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Different axes of environmental variation explain the presence versus extent of cooperative nest founding associations in *Polistes* paper wasps

Michael J Sheehan^{1-3*}, Carlos A Botero^{4,5}, Tory A Hendry^{3,6}, Brian E Sedio^{3,7}, Jennifer M. Jandt⁸, Susan Weiner⁹, Amy L Toth⁸, Elizabeth A Tibbetts³

1. Integrative Biology and Museum of Vertebrate Zoology, UC Berkeley, Berkeley, CA 94720
2. Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721
3. Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109
4. Department of Biology, Washington University in Saint Louis, St. Louis, MO 63130
5. Initiative for Biological Complexity, North Carolina State University, Raleigh, NC 27695
6. Environmental Science, Policy, and Management, UC Berkeley, Berkeley, CA 94720
7. Smithsonian Tropical Research Institute, Balboa, Ancon, Panamá
8. Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011
9. Biological, Chemical and Physical Sciences, Roosevelt University, Chicago, IL 60605

Author contributions:

MJS conceived and designed the study; MJS constructed the database of cooperative nesting; TAH performed phylogenetic analysis; MJS, JMJ, SW, ALT and EAT contributed field data on wasp nesting behavior; MJS, CAB and BES analyzed the nesting data in relation to climate; MJS wrote the paper with input from other authors.

Author emails:

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30 MJS – ms3246@cornell.edu; CAB – cbotero@wustl.edu; TAH – th572@cornell.edu; BES –
31 briansedio@gmail.com; JMJ – jandt@iastate.edu; SW – sweiner02@roosevelt.edu; ALT –
32 amytoth@iastate.edu; EAT – tibbetts@umich.edu

33

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44 *Corresponding Author Information:

45 Michael J Sheehan

46 Department of Neurobiology and Behavior

47 Cornell University

48 Mudd Hall

49 215 Tower Road

50 Ithaca, NY 14853

51 ms3246@cornell.edu

52 tel. 607 254 4302

53 fax 607 254 1303

54

55 **Abstract**

56 Ecological constraints on independent breeding are recognized as major drivers of cooperative breeding
57 across diverse lineages. How the prevalence and degree of cooperative breeding relates to ecological
58 variation remains unresolved. Using a large dataset on cooperative nesting in *Polistes* wasps we
59 demonstrate that different aspects of cooperative breeding are likely to be driven by different aspects of
60 climate. Whether or not a species forms cooperative groups is associated with greater short-term
61 temperature fluctuations. In contrast, the number of cooperative foundresses increases in more benign

62 environments with warmer, wetter conditions. The same dataset reveals that intraspecific responses to
63 climate variation do not mirror genus-wide trends and instead are highly heterogeneous among species.
64 Collectively these data suggest that the ecological drivers that lead to the origin or loss of cooperation
65 are different from those that influence the extent of its expression within populations.

66 INTRODUCTION

67 Although the importance of relatedness in shaping patterns of cooperation has recently been
68 debated (Nowak *et al.* 2010; Liao *et al.* 2015), there is broad theoretical and empirical consensus that
69 ecological constraints on independent breeding can favor cooperation (Brockmann 1997; Hatchwell &
70 Komdeur 2000; Nowak *et al.* 2010; Jetz & Rubenstein 2011; Purcell 2011). Comparative and field studies
71 have documented diverse ecological constraints on independent breeding including habitat saturation
72 (Komdeur 1992), harsh foraging conditions (Faulkes *et al.* 1997), predation (Strassmann *et al.* 1988), and
73 parasitism (Feeney *et al.* 2013). Despite several early comparative studies comparing cooperation and
74 environmental factors (Reeve 1991; Faulkes *et al.* 1997; Arnold & Owens 1999), the nature of the
75 environmental constraints that favor cooperative breeding and the extent of their influence across
76 lineages remain largely unresolved.

77 There has been renewed interest in recent years in using phylogenetic comparative methods
78 and global climate datasets to identify aspects of environmental variation that are associated with
79 cooperative breeding (e.g. Jetz & Rubenstein 2011; Gonzalez *et al.* 2013). However, two major critiques
80 of comparative studies of cooperative breeding have emerged. First, comparative analyses of
81 cooperative breeding tend to rely on binary classifications of social systems, while ignoring the variation
82 in the intensity of cooperation among taxa (Ligon & Burt 2004; Cockburn 2013). Second,
83 macroevolutionary patterns in some groups contradict findings from many population-level studies,
84 complicating the interpretation of results (Cockburn & Russell 2011; Cockburn 2013). At the heart of
85 both critiques is our ability to distinguish which environmental factors are associated with the presence
86 versus extent of cooperative breeding. Categorical classification systems may reveal which
87 environmental factors are associated with the presence of cooperative strategies, but only data
88 comparing the degree of cooperation across taxa can provide insights into what factors shape the extent
89 of cooperation among lineages.

90 There are at least two alternative views on the role that environmental factors play on the
91 occurrence and intensity of cooperative breeding. One view argues for cooperation being considered as
92 a continuum (Sherman *et al.* 1995; Avilés & Harwood 2012). Under such a scenario, elevated values of a
93 particular environmental feature might be associated with cooperation and the most cooperative

94 species are expected to occupy ranges with the most extreme environmental values. Changes in
95 cooperation levels in this scenario are also expected to be associated with the tightening or relaxation of
96 environmental constraints. Under such a model, cooperative breeding is expected to evolve as a
97 continuum, such that a shift from singular breeding to breeding in groups of two should not be
98 fundamentally different from a shift going from two to three and even further increases thereafter
99 (Sherman *et al.* 1995). If cooperation is a continuum, we may also expect the environmental features
100 that shape macroevolutionary patterns to explain intraspecific patterns of variation in cooperative
101 breeding as well (Cockburn 2013).

102 Alternatively, several authors have argued that non-cooperative and cooperative breeding
103 systems represent shifts between qualitatively distinct social regimes (Brown 1987; Wcislo & Tierney
104 2009), and that the factors influencing whether or not a species cooperates are likely to differ from
105 those that shape the proportion of the population that pursue a helping strategy (West *et al.* 2007). This
106 hypothesis predicts that the presence of cooperation should be favored on one side of an environmental
107 threshold and that the rates of helping among cooperative species are not necessarily driven by the
108 same environmental factors.

109 Whether variation in cooperative breeding among species is best explained by a continuous or a
110 threshold model has important implications for understanding the evolution of cooperation. The major
111 challenge in distinguishing between these alternatives has been a lack of quantitative estimates of
112 variation in rates of cooperation across species as the few data available on social systems tend to be
113 coarse-grained, and potentially arbitrarily categorized (Cockburn 2013). High-resolution datasets that
114 provide quantitative estimates of the extent of cooperation across species are sorely needed.

115 To test the relationship between climate and cooperative breeding in *Polistes* paper wasps, a
116 model genus in sociobiology (Jandt *et al.* 2014), we constructed a dataset of nesting behavior for over
117 30,000 wasps from 51 species (Table S1). Paper wasp colonies are initiated by adult females, known as
118 foundresses or queens (Reeve 1991). In temperate habitats, colony foundation occurs in the spring,
119 after adult wasps emerge from winter diapause. Colony foundation is more asynchronous in the tropics
120 (Reeve 1991). While *Polistes* wasps are eusocial (i.e., there are queens and workers), there is marked
121 variation across species in the extent to which new nests are founded by solitary foundresses (non-
122 cooperative) or associations of multiple foundresses (cooperative) (Fig 1). Thus, species appear to differ
123 in the extent to which foundresses seek to join established nests, accept potential cooperators or some
124 combination of those two. Within cooperative associations, foundresses engage in dominance contests
125 with the most dominant foundress assuming the role of the primary egg layer while lower ranking

126 individuals engage in more foraging and less reproduction (Jandt *et al.* 2014). Thus, *Polistes* foundress
127 associations present a classic example of cooperative breeding with skewed reproduction among nest
128 members (Reeve *et al.* 2000; Seppa *et al.* 2002; Leadbeater *et al.* 2011).

