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Life history responses of meerkats to seasonal changes in extreme environments

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Abstract: Species in extreme habitats increasingly face changes in seasonal climate, but the demographic mechanisms through which these changes affect population persistence remain unknown. We investigated how changes in seasonal rainfall and temperature influence vital rates and viability of an arid environment specialist, the Kalahari meerkat, through effects on body mass. We show that climate change–induced reduction in adult mass in the prebreeding season would decrease fecundity during the breeding season and increase extinction risk, particularly at low population densities. In contrast, a warmer nonbreeding season resulting in increased mass and survival would buffer negative effects of reduced rainfall during the breeding season, ensuring persistence. Because most ecosystems undergo seasonal climate variations, a full understanding of species vulnerability to global change relies on linking seasonal trait and population dynamics.

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1 **Title: Life-history responses of meerkats to seasonal changes in extreme**

2 **environments**

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12 **Abstract:**

13 Species in extreme habitats increasingly face changes in seasonal climate, but the demographic

14 mechanisms through which these changes affect population persistence remain unknown. We

15 investigated how changes in seasonal rainfall and temperature affected vital rates and viability of

16 an arid-environment specialist, the Kalahari meerkat, through effects on body mass. We show

17 that climate change reducing adult mass in the pre-breeding season would decrease fecundity

18 during the breeding season and increase extinction risk, particularly at low population densities.

19 In contrast, a warmer non-breeding season resulting in increased mass and survival would buffer

20 negative effects of reduced rainfall during the breeding season, ensuring persistence. As most

21 ecosystems are seasonal, a full understanding of species vulnerability to global change relies on

22 linking seasonal trait and population dynamics.

23

24   **One Sentence Summary:**

25   Trait-mediated survival and reproduction determine population persistence under seasonal

26   changes in extreme rainfall and temperature

27   **Main Text:**

28   Ecosystems subject to climatic extremes, such as arid regions, which cover > 40 % of the

29   terrestrial landmass, are among the most vulnerable to climate change (*1–3*). Changes in rainfall-

30   drought cycles (*2, 4*) and increasing temperatures (*5*) are likely to severely affect population

31   dynamics of arid-environment species (*6*). This is because key vital rates, such as survival,

32   growth, and reproduction, of these species respond unusually strongly to seasonal and

33   interannual climatic patterning (*2, 5, 7*). Despite this increased vulnerability, population viability

34   analyses of arid-environment specialists are scarce (*6*). Studies on seasonal changes in vital rates

35   and phenotypic traits, which strongly mediate climatic effects on viability (*8–10*), are thus far

36   absent.

37   In this study, we used long-term demographic and trait (body mass) data of meerkats

38   (*Suricata suricatta*) from the Kalahari desert in southern Africa to investigate how future

39   changes in seasonal rainfall and temperature may affect vital rates and population persistence.

40   Meerkats are an ideal study species since vital rates can be measured precisely (*11*) and respond

41   strongly to climatic factors, generating large variation in population size (*8, 12*). In addition,

42   meerkats are cooperative breeders, where young born to a dominant female are co-reared by non-

43   breeding helpers (*13*), and the number of helpers in the population increases reproductive success

44   (*8, 14*). This relationship allows us to assess how interactions between population density and

45   climate affect vital rates (*12, 15*). To establish a basis for detailed projections of population

46   change over time, we first used 20 years of individual data from female meerkats to fit

47   generalized additive models (GAMs) (*8*). In these models, vital rates (survival, growth,

48   reproduction, stage transitions, and emigration) of nine life-history stages (pups, juveniles,

49   subadults, and non-pregnant, pregnant, and litter-weaning helpers and dominants; fig. S1) were

50   fitted as functions of body mass, population density, season (month-of-year), interannual rainfall

51   and temperature deviations (from seasonal means), and interactions among these drivers (*8*)

52   (Table S1).

