

1 Title: Precipitation-dependent source-sink dynamics in a spatially structured population of an
2 outbreaking caterpillar

3

4 Authors: Patrick Grof-Tisza¹, Adam Pepi^{1,2}, Marcel Holyoak³, and Richard Karban¹

5 1. Department of Entomology and Nematology, University of California, 1 Shields Ave.,
6 Davis, CA 95616

7 ORCID 0000-0002-0217-4253

8 2. Ecology Graduate Group, University of California, 1 Shields Ave., Davis, CA 95616
9 pgroftsiza@ucdavis.edu

10 3. Department of Environmental Science and Policy, University of California, 1 Shields
11 Ave., Davis, CA 95616

12 Abstract:

13 Context

14 Patch-based population models predominately focus on factors that affect regional processes
15 namely, patch size and connectivity, as the primary drivers explaining patch occupancy. This
16 trend persists despite the recognition that patch quality can strongly influence population
17 demography at the local scale. The quality of patches is often temporally variable and influenced
18 by abiotic conditions. However, few studies have explicitly investigated how climatic variables
19 influence the spatial and temporal dynamics of spatially structured populations either directly or
20 indirectly through changes in patch quality.

21 Objectives

22 Using a 10-year census of a spatially structured population of an outbreaking caterpillar, we
23 determined the relative importance of patch quality (determined demographically), connectivity,
24 precipitation, and their interactive effects on patch abundance, occupancy, colonization, and
25 extinction.

26 Methods

27 We generated a series of statistical models and performed comparisons using Akaike's
28 information criterion. We subsequently used likelihood ratio tests to determine the influence of
29 each parameter on model fit.

30 Results

31 Patch quality and precipitation were the strongest predictors of the observed dynamics. We found
32 that the dynamics of the spatially structured population of *A. virginalis* were strongly influenced
33 by precipitation: all patches had a higher probability of occupancy, contained higher abundances
34 of caterpillars, and experienced fewer extinctions following wet winters compared to years
35 following droughts.

36 Conclusion

37 These findings suggest that precipitation may act to influence the strength of heterogeneity of
38 patch quality. This work demonstrates that patch-based models that do not include local and
39 climatic factors may produce poor predictions under future climatic regimes.

40 Keywords: area-isolation paradigm, hilltopping, metapopulation, patch quality

41 Introduction:

42 Empirical studies spanning several taxa have validated theoretical patch-based models
43 demonstrating that patch size and isolation explained extinction-colonization dynamics (Thomas
44 and Harrison 1992; Hanski and Thomas 1994; Rabasa et al. 2008); the probability of stochastic
45 extinctions was found to be negatively correlated with patch size and the probability of
46 (re)colonization was positively correlated with increased connectivity (or inversely, isolation;
47 Hanski, 1994). A seminal paper by Moilanen & Hanski (1998) concluded that the inclusion of
48 patch-level environmental variables into metapopulation models did not increase explanatory
49 power. Consequently, over the next two decades, most studies investigating the spatial dynamics
50 of spatially-structured populations focused on patch geometry and ignored patch quality (but
51 see Thomas et al. 2001; Fleishman et al. 2002). A meta-analysis, however, found that patch area
52 and isolation accounted for only 25% of the variation in patch occupancy (Prugh et al. 2008).
53 Indeed, several studies demonstrated that the observed spatial dynamics were not consistent with
54 the area-and-isolation paradigm [Hanski, 1998], reporting that factors other than patch geometry,
55 namely proxies for patch quality, were the strongest predictors (Schooley and Branch 2009;
56 Franzén and Nilsson 2010; Robles and Ciuad 2012). Learning from the resolution of the decade-
57 long bottom-up, top-down debate (Hunter and Price 1992), the field is shifting from determining
58 if local (e.g., quality) or regional (e.g., patch geometry) factors are more important to
59 determining the relative importance of both and under what conditions they may predominate.

