LETTER

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Environmental quality mediates the ecological dominance of cooperatively breeding birds

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Abstract

Although social species as diverse as humans and ants are among the most abundant organisms on Earth, animals cooperate and form groups for many reasons. How these different reasons for grouping affect a species' ecological dominance remains unknown. Here we use a theoretical model to demonstrate that the different fitness benefits that animals receive by forming groups depend on the quality of their environment, which in turn impacts their ecological dominance and resilience to global change. We then test the model's key predictions using phylogenetic comparative analysis of >6500 bird species. As predicted, we find that cooperative breeders occurring in harsh and fluctuating environments have larger ranges and greater abundances than non-cooperative breeders, but cooperative breeders occurring in benign and stable environments do not. Using our model, we further show that social species living in harsh and fluctuating environments will be less vulnerable to climate change than non-social species.

KEYWORDS
cooperation, cooperative breeding, ecological consequences, range size, sociality, species distribution

INTRODUCTION

Over 150 years ago, Charles Darwin proposed in *On the Origin of Species* that explaining interspecific variation in geographic range size is critical for understanding both the "present welfare" and the "future success" of species (Darwin, 1859). Linking species distributions and organismal success takes on greater meaning today in an era of anthropogenic climate change where environments are becoming increasingly unpredictable (IPCC, 2021) and extreme weather events are occurring with greater frequency (Mora et al., 2017; Prein et al., 2017). One of the primary ways that organisms cope with these and other forms of global change is to adjust their distributions, moving, for example, up mountain ranges

as temperatures increase (Chen et al., 2011; Lenoir et al., 2020) or into new habitats as precipitation patterns shift (Pearce-Higgins et al., 2015). Environmental change most often negatively impacts the demography of populations or species, including both reductions in range size (Erasmus et al., 2002) and abundance (Both et al., 2010; Pearce-Higgins et al., 2015), yet animals that cooperate and form societies may be able to compensate and outcompete their non-social neighbours or relatives under periods of global change (Cornwallis et al., 2017; Sun et al., 2014). Although the ability to form cooperative societies has been argued to be one of the primary reasons for the dominance of social organisms on Earth, there are not only many fewer social species than non-social ones (Brooks et al., 2017; Wilson, 1990, 2012), but

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there is also no formal framework explaining why some social species have become ecologically dominant while others have not. To understand how cooperation influences ecological dominance, we must determine not only how ecology impacts the evolution of social living, but also how sociality influences ecological success and population demography for species living in environments of varying quality (Lin et al., 2019; Shen et al., 2017).

Several comparative studies in a variety of taxa suggest that both the mean and variation in climatic conditions have shaped the evolution of animal societies (Fisher et al., 2021). For example, harsh mean environmental conditions and/or fluctuating environments have favoured the evolution of cooperative breeding behaviour in ants (La Richelière et al., 2022), wasps (Sheehan et al., 2015), bees (Kocher et al., 2014), birds (Jetz & Rubenstein, 2011; Rubenstein & Lovette, 2007), and mammals (Firman et al., 2020; Lukas & Clutton-Brock, 2017), including humans (Martin et al., 2020). Yet, high population density and habitat saturation, both characteristics of species living in benign and/or stable environments, have also been suggested to favour the evolution of cooperative breeding behaviour in insects (Choe & Crespi, 1997; Costa, 2006), arachnids (Choe & Crespi, 1997), birds (Gonzalez et al., 2013), and mammals (Solomon & French, 1997). This phenomenon of cooperative breeding behaviour being favoured in both harsh and fluctuating environments as well as under benign and stable conditions constitutes the paradox of environmental quality and sociality (Lin et al., 2019; Shen et al., 2017). To help resolve this paradox, researchers proposed that cooperative breeding behaviour may evolve for different reasons in different environments (Shen et al., 2017). According to this "dual benefits framework", animals form social groups to gain resource defence (RD) benefits against intraspecific competitors in stable and/or benign environments, but they form groups to gain collective action (CA) benefits in the face of interspecific competition or environmental challenges in harsh and/or fluctuating environments (Lin et al., 2019; Shen et al., 2017). Despite contrasting and testable predictions from the dual benefits framework (Shen et al., 2017; Shen & Rubenstein, 2019), we still lack a mathematical formulation of these ideas, as well as broad-scale comparative and biogeographic studies investigating how the relationships among cooperative breeding behaviour and ecology influence the demography and ecological success of social organisms.

Here, we integrate socioecological and macroecological perspectives on animal behaviour, demography, and global change by combining theory and phylogenetic comparative approaches to test the paradox of environmental quality and sociality. First, we construct a spatially explicit, individual-based model to explore how the effects of both mean environmental conditions and environmental fluctuation (variation in environmental conditions) influence the evolution of cooperative investment in

different types of grouping benefits, and how these combined environmental effects impact the ecological and demographic consequences (range size and abundance) of social species that form groups for different reasons (RD or CA benefits). Using phylogenetic comparative methods, we subsequently test the model's key predictions by first examining how environmental and social factors affect the evolution of cooperative breeding behaviour in birds, and then determining whether cooperative breeding has different ecological and demographic consequences (range size and abundance) for species that exhibit cooperative breeding behaviour under different environmental conditions. Because birds are known to show variation among clades in the relationship between cooperative breeding and environmental quality (Lin et al., 2019), we begin by conducting a clade-level analysis within avian lineages that have evolved cooperative breeding behaviour to investigate how different environmental factors influence cooperative breeding. To examine the alternative ecological and demographic consequences of cooperative breeding, we then separate these avian clades into two categories, those in which cooperative breeding behaviour is either positively associated with environmental harshness/stability or with environmental benignness/fluctuation, and compare species range sizes and abundances in cooperative and non-cooperative species in these two categories. To explore further, we combine all clades and species into a single comparative analysis examining range size and abundance in cooperative and non-cooperative species. Finally, we use our model to further investigate the vulnerability to climate change of species that form cooperatively breeding groups for different reasons in different environments. Ultimately, we show not only that the relationships between cooperative breeding behaviour and demography (range size and abundance) depend on the relationship between cooperative breeding and environmental quality, but that social species living in harsh or fluctuating environments will be less vulnerable to climate change than non-social species.

