

Environmental Uncertainty and the Global Biogeography of Cooperative Breeding in Birds

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Summary

Understanding why organisms as different as amoebas, ants, and birds cooperate remains an important question in evolutionary biology. Although ecology can influence cooperation and conflict within animal societies and has been implicated in species differences in sociality [1], the environmental predictors of sociality across broad geographic and taxonomic scales remain poorly understood [2]. In particular, the importance of temporal variation in selection pressure has been underestimated in most evolutionary studies [3, 4]. Environmental uncertainty resulting from climatic variation is likely to be an important driver of temporal variation in selection pressure and therefore is expected to impact the evolution of behavioral, morphological, and physiological traits, including cooperation [5]. Using a data set of over 95% of the world's birds, we examine the global geography and environmental, biotic, and historical biogeographic predictors of avian social behavior. We find dramatic spatial variation in social behavior for which environmental and biotic factors—namely, among-year environmental variability in precipitation—are important predictors. Although the clear global biogeographic structure in avian social behavior carries a strong signal of evolutionary history, environmental uncertainty plays an additional key role in explaining the incidence and distribution of avian cooperative breeding behavior.

Results and Discussion

Cooperative breeding systems, in which more than two individuals in a group care for young, are more common in birds than once thought [6], with at least 9% of all passerines [7] and nearly 20% of those species with biparental care [8] exhibiting this complex social behavior. Although the inclusive fitness benefits of helping relatives ultimately set the stage for the evolution of cooperative breeding in most cases [6], environmental factors have long been thought to influence the reproductive costs and benefits of this behavior, as well as its incidence across species and regions [9]. Numerous studies have demonstrated the importance of territory quality, access to breeding sites, resource availability, and other ecological factors in influencing reproductive and dispersal decisions in cooperatively breeding species (e.g., [10, 11]). Despite this long-standing emphasis on the role of ecology

in the evolution of cooperative breeding behavior in birds, few early studies showed a strong relationship between the interspecific incidence of cooperative breeding and environmental conditions [12–16]. Although more recent comparative analyses have suggested that climatic variables like temperature [17] and rainfall [5] may be related to patterns of sociality in some groups of birds, evidence for interspecific differences in the ecologies of cooperative and noncooperative vertebrates has been equivocal at best [2]. Other studies argue that evolutionary history explains the patterns of avian sociality better than environmental factors do [18–21]. Whereas some suggest that life history traits and other biotic factors predispose certain avian lineages to cooperative breeding, with ecological conditions only acting to further facilitate the behavior [20, 22], others argue that the two factors work in concert to promote avian sociality [23].

Strong environmental effects on avian sociality should leave a visible geographic signature. Although the prevalence of cooperative breeding in places like Australia [16, 24] and Sub-Saharan Africa [13, 14] has long been recognized, to date, patterns have not been assessed on a global scale. If environmental determinants of avian sociality in birds exist, how much of its geographic distribution can they explain? And for which clades and regions are other drivers, such as evolutionary history, clade biogeography, and other determinants unconnected with contemporary environment [18, 19, 21], important? Here, we integrate these different environmental, biotic (life history), and historical biogeographic (phylogenetic) factors and evaluate their relative contributions to avian sociality. We begin by addressing, for the first time, the explicit biogeographic distribution of cooperatively breeding species using a data set of nearly all birds (see [Supplemental Experimental Procedures](#) available online) [7]. We then evaluate the relative importance of environmental (mean annual, among-year, and within-year variation in rainfall and temperature) and biotic (body mass, diet breadth, and diet type) factors on the global patterns of sociality in birds in a historical biogeographic framework [25].