60 One issue with including a quality metric in metapopulation and other similar patch-
61 based models hinges on the difficulty of assessing habitat patch quality. Indeed, simply defining
62 quality has proved challenging (see Morteli et al. 2010 for an overview of quality definitions).
63 While debated, the definition posited by Hall et al. (1997) is widely accepted: “habitat quality is

64 the ability of the environment to provide conditions appropriate for individual and population
65 persistence.” Abundances and density are often used as an indicator of patch quality. However,
66 in systems characterized by high patch heterogeneity, only a small fraction of a population may
67 occur in patches with sufficient quality to support successful breeding (Pulliam 1998). Moreover,
68 relying on periodic censuses does not account for dispersal between patches, a hallmark of
69 spatially-structured populations; changes in abundance may erroneously be attributed to patch-
70 dependent mortality or birth rates and not individual movement. Other common proxies of patch
71 quality include physical attributes such as area (e.g., Anzures-Dadda and Manson) or limited
72 resources thought to important for focal species such as trophic resources,(e.g., Fleishman et al.
73 2002; Franzén and Nilsson 2010) and breeding habitat (e.g., Robles and Ciudad 2012). Less
74 common is using top-down factors. Often considered separately from patch quality, the presence
75 of predators can influence the establishment or persistence of species in a patch (Shurin 2001;
76 Kneitel and Miller 2003; Grainger et al. 2017) or deter colonization processes (i.e., habitat
77 selection and immigration; Resetarits *et al.*, 2018). The utility of using these proxies is
78 contingent upon the strength of the relationship between the quantifiable variable and actual
79 patch quality. However, experimentally establishing a quantitative understanding between
80 proxies and survival or reproductive success while controlling for individual movement is rare
81 (Diffendorder 1998).

82 While the incorporation of local, patch-level factors is increasing, few studies have
83 explicitly modeled how changes in weather patterns influenced the spatial and temporal
84 dynamics of spatially structured populations (but see Pardikes et al. 2015, Tack et al. 2015,
85 Kahilainen et al. 2018). Yet changes in precipitation and temperature can either directly (Huey
86 and Kingsolver 1989; Karban et al. 2015) or indirectly influence local and regional processes

87 through loss of habitat (Johnson 2004) or changes in bottom-up (Boughton 1999) and top-down
88 (Pepi et al. 2018) forces driving patch-quality. One explanation for the paucity of studies
89 incorporating climatic variables is that early metapopulation models pooled occupancy data over
90 multiple years to account for stochastic environmental fluctuations as opposed to explicitly
91 quantifying their effects (Hanski et al. 1996; Moilanen 1999). Scientists are in broad agreement
92 that the climate is changing (IPCC, 2014), and climate models predict a more variable future
93 with increased frequency of extreme weather events leading to droughts and floods (Coumou and
94 Rahmstorf 2012). Elucidating the mechanisms underlying the link between variation in weather
95 and processes at the local and regional scales will increase our understanding of how a changing
96 climate will affect the persistence of spatially structured populations.

97 Our research investigated the dynamics of a spatially structured population of a
98 hilltopping tiger moth, *Artcia virginalis*. This research was motivated by our previous work
99 analyzing a 5-year caterpillar census (Karban et al. 2012) and subsequent caging studies in the
100 field (Karban et al. 2013, 2017); through this work, we found that within-patch demography was
101 dependent on patch quality. The contributions of patch geometry and seasonal weather to the
102 dynamics of *A. virginalis* have yet to be assessed. Using an additional five years of census data
103 (10 years total), we evaluated the relative importance of local, regional, and climatic drivers and
104 their interactive effects on several common metapopulation parameters. Specifically, we
105 quantified the relative effects of patch quality, patch connectivity, total annual precipitation and
106 their interactions on common metapopulation parameters we measured as responses including
107 patch-level caterpillar abundance, and the probabilities of patch occupancy, colonization, and
108 extinction. Previous work in this system demonstrated that precipitation positively correlated
109 with caterpillar abundance potentially through the displacement of predatory ants (Karban et al.