METHODS

Modelling social evolution and its ecological consequences

To examine the ecological and demographic consequences of cooperation, we began by building a spatially explicit, individual-based model that assumes a population evolves in a habitat matrix of 23×23 patches. Each patch can be occupied by more than one individual, and individuals in the same patch interact, or cooperate, to generate either CA or RD benefits. Individuals are classified into (1) those that invest in generating CA benefits by cooperating to outcompete interspecific competitors or to cope with

environmental challenges (CA cooperators), thereby increasing the amount of group resources that are shared equally among group members, (2) those that invest in creating RD benefits through the cooperative defence of group resources within the patch against intraspecific competitors (RD cooperators), or (3) those that neither cooperate nor produce anything, but that share group resources (free-loaders) (Shen et al., 2017). Cooperators contribute to the grouping benefits at a cost to themselves, whereas non-cooperators bear no cost. Within each simulation time step, the reproductive rate is determined by the amount of resources that individuals consume. After individuals produce offspring, those offspring either stay or disperse to other patches, and then some of the reproductive individuals die.

To account for the relationship between the mean and variation in environmental conditions, and to introduce temporal variation into our model by simulating a fluctuating environment, we sampled the resource availability of the whole grid every time step from a uniform distribution. To tease out the ecological and demographic consequences of cooperation, we recorded the proportion of cooperators in the population and the average degree of cooperation that each individual exhibits over time, as well as the total abundance and range size (i.e., the number of occupied patches in the habitat matrix). We then compared the results of this model to those of a non-social population composed exclusively of non-cooperators. Finally, we simulated scenarios under which climate change results in lower mean available resources or higher fluctuation in resources. We investigated the impacts of climate change on CA and RD collaborators by adjusting the mean resource level of the environment and increasing the degree of fluctuation in environmental resources. More detailed model descriptions are provided in the Supplementary Methods.

Phylogenetic comparative analysis

Trait and environmental data

The avian species used in this study came from published data (Jetz & Rubenstein, 2011). Because we were interested in how climatic factors influence the evolution of cooperatively breeding behaviour, we excluded clades containing 100% non-cooperatively breeding species (2409 species belonging to 52 clades) and 100% cooperatively breeding species (58 species belonging to 5 clades). We also compared the species list with the most recent *Handbook of the Birds of the World* and BirdLife Taxonomic Checklist v5 (BirdLife International, 2020) to exclude subspecies from our analysis ($N = 290$ species). The social system of each species was classified as "cooperative" or "non-cooperative"

and was determined through published accounts (Cockburn, 2006; Jetz & Rubenstein, 2011). Following Griesser and Suzuki (2016), we also reran our comparative analyses excluding 152 species that only occasionally breed cooperatively, finding nearly identical results (see Tables S1–S3). Since 47 of these occasional cooperative breeders were present in the clades containing all non-cooperative species and already removed, we ended up excluding 105 species in our re-analysis without occasional cooperative breeders. Body mass was also collected from published data (Dunning Jr, 2007; Tobias et al., 2022) and included in our analysis because of its potential effect on influencing social behaviour (Jetz & Rubenstein, 2011). Range sizes of every species in the dataset were extracted from digital bird species distribution maps of the world (BirdLife International, 2020), and global species abundances (i.e., the estimated number of individuals within a species) were taken from a previously published study (Callaghan et al., 2021). To ensure sufficient statistical power to assess the relationship between climatic factors and cooperative breeding behaviour, we restricted our analysis to clades containing more than 20 species (Blomberg et al., 2003). Thus, our clade-level analysis includes 6553 species belonging to 52 clades (Table S4). Finally, 100 phylogenies were generated from the open-access dataset of BirdTree.org (Jetz et al., 2012) using the Hackett backbone (Hackett et al., 2008). To account for phylogenetic uncertainty, we used posterior tree samples to create a maximum clade credibility (MCC) consensus tree, using 10% burn-in and common ancestor height in TreeAnnotator v2.6.6 (Bouckaert et al., 2019).

We extracted environmental data from the distributional ranges of each species using the CRU TS 4.05 database (Harris et al., 2020) and calculated the mean values of six climate variables for each grid cell within the geographic distribution range of each species: (1) mean annual temperature (°C); (2) diurnal temperature range (DTR, °C); (3) seasonal temperature range (STR, °C); (4) mean annual precipitation (MAP, mm); (5) within-year variation in precipitation (i.e., the mean among all years of the within-year standard deviations of the 3-month values); and (6) among-year variation in precipitation (i.e., the standard deviation within the same 3-month period across all years) (Chan et al., 2016; Ficetola et al., 2017; Gonzalez et al., 2013; Rubenstein & Lovette, 2007). We then calculated within- and among-year variation in precipitation as the mean of log10-transformed values across all 55 × 55 km grid cells occupied by a species over 120 years (Jetz & Rubenstein, 2011). Following similar comparative studies, harsh and fluctuating environments were defined as those with high mean annual temperature (Cornwallis et al., 2017), low mean annual precipitation (Botero et al., 2014; Firman et al., 2020), high variability in precipitation (Cornwallis et al., 2017; Rubenstein & Lovette, 2007), and high variability in

temperature (Botero et al., 2014; Firman et al., 2020), and vice versa for stable and predictable environments.