We find that the world's 831 cooperatively breeding bird species (8.9% of all nonmarine birds) exhibit a distinctly nonuniform geographic distribution, with the highest species richness in many parts of Sub-Saharan Africa, southwestern Australia, parts of the Amazon basin, the Himalayas, and New Guinea (Figure 1A). Across the world's primary biogeographic realms [26, 27], the Afrotropics (268 species, 15%) and Australasia (169 species, 12%) harbor proportionally more cooperative breeders than the Nearctic (25 species, 7%), Palearctic (45 species, 6%), Indomalaya (98 species, 7%), and Neotropics (218 species, 6%). These broad-scale differences are exacerbated at finer scales (Figure 1B), with cooperative breeders representing over 20% of all bird species in some African, and over 30% of all bird species in select Australian, bird assemblages (Figure 1B). Additionally, cooperative breeding behavior is slightly more common in passerine (583 species, 10%) than nonpasserine (248 species, 7%) species, the two major evolutionary groups in birds (generalized linear model, Akaike information criterion [AIC] of null model = 5604; AIC of model fitting group

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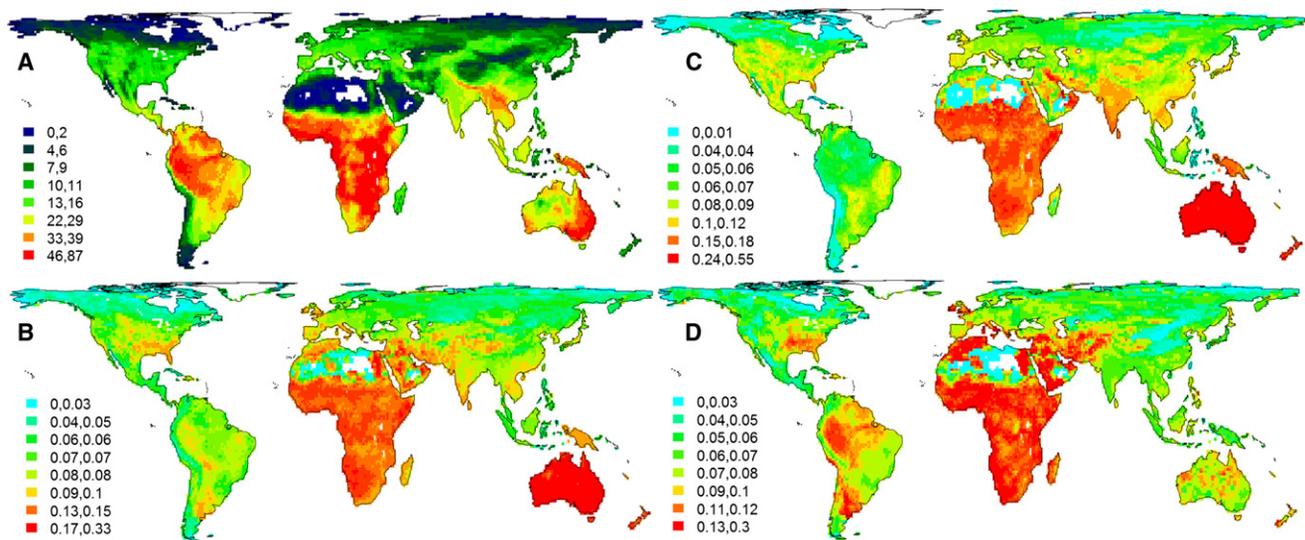


Figure 1. Biogeographic Distribution of Cooperative Breeding Behavior in Birds

Total richness of cooperative breeders (all 9310 nonmarine species) (A) and proportional richness of all (B), passerine (C), and nonpasserine (D) cooperative breeders. Maps are calculated across 110×110 km grid cells and displayed in quantile classification (i.e., equal number of cells in each class). The legend depicts lower and upper values for each color class. See also Table S2.

membership = 5578; $z = 5.16$, $p < 0.001$). Although both groups contribute to the exceptional prevalence of cooperative breeders in Africa, the high levels in Australasia are almost exclusively driven by passerine species (Figures 1C and 1D). In contrast, nonpasserine cooperative breeders are more prevalent in the Neotropics and account for much of the richness of cooperative breeders seen in the Amazon basin (Figures 1C and 1D). In general, cooperative breeders are much less common at higher latitudes, as has been pointed out previously for some groups of birds [19]. Overall, the dramatic spatial variation reported here is remarkable because its apparent geographic idiosyncrasy strongly surpasses other avian traits analyzed at global scale thus far (e.g., clutch size) [25], suggesting an important role for clade biogeographic (evolutionary) history in addition to combined effects of environmental (e.g., habitat structure and availability, climate) and/or biotic (life history) predictors of avian social behavior.