110 2017). Because of this a priori knowledge and our interest in interactive effects but with limited
111 data, we focused solely on precipitation as the climatic driver. In light of previous findings, we
112 hypothesized that 1) patch quality is the primary factor driving the dynamics of *A. virginalis*, but
113 the magnitude of its effect is dependent on precipitation and 2) a positive relationship between
114 connectivity and all responses except for extinction, which should have a negative relationship
115 with this parameter. Our measure of connectivity accounts for lekking behavior on local summits
116 (i.e., hilltopping). This metric better reflects constrained dispersal exhibited by hilltopping
117 species as compared to conventional connectivity metrics that assume that dispersal occurs
118 randomly among patches. Consequently, patches closest to hilltops with large mating
119 aggregations (and thus sources of mated females; i.e., high connectivity) should exhibit higher
120 occupancy with more caterpillars and colonization events but fewer extinctions compared to
121 those patches with lower connectivity (see online resource 1 for map showing connectivity).

122 Methods:

123 *The study system*

124 Surveys and experiments were conducted within the Bodega Marine Reserve (BMR), Sonoma
125 County, California (38.3184° N, 123.0718° W). Our study site experiences hot, dry summers and
126 cool, wet winters, typical of a Mediterranean climate. *Arctia virginalis* [Lepidoptera; Erebidae] is
127 a patchily distributed, day-flying moth in the western United States (Powell and Opler 2009).
128 Caterpillars leave larval patches and pupate in late spring (April–June). Adults engage in
129 hilltopping behavior during June – August (Grof-Tisza et al. 2016). Similar to lek mating
130 systems, hilltopping is a common mate-locating strategy used by insects: individuals aggregate
131 on summits and ridges, thereby increasing their likelihood of finding a mate (Shields 1967;
132 Alcock 1987). Only a few hilltopping sites are used within BMR, with most individuals (>70%)

133 aggregating on the highest elevation summits (Grof-Tisza et al. 2017; online resource 1). After
134 mating, females disperse from summits and search for suitable habitat patches to oviposit.
135 Consequently, dispersal is constrained by these mating aggregations and does not originate from
136 larval patches as commonly assumed in most patch-based models.

137 Larval patches are comprised of bush lupine (*Lupinus arboreus*) stands, the primary host
138 plant at our study site. *L. arboreus* patches are common within the dominant coastal prairie
139 habitat and on the periphery of low-lying, fresh water marsh habitat. A 5-year caterpillar census
140 showed that this system conformed to predictions consistent with source-sink dynamics;
141 caterpillar abundances were consistently higher in marsh habitat patches than coastal prairie
142 patches, where caterpillar abundances were often low, such that some patches went locally
143 extinct in some years (Karban et al. 2012). Experimental work demonstrated that both bottom-up
144 and top-down forces were drivers of this pattern. Survival was higher for early instar caterpillars
145 in marsh than prairie habitat when reared on *L. arboreus* plants using fine mesh cages that
146 excluded predatory ants (in preparation); predation of caterpillars by ants was also higher in
147 prairie than marsh habitat (Karban et al. 2013). Following Hall *et al.*, (1997), we used these
148 demographic studies to assign patch quality; patches within marsh and prairie habitat were
149 categorized as high- and low-quality, respectively. As previously mentioned, quantifying patch-
150 associated mortality to assess patch quality is a more direct measure than relying on census data
151 or the abundance of trophic resources.

152 *Census*

153 An ongoing census program for *P. virginals* has surveyed 13 larval patches within BMR since
154 2007 described elsewhere (Karban *et al.*, 2012 Online resource 1). Briefly, we counted the

155 number of caterpillars observed on haphazardly selected lupine plants (n=10, 2007-2011; n=15,
156 2011-2016) of similar size in March of each year and we tallied the total number caterpillars
157 observed per patch. For this study, we compiled 10 years (2007-2016) of patch-level annual
158 caterpillar census data, including caterpillar counts, occupancy, extinction (i.e., no caterpillars
159 observed in a previously occupied patch; 2008-2016) and colonization (observing at least 1
160 caterpillar in a site that was deemed extinct during the previous year; 2008-2016). In addition to
161 summarizing our census data across all patches for all years, we provide a summary table
162 grouped by patch quality (Table 1).