Phylogenetically-informed tests

To explore the ecological causes and consequences of cooperative breeding behaviour comparatively in birds, we used a series of phylogenetically-informed tests (see flow diagram in Figure S1). First, to assess the relationship between social system and climate for each of the 52 avian clades (selected according to the criteria described above), we examined whether the six environmental variables and body mass predicted the occurrence of cooperative breeding behaviour in each clade. We first tested a full model using the *phyloglm* function with all of the environmental variables and life history traits in the R package *phylolm* (Ho et al., 2018), with the binary dependent variable (cooperative breeding, hereafter referred to as "cooperative" or non-cooperative breeding, hereafter "non-cooperative"). We then examined the variance inflation factor (VIF) of the full model for each climatic factor to assess potential multicollinearity. We identified and retained variables with robust effects after iteratively removing variables with VIF>5 (O'brien, 2007). Finally, we determined the best-fitting models with a corrected Akaike information criterion (AICc) (Hurvich & Tsai, 1989), using model averaging for models with AICc<2 (Anderson & Burnham, 2004) in the R package *AICcmodavg* (Mazerolle, 2013). We then classified each clade into one of the three groups based on the relationship between environmental factors and social system from *phyloglm*: (1) cooperative breeding behaviour is positively associated with environmental harshness/stability; (2) cooperative breeding behaviour is positively associated with environmental benignness/ fluctuation; or (3) there is no association between cooperative breeding behaviour and environmental quality. To include as many clades as possible in our analysis, we used a liberal threshold of *p*<0.25 for classifying clades into one of the three categories.

Next, we performed a clade-level analysis, testing the effects of both cooperative breeding behaviour and climate on demography (both species range size and abundance) using phylogenetic least squares (PGLS) models separately for species in clades that cooperate in benign and/or stable environments (*N*=1786 species), those that cooperate in harsh and/or fluctuating environments (*N*=2426 species) by implementing the *phylolm* function using lambda model (Pagel, 1999) in the R package *phylolm*. We also tested the VIF of the full model between each climatic factor to examine for potential multicollinearity. As before, we identified and retained variables with robust effects after iteratively removing variables with VIF>5 (O'brien, 2007) and used model averaging methods to average the models with ΔAICc<2. We also ran a PGLS analysis using the same approach but

combining all clades and species (*N*=6553 species) into a single model. Finally, we explored the potential causal relationships among climate, body mass, social system, and demography in the two categories in which cooperative breeding was associated with environmental quality using phylogenetic confirmatory path analysis (PCPA) (Hardenberg & Gonzalez-Voyer, 2013) with the lamda model in the R package *phylopath* (van der Bijl, 2018). More detailed descriptions of PCPA are provided in the Supplementary Methods.

RESULTS

Model results

First, we explored which environmental conditions favour CA or RD cooperation strategies. Since high quality patches are only worth defending when environmental conditions are predictable, we found that RD benefits only evolve in a temporally stable environment with low variability in resource availability (Figure 1a). In addition, both stable and benign environments (i.e., those with high resource availability) will lead to higher intraspecific competition over resources and thus, favour cooperative investment in resource defence (Figure S2). In contrast, CA benefits are more likely to emerge when mean environmental conditions are harsh (i.e., low resource availability) and when resource availability fluctuates greatly (Figure 1b and Figure S2). This is because extra group resources produced by cooperators are essential for individuals to reproduce successfully in both harsh and fluctuating environments. As a result, we found that CA and RD benefits occur in environments with distinct properties. Finally, our model also shows that non-cooperators have a reproductive advantage over cooperators under a wide range of environmental conditions, including in both benign environments for CA benefits and fluctuating environments for RD benefits.