Comparative studies of avian cooperative breeding behavior have generally emphasized evolutionary history [18, 19, 21] and life history predictors [17, 20] as being more important than environmental predictors (but see [5]). Much of the difficulty in testing for general environmental correlates of cooperative breeding behavior in birds stems from inconsistencies in the types of environmental variables used to describe the ecological settings where most cooperatively breeding birds occur. Cooperative breeders occur in both stable [17, 28] and unstable [5, 16, 29], as well as in both seasonal [5, 13] and aseasonal [15], environments. However, most comparative studies have not actually quantified climatic seasonality or stability, measures of environmental predictability that quantify among- and within-year variability in climate [5, 30]. Instead, those studies that have examined more quantitative environmental correlates of avian cooperative breeding have generally emphasized climatic means or extremes [12, 13, 17]. To evaluate the relative importance of different environmental predictors of avian social behavior, we set prevalence of cooperative breeding in relation to broad-scale environmental niches of species, measured as both mean and

variation in environmental conditions found throughout species' global geographic ranges (see Supplemental Experimental Procedures). Specifically, we characterized species in terms of mean annual conditions (EnvMean), within-year variation (EnvVar within), and among-year variation (EnvVar among) across their range using a 30-year climatic database of precipitation and temperature. In general, we found that among- and within-year variation in temperature show latitudinal trends of increasing variation with increasing latitude (Figures 2A and 2B), whereas among- and within-year variation in precipitation exhibit more complicated patterns with generally greater variation in the tropics (Figures 2C and 2D). Analyses were performed on the entire data set of all 9310 nonmarine avian species (All across), but we also ran analyses separately on passerines and nonpasserines because of their different evolutionary histories and biogeographies [21, 31]. To control for shared evolutionary history within lineages and to look for evidence of phylogenetic signal in our data set, we also performed a nested phylogenetic, or within-clades, analysis on all species (All within) [25] using the 121 major avian clades (see Supplemental Experimental Procedures).

In the across-all-species analysis (All across), we found that although cooperative breeders tend to occupy regions with relatively low annual rainfall and high mean temperatures, variables capturing environmental variability (EnvVar) emerge as much stronger predictors than variables capturing environmental mean values (EnvMean) (Table 1). Specifically, both high among- and within-year variation in precipitation positively affect cooperative breeding (Table 1; Figure 3A). In contrast, cooperative breeders are slightly negatively associated with among-year temperature variation and are not affected by within-year temperature variation (Table 1; Figure 3B). When considered in a framework that accounts for evolutionary history, patterns in the nested phylogenetic analysis (All within) largely track those of the all-species analysis (All across); the within-clades analysis confirms the importance of both high among- and within-year variation in precipitation (Table 1). Despite generally small magnitudes in the