163 *Patch structure*

164 Using a high-resolution satellite image of BMR (Google Earth Pro; image date, 6 June 2017),
165 we obtained spatial coordinates of the centroids of larval patches (n=13; Online resource 1) and
166 previously identified adult mating aggregation summits (n=5; Grof-Tisza *et al.*, 2017). Distance
167 from the centroid of each larval patch to each aggregation summit was obtained using the ‘Imap’
168 package in R (R Development Core Team 2011). Centroids, as opposed to patch edges, were
169 used because the perimeter of patches varied annually depending on death and recruitment of *L.*
170 *arboreus* plants. The area of patches was estimated for the extant patches in 2017 using the
171 satellite image described above. Because we only had one year of patch area data (one year
172 beyond our 10-year census; 2007-2016) and it fluctuated annually, we did not consider patch
173 area in our analysis but report patch area for 2017 in an appendix (Online resource 2).

174 We used distance between each larval patch and aggregation summit centroid to calculate
175 a connectivity index. Unlike most connectivity indices that assume random dispersal between
176 patches, our connectivity metric incorporates mating behavior; for hilltopping insects, females

177 use elevational cues to navigate to summits, mate, and then descend to locate suitable oviposition
178 sites. Consequently, dispersal is a directed (i.e., non-random) process influenced by topography
179 (Pe'er et al. 2004, 2013; Painter 2014; Grof-Tisza et al. 2017). Our model assumes a fragmented
180 landscape with discrete adult aggregation sites (summits) and larval patches,

181
$$C_i = \sum_{j \neq i}^n e^{-d_{ij}/\alpha} H_j$$

182
183 where C_i is the connectivity of patch i , d is the Euclidean distance between any patch i and any
184 adult aggregation summit j , α is the mean dispersal distance of *A. virginalis* moths, and H is the
185 density of female moths at hilltop j determined in a previous study (Grof-Tisza et al. 2017). H in
186 our model is analogous to the area of source patches in conventional connectivity models
187 (Hanski and Thomas 1994), which is thought to be proportional to population size and
188 accordingly, the number of dispersing propagules. Though we only estimated mating aggregation
189 size in one year, surveys over the 10-year period indicated that the same summits are used
190 annually at similar relative frequencies (Grof-Tisza et al. 2016, 2017). We used an α of 300 m,
191 derived from the average of the maximum flight distance recorded during a mark-recapture study
192 for male (340 m) and female (260 m) moths, respectively (Grof-Tisza *et al.*, 2017).. We also
193 tested an α of 1000 m, a value commonly used for connectivity analyses when the dispersal
194 ability of a focal butterfly is unknown. The relative importance of parameters (i.e., connectivity,
195 patch quality, precipitation), did not change under this scenario of low dispersal limitation (data
196 not shown). The connectivity index can be interpreted as the sum of the predicted movement by
197 mated female moths from aggregation summits to a focal larval patch weighted by moth density,

198 assuming that the frequency of movement decreases exponentially with distance and dispersal
199 capacity.

200 *Statistical modeling*

201 We constructed generalized linear mixed models representing all possible combinations of
202 predictors and two-way interactions to test the influence of connectivity, patch quality,
203 precipitation and their interactive effects on four response variables: caterpillar abundance and
204 the probabilities of occupancy, colonization, and extinction (Table 2). Because previous work
205 demonstrated that precipitation in year $t-1$ was a good predictor of *A. virginalis* caterpillar
206 abundance in year t (Karban and de Valpine 2010; Karban et al. 2017), we used total annual
207 precipitation of the previous water year (i.e., hydrological year; 1 October to 31 September of $t-$
208 1) in our analyses. We fit models in R using the glmmADMB package. Patch abundance was
209 modeled using a negative binomial error distribution with a log-link function to account for
210 overdispersion in our count data (Ver Hoef and Boveng 2007). For all other models, we used a
211 binomial error distribution with a logit-link function. We included “patch” as a random effect to
212 account for repeated measures covariance structure.