129 In this paper we set out to answer three fundamental questions regarding the relationship
130 between climate and cooperative nesting in *Polistes*. First, what aspects of climate are associated with
131 the presence or absence of cooperative nesting? Second, are these same climatic features associated
132 with the extent of cooperation among species? Third, to what extent do climatically driven patterns of
133 variation in cooperative nesting within species match patterns of variation among species within a
134 genus?

135

136 **METHODS**

137 **Data on cooperative behavior**

138 We collected information on cooperative behavior from published data on wasp nesting, our
139 own unpublished field records, and data from online natural history databases including Bugguide
140 (<http://bugguide.net>) the Atlas of Australia (<http://www.ala.org.au>) and iNaturalist
141 (www.inaturalist.org) of foundress associations in wasps. The uncovered nests of *Polistes* wasps allow
142 for the easy determination of the stage of colony progression, even from photographs. As a general rule,
143 published accounts of wasp nests (and our own field data) report counts made during the early morning
144 or late evening, when all foundresses are present and quantifying the number of wasps on a nest is
145 straightforward. However, because the number of foundresses observed at a nest can fluctuate over the
146 course of colony development and throughout the day, the numbers reported here should be seen as
147 estimates rather than the 'true' numbers of foundresses per species (West Eberhard 1969). Because we
148 were interested in the number of foundresses that associate in the formation of colonies, we included
149 observations of colonies during the pre-emergence phase of the colony cycle during which only
150 foundresses are present (West Eberhard 1969; Reeve 1991). If observations of the pre-emergence phase
151 nests were not available we used records of the number of foundresses present on nests as determined
152 by dissection of ovarian development or the number of foundresses that contributed to the brood via
153 genetic analysis. Indirect measures of foundress number (i.e., photographs and ovarian counts)
154 constituted only 1.17% (101/8613) of the nests observed in *Polistes* in our dataset (Supplemental text).

155 Analyzing the present dataset requires a balance between including data on more species and
156 stringent filtering for data quality. We strike a balance between inclusivity and data quality by
157 conducting two separate analyses. In the first analysis we use all the data available and report aggregate

158 values for each species (hereafter referred to as the 'aggregate' analysis). The aggregate dataset has the
159 benefit of including as many species as possible, though estimates of the size of cooperative nesting
160 groups are based on small numbers of foundresses in some cases (Table S1). In the second analysis, we
161 stringently filtered the data by only considering well-sampled localities for each species (hereafter
162 referred to as the 'locality' analysis). The locality analysis includes fewer species and phylogenetic
163 contrasts, but the continuous estimates are robust as they are based on the behavior of many
164 foundresses from the same location (Supplemental Text).

165 In the aggregate dataset, we made use of all available data for each species to estimate rates of
166 cooperation, aggregating nest observation data from all sources (Table S1). We use the aggregate
167 dataset (Table S1) for three analyses: (1) the distribution of rates of cooperation across species, (2)
168 ancestral state reconstructions, (3) comparative analyses of the relationship between cooperation and
169 climate. In addition to continuous estimates of the average size of cooperative foundress associations,
170 we also categorized species as either 'cooperative' or 'non-cooperative' based on categorizations used
171 in the literature. We note that the continuous estimates of cooperation are in agreement with
172 traditional descriptive categories.

173 In the locality dataset (Table S2), we made an attempt to define localities as narrowly as
174 possible, to the level of municipality, using the verbal descriptions or specific place names of sampling in
175 each study. Although some variation in climate can be expected within large metropolitan areas or
176 municipalities, it is unlikely that characterizing the climate variables of such localities from a single
177 georeference will bias our results because variation in precipitation and temperature at a local scale is
178 minimal in comparison to the regional differences observed between distant localities from the same or
179 different species. We were conservative in our locality dataset and only considered localities where the
180 nesting behavior of at least 20 foundresses from a given species had been observed (N = 129 localities
181 across 28 species, range 1-22 localities per species, Table S2).

182 For both the aggregate and locality datasets, we calculated the mean number of foundresses as
183 well as the percentage of foundresses in a subordinate role, measures that have been previously used to
184 compare rates of cooperative nesting in *Polistes* (Hughes *et al.* 1993). We chose to measure cooperative
185 nesting behavior as mean number of foundresses and percent subordinates because it was possible to
186 calculate these statistics for the largest number of records in our dataset. We considered the number of
187 foundresses observed in excess of the number of nests as subordinate foundresses because, by
188 extension, such foundresses could not have nested solitarily and because each nest has a single most
189 dominant female. For example, if 150 foundresses were observed on a total of 100 nests, then the 50

190 excess foundresses were considered subordinate, meaning that 33% of the foundresses observed in the
191 population were subordinate. These measures are related to each other, though not in a linear manner
192 (Fig S1). In particular, calculating percentage of foundresses in a subordinate role places greater
193 emphasis on variation between means of 1 and 2 foundresses (i.e., 0-50%) than between higher rates of
194 cooperation, e.g. an increase from a mean of 2-3 foundresses corresponds to 50-66.67%. Overall, we
195 believe that these measures reasonably capture variation in the extent of cooperation across species as
196 they distinguish between species with nests of different foundress-association sizes.

197 It is important to emphasize that our measures deal with size of cooperative foundress
198 associations and are not measures of how reproduction is apportioned within groups. In general,
199 multiple foundress associations in *Polistes* wasps show evidence of reproductive skew among foundress,
200 though the extent of skew is highly variable even within populations (Reeve *et al.* 2000; Seppa *et al.*
201 2002). While dominant foundresses typically enjoy a disproportionate share of reproduction within
202 multiple foundress associations, they are not the sole breeders; subordinate reproduction is commonly
203 reported in *Polistes* (Reeve *et al.* 2000; Seppa *et al.* 2002). Regardless of the amount of skew, multiple
204 foundress associations are cooperative in the sense that foundresses provide care to offspring that are
205 not their own (West Eberhard 1969; Reeve 1991; Jandt *et al.* 2014).

206

207 **Phylogenetic reconstruction**

208 Phylogenetic reconstruction was performed on 71 taxa, 17 out-group species in the genera
209 *Apoica*, *Mischocyttarus*, *Polybia*, *Protopolybia* and *Ropalidia*, and 54 *Polistes* taxa, using sequences from
210 two mitochondrial loci. All sequence data was taken from GenBank (Table S3). A 563 base pair portion of
211 the 16S ribosomal RNA gene was used for all taxa except ten, *P. apachus*, *P. carnifex*, *P. biglumis*, *P.*
212 *olivaceus*, *P. erythrocephalus*, *P. satan*, *P. instabilis*, *P. versicolor*, *M. immarginatus*, *M. mexicanus*, and *R.*
213 *fasciata*, for which only 350 or fewer bases were available. Additionally, a 1234 base pair portion of the
214 cytochrome oxidase subunit I (COI) gene was used. For COI sequences 56 taxa had at least 75% shared
215 sequence length included, however, only 376-658 bases were available for 19 of the taxa. Sequences for
216 each gene were aligned separately using ClustalW (Thompson *et al.*, 1994) and manually adjusted for
217 accuracy. These alignments were then concatenated and used for Bayesian analyses in MRBAYES v3.1.2
218 (Huelsenbeck and Ronquist, 2001). Two runs of four parallel Markov chain Monte Carlo chains under the
219 GTR + I + Γ model were performed for 800,000 generations, sampling every 1000 generations, at which
220 point the standard deviation of split frequencies was effectively zero. From each analysis a 50% majority
221 rule consensus tree was produced from 1000 samples with a 25% burn-in of trees. Multiple polytomies

222 with low support were recovered in the analysis. However, the overall topology of the tree is very
223 similar to that resolved previously using morphological data (Pickett & Carpenter 2010), suggesting that
224 the low support values stem from a need for more informative sequence data rather than inaccurate
225 tree reconstruction. A full version of the phylogeny is shown in Fig S2.