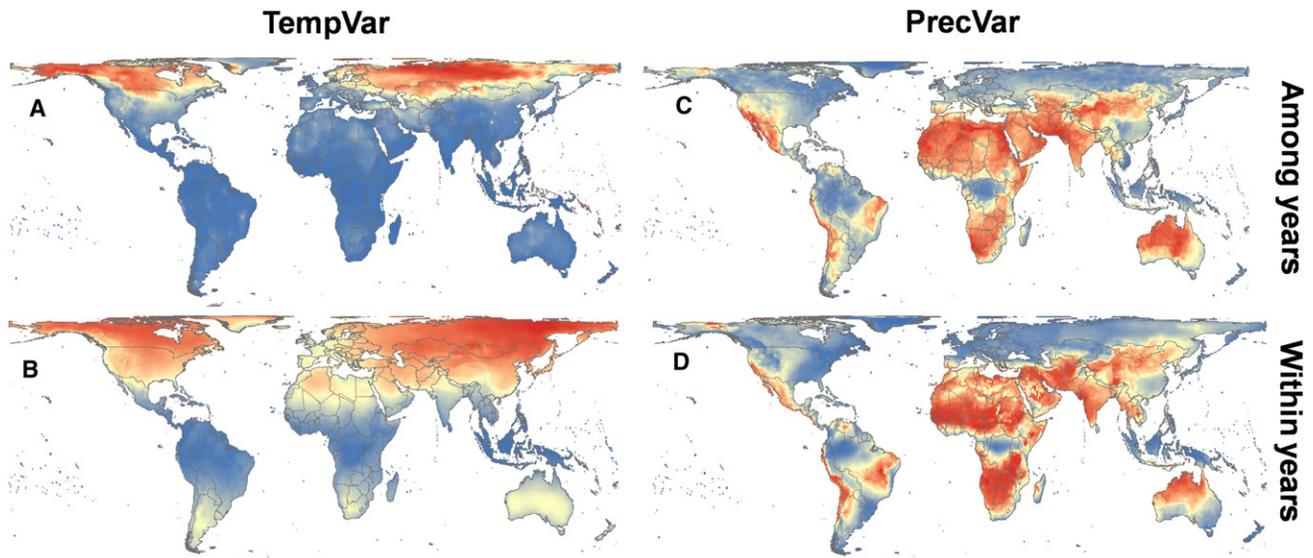


Figure 2. Global Patterns of Climatic Variability

Temperature (A and B) and precipitation variation (C and D) among (A and C) and within (B and D) years (the basis for log₁₀-transformed species variables TempVar within, TempVar among, PrecVar within, and PrecVar among in Table 1), calculated as standard deviations of log-transformed original values. Colors range from most variable (dark red) to least variable (dark blue) (TempVar among: min 0.06, median 2.59, max 12.71; TempVar within: min 0.25, median 18.83, max 79.21; PrecVar among: min 0.01, median 2.36, max 10.16; PrecVar within: min 0.23, median 2.98, max 19.94). Visualized across 55 km equal grid cells, natural breaks classification.

differences between cooperative and noncooperative species (Figure 3; see below for further analysis), our results demonstrate that environmental variation in precipitation among and within years is a key predictor of cooperative breeding behavior in birds. Overall, our analysis of the environmental predictors of avian sociality suggests that in general, (1) environmental variability (uncertainty) is a relatively stronger predictor than mean annual conditions, (2) variation in precipitation is a relatively stronger predictor than variation in temperature, and (3) among-year variation is a relatively stronger predictor than within-year variation (Table 1).

Although our analysis demonstrates that environmental variation—particularly in precipitation among years—is an important predictor of avian social behavior, the patterns are different for passerine and nonpasserine species. Whereas environmental variability is a better predictor than mean annual conditions for both passerines (Pass across) and nonpasserines (Nonpass across), the relative importance of among-versus within-year variation, and variation in precipitation versus temperature, differs (Table 1). Cooperative passerines are more likely to be found in areas of low mean annual and high variation in rainfall, whereas cooperative nonpasserines are found in areas of high mean annual and low variation in temperature. We note that environmental associations are much weaker in nonpasserines, where, unlike in passerines, they become nonsignificant in a nested phylogenetic analysis (Nonpass within, Table S1). Although this likely indicates key behavioral ecological differences between the two groups, it could also be due to the different evolutionary histories of the groups and the fact that the passerine clades diverged more recently than nonpasserine clades [31]. Nonetheless, this distinction between the environmental predictors of cooperative breeding behavior in passerine and nonpasserine species likely explains much of the long-standing disagreement over the role of environmental factors in the evolution of avian cooperative breeding [5, 12, 13, 15–17, 28, 29].

Because life history traits are also thought to be important for explaining the incidence of cooperative breeding behavior in birds [20, 22, 23, 28], we examined a suite of potential biotic predictors (body mass, diet breadth, and diet type) of cooperative breeding. We found no effect of body mass in the across-all-species analysis (All across), but the within-clades analysis (All within) suggests that cooperative breeders tend to be larger than noncooperative breeders; this pattern is driven by trends in passerines and not in nonpasserines (Table 1). Additionally, there is a weak but significant trend for cooperative breeders to have a wider diet breadth than noncooperative breeders in the across-all-species analysis, but not in the within-clades analysis; in general, cooperative breeders (both passerines and nonpasserines) are less likely to be carnivorous or herbivorous than noncooperative breeders (Table 1). Overall, whereas in the across-species analysis, biotic effects ($AIC_d = 102$) are slightly stronger than those of environmental conditions ($AIC_d = 94$), this reverses in the within-clades analysis ($AIC_d = 40$ biotic versus 44 environmental). This switch in relative importance confirms the stronger clade-level phylogenetic signal in biotic predictors compared to environmental predictors, something that was also recently documented for other life history traits [25]. Moreover, the increase in overall model fit (to AIC_d 212 and 74 for All across and All within, respectively) when including biotic predictors to a model that just includes environmental predictors supports the strong complementary role of life history traits in addition to broad-scale environmental conditions in explaining the incidence of avian cooperative breeding (Table 1).