53   Our results from the most parsimonious GAMs agreed with previous findings, showing

54   strong seasonal effects, both positive and negative, of all considered variables on meerkat vital

55   rates (*8, 12*). For instance, monthly growth in adult helpers was generally highest ($P < 0.01$) in

56   the rainy season when food resources were most abundant (Fig. 1A). Interactions between

57   population density and rainfall/temperature deviation mediated these seasonal effects. High

58   density and rainfall increased helpers' growth (Fig 1A). High density under low temperatures

59   however decreased the probability of dominant reproduction at the onset of the dry season (Apr-

60   May) (Fig 1B). Overall, body mass had a consistently positive effect on vital rates, strongly

61   mediating environmental impacts (*8*). Rainfall also positively affected vital rates (*12, 16*),

62   whereas the effect of higher temperatures was positive only in dry and cool seasons (Apr-Aug)

63   (Table S2, fig. S18). Under most environmental conditions, population density showed a

64   negative effect on survival and on emigration of adult helpers (*12*). In dominants, however,

65   survival increased with density at the onset of the breeding season but decreased at high densities

66   in the non-breeding season, when resources were scarce. Highest reproductive output was

67   achieved at intermediate densities (Table S2). Population density therefore both amplified and

68   compensated negative responses to the environment, depending on the vital rate affected (*15*)

69   (Fig. 1).

70   We next assessed how changes in climate variation across seasons might affect

71   population dynamics through direct effects on vital rates and through effects mediated by body

72   mass and density. We first used the most parsimonious GAMs of vital rates to assemble a

73   density-dependent, environment-specific, mass-stage classified integral projection model for

74   each study month and year (*17*; supplementary materials). This enabled us to project trait and

75   population dynamics simultaneously in discrete one-month intervals, which could then be

76   integrated over the entire year (fig. S2). Our population model assumed that past conditions

77   affecting meerkats were captured by the current mass distribution and were propagated through

78   time, allowing us to assess trait-mediated population processes (*10*). These assumptions were

79   justified as we could not detect life-history tradeoffs (*i.e.*, fitness decreases due to high growth or

80   reproductive effort; supplementary text) (*16*).

81   The population model replicated observed seasonal population and mass fluctuations

82   (1997-2016) with high accuracy (for total population density: Pearson's correlation coefficient *r*

83   = 0.74, P < 0.001) (Fig.1B), and did not extrapolate beyond biologically realistic values of

84   masses (figs. S3 and S4). Model projections were also robust, showing low uncertainty due to

85   parameter estimates (Tables S3 and S4). We then used this model to project population dynamics

86   for 50 years based on 12 scenarios of changes in rainfall (drier) and temperature (hotter)

87   extremes. These scenarios were derived from four projections of greenhouse-gas emissions,

88   showing a plausible range of season-specific climate change in the Kalahari (figs. S5 and S6).

89   Projected changes in climatic patterning, and increases in extreme events in particular,

90   increased the risk of population quasi-extinction (< 20 individuals or < 5 dominants) up to 55 %

91   by 2066 (Fig. 2A, B). Simultaneous changes in rainfall and temperature led to a higher extinction

92   risk (figs. S7 and S8), highlighting potentially detrimental compound climate-change effects on

93   the viability of arid-environment species (*18*). Density was important in regulating persistence

94   (Fig. 2C); projections that kept populations at either low or high densities resulted in

95   significantly higher probability of quasi-extinction (to 100 %, P < 0.01) and decreased time to

96   extinction on average by 20 years (SE = 10; P < 0.01). At low population densities, when the

97   benefits of cooperation decrease and the environment favors the settlement of new groups (*12*,

98   *19*), emigration was relatively high. This reduced both the overall number of helpers and

99   reproductive success (*20*; fig. S14). At high densities, when resource competition and intergroup

100 conflicts increase, particularly under scarce rainfall (Table S2), reproduction and survival were

101 reduced, increasing the risk of extinction (*21*). Maintaining densities at intermediate levels, when

102 the benefits of cooperation are largest, eliminated extinction risk (Fig. 2C), similar to patterns

103 seen in other social species (*20*).