226

227 **Ancestral State and Area Reconstruction**

228 We reconstructed the evolutionary history of cooperative nesting in *Polistes* using the
229 parsimony reconstruction model of continuous data in Mesquite v 2.75 (Maddison & Maddison 2001)
230 using the mean number of foundresses and percent of subordinate foundresses as a continuous
231 measures respectively. Additionally, we considered the evolution of cooperative breeding as a
232 categorical variable, using the likelihood reconstruction model for categorical data in Mesquite v 2.75.
233 We ran the analyses using the previously constructed Bayesian tree pruned to 47 species for which we
234 had data on social systems: 40 species of *Polistes* and 5 species of *Mischocyttarus*, 1 species of
235 *Belonogaster* and 1 species of *Ropalidia* as outgroups.

236 We reconstructed the evolution of geographic ranges in *Polistes* and its relatives using the
237 maximum likelihood dispersal-extinction-cladogenesis model as implemented in “Lagrange” (Ree &
238 Smith 2008). We employed a temporally unconstrained model in which dispersal probabilities between
239 regions were assumed to be symmetric.

240 The following six biogeographic regions were used in the analysis: a) Neotropics (South America,
241 Central America and the Caribbean), b) the Nearctic (North America); c) the Western Palearctic (Europe,
242 Central Asia, Middle East, and North Africa); d) the Eastern Palearctic (temperate East Asia); e) Indo-
243 Malaya and Oceania (South Asia, Peninsular and Insular Southeast Asia, New Guinea, and Australia); and
244 f) the Afrotropics (Sub-Saharan Africa). See the supplemental methods for further justification of the
245 choice of regions. We calculated a geographic reconstruction pertaining to one fully dichotomous
246 phylogeny randomly resolved from the multichotomous tree using the R package ‘picante’ (Fig S3,
247 Kembel *et al.* 2010).

248

249 **Climate analysis**

250 We used a total of 4103 georeferenced observations of species from museum specimens (GBIF:
251 <http://www.gbif.org>), field observations (Bugguide: <http://bugguide.net>; Atlas of Australia:
252 <http://www.ala.org.au>) and localities described in the published literature on each species (median
253 number of records = 58, range: 4 to 1108). For each record of each species we extracted 13 variables

254 capturing the mean, variance and predictability of temperature, precipitation and primary productivity
255 variables from Bioclim and the CRU-TS 3.1 Climate Database (Mitchell & Jones 2005, see Table S4 for
256 further information on the variables considered). Predictability of climate variables was measured as
257 Colwell's P (Colwell 1974), which takes into account both the contingency and constancy of climate
258 patterns between years. The aggregate species mean for each of the variables was calculated and a
259 principal component analysis performed on the 40 *Polistes* species used in the comparative analyses.
260 The first two principal components explained approximately 75% of the variation in the aggregate
261 dataset and can be interpreted as corresponding to variation in environmental harshness (PC1, 57% of
262 the variance) and short-term temperature fluctuation (PC2, 17% of the variance) (Supplemental text, Fig
263 S4a). For PC1, higher values are associated with lower mean temperatures and rainfall with lower values
264 associated with warmer, wetter conditions. High values of PC2 are associated with low differences
265 between the high and low temperatures within a month and lower values have higher amplitude short-
266 term temperature fluctuations. We ran an additional PCA analysis with the climate data limited to
267 georeference points used in our locality dataset (Table S2). The results of this analysis are similar to
268 those found for the aggregate dataset climate PCA (Fig S4b): the first two principal components explain
269 approximately 66% of the variation and correspond roughly to the same environmental features as
270 those captured in the aggregate species PCA. That is, environmental harshness or PC1 captured 47% of
271 the variance, and short-term temperature fluctuation or PC2 captured 20% of the variance. Indeed, the
272 loadings on PC1 for both the species-level and population-level datasets are nearly identical (linear
273 regression, $r^2 = 0.95$, $B = 1.01$, $P < 0.0001$) and the loadings on PC2 are very similar (linear regression, r^2
274 $= 0.71$, $B = 0.79$, $P = 0.0003$), reflecting the fact that both of these analyses ultimately have similarly
275 balanced global coverage. Loading of the variables on different PC axes can be found in Table S5.
276 Although the PC axes in both cases are not exact replicas, the high level of similarity allows for
277 reasonably direct comparisons between the inclusive aggregate and more stringently filtered locality
278 datasets (Fig S5).

279 Four temperate species - *P. dominula*, *P. exclamans*, *P. fuscatus*, and *P. metricus* - were sampled
280 at a sufficiently large and geographically disparate set of localities to allow us to investigate intraspecific
281 relationships between climate and cooperative nesting. Using subsets of the locality dataset for each
282 species, we modeled the mean number of foundresses observed in a given locality as a function of
283 environmental factors.

284

285 **Comparative Analyses**

286 We examined the relationships between the principal components of climate variation and our
287 different measures of cooperation. First, we examined both PC axes as predictors of cooperation coded
288 as a categorical variable (cooperative v. non-cooperative). Next, we considered both PC axes as
289 predictors of continuous measures of cooperative nesting (i.e., mean number of foundresses and the
290 percent of subordinate foundresses). We next examined the effects of both climate axes on continuous
291 variation in cooperation in a reduced dataset including only the cooperative species. Species were
292 categorized as either cooperative or non-cooperative based on traditional categorizations and
293 descriptions of the species in the literature. We examined the relationship between climate and
294 cooperative breeding with Bayesian phylogenetic mixed models using the package MCMCglmm in R
295 (Hadfield 2010) with flat non-informative priors, 600000 iterations, a burnin of 200000 and a thinning
296 interval of 100 iterations used in all analyses. Visual inspection of the MCMC chain demonstrated
297 convergence in all cases. Additionally, we analyzed our data using phylogenetic generalized least
298 squares analyses using the R package Caper (Orme *et al.* 2012) to ascertain their robustness to different
299 modeling procedures. For each analysis we pruned the overall phylogenetic tree (FigS2) to taxa for
300 which we had data. In the locality analysis, species observed at multiple localities were represented by a
301 polytomy with multiple tips.