How well can the assessed environmental and biotic factors together explain the incidence of cooperative breeding among species and across geographic regions? Models combining all environmental and biotic effects in the across-all-species (All across) analysis are the best supported (Table 1) and differentiate reasonably well among cooperative and noncooperative species in both passerines and nonpasserines (Figures 4A

Table 1. Environmental and Biotic Predictors of Cooperative Breeding Behavior in Birds

	All across		All within		Pass across		Nonpass across		Pass versus Nonpass	
	z	AIC _d	z	AIC _d	z	AIC _d	z	AIC _d		
EnvMean		70		27		55		27		
Annual Temp	4.76 ***	22	2.02 *	2	2.55 *	5	4.52 ***	26	**	
Annual Prec	-3.18 **	6	-5.14 ***	24	-4.97 ***	22	1.78	1	***	
EnvVar		82		35		82		33		
TempVar within	-1.72	-1	-0.80	-2	1.22	-1	-4.12 ***	20	***	
PrecVar within	6.98 ***	42	6.73 ***	41	6.12 ***	33	3.25 **	8		
TempVar among	-4.01 ***	14	-0.67	-2	-1.73	1	-3.99 ***	18	*	
PrecVar among	7.32 ***	47	6.68 ***	41	7.89 ***	56	1.08	-1	**	
Both among		78		43		66		20		
Both within		46		42		32		31		
TempVar both		26		-3		23		19		
PrecVar both		44		43		55		19		
Biotic		102		40		99		40		
Body mass	-0.06	-4	6.46 **	39	8.61 ***	69	-1.85	1	***	
Diet breadth	3.69 ***	10	1.59	0	2.73 **	5	3.21	8		
Diet										
Vert	-4.02 ***		-3.18 **		-0.04		-2.97 **			
Invert	6.11 ***		1.43		3.55 ***		3.22 **			
Mixed	5.16 ***	93	3.80 ***	19	4.92 ***	41	2.42 *	35		
Plants, seeds	-6.24 ***		-0.69		-4.20 **		-4.27 ***			
Fruits, nectar	-1.62		-2.02 *		-2.52 *		1.70		**	
EnvMean + EnvVar		94		44		94		38		
EnvMean + EnvVar + Biotic		212		74		201		74		

Results are based on generalized linear models across all bird species (All across, $n = 9310$ nonmarine species), all passerines (Pass across, $n = 5756$ species), all nonpasserines (Nonpass across, $n = 3555$ species), and a nested phylogenetic or within-clades model for all birds that controls for evolutionary nonindependence of clades (All within, distinguishing 121 clades, generalized linear mixed effects model). The column “Pass versus Nonpass” indicates whether the slopes of single predictors for Nonpass across and Pass across are significantly different (based on the interaction between a predictor and a categorical Nonpass/Pass variable in the All across data set). Positive z values indicate increased probability of cooperative breeding and for the categorical predictor Diet are based on linear contrasts. AIC_d values are the difference between the Akaike information criterion (AIC) of the predictor model and the null model with only intercept fitted (null AIC values: All across 5602; All within 4458; Pass across 3777; Nonpass across 1801); the AIC_d values refer to single/two-predictor models within the three variable groups and to multipredictor models across them (count of predictor variables: EnvMean: 2, EnvVar: 4, Biotic: 3). Values are comparable within and across each of the three variable groups, with larger values indicating stronger fit and allowing comparisons of relative importance of single predictors or predictor categories. Within each category, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. For evaluation plots of these models, see Figure 4 and Figure S1. See also Table S1.