213 We performed model comparisons using Akaike’s information criterion corrected for
214 sample size (AICc) and ranked models using delta-AICc values ($\Delta_i = \text{AICc}_i - \text{AICc}_{\min}$). We report
215 parameter estimates for both the best performing model (AICc_{\min}) and results from likelihood
216 ratio tests, which were used to determine the influence of each parameter on model fit.
217 Parameters were estimated by the maximum likelihood method (using the Laplace
218 approximation for GLMMs; Bolker *et al.*, 2009). Prior to analysis, we standardized all predictor
219 variables by subtracting the mean and dividing by two times the standard deviation (Gelman

220 2008). This standardization allowed for the direct comparison of parameter effects, including
221 those between continuous and categorical variables. We assessed multicollinearity between
222 predictor variables by measuring the variance inflation factor (VIF), which was low in all cases
223 (VIF<1). Figures used parameter estimates from the best performing model for each response
224 variable and included only fixed effects due to issues with estimating confidence intervals of
225 generalized linear mixed models with random effects (Bates et al. 2015).

226 Results

227 *Census*

228 Over the 10-year sampling period, caterpillar abundance varied from 0 to 200 caterpillars per
229 patch (mean±SD, 16.0±29.2). The proportion of patches that were occupied ranged from 0.14 to
230 1 per year (mean±SD, 0.79±0.27). The number of patch colonization and extinction events was
231 11 and 16, respectively. Differences in caterpillar abundance, proportion of occupied patches,
232 and the number of colonization and extinction events across high-and low-quality patches are
233 illustrated in Table 1 (but see results; statistical modeling).

234 *Patch structure*

235 Two patches were dropped from the annual census due to the bulldozing of ‘Dorm Marsh’ in
236 2012 by reserve managers and the natural senescence of *L. arboreus* bushes comprising ‘Bay
237 Marsh’ in 2015. The following description of patch structure includes all patches (i.e., years
238 2007-2011; see Online resource 3 for descriptive statistics during all census years). The mean
239 distance (±SD) between aggregation summits and larval patches was 906.7±462.2 m. These
240 distances were used to calculate a dimensionless connectivity index. The connectivity index
241 values ranged from 4.9 to 75.9, with an aggregate mean±SD of 25.9±18.0; connectivity did not

242 differ between low-quality (mean \pm SD, 31.0 \pm 20.3) and high-quality (mean \pm SD, 19.1 \pm 11.4)
243 patches (t=1.41, df=9.73, P=0.19).

244 *Statistical modeling*

245 The best fitting model (AIC_c_{min}) explaining patch-level caterpillar abundance included patch
246 quality, precipitation, and connectivity (Table 2, Table 3); caterpillar abundance was nearly 2 \times
247 higher in high-quality than low-quality patches (Table 1; Fig. 1). A 1 cm increase in rain in year
248 t-1 corresponded to an increase of 3.7 caterpillars. We found a positive relationship between
249 patch connectivity and caterpillar abundance, but this connectivity parameter did not improve
250 model fit according to a likelihood ratio test (Table 3, Fig. 1).

251 The probability of patch occupancy was best explained by patch quality, precipitation,
252 and connectivity (Table 2, Table 3). The proportion of occupied patches was 1.6 \times higher in high-
253 quality than low-quality patches (Table 1). The overall effect size for connectivity was less than
254 half of that for patch quality. As we expected, increased connectivity was positively correlated
255 with occupancy; this was especially true for low-quality patches (Fig. 2). Despite some model
256 support, the connectivity parameter, neither alone nor in an interaction with path quality,
257 improved model fit (Table 2, Table 3).

258 The best fitting model predicting the probability of colonization included two interaction
259 terms: precipitation \times connectivity and precipitation \times quality, but only the latter term
260 moderately improved model fit (Table 2, Table 3); precipitation positively correlated with
261 colonization, but for low-quality patches (Fig. 3). Total colonization events were 4.5 \times more
262 frequent in low-quality than high-quality patches (Table 1). This is likely a function of

263 colonization potential; low-quality patches were more often extinct and consequently had more
264 opportunities to be recolonized than high-quality patches during summers following wet years.