302

303 RESULTS

304 Distribution and evolutionary history of cooperative breeding

305 The average number of foundresses observed on pre-emergence nests in *Polistes* species ranges
306 from 1 to 7.5, showing a positive skewed distribution (Fig 2A, skewness = 1.19). The percent of
307 subordinate foundresses varies from 0 to 87% across species and shows a strongly bimodal distribution.
308 (Fig 2B, Hartigan's dip test, $D = 0.098$, $P = 0.0004$, $N = 51$ species). Removing poorly sampled species (<
309 15 foundresses observed) does not alter this result (Hartigan's dip test, $D = 0.10$, $P = 0.0003$, $N = 40$
310 species). Notably, the species on either side of the break in the distribution (greater or less than 10%
311 subordinates) have historically been categorized as non-cooperative and cooperative, suggesting that
312 these categorical descriptors may capture a biologically relevant break in patterns of cooperative
313 nesting.

314 Ancestral state reconstruction indicates that cooperative nest founding has been evolutionarily
315 labile. There is broad agreement across reconstructions using mean number of foundresses, percent
316 subordinate foundresses, and categorical measures (Fig 2C, S6). Cooperative breeding has been lost
317 multiple independent times in *Polistes*, with increased rates of cooperation seen in some lineages (Figs

318 2C). At least three independent losses of cooperative nesting in *Polistes* involve species or clades that
319 have independently invaded eastern Asia (Fig 2C-D, S3). Additionally, species with the highest rates of
320 cooperation are found in the Neotropics (Fig 2D). The clustering of non-cooperative and highly
321 cooperative species in different geographic regions suggests that climatic factors may have played a role
322 in the evolution of cooperative nesting behavior in this genus.

323

324 **Climatic correlates of cooperative breeding across species**

325 Different aspects of climate variation are correlated with the formation versus the size of
326 cooperative foundress associations in *Polistes*. Table 1 shows the output for models of categorical and
327 continuous measures of cooperation with the first two PC axes, environmental harshness and short-
328 term temperature fluctuation as main effects. Categorical models using both the aggregate and locality
329 datasets show that non-cooperative species occur in regions with greater short-term temperature
330 stability (Fig 3). Conversely, cooperative nesting is associated with higher amplitude fluctuations in
331 temperature. Continuous models show that the size of cooperative nesting associations is inversely
332 related to environmental harshness, with higher rates of cooperative nesting occurring in more benign
333 regions, i.e. the tropics (Fig 3). Notably, environmental harshness is a better predictor of rates of
334 cooperation when non-cooperative species are excluded from both the aggregate and locality datasets
335 (Table 1). The overall pattern of results is equivalent whether we measure cooperation as the mean
336 number of foundresses (Table 1) or the percentage of subordinate foundresses (Supplemental text,
337 Table S6).

338 Categorical analyses are a better fit to the aggregate dataset whereas continuous analyses are a
339 better fit to the locality dataset. A model that considers short-term temperature fluctuation as the sole
340 predictor of categorical cooperation data is a substantially better fit in the aggregate (PGLS, $F_{2,38} = 25.63$,
341 $r^2 = 0.39$, $P < 0.0001$) compared to the locality dataset (PGLS, $F_{2,127} = 6.96$, $r^2 = 0.04$, $P = 0.009$). For the
342 continuous data, a model that considers solely environmental harshness as a predictor of extent of
343 cooperation in cooperative species within the locality dataset fits better (PGLS, $F_{2,84} = 34.55$, $r^2 = 0.28$, P
344 < 0.0001) than its equivalent model with the cooperative-only aggregate dataset (PGLS, $F_{2,24} = 4.57$, $r^2 =$
345 0.13 , $P = 0.021$).

346

347 **Climatic correlates of cooperation within species**

348 Global axes of climate variation that explain patterns of cooperative nesting across the genus
349 are relatively poor predictors of variation in cooperative nesting within individual species. In the genus-

350 wide analysis of the locality dataset environmental harshness correlates with variation in the extent of
351 cooperative nesting (Fig 3C). However, short-term temperature stability tends to better explain variation
352 in size of cooperative nesting associations within the four species examined here (Fig 4A-B, Table 2). In
353 both *P. dominula* and *P. exclamans*, short-term temperature stability tends to be negatively associated
354 with the mean number of foundresses. In contrast, in *P. fuscatus* short-term temperature stability tends
355 to be positively associated with cooperative nesting. Neither of the genus-wide climate PCs explained
356 variation in cooperative nesting in *P. metricus*. The same pattern of results is found when analyzing
357 variation in the percent subordinate foundresses for *P. exclamans*, *P. fuscatus* and *P. metricus* (Table 2).
358 For *P. dominula*, however, the percentage of subordinate foundresses is associated with environmental
359 harshness rather than short-term temperature stability. This difference arises because mean foundress
360 number and percent subordinate foundresses differentially emphasize variation among populations
361 showing high or low rates of cooperative nesting respectively (Fig S1).

362 Genus-wide PC axes are derived from a global dataset of localities, and although they are
363 relevant axes of climate variation at a global scale, they may not accurately reflect patterns of climatic
364 variation within the range of single species. For example, the environmental factors that explain broad
365 patterns of variation in cooperation between temperate and tropical zones or between rainforests and
366 deserts may be highly uninformative when it comes to the variation in cooperation observed within a
367 species that is only present in temperate deciduous forests. Thus, we conducted a second-set of
368 intraspecific analyses where we calculated climate PCs specific to the population datasets for each
369 species. As expected from the limited distributions of the focal species, species-specific climate PCs
370 differ considerably from genus wide PCs (Fig S7). Analyses of patterns of variation in cooperative nesting
371 relative to species-specific climate PCs reveals considerable heterogeneity among species (Table S7) – in
372 *P. dominula* cooperation is positively associated with warmer, predictable temperature regimes (Fig S8A,
373 $F_{1,17} = 10.78$, $r^2 = 0.35$, $P = 0.004$); in *P. fuscatus* cooperation is higher with more predictable precipitation
374 patterns (Fig S8B, $F_{1,18} = 6.60$, $r^2 = 0.23$, $P = 0.019$); in *P. metricus* cooperation is highest with less
375 predictable precipitation patterns (Fig S8C, $F_{1,20} = 7.27$, $r^2 = 0.23$, $P = 0.014$); in *P. exclamans* neither of
376 the first two principal components explain variation in cooperation rates (Fig S8D).

377 378 **DISCUSSION**

379 Our results demonstrate that the axes of global environmental variation associated with shifts
380 between cooperative and singular nesting are different from those that explain variation in the size of
381 cooperative nesting associations across species. Put simply, the environmental pressures associated

382 with increasing from one to two foundresses do not explain the increase from two to three foundresses.
383 We find the same pattern of results using both a comprehensive, though noisy dataset of aggregate
384 measures for all species and a stringently filtered dataset based solely on well-sampled localities,
385 demonstrating that our findings are robust. Our results therefore suggest that being willing or able to
386 form any cooperative nesting association is a fundamental step in social evolution. Notably, the bimodal
387 distribution of the rates of cooperation across species is consistent with a model where non-cooperative
388 and cooperative breeding represent two distinct states. In other realms of ecological research, bimodal
389 distributions have been interpreted to be driven by regime shifts in other systems as well (Scheffer *et al.*
390 2014) or to be indicative of bistability of ecosystems (Staver *et al.* 2011). Specifically, the bimodal
391 distribution in rates of cooperative nesting observed in *Polistes* wasps appear to be the result of
392 opposing selection pressures favoring either cooperative or non-cooperative strategies at either side of
393 an environmental threshold.

394 The loss of cooperative nesting is associated with reduced temperature fluctuations over short
395 time scales. Comparative studies of cooperative breeding in vertebrates have focused on the role of
396 year-to-year environmental predictability in shaping cooperative behavior (Faulkes *et al.* 1997; Jetz &
397 Rubenstein 2011; Gonzalez *et al.* 2013). Compared to relatively long-lived cooperatively breeding
398 vertebrates, paper wasps have a short lifespan with annual colony cycles (Reeve 1991; Brockmann
399 1997). Thus it is perhaps less surprising that variation during the course of a wasp's life rather than
400 between generations is more salient in this case.