Next, we explored the effects of cooperation on demography by determining the consequences of CA and RD benefits on range size and abundance. We found that RD cooperators and non-cooperators have very similar range sizes (Figure 2d) and abundances (Figure 2e,f) in harsh environments with low resource availability. In contrast, the population and range sizes of CA cooperators are larger than those of non-cooperators (Figure 2d–f) because individuals are more cooperative in harsh environments with low resource availability (Figure 1b). Nevertheless, CA cooperators and non-cooperators have similar range sizes and abundances in benign environments with high resource availability (Figure 2a–c), but the range sizes (Figure 2a) and abundances (Figure 2b,c) of RD cooperators are smaller or similar to non-cooperators. We also found that CA cooperators always have larger
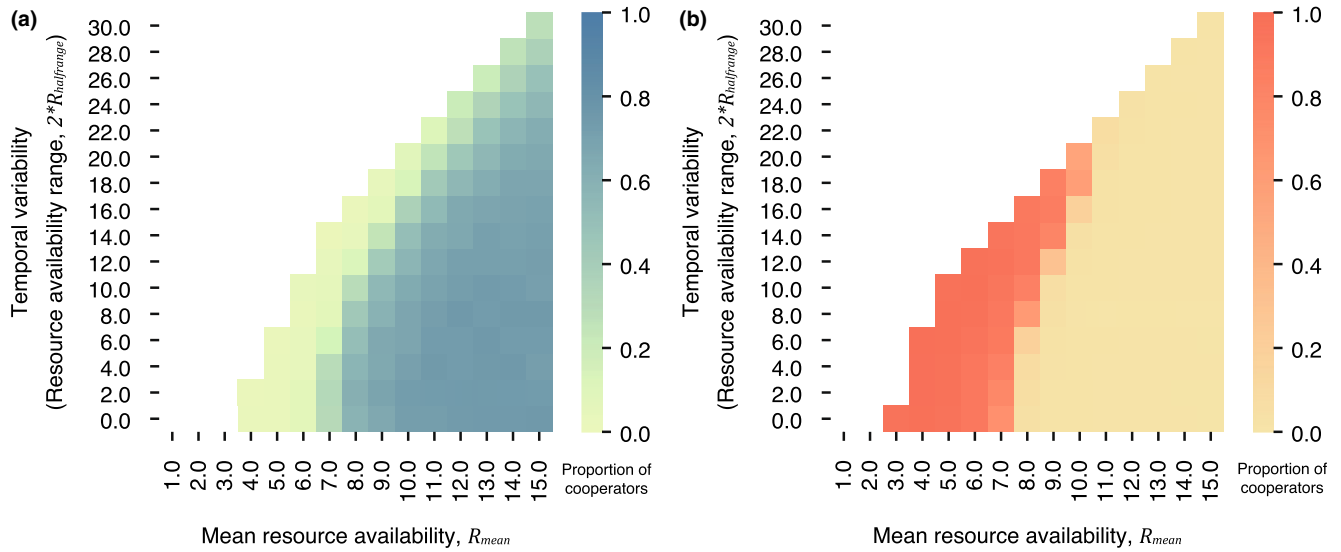
FIGURE 1 Model predictions of the relationships among grouping benefits, the mean and variability of resource availability, and the evolution of cooperation. Proportions of (a) resource defence (RD) cooperators and (b) collective action(CA) cooperators in each population in relation to mean resource availability. Each grid of the heat map is an average of over 100 repeated simulations, and each simulation lasts 10,000 time steps. We calculated the proportion of cooperators (i.e., individuals with non-zero degrees of cooperation) at the end of the simulations. Descriptions for resource availability in the simulation model are provided in the Methods.
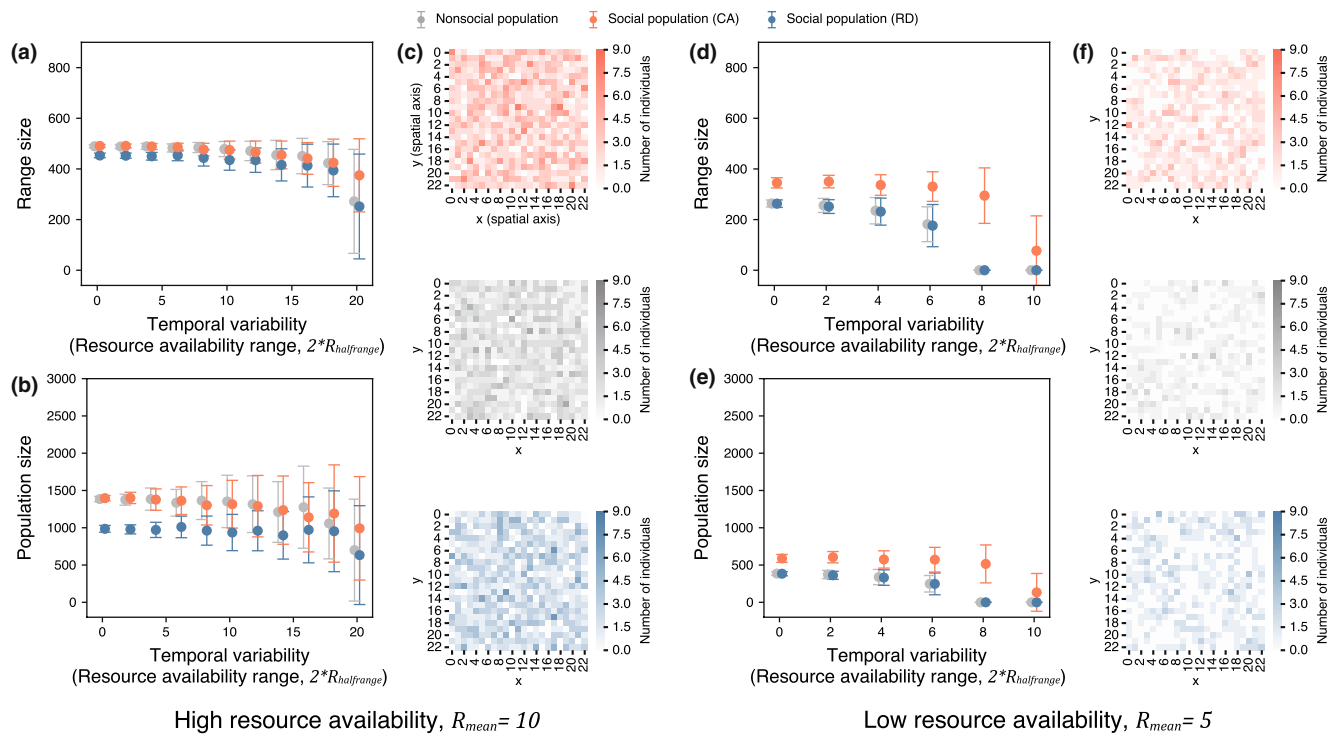

FIGURE 2 Model predictions about the relationships among grouping benefits, the mean and variability of resource availability, and the ecological consequences of cooperation. Comparisons of (a) range size, (b) species abundance, and (c) the spatial distribution of individuals of social populations that form because of collective action (CA) benefits (orange), social populations that form because of resource defence (RD) benefits (blue), and non-social populations (grey) in relation to the temporal variability in benign environments with high resource availability. (d) Range size, (e) species abundance, and (f) the spatial distribution of individuals of social populations in harsh environments with low resource availability. Points represent means, and error bars represent standard deviations. The colour darkness of heat maps indicates the number of individuals occupying a patch. All data are collected in the same way as in Figure 1.

range sizes and abundances than non-cooperators in harsh environments (Figure 2d–f). Fluctuating environmental conditions generally lead to a reduction in the range size (Figure 2d) and abundance (Figure 2e,f)

of both cooperators and non-cooperators in harsh environments with low resource availability. However, the reductions in range size (Figure 2d) and abundance (Figure 2e,f) of CA cooperators are relatively

small, except in extremely fluctuating environments. In contrast, the range sizes and abundances of CA co-operators are comparable to those of non-cooperators when mean resource availability is high (Figure 2a–c). Nevertheless, RD cooperators have smaller or similar range sizes (Figure 2a) and abundances (Figure 2b,c) to non-cooperators because most individuals defend high-quality patches (i.e., high resource availability; larger R_{mean} in Figure 1a). Interestingly, our model makes the same predictions for populations in both harsh and fluctuating environments, as well as similar predictions for those in both benign and stable environments, suggesting that the effect of highly fluctuating environments on the evolution of cooperative breeding behaviour is equivalent to the effect of harsh mean environmental conditions.