104   As well as influencing viability, projected changes in climate significantly altered

105 population structure due to changes in the distribution of mass. In projections where climatic

106 extremes became more likely but the population persisted, the proportion of non-pregnant

107 dominant females increased (compared to baseline simulations) at the end of the breeding season

108 (Apr-Jul); as well as the proportion of pregnant dominant females and of females with dependent

109 litters at the onset of the breeding season (Aug-Nov; Fig 3A). This occurred due to mass

110 increases of helpers (from 600 to up to 670 grams) and dominants in the dry season (May-Sep;

111 Fig. 3B), which led to higher reproductive output in subsequent months and compensated for the

112 loss of adult helpers from the population (Fig. 3A). These changes in the proportion of helpers

113 and dominants indicate a reduction in average group size under climate change (*21*). In contrast,

114 in projections where the population collapsed, the proportion of non-pregnant helpers dropped to

115 20 % (from 40 % in baseline simulations), as helpers emigrated more readily under low

116 population densities (Fig. 3). Density was further reduced by a lower reproductive output that

117 resulted from decreased masses of reproductive females at the onset of the breeding season (Fig.

118 3B), providing a potential early-warning signal for an impending population crash (22).

119 Therefore, for social species, in particular cooperative breeders, density feedbacks (23) may

120 exacerbate a breakdown of social groups under climate change (21).

121   To explore the seasonal demographic mechanisms behind projected quasi-extinctions, we

122 assessed how perturbations of our population model affected population growth. We replicated

123 simulations which had resulted in extinction but maintained the effects of rainfall and

124 temperature deviations at observed past values (1997-2016) for either specific vital rates or

125 simultaneously for all vital rates, accounting for covariation (fig. S11). We maintained the effects

126 either for the entire year or across four seasons: rainy (Oct-Apr), dry (May-Sep), hot (Nov-Feb),

127 and cool (Jun-Aug). Our results demonstrate highly season-specific contributions of demography

128 to extinction. The time to extinction can be slowed by 4 years on average (SE = 2.1) if the

129 reproduction of dominants is not affected by climate change in the rainy season (Fig 4; Fig. S10).

130 On the other hand, increasing warming can potentially decrease emigration, particularly in the

131 dry and cool seasons, despite potential mass gains of prospective emigrants. Maintaining

132 emigration under observed rainfall and temperature regimes therefore leads to faster extinction

133 (Fig. 4). These results agreed with analytical perturbations of population growth, which showed

134 high but seasonally varying relative contributions of helper and dominant vital rates to

135 population growth (figs. S12 and S13).

136   This work highlights that assessing the dynamics of seasonal influences on phenotypic

137   traits may be key to understanding how changes in demography and population structure can

138   ensure population persistence when rainfall and temperature patterns change (*5, 10*). In

139   particular, we show that climate-driven changes in body mass affect vital rates differently in

140   different seasons. These trait-mediated effects can either buffer populations from extinction (*15*)

141   or exacerbate extinction risk under climate-density interactions for species where density

142   positively affects vital rates (*15, 24*). Seasonal, demographic analyses that include phenotypic-

143   trait changes are therefore required to gain much-needed information on population responses to

144   global change, such as interactions of climatic components that are increasingly extreme (*18, 24,*

145   *25*).

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265

270   **Author Contributions:** T.C.B. led the long-term study and data collection; M.P. and A.O.

271   conceived the ideas for the paper and its structure; M.P., A.O., N.M. and G.C. designed the

272   analyses; M.P. conducted the analyses and wrote the manuscript; all authors discussed

273   the results and commented on the manuscript.

274   **Competing interests:** The authors have no competing interests to declare.

275   **Data and materials availability:** The parameters and datasets generated and analyzed during

276   the current study, required to build and project meerkat population dynamics are freely available

277   in the *GitHub* repository: https://github.com/MariaPaniw/meerkats. All analyses in this study

278   were performed using the freely available, statistical software *R*. All R script to run the analyses

279   are available in the *GitHub* repository: https://github.com/MariaPaniw/meerkats. All

280   correspondence and material requests should be addressed to M. Paniw at m.paniw@gmail.com.