401 A number of investigators have examined the influence of microhabitat temperature on nest
402 site choice and colony productivity in *Polistes* (Cervo & Turillazzi 1985; Jeanne & Morgan 1992; Nadeau
403 & Stamp 2003). However, little work has explicitly examined the influence of the amplitude of
404 temperature fluctuations. We suggest two non-mutually exclusive routes through which short-term
405 temperature fluctuations may influence cooperation in paper wasps. First, large diurnal and day-to-day
406 temperature fluctuations can have negative implications for growth and development in insects (Colinet
407 *et al.* 2015). Unlike many bees and ants, paper wasps have small, exposed nests, which offer little buffer
408 from environmental fluctuations (Jones & Oldroyd 2006). This is especially true at the founding stage
409 when nests are small (Hozumi & Yamane 2001). Higher amplitudes of temperature fluctuation may
410 represent more stressful conditions for both larval development and adult physiology given the limited
411 thermoregulatory capacity of *Polistes* wasps (Weiner *et al.* 2010). More stressful nesting conditions, in
412 turn, may favor cooperation. Second, fluctuating temperatures may also affect wasps by reducing the
413 amount of time available for foraging. Wasps tend to be inactive at lower temperatures and some

414 species have narrow temperature ranges for optimal flight (Weiner *et al.* 2012). At higher temperatures,
415 adults forgo nutrient foraging and invest in nest-directed thermoregulatory behaviors including fanning
416 the nest and collecting water to drench the nest for evaporative cooling (Rau 1931). Cooperation may be
417 advantageous when there are larger amplitude temperature fluctuations as groups of foundresses may
418 be able to more effectively take advantage of windows suitable for foraging. The current findings call for
419 work integrating studies of thermal physiology and cooperative nesting in *Polistes* wasps to elucidate
420 the mechanisms driving the pattern uncovered in this study.

421 The largest cooperative groups are not found among species with the most extreme
422 temperature fluctuations, but rather those occupying benign climates with warm and wet conditions. At
423 face-value this finding appears to challenge much of the work emphasizing the role of ecological
424 constraints on independent breeding in favoring cooperative breeding (Faulkes *et al.* 1997; Hatchwell &
425 Komdeur 2000). Benign environmental conditions, however, have also been argued to potentially lead
426 to increased rates of cooperation due to habitat saturation (Selander 1956; Arnold & Owens 1999;
427 Gonzalez *et al.* 2013). There is some evidence of higher rates of cooperative nesting in denser *Polistes*
428 populations (Brockmann 1997) though there is no evidence that Neotropical species with the highest
429 rates of cooperation nest at higher density or are closer to their carrying capacity than *Polistes* in other
430 parts of the world. Alternatively, it is possible that wasps in regions with benign abiotic conditions are
431 faced with harsher biotic interactions. In particular, rates of ant predation on wasp larvae have been
432 experimentally shown to be higher in the Neotropics compared to temperate North America (Jeanne
433 1979), and are thought to have been a major evolutionary force shaping nest site selection in tropical
434 Polistine wasps (Corbara *et al.* 2009). Currently, data on any moderating effects of foundress number on
435 mitigating ant attacks is lacking. More broadly, larger foundress associations have been shown to be
436 more resilient against vertebrate predation as well as defending against parasitoids (Strassmann 1981;
437 Strassmann *et al.* 1988). The Neotropics also has elevated levels of species diversity in *Polistes* and
438 related genera (Corbara *et al.* 2009), raising the possibility that competition may be greater in the paper
439 wasp niche in the Neotropics compared to temperate regions. Relatively little is known about the
440 comparative population demography, predation and parasitism pressures across *Polistes* though future
441 work in this area holds important promise for understanding patterns of cooperation across species.

442 The axis of climate variation that explains genus-wide patterns of variation in the size of
443 cooperative nesting associations do not explain intraspecific patterns of cooperative nesting in the four
444 temperate species examined. This result is especially noteworthy for two reasons. Previous authors have
445 criticized phylogenetic comparative studies of cooperative breeding because they did not match species-

446 level patterns (Cockburn 2013), even though studies at different scales have used different climate data.
447 In the present study, the climate and cooperation data used to assess variation in each species was
448 simply a subset of the locality data used in the genus-wide analysis. Arguably, this result provides the
449 clearest evidence to date that different processes shape variation in the rates of cooperation within and
450 between species. Indeed, analyses of intraspecific variation in rates of cooperation demonstrate that
451 variation in cooperative nesting is often associated with environmental variation, though the relevant
452 gradients differ across species (Fig. 4). The major axes of climate variation at the global scale are rarely
453 replicated within the range of an individual species, so it is not surprising that important features of
454 climate variation may differ at local and global scales (Fig S6). Notably, the species we examined shared
455 partly overlapping ranges and still showed heterogeneous responses to climate variation suggesting that
456 species' cooperative nesting responses to climate variation are evolutionarily labile within *Polistes* (Fig
457 4). The heterogeneity in the relationships between cooperation and environmental conditions among
458 species urges caution in extrapolating findings on the climatic drivers of cooperation from a single
459 population or species to broader geographic and spatial scales. Thus, criticisms that the results of
460 comparative studies examining the relationship between cooperation and the environment do not
461 concur with intraspecific studies (Cockburn & Russell 2011; Cockburn 2013) should be re-evaluated in
462 light of the fact that predictors of the formation of cooperative groups and size of those groups need not
463 be the same (West *et al.* 2007, this study).

464

465 **Conclusion**

466 Detailed records of wasp nesting behavior have allowed us to examine the relationships
467 between cooperative nesting and climate using different metrics across phylogenetic and spatial scales.
468 These analyses reveal that different aspects of climatic variation are associated with the presence and
469 extent of cooperation both within and across species. Interestingly, estimates of the average climate for
470 each species are a better predictor of the presence of cooperation than climate variables from the
471 limited subset of populations where species have been observed and vice versa for continuous
472 measures of cooperation. This result suggests that the propensity to engage in cooperative nesting is a
473 trait that evolves at the species-level in paper wasp while the extent of its expression (as measured by
474 foundress group size) is potentially more plastic and dependent on local conditions. Taken together, our
475 data provide support for variation in cooperative breeding as both an ecologically labile continuum and
476 distinct evolutionary strategies. The disconnect between inter- and intra-specific patterns of cooperative
477 nesting in responses to climate begs for further research documenting patterns of cooperation across

478 species' ranges, opening up a new line of questioning to understand the demographic, ecological and
479 evolutionary processes that give rise to heterogeneity in climate responses across species.