Comparative tests of ecological dominance in avian cooperative breeders

To comparatively test the set of predictions of our model (summarized in Table S5), together with previous work showing that the ecological drivers of cooperative breeding behaviour in birds may be different in different clades (Cockburn, 2020; Lin et al., 2019; Shen et al., 2017), we first examined how environmental factors affect the evolution of cooperatively and non-cooperatively breeding species separately in each avian clade (those showing either an association between cooperative breeding behaviour and environmental harshness/fluctuation, an association between cooperative breeding behaviour and environmental benignness/stability, or no association between cooperative breeding behaviour and environmental quality), and then compared species range sizes and abundances between cooperative and non-cooperative breeders in just the clades that showed an association between cooperative breeding behaviour and environmental quality. Although cooperative breeding behaviour is unrelated to environmental quality in 22 clades containing 2341 species (including 236 cooperative breeders), cooperatively breeding species tend to occur in harsh and fluctuating environments in 15 clades containing 2426 total species (including 306 cooperative breeders), but in benign and stable environments in 15 clades containing 1786 total species (including 169 cooperative breeders) (Table S4). Thus, as has been argued previously for birds (Lin et al., 2019), cooperative breeding behaviour varies greatly across the avian tree of life and appears to have evolved for different reasons in different groups of birds: 30% of clades show an association between cooperative breeding behaviour and environmental harshness/fluctuation (indicating that groups are likely to form because of CA benefits), 30% show an association between cooperative breeding behaviour and environmental benignness/stability (indicating that groups are likely to form because of RD benefits), and

40% show no association between cooperative breeding behaviour and environmental quality.

Next, we explicitly tested our simulation model predictions about the ecological and demographic consequences of sociality by comparing species range sizes and abundances in cooperative and non-cooperative breeders separately in clades that showed an association between cooperative breeding and environmental quality. In clades where cooperative breeding is associated with environmental benignness/stability (Table S6a), cooperative and non-cooperative breeders have similar range sizes (Figure 3a and Table S6b) and abundances (Table S6c). However, in clades where cooperation is associated with environmental harshness/fluctuation (Table S7a), cooperatively breeding species tend to have marginally larger range sizes than non-cooperative species (Figure 3b and Table S7b) and species with larger range sizes have greater abundances (Table S7c). Both of these results are consistent with the predictions of our simulation model. CA cooperators are more likely to evolve in harsh/fluctuating environments, and thus, those cooperatively breeding species occurring in such environments are more likely to have larger species range sizes and abundances than non-cooperative species. In contrast, RD cooperators are more likely to evolve in benign/stable environments, and thus, those cooperatively breeding species occurring in such environments are more likely to have similar species range sizes and abundances to non-cooperative species.

Although the results of our clade-level analysis were consistent with the key predictions of our simulation model, they excluded the 40% of avian species in clades that did not show an association between cooperative breeding behaviour and environmental quality. Therefore, to further test our model predictions using the complete dataset, we combined all of the avian clades into a single analysis (52 clades, including 6553 species). As has been shown previously for birds (Cornwallis et al., 2017; Jetz & Rubenstein, 2011; Rubenstein & Lovette, 2007), we found that both high environmental variability (high among-year variation in precipitation) and harsh mean environmental conditions (low mean annual precipitation) best explain the evolution of cooperative breeding behaviour (Table S8a). However, we went a step further than previous analyses and also show that cooperatively breeding species, which are more likely to occur in harsh and fluctuating environments, have significantly larger range sizes (Figure 3c and Table S8b) and marginally larger species abundances than non-cooperatively breeding species (Table S8c), as predicted by our model and consistent with the clade-level analysis.