281
282   **Supplementary Materials**
283
284   Materials and Methods

285   Supplementary Text

286   Figs. S1 to S17

287   Tables S1 to S4

288   Caption for Fig. S18

289   Captions for R scripts S1 to S3

290   Captions for databases S1 to S17

291   References (*26-57*)

292   **Figures:**

293   **Figure 1. Interactive effects of seasonality, population density, and rainfall/temperature**

294   **variation on meerkat vital rates and population dynamics.** (A) Line colors and different plot

295   panels depict predictions of body mass (g) and reproduction using maximum (+) and minimum (-

296   ) observed temperature and rainfall deviation from seasonal averages, respectively. Shaded areas

297   show 95% prediction intervals. Plot backgrounds highlight the rainy (Oct-Apr) and dry (May-

298   Sep) seasons. (B) Average (lines) ± 95% bootstrap confidence intervals (shaded areas) projected

299   population densities (individuals/km^2) obtained from modeling the relationships described in

300   (A).

301   **Figure 2. Projected density and viability of meerkats under changes in rainfall and**

302   **temperature variation.** (A) Average (lines) population density (individuals/km^2) ± 95%

303   projection interval (shaded areas) based on 280 and 120 simulations where the population

304   persisted or went extinct, respectively. (B) Cumulative probabilities of quasi-extinction under

305   four scenarios of greenhouse-gas Representative Concentration Pathways (RCPs). Shaded areas

306   show 95 % projection intervals among sequential vs. stochastic projections of climate. (C)

307   Effects on extinction probability of imposing constant low, intermediate, and high densities

308   during projections. Plot backgrounds highlight the rainy (Oct-Apr) and dry (May-Sep) seasons.

309   **Figure 3. Projected changes in population structure and trait dynamics for meerkats under**

310   **climate change.** Seasonal distribution of proportion of different life-history stages (A) and

311   average masses (g) within each stage (B). Boxplots show the distribution of values across years

312   and simulations grouped based on different simulations of future rainfall and temperature

313   variation. The stages include pups, juvenile (Juv), subadults (SubA), and non-pregnant (NP),

314   pregnant (P) and litter-weaning (L) helpers (H) and dominants (D). Plot backgrounds highlight

315   the rainy (Oct-Apr) and dry (May-Sep) seasons.

316   **Figure 4. Seasonal differences in probability of quasi-extinction under climate-change**

317   **simulations.** Averages (points) ± 1 SE (error bars) changes in the time (years) to extinction

318   across 120 simulations when a given vital rate is affected by observed (1997-2016), instead of

319   projected (2017-2066), rainfall/temperature variation. The observed variation was maintained