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690

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699 **Table 1: Comparative results**

Cooperation measure	Climate PC axis	Bayesian			PGLS		
		posterior mean	95% CI Bounds	pMCM C	t	P	r ²
All species-level data (N = 40 species)							
Categorical	Env. Harshness	-8.68	-56.92 - 38.17	0.72	0.28	0.78	0.37
	Fluctuating				-		
	Temp.	175.66	36.69 - 318.94	0.0013	5.00	<0.0001	
Mean							
Mean	Env. Harshness	-0.112	-0.30 - 0.065	0.21	1.19	0.24	0.02
	Fluctuating				-		
	Temp.	-0.191	-0.52 - 0.15	0.26	1.11	0.28	
Cooperative only species-level data (N = 26 species)							
Mean							
Mean	Env. Harshness	-0.186	-0.435 - 0.065	0.12	1.89	0.07	0.09
	Fluctuating				-		
	Temp.	0.090	-0.51 - 0.72	0.77	0.41	0.69	

All Population-level data (N = 129 populations, 28 species)

Categorical	Env. Harshness	-7.76	-62.85 - 49.87	0.72	1.37	0.17	0.05
	Fluctuating				-		
	Temp.	58.06	-2.10 - 136.13	0.041	2.68	0.008	
Mean	Env. Harshness	-0.177	-0.293 - -0.062	0.003	2.97	0.004	0.05
	Fluctuating				-		
	Temp.	-0.032	-0.191 - 0.130	0.69	0.36	0.72	

Cooperative only population-level data (N = 86 populations, 19 species)

Mean	Env. Harshness	-0.262	-0.383 - -0.124	0.001	1.89	0.071	0.09
	Fluctuating				-		
	Temp.	0.046	-0.172 - 0.256	0.66	1.11	0.69	

700

701

702

Table 2: Interspecific analyses

Genus-wide Population-level Climate PCs

Species		Mean Foundresses			Percent Subordinate		
		<i>F</i> or <i>t</i>	<i>r</i> ²	P	<i>F</i> or <i>t</i>	<i>r</i> ²	P
P. dominula	Whole model	6.07	0.36	0.010	6.24	0.37	0.010
	Env. Harshness	-0.62		0.54	2.3		0.036
	Fluctuating Temp.	-2.08		0.054	-0.39		0.71
P. exclamans	Whole model	2.21	0.13	0.15	1.86	0.097	0.19
	Env. Harshness	-1.07		0.3	0.87		0.398
	Fluctuating Temp.	-2.10		0.055	-1.90		0.078
P. fuscatus	Whole model	1.9	0.09	0.18	3.85	0.23	0.042
	Env. Harshness	-0.36		0.73	1.14		0.27
	Fluctuating Temp.	1.89		0.076	2.77		0.013
P. metricus	Whole model	1.65	0.06	0.22	1.88	0.08	0.18

Env. Harshness	0.91	0.37	-0.86	0.40
Fluctuating Temp.	0.39	0.698	0.54	0.60

703

704 **FIGURE LEGENDS**

705

706 **FIGURE 1**

707 Polistine wasp nests are initiated by single foundress or groups of foundresses. The open-structure of
 708 the nest makes determination of group size and colony stage straightforward. Species shown left to
 709 right are *P. fuscatus*, *P. annularis* and *P. bahamensis* (Photos by M.J. Sheehan).

710

711 **FIGURE 2**

712 (A) The mean number of foundresses shows a leptokurtotic distribution across *Polistes* species. (B) Rates
 713 of cooperation measured as the percent of subordinate foundresses are bimodally distributed among
 714 *Polistes* paper wasp species. (C) Phylogeny of *Polistes* wasps with rates of cooperative nesting mapped
 715 onto the tree. Rates of cooperation have been evolutionary labile, with multiple independent losses of
 716 cooperative breeding. (D) Range centers for species examined in our cooperation data set. The dots
 717 each represent the average latitude and longitude for each species examined, with the color denoting
 718 the level of cooperation observed in that species. Non-cooperative species are clustered in eastern Asia
 719 while the most cooperative species are found in the Neotropics.

720

721 **FIGURE 3**

722 Similar patterns of results are found for analyses using aggregate (A-B) and locality datasets (C-D). In the
 723 aggregate dataset, the climate and cooperation data are based on the aggregate of all available data for
 724 each species. For the locality dataset, climate and cooperation data are specific to particular localities. In
 725 both datasets, environmental harshness PC is negatively associated with the rate of cooperative nesting
 726 among cooperative species but does not separate cooperative from non-cooperative species (A, C).
 727 Greater short term temperature stability is associated with non-cooperative nesting species in both the
 728 aggregate and locality datasets (B,D). The scatterplots show the continuous variation in raw data for
 729 each analysis with trend lines denoting a significant phylogenetically corrected relationship. Boxplots
 730 show the distribution of climate variables for each category of species. Cooperative species are denoted
 731 with red and non-cooperative with blue.

732

733 **FIGURE 4**

734 (A) Environmental harshness that correlates with interspecific variation in the extent of cooperation
735 across the genus, but does not explain intraspecific variation in rates of cooperation in any of the four
736 species examined: *P. dominula* (red), *P. fuscatus* (blue), *P. metricus* (purple), and *P. exclamans* (green).