Finally, to infer causal relationships among climate, cooperative breeding behaviour, and demography, we performed phylogenetic path analysis for both the clade-level and combined analyses. For clades in which cooperative breeders are more likely to occur in benign and stable environments, cooperation does not influence
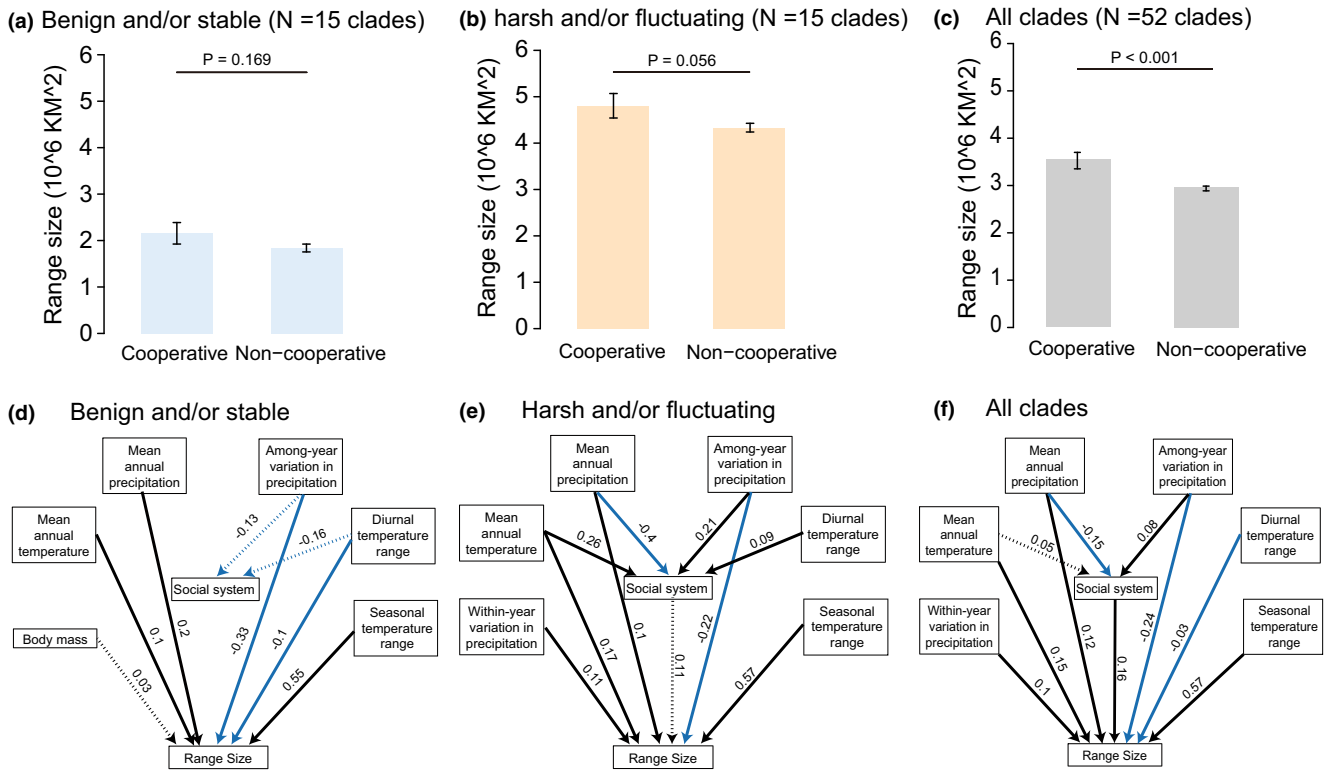
FIGURE 3 Relationships among environmental factors, social system, and range size. Comparison of geographic range sizes of cooperatively and non-cooperatively breeding species in (a) benign and/or stable environments ($N=15$ clades), (b) harsh and/or fluctuating environments ($N=15$ clades), and (c) in all clades in all environments, including those that did not show relationships between cooperative breeding behaviour and environmental quality ($N=52$ clades). Causal relationships among environmental factors, cooperative breeding, and range size in clades that cooperate in (d) benign and/or stable environments, (e) harsh and/or fluctuating environments, and (f) in all clades of cooperatively breeding birds in all environments. Arrows indicate direct effects, and colours represent direction (black: positive; blue: negative), with solid lines signifying significant causal relationships and dash lines signifying marginally significant causal relationships. Numbers represent standardized regression coefficients.
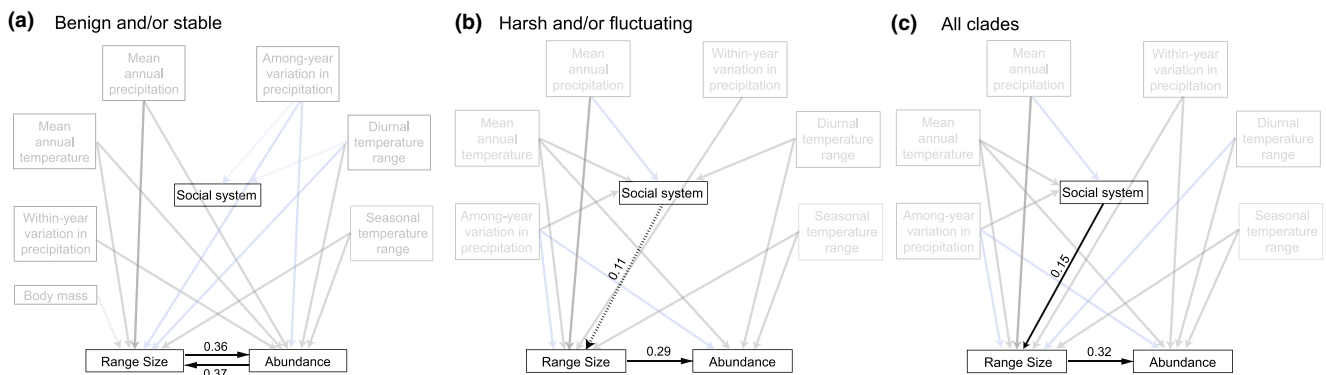

FIGURE 4 Causal relationships among social system, range size, and species abundance for (a) cooperatively breeding species that occur in benign and/or stable environments, (b) cooperatively breeding species that occur in harsh and/or fluctuating environments, and (c) all clades of cooperatively breeding birds. Arrows indicate direct effects, and colours represent direction (black: positive; blue: negative; grey: relationships that have been described in Figure 3), with solid lines signifying significant causal relationships and dash lines signifying marginally significant causal relationships. Numbers represent standardized regression coefficients. Since 424 species did not have species abundance information, we performed the same phylogenetic path analysis using this subset of the data ($N=6129$ species) that includes both species range size and abundance. The faded text and lines in the figure represent similar relationships to those presented in Figure 3, so we have faded them to improve the readability of this figure.

range size (Figure 3d and Table S9a), but species with larger ranges still have greater abundances (Figure 4a and Table S9b). However, for clades in which cooperative

breeders are more likely to occur in harsh and fluctuating environments, cooperative species have marginally larger range sizes (Figure 3e and Table S10a) and greater

abundances than non-cooperative species (Figure 4b and Table S10b). In the combined analysis of all clades, we similarly found that cooperative breeding behaviour is more likely to occur in harsh and fluctuating environments, and that cooperative species in these environments have larger range sizes (Figure 3f and Table S11a) and greater abundances than non-cooperative species (Figure 4c and Table S11b).

Considering all of these comparative analyses together indicates that cooperation appears to enable social species to outcompete non-social species to achieve greater abundances in environments where resource availability is low and variability high, a result consistent with the key prediction of our simulation model. In contrast, species that cooperate in benign and stable environments do not have greater abundances than non-cooperative species in those same environments, a result that is also consistent with the prediction from our theoretical model. In other words, cooperative breeding behaviour does not affect species range size or abundance in benign and/or stable environments, only in harsh and/or fluctuating environments. Thus, our comparative analyses suggest that cooperation appears to be a consequence—rather than a cause—of high intraspecific competition when species are abundant.

Vulnerability of social species to climate change

Given our finding that cooperation enables social species to outcompete non-social species and achieve greater abundance in environments where resource availability is low and fluctuates, we returned to our simulation model to investigate the possible effects of climate change (e.g., an increase in environmental fluctuation) on populations of CA cooperators, RD cooperators, and non-cooperators. Our model compares CA benefit species (populations containing both CA cooperators and non-cooperators), RD benefit species (populations containing both RD cooperators and non-cooperators), and non-social species (populations consisting entirely of non-cooperators). We found that in an originally harsh environment with low resource availability, CA cooperators are more resilient when climate change causes a decrease in the average availability of resources (Figure 5a–f). Therefore, the proportion of CA cooperators increases as the environment becomes increasingly harsh (Figure 5b,e), and CA cooperators maintain a relatively higher abundance compared to RD cooperators and non-cooperators (Figure 5a,d). In contrast, RD cooperators persist at a lower proportion in the population when the average environmental conditions deteriorate (Figure 5c,f,i,l), but environmental change has only a minimal or negative impact on the population abundance of RD cooperators compared to that of non-cooperators (Figure 5a,d,g,j). We also find that the effect of greater environmental fluctuations on both

the population abundance and the proportion of cooperators in the population is similar to that of reduced average resource availability (Figure S3). Thus, species that cooperate in harsh and/or fluctuating environments will be less vulnerable to climate change than both non-social species and those that cooperate in benign and/or stable environments.