and 4B insets). Area under the curve (AUC) values of the receiving operator characteristic (ROC) curve suggest sound discrimination of the two groups by the across-species models (AUC_{Pass} = 0.67, AUC_{Nonpass} = 0.70; Figure S1). Applying the predictions of these best-supported models (i.e., combining all variables) to the geographic occurrences allows us to calculate the mean predicted probability that bird species in a given assemblage are cooperative breeders. We find that this prediction provides a strong fit (i.e., goodness of fit) for the observed geographic variation in proportional occurrence of cooperative breeders (Figures 1C and 1D; Figures 4A and 4B; passerines $r_s = 0.66$, nonpasserines $r_s = 0.68$; $n = 11,098$ 110 km cells). However, significant variation remains, particularly in the case of passerines, where the variation is strongly geographically structured with the model unable to predict the high and low prevalence of cooperative breeders in Australian and Asian assemblages, respectively (Figure 4A). Additionally fitting clade membership of species, as done in the within-clades analyses, strongly improves the interspecific predictions of cooperative breeding (Figures 4C and 4D insets; Table S1), resulting in very good discrimination, particularly for nonpasserines, where environmental and biotic factors are weaker predictors than in passerines (AUC_{Pass} = 0.87; AUC_{Nonpass} = 0.92). Evaluation plots indicate higher levels of specificity and sensitivity compared to the across-species

models (Figure 4; Figure S1). Accordingly, geographic fits for all birds are strongly improved when controlling for clade-level variation (Figures 4C and 4D; passerines $r_s = 0.71$, nonpasserines $r_s = 0.80$; $n = 11,098$ 110 km cells), particularly for Australian passerine assemblages (Figure 4C). Thus, our best-supported model—particularly when including phylogenetic signal—does well in explaining interspecific differences in avian social behavior. Lacking a fully resolved avian phylogeny that would allow for the calculation of, e.g., Pagel’s lambda and an analysis in a generalized least-squares setting [32], the mixed-effects model used for the within-clades analysis offers a powerful alternative [25]. However, we note that this approach implies that some of the signal in the predictor variables is subsumed in that of phylogeny, as a result of conservation of traits and environmental niches of clades. Because several highly cooperative clades are restricted to regions that also have high environmental variability (e.g., select passerine groups in Australia), the attribution of relative phylogenetic versus environmental signal is not straightforward. For interpretation, we therefore emphasize the consistent emergence of key environmental variables associated with cooperative breeding above and beyond the signal of evolutionary history.

Overall, we show that birds exhibit dramatic spatial and biogeographic structure in cooperative breeding behavior

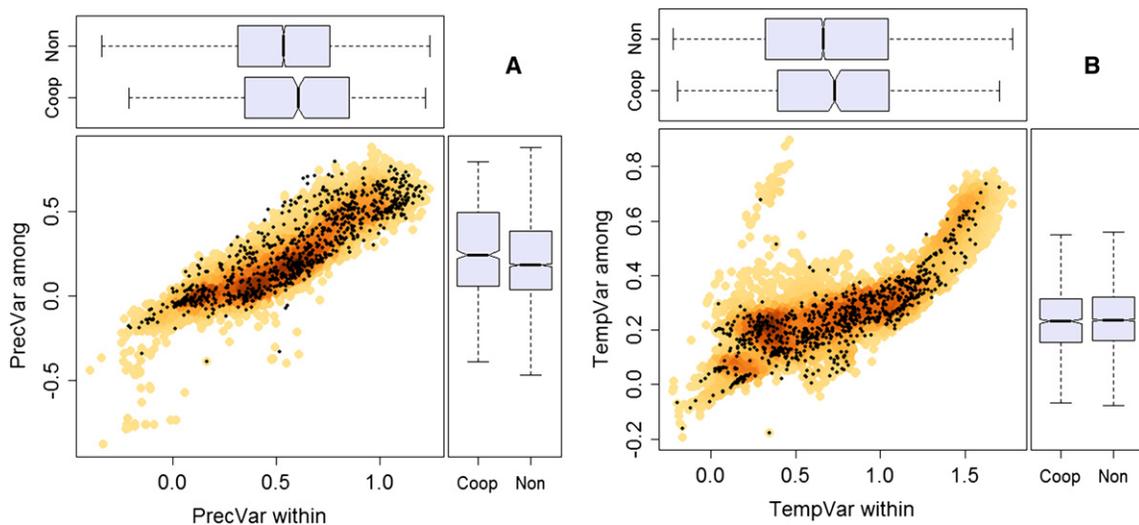


Figure 3. Environmental Variability as a Predictor of Cooperative Breeding Behavior in Birds

