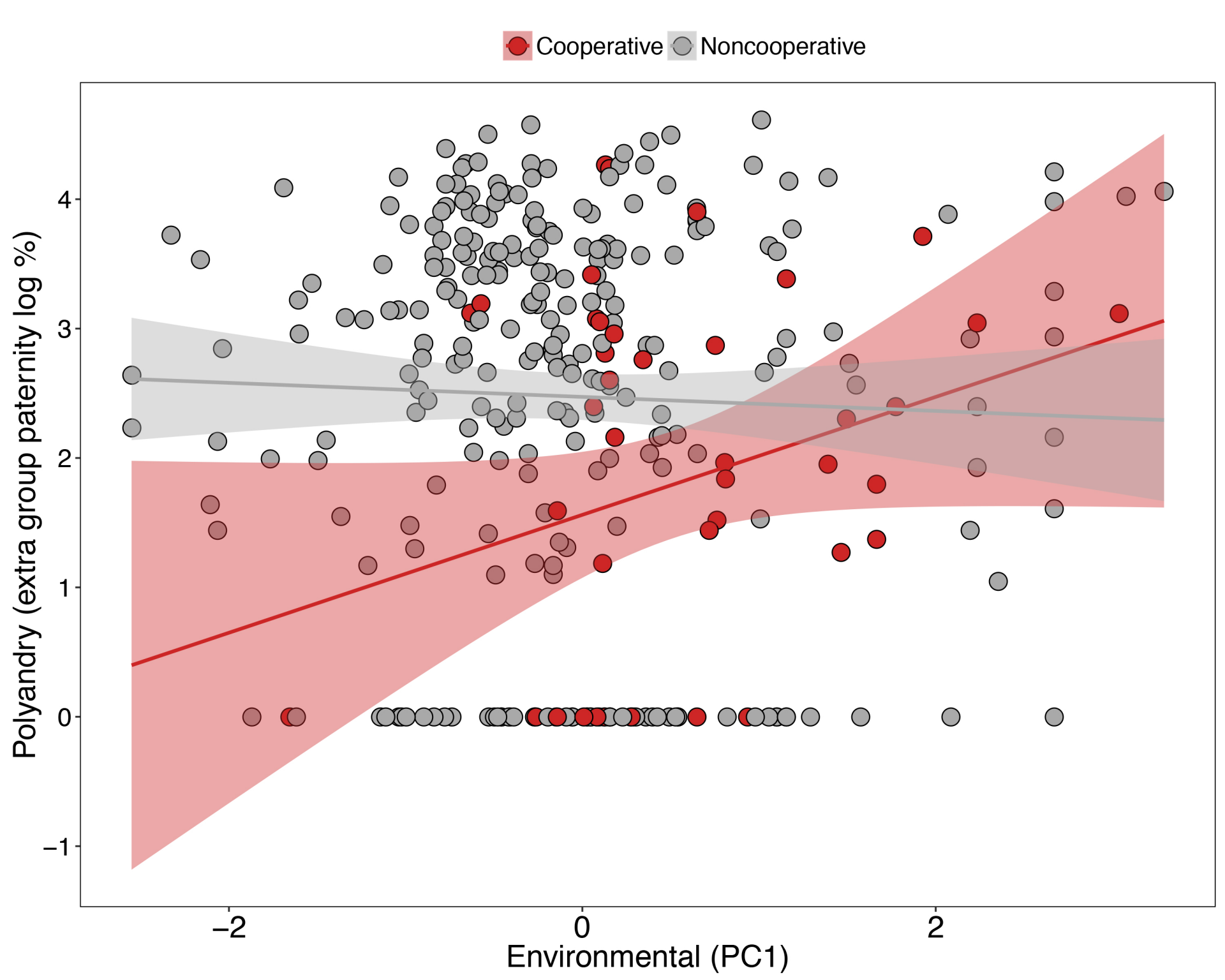

Polyandry (extra group paternity %)
100
75
50
25
0
Cooperative
Noncooperative


Cooperative breeders
Environmental PC1
Polyandry

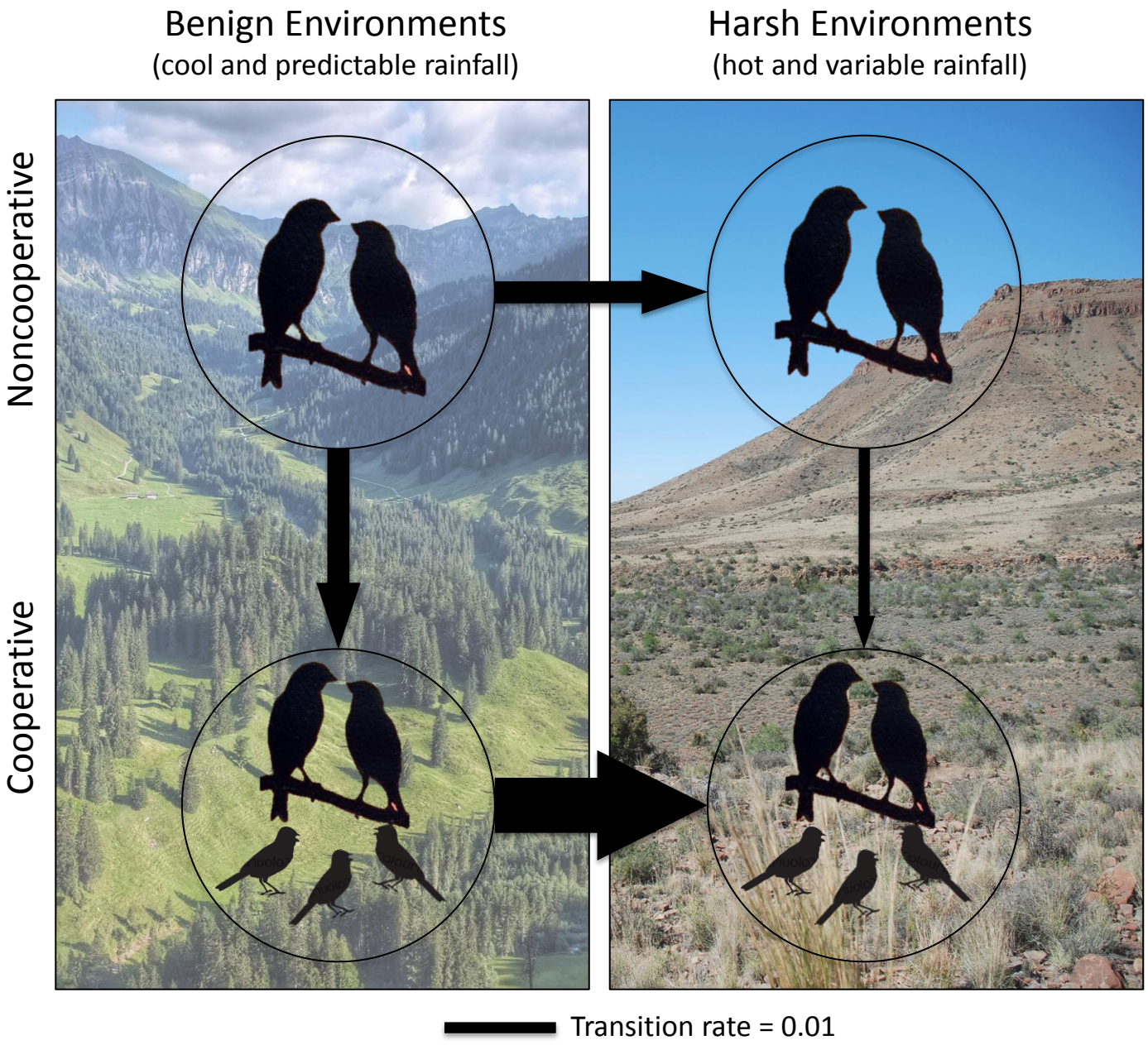

Ancestral Environment (PC1)
0.51
0.50
0.49
0.48
0.47
Non to Coop
Non to Non


Ancestral Polyandry (extra group paternity %)
40
30
20
10
0
Non to Coop
Non to Non


Benign
Harsh
0.06
0.05
0.04
0.03
0.02
Transition rate to higher polyandry (q)
Noncooperative
Cooperative


Cooperative
Noncooperative
Polyandry (extra group paternity log %)
4
3
2
1
0
−1
−2
0
2
Environmental (PC1)

Polyandry
Monogamous
Environment (PC1)
3
2
1
0
−1
20
40
60
80
Cooperative nests (%)


Benign Environments
(cool and predictable rainfall)
Harsh Environments
(hot and variable rainfall)
Noncooperative
Cooperative
Transition rate = 0.01