DISCUSSION

To more directly test the paradox of environmental quality and sociality, we combined simulation modelling and phylogenetic comparative analysis to examine the ecological and demographic consequences of sociality (summarized in Table S5). Our model showed that CA cooperators living in harsh and/or fluctuating environments have larger range sizes and species abundances than non-cooperators in those environments, but that RD cooperators and non-cooperators living in stable and/or benign environments have similar range sizes and species abundances. Results from our comparative analyses were consistent with the model predictions, which help explain the paradox of why similar forms of social organization occur under such seemingly disparate ecological circumstances (Emlen, 1982; Shen et al., 2017). Yet, previous studies have argued that the influence of ecology on social evolution is not as easily quantified across species as kinship, making it difficult to develop a general understanding of how ecology influences on social evolution (Korb & Heinze, 2008; West et al., 2021). The obvious challenge is that a species often faces various types of environmental pressures (i.e., CA and RD benefits can occur in the same species). Thus, although environmental factors have been consistently recognized as key causes of social evolution, surprisingly, the specific environmental factors—agents of selection—influencing the evolution of cooperative breeding behaviour have only been well-studied in a few empirical studies (Shen et al., 2017; Wcislo & Tierney, 2009).

The dual-benefits framework provides a series of predictions that allow us to conduct broad-scale comparative studies to understand the ecological causes and consequences of cooperative breeding behaviour. Our analysis of the global distribution of avian species suggests that different taxa form cooperatively breeding groups for different reasons and in environments of contrasting quality. Among all birds, we found that species tend to cooperate in harsh environments with low mean annual precipitation and fluctuating environments with high among-year variation in precipitation, as has been shown previously for birds (Cornwallis et al., 2017; Jetz & Rubenstein, 2011; Rubenstein & Lovette, 2007). However, at the clade level, we found that similar numbers of clades containing roughly equal numbers of species cooperate in harsh and/or fluctuating environments and in benign and/or stable environments. We interpret these results to
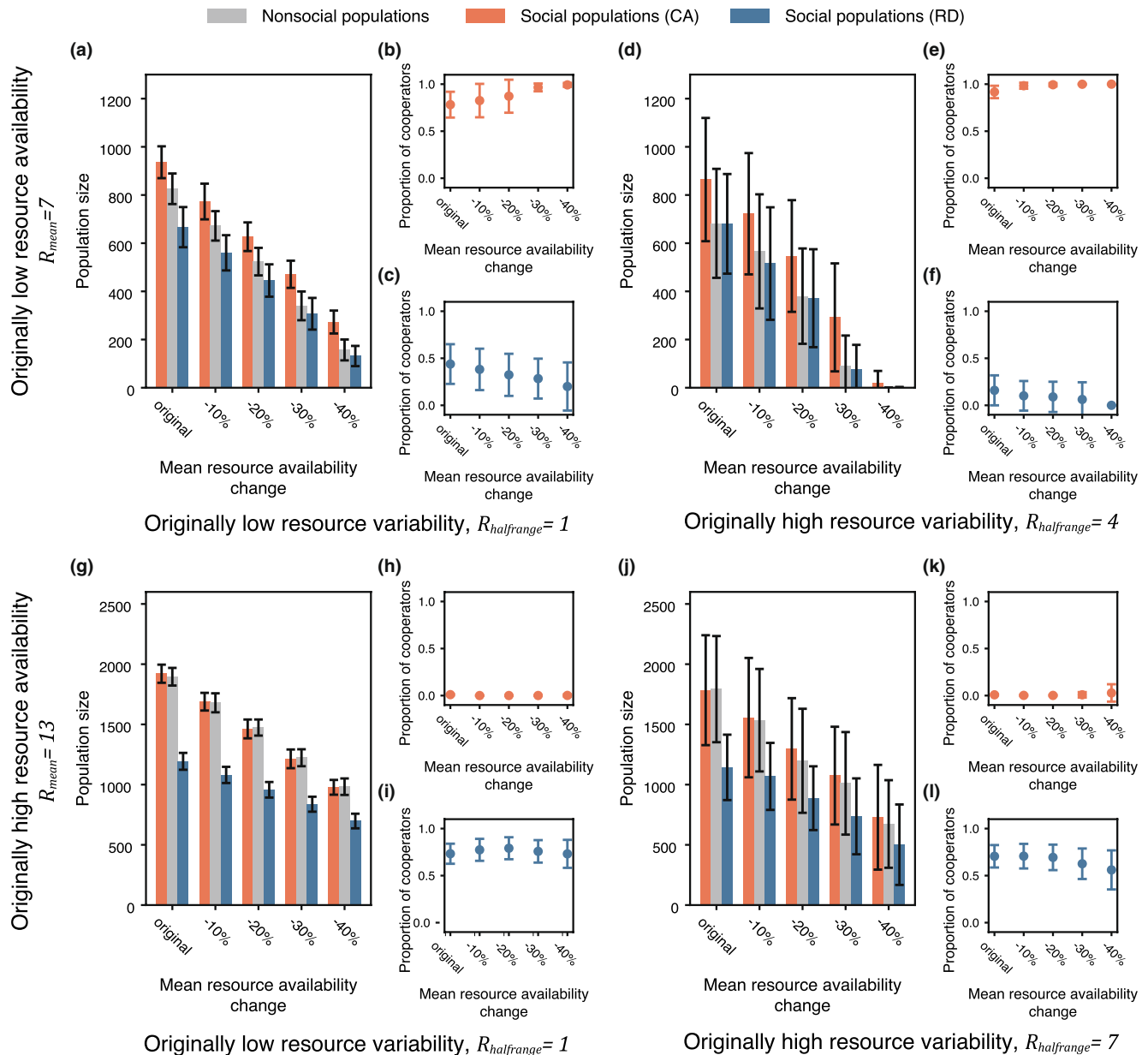
FIGURE 5 Model predictions of the effects of decreasing mean resource availability due to climate change. Comparison of (a) species abundance, (b) proportion of collective action (CA) cooperators, and (c) proportion of resource defence (RD) cooperators in an environment originally with low mean resource availability and small fluctuations in resources. Comparison of (d) species abundance, (e) proportion of CA cooperators, and (f) proportion of RD cooperators in an environment originally with low mean resource availability and large fluctuations in resources. Comparison of (g) species abundance, (h) proportion of CA cooperators, and (i) proportion of RD cooperators in an environment originally with high mean resource availability and small fluctuations in resources. Finally, a comparison of (j) species abundance, (k) proportion of CA cooperators, and (l) proportion of RD cooperators in an environment originally with high mean resource availability and large fluctuations in resources.