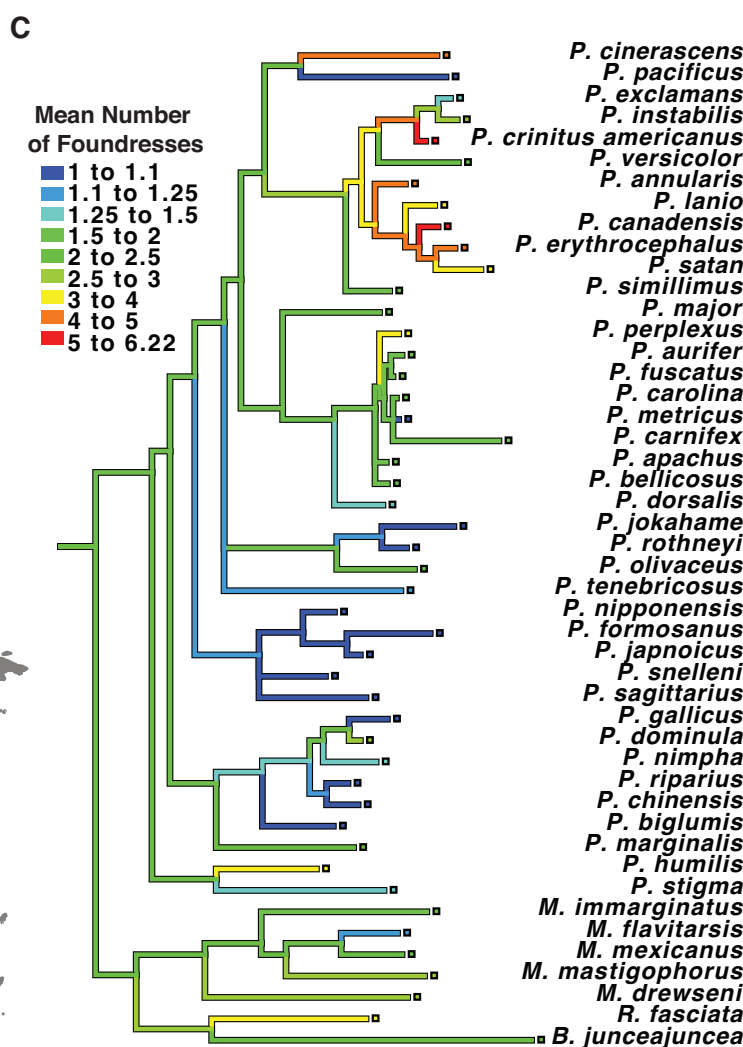
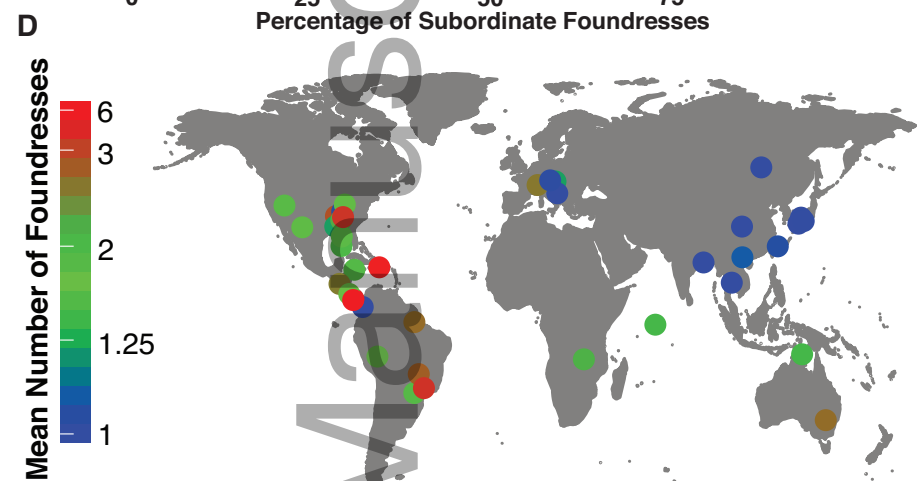
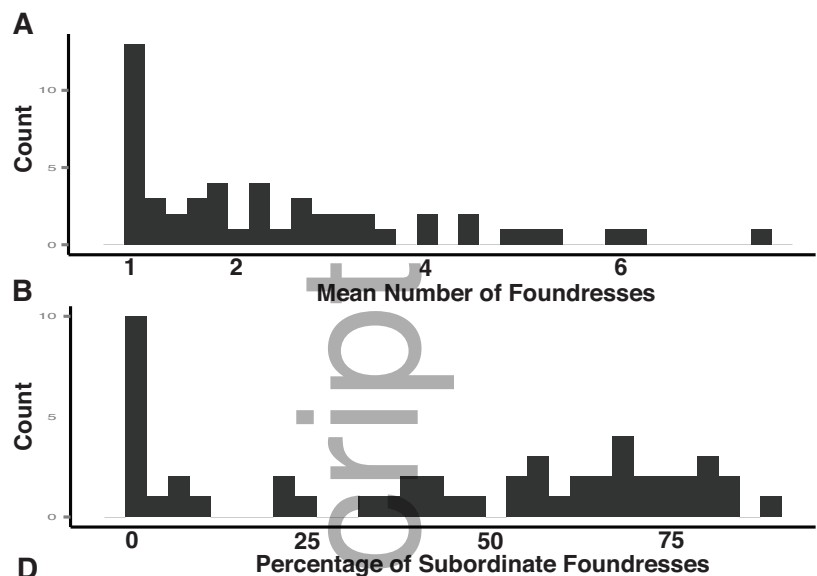
737 (B) Short term temperature stability, which is associated with the presence of cooperation at the
738 macroevolutionary scale, tends to explain variation in the extent of cooperative nesting among
739 populations in three of the species. The trends in *P. dominula* and *P. exclamans* are in line with the
740 genus-wide patterns though *P. fuscatus* shows an opposite response to fluctuating temperatures.

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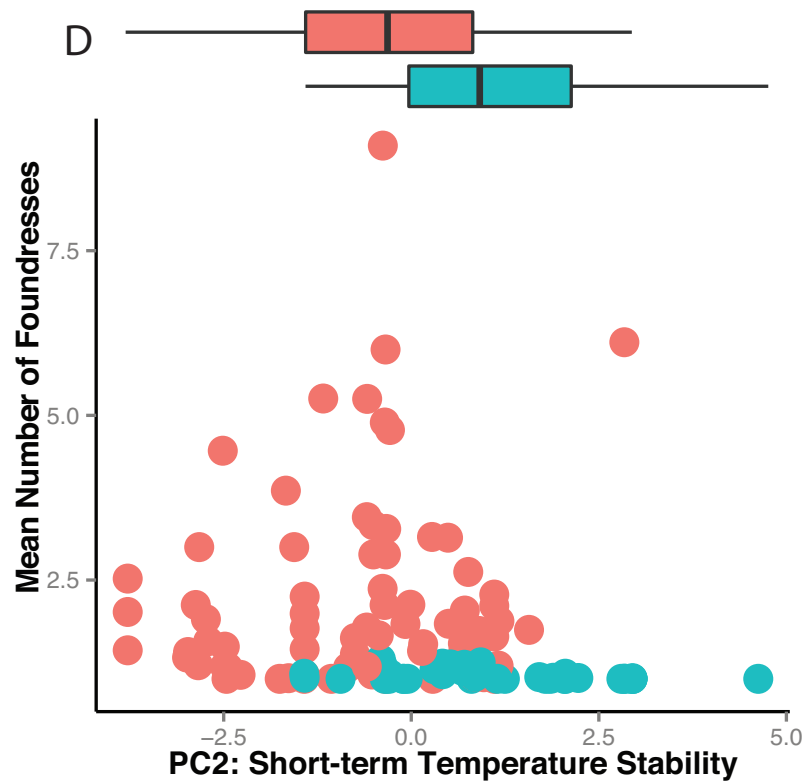
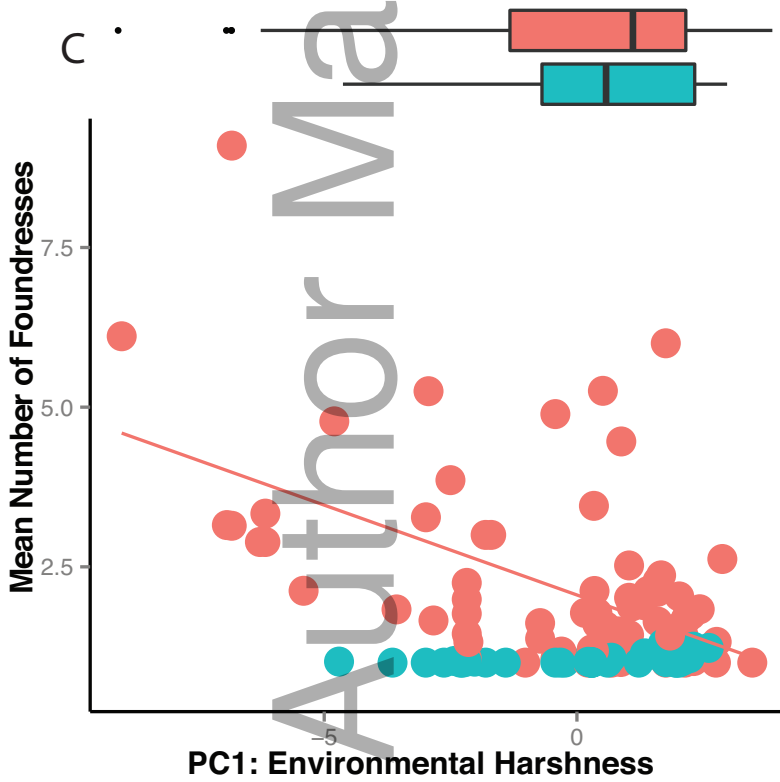
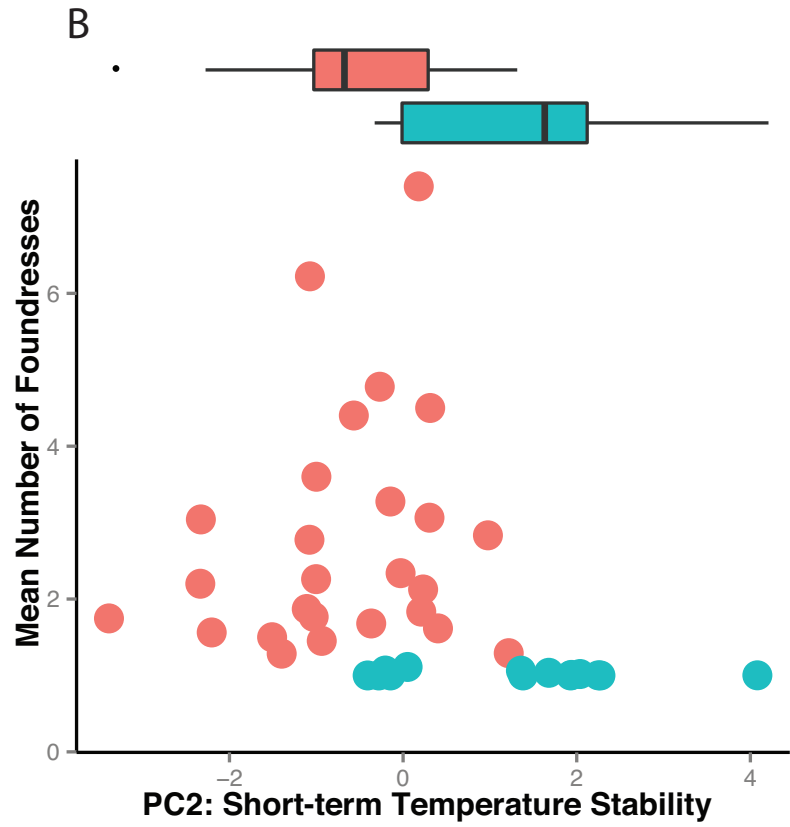
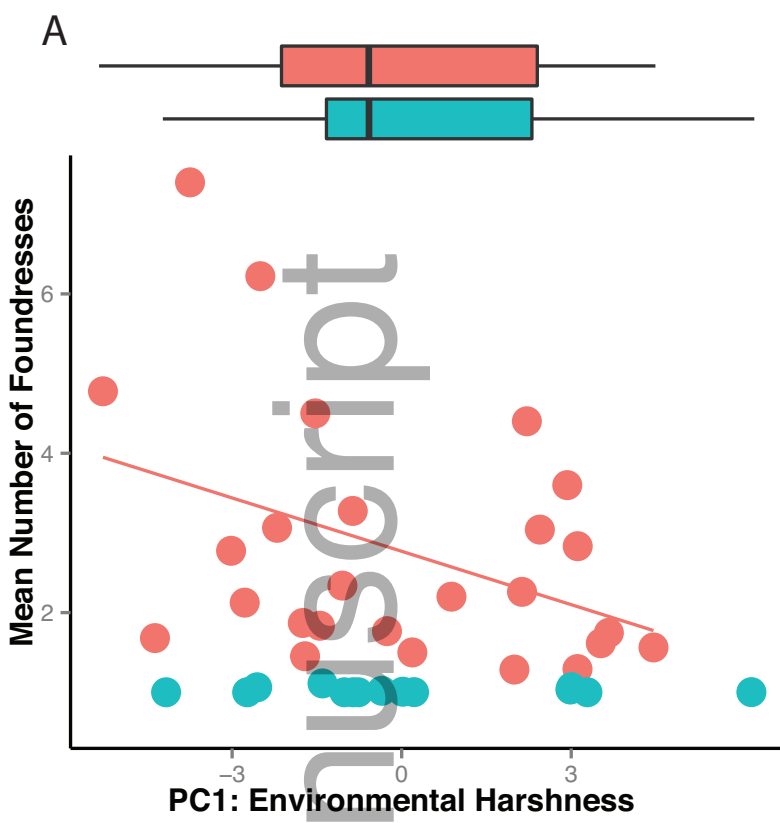