265 The probability of patch extinction was best explained by patch quality and precipitation,
266 with the effect size for precipitation being nearly 2× larger than for patch quality (Table 3). Total
267 extinction events were over 7× more frequent in low-quality than high-quality patches and were
268 more likely to occur following drought years (Table 1; Fig. 4).

269 For all response variables tested, we found substantial support (Δ -AICc <2) for additional
270 models, especially those containing interactions with connectivity (Table 2, online resource 4).
271 For example, we found support (Δ -AICc =0.1) for a model containing a precipitation ×
272 connectivity parameter for predicting the probability of occupancy (Online resource 5); there was
273 a strong positive relationship between precipitation and the probability of occupancy but only for
274 less connected (i.e., more isolated) patches. However, most of the parameters in these models did
275 not significantly increase model fit according to likelihood ratio tests. Because we only had 10
276 years of precipitation data, we had low power to test interactive effects.

277 Discussion

278 In agreement with other studies (Thomas et al. 2001; Fleishman et al. 2002; Schooley and
279 Branch 2009; Franzén and Nilsson 2010; Robles and Ciuad 2012), our results support the
280 inclusion of local factors in patch-based population models; patch quality was a strong driver of
281 the observed dynamics of *A. virginalis* caterpillars. Over the ten-year study, high-quality patches
282 were generally occupied with higher caterpillar abundances and experienced fewer local
283 extinctions compared to low-quality patches, regardless of connectivity. These results were
284 largely dependent on precipitation; the probability of occupancy and extinction were

285 indistinguishable in years following wet winters but differed following droughts, with droughts
286 being the most important factor predicting patch extinctions. Additionally, we found an
287 interaction between precipitation and patch quality explaining the probability of patch
288 colonization. In light of our earlier work, these findings suggest that increased precipitation may
289 reduce heterogeneity of patch quality, potentially through the displacement or numerical
290 reduction of predatory, ground-dwelling ants that prefer dry soil (Karban et al. 2017).
291 Alternatively, or in addition, rainy winters may decrease patch-to-patch variation in bottom-up
292 processes the following season. However, because the demographic studies which we used to
293 assign patch quality were only conducted in a subset of years and not in each year of this study,
294 we cannot make strong inferences regarding the influence of precipitation on patch quality. This
295 work demonstrates that in addition to underlying heterogeneity of patch quality, climatic
296 variables may drive source-sink dynamics of spatially structured populations, potentially by
297 affecting the spatial variation of trophic processes influencing patch conditions and
298 consequently, caterpillar survival.

299 Source-sink metapopulations are characterized by persistent populations in good habitat
300 ('sources') coupled to extinction prone populations in poor habitat ('sinks') by one-way
301 migration (Harrison 1991). For example, the checkered white butterfly continually occupies
302 riparian habitat where it can overwinter successfully. Peripheral patches become occupied in the
303 spring but only persist for a few generations until the onset of winter (Shapiro 1979). In this
304 example, habitat quality is seasonally dependent; non-riparian habitat is only a sink in the winter.
305 Like temporal dependence, temporary unfavorable conditions such as those associated with
306 extreme weather events can cause a traditional metapopulation to temporarily exhibit source-sink
307 dynamics. Rare freezes can rapidly degrade habitat and cause mass extinction events except in

308 refuge habitat (Boughton 1999). Flooding events can inundate generally high-quality habitat;
309 populations beyond the flood reaches act as sources to repopulate lower-lying habitat during
310 non-flooding periods (Johnson 2004). We found that interannual variation in precipitation
311 strongly influenced the observed dynamics of *A. virginalis*. During favorable seasons following
312 wet winters all patches were occupied and contained more caterpillars than on average, but
313 during unfavorable conditions following droughts, low-quality patches became extinction prone
314 and a higher proportion were unoccupied or had lower caterpillar abundances.