320   over an entire year or for the rainy (Oct-Apr), dry (May-Sep), hot (Nov-Feb) or cool (Jun-Aug)
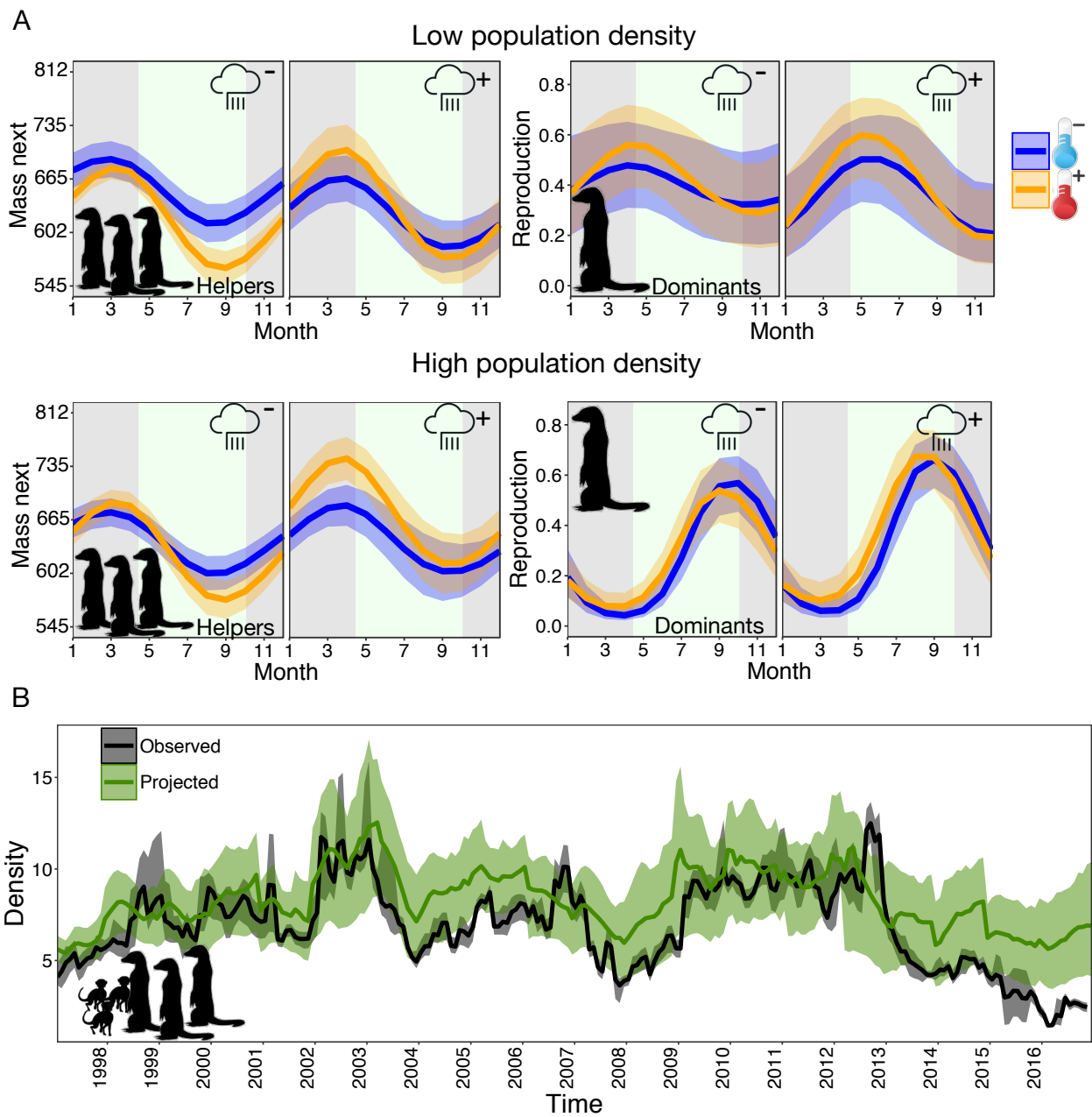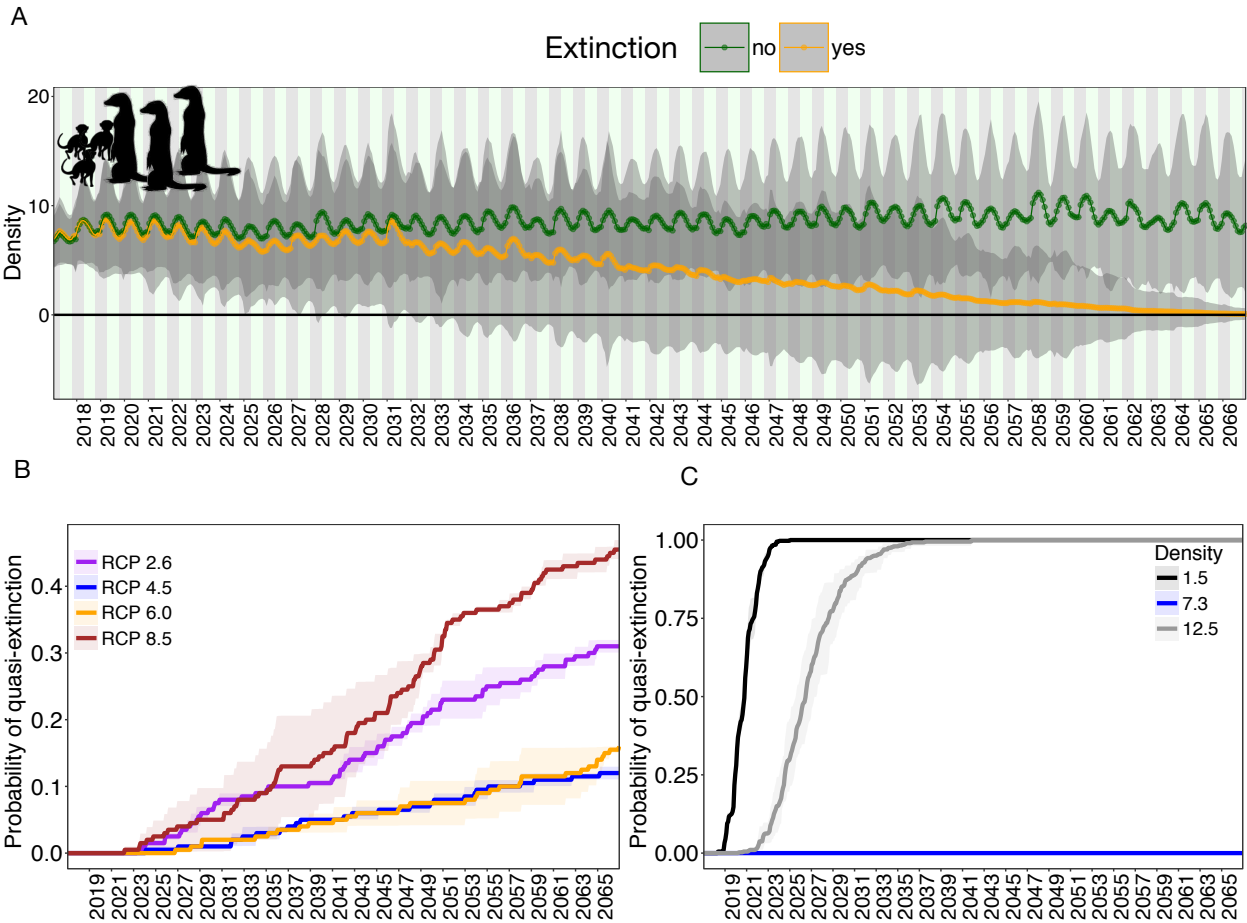
321   seasons.