In the scatter plots, each dot represents the mean niche position of a single species; box plots summarize these positions for a single axis. Small black dots refer to cooperative (“Coop”) breeders, whereas large colored dots refer to noncooperative (“Non”) breeders. The climatic niche axes represent within- and among-year variation of precipitation (PrecVar) (A) and temperature (TempVar) (B). In noncooperative species, darker colors indicate greater density (overlap) of points (box plots: notches indicate approximated 95% confidence intervals; hinges indicate position of lower and upper quartile of data; whiskers indicate the position of the extreme points at the 1.5 interquartile range of the lower and upper quartile of the data). See Table 1 for single- and two-predictor model results.

and highlight the global “hot spots” (e.g., Australia and Afrotropics) and “cold spots” (e.g., Neotropics and Indomalaya) of avian social diversity. We further demonstrate that geography and clade history, together with environmental and biotic (life history) factors, explain the worldwide distribution of avian social behavior. Importantly, although exerting a strong signal, phylogenetic history alone cannot fully explain the observed overrepresentation of cooperatively breeding species in places like Australia and Africa. Biotic factors like body mass and diet are among the strongest overall predictors; however, they exhibit strong phylogenetic signal, consistent with the hypothesis that life history traits may predispose certain lineages toward cooperative breeding behavior [17, 22] but then work in concert with environmental factors within those lineages [23]. Notably, environmental factors are strong predictors of avian sociality above and beyond the effects of clade membership. In particular, environmental variability is a stronger predictor of avian sociality than mean annual conditions, and variation in precipitation—particularly among years—is a stronger predictor than variation in temperature, as has been suggested previously [5].

Our results demonstrate that even on a global scale, the incidence of complex avian social behavior may be greatly influenced by the fitness consequences of living in unpredictable environments. Variable environments encompass a broad range of climatic conditions that likely have important consequences for behavioral, morphological, and physiological adaptation because they pose a greater range of challenges to survival and reproduction than predictable environments. Individuals may be forced to adopt more generalist reproductive strategies, and cooperative breeding may therefore be a conservative, “best of a bad job” strategy to maximize fitness when breeding conditions vary unpredictably from year to year. Although this hypothesis emphasizes the role of environmental variability and variation in offspring mortality and production, adult mortality and longevity are also likely

to be important and similarly influenced by environmental uncertainty [17, 20]. This idea is supported by recent empirical studies of avian cooperative breeding behavior showing that the fitness benefits of helping are most apparent in harsh conditions [33] and that flexible reproductive strategies allow for more individuals to maximize their fitness during benign conditions [34]. Thus, cooperative breeding as a flexible but conservative reproductive strategy may allow individuals to maximize fitness in both good and bad times.

Supplemental Information

Supplemental Information includes one figure, two tables, and Supplemental Experimental Procedures and can be found with this article online at [doi:10.1016/j.cub.2010.11.075](https://doi.org/10.1016/j.cub.2010.11.075).