315

316 *Local vs regional factors*

317 Local patch quality had stronger effects than connectivity on caterpillar abundance and
318 extinction-colonization dynamics. Unlike most studies that use density to determine patch
319 quality, we determined quality through manipulative experiments investigating demography in
320 different habitat patches as suggested by Hall *et al.*, (1977). Strong bottom-up (unpublished
321 manuscript) and weak top-down forces (predominantly predation by ants; Karban *et al.*, 2013,
322 2017) conferred a survival advantage to early instar caterpillars in host plant patches occurring
323 within marsh habitat (high-quality) over those in coastal prairie habitat (low-quality). Finding
324 spatial variation of trophic forces is common for ecological studies conducted at the landscape
325 scale (Gripengberg *et al.* 2007). Accordingly, plant abundance or quality are often used as proxies
326 of patch quality (Mortelliti *et al.* 2010). It is less common to use predator density or predation
327 intensity as indicators of patch quality. Considering that predators can cause local extinctions
328 (Weisser 2000; van Nouhuys and Hanski 2002), determining patch quality through bottom-up
329 studies only (i.e., laboratory feeding assays or in-situ caging experiments, where predators are

330 excluded) could lead to erroneous conclusions. Moreover, because predators can affect
331 colonization decisions, incomplete understanding of top-down influences could obscure the
332 relative importance of local and regional processes (Shurin 2001; Kneitel and Miller 2003;
333 Grainger et al. 2017; Resetarits et al. 2018).

334 We found a positive but non-significant relationship between connectivity and caterpillar
335 abundance and patch occupancy. There are three potential explanations for this weak effect.
336 First, connectivity may be less important in this system. In metapopulation studies that included
337 patch quality (Thomas et al. 2001), and those solely concerned with patch geometry (Thomas et
338 al. 1992), connectivity often had little predictive power. Second, connectivity may be important
339 but at a larger spatial scale than considered here (Jackson and Fahrig 2015). However, we did
340 find some evidence that suggested that connectivity had a stronger effect on occupancy for low-
341 quality patches compared to high-quality patches (Table 2, Fig. 2). If conditions are sufficiently
342 poor (e.g., strong predation by ants of caterpillars) in low-quality patches such that the
343 probability of caterpillar survival is low, then it is likely that only those low-quality patches
344 which receive a high level of oviposition (i.e., highly connected) will remain occupied by the
345 time of our annual census.

346
347

348 *Precipitation:*

349 We found that precipitation from the previous hydrological year was a good predictor of the
350 dynamics exhibited by *A. virginalis*. Relatively few studies have explicitly quantified the effects
351 of weather on metapopulation dynamics (but see Pardikes et al. 2015, Tack et al. 2015,
352 Kahilainen et al. 2018). One explanation of this paucity is that early studies pooled occupancy

353 data over multiple years to account for stochastic environmental fluctuations (Hanski et al. 1996;
354 Moilanen 1999). The few studies that have modeled the effects of precipitation and temperature
355 or done so indirectly through changes in patch quality (Fleishman et al. 2002), have found strong
356 effects on spatio-temporal population dynamics. Padikes et al. (2015) found that warmer and
357 wetter years associated with sea-surface temperature anomalies generated by the El Nino
358 Southern Oscillation were correlated with increased sightings of numerous butterfly taxa across
359 the study region. In another example, using a 21-year Glanville fritillary butterfly census of over
360 4000 patches, Tack et al., (2015) demonstrated that the frequency of droughts synchronized
361 populations. This finding was confirmed by Kahilainen et al. (2018), who also ruled out the
362 possibility of predator-driven synchrony. We found the opposite; increased precipitation
363 synchronized the demographic variables across high- and low-quality patches. Synchronous
364 dynamics of local populations are expected to decrease the persistence time of a metapopulation
365 (Harrison and Quinn 1989; Liebhold et al. 2004). Synchrony reduces the potential for rescue
366 effects (Brown and Kodric-Brown 1977), which are the primary mechanisms promoting regional
367 stability. However, in a system characterized by deterministic extinctions brought about by low
368 patch quality, rescue effects are likely less effective.

369 Climate models predict a more variable climate with increased frequency and severity of
370 extreme weather events (Coumou and Rahmstorf 2012). This prediction is being borne out in
371 California, where summer droughts are becoming more common (Berg et al. 2015). Indeed,
372 several droughts occurred over the duration of this study (Table 1). If our inference that
373 