322

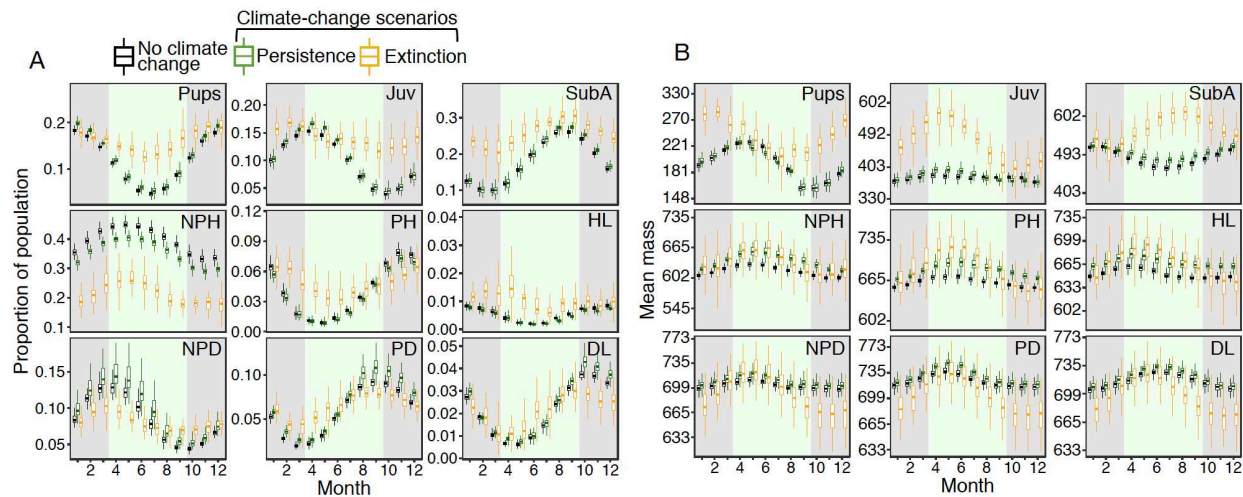323 **Figure 1**

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Figure 2

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Figure 3

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Figure 4

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