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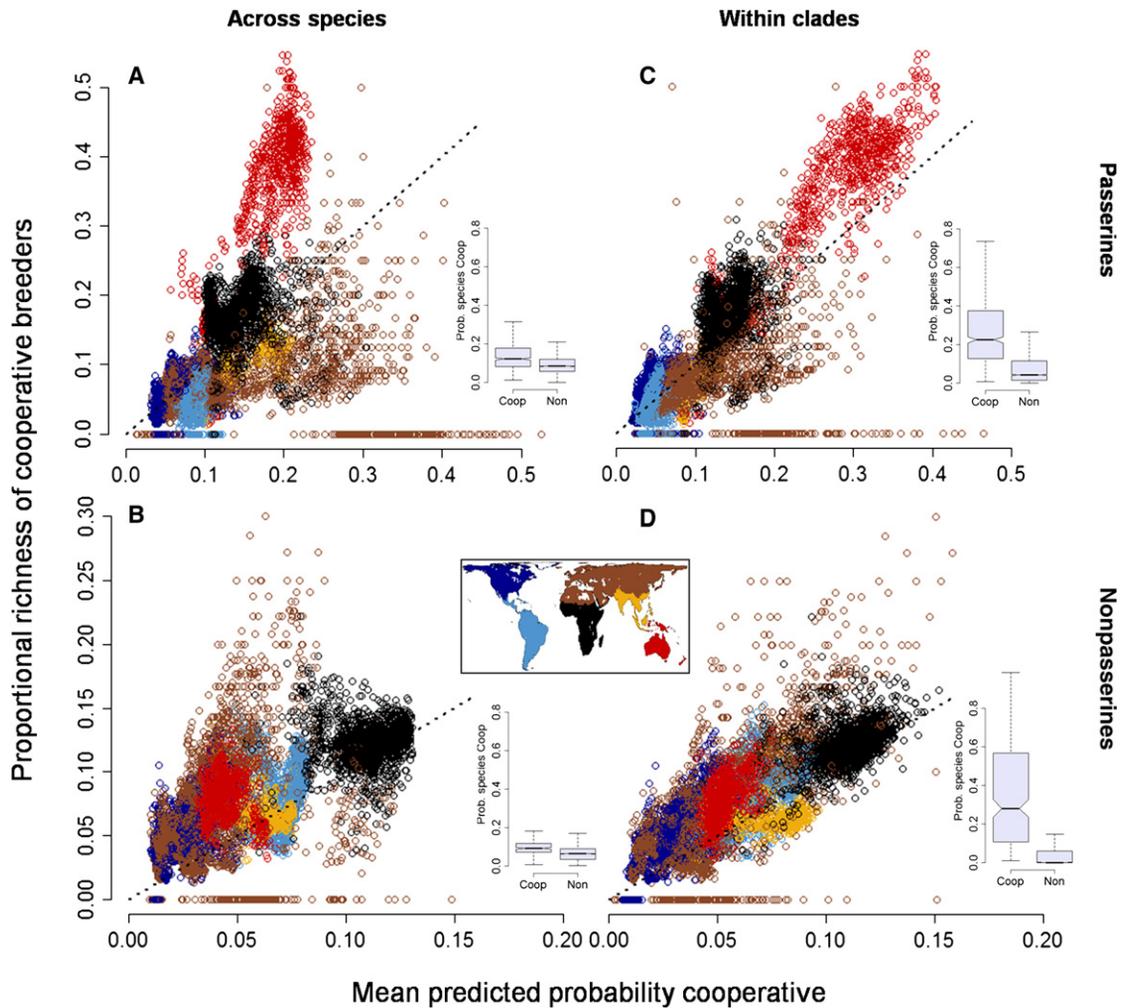


Figure 4. Model Fits across Species and Grid Assemblages

Ability of the best-supported model (EnvVar + EnvAvg + Biotic) to predict species (box plots, insets) and geographic (scatter plots) variation in cooperative breeding for passerines (A and C) and nonpasserines (B and D). Box plots show the predicted probability of a species to be cooperative according to the EnvVar + EnvAvg + Biotic model (see Table 1) for known cooperative and noncooperative breeders ($n = 9310$ species; see Figure S1 for additional evaluation plots); for details on box plots, see Figure 3. Scatter plots illustrate how these species predictions, averaged across all members of a 110 km grid cell assemblage (“mean predicted probability cooperative”), are able to predict the observed proportional richness of cooperative breeders, i.e., the geographic patterns shown in Figure 1B ($n = 11,098$ cells). The across-species (All across) model does not account for phylogeny, whereas the within-clades (All within) model addresses phylogeny by fitting clade membership (see Table 1). In the scatter plots, dotted lines illustrate a 1:1 fit, and symbol colors indicate which of the six primary biogeographic realms (see inset map) a grid cell belongs to. See also Figure S1.

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