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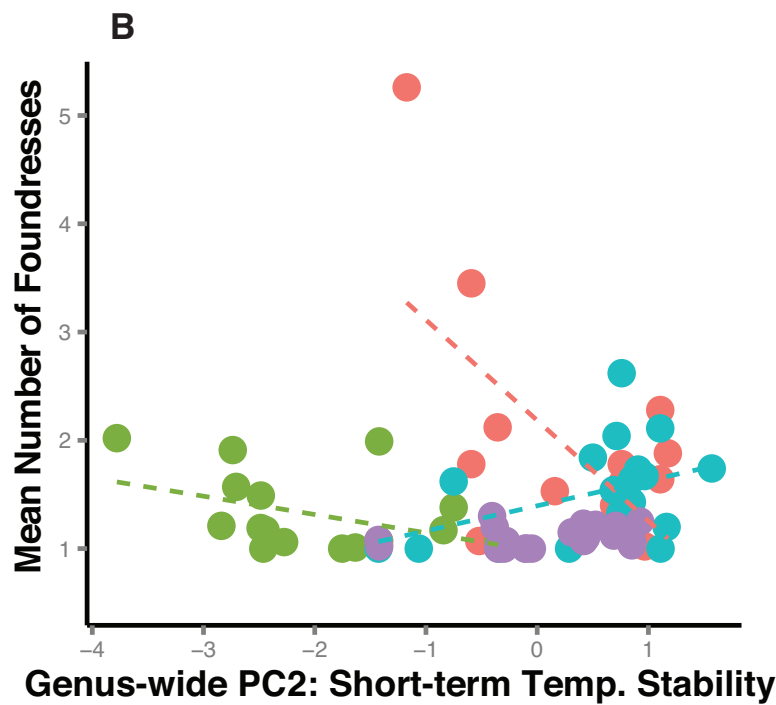
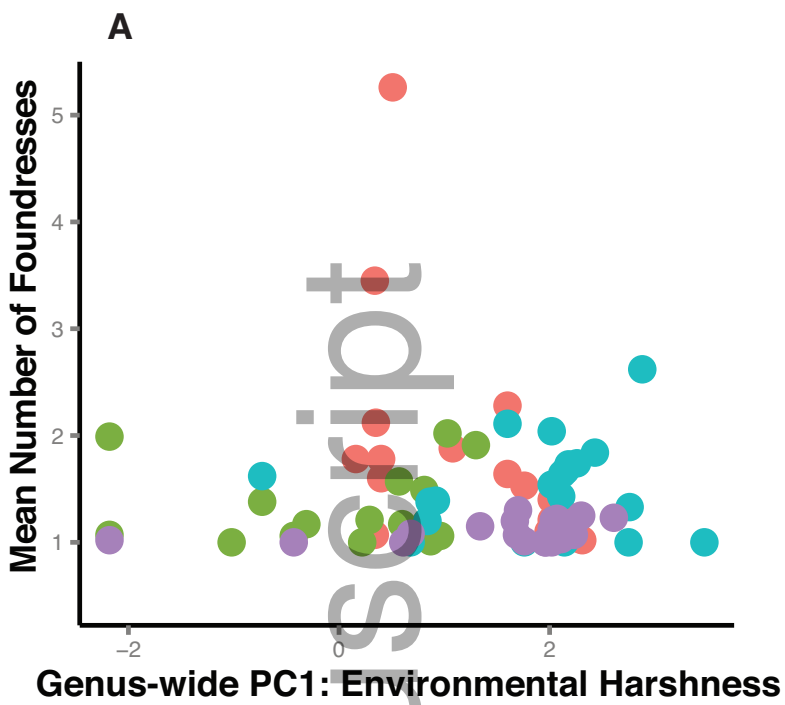
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