mean that although there is a general trend for cooperative breeding behaviour to evolve in harsh and/or unpredictable environments, birds appear to cooperate in these contrasting environments for different reasons, as argued by the paradox of environmental quality and sociality (Lin et al., 2019; Shen et al., 2017). Importantly, without performing clade-level analyses as we did here, researchers are likely to overlook the effects of benign/stable environments on the evolution of cooperative breeding behaviour.

Our results are consistent with the idea that cooperative breeding behaviour should be considered as an umbrella category, and care should be taken to differentiate between clades that form cooperatively breeding groups for different ecological reasons when conducting large-scale comparative studies (Shen et al., 2017). In addition, there are many clades of birds for which we were unable to find a relationship between environmental quality and cooperative breeding behaviour, either because CA and RD benefits

may both play a part in these lineages, or other factors may influence the propensity to cooperate. Therefore, we believe that future studies that examine the effects of environmental and social factors on cooperative breeding behaviour at the clade level—rather than just lumping all the data together—will be fruitful. Equally important, although CA and RD benefits are likely to act together in the same species, we believe that in most species one particular type of benefit will be more important for influencing the evolution of cooperative breeding behaviour. For example, while alloparents typically feed offspring and help increase the overall provisioning rate (a type of a CA benefit) (Hatchwell, 1999), a lack of outside breeding vacancies often favours offspring remaining on the natal territory (a type of RD benefit) and is therefore likely to be the primary ecological cause of cooperative breeding in these species (Emlen, 1982, 1991). According to the dual-benefits framework, we can understand which CA or RD benefits play the most important role in shaping the cooperatively breeding behaviour of species (or population) through observations (e.g., the relationship between group size and per capita productivity) or experimental manipulations (e.g., alteration of reproductive vacancies or population density; see table 1 in Shen et al., 2017) (Liu et al., 2020; Sun et al., 2014). Ultimately, determining the influence of CA or RD benefits on the evolution of cooperative breeding behaviour at the species level will be key to our understanding of environmental influences on the evolution of sociality (Shen & Rubenstein, 2019).

It is worth noting that our simulation model generates similar effects of high environmental fluctuation and poor mean environmental conditions on the evolution of cooperative behaviour, a result that is likely to occur because environments with high climatic fluctuations are, by definition, bound to include periods of both low and high environmental quality. Thus, in environments with greater environmental fluctuations, there is a stronger selection for social group formation during harsh periods with small population sizes than during benign periods with relatively large population sizes. Most studies examining the effects of population size fluctuations on the strength of selection have focused on the effects of genetic drift in small populations (Carson, 1990; Lande, 1976), or have examined how environmental fluctuations affect changes in gene frequency across genotypes at a fixed population size, thus focusing on reductions in fitness variance (Slatkin, 1974; Starrfelt & Kokko, 2012). However, based on our model that assumes population size varies with environmental fitness (a biologically realistic assumption for most species), strategies to cope with harsh environments may be key to understanding how organisms adapt to fluctuating environments.

Finally, although some of the most ecologically successful species on Earth form cooperative societies, it is often assumed that cooperation enables their 'social conquest' (Wilson, 1987, 2012). Here, we provide a formal mathematical framework for understanding precisely how cooperation could lead to ecological dominance in some taxa but not in others. Our model results also suggest that species that cooperate in harsh and/or fluctuating environments (Firman et al., 2020; Jetz & Rubenstein, 2011; Kocher et al., 2014; La Richelière et al., 2022; Lukas & Clutton-Brock, 2017; Martin et al., 2020; Rubenstein & Lovette, 2007; Sheehan et al., 2015) will be less vulnerable to climate change than both non-social species and those that cooperate against intraspecific competitors in benign and/or stable environments (Borger et al., 2023; Choe & Crespi, 1997; Cornwallis et al., 2017; Costa, 2006; Gonzalez et al., 2013; Solomon & French, 1997). This framework linking the ecological causes and consequences of cooperation can thus be used to explore a range of topics relevant to the changing world in which we now find ourselves, including the fluctuation and resilience of species abundances of social and non-social species over evolutionary and ecological timescales, as well as range size shifts in relation to changes in social behaviour under different climate change scenarios. Under intensifying anthropogenic climate change (Bonfils et al., 2020; Paik et al., 2020; Zhang et al., 2013), now more than ever, we urgently need to understand how social behaviours and environmental conditions synergistically influence the ecological success—or failure—of animals.

AUTHOR CONTRIBUTIONS
S.-F.S. conceived the idea of the paper. Y.-Y. C. and S.-F.S. constructed the simulation model. Y.-H. L., S.-F. S., and D.D.R. analysed the empirical data. S.-F. S., Y.-Y. C, Y.-H. L., M.L., M.L., and D.D.R. designed the study and wrote the manuscript.

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DATA AVAILABILITY STATEMENT
All code and data are available on GitHub (https://github.com/mingpapilio/Codes_Social_Conqeust) and archived on Zenodo (doi.org/10.5281/zenodo.7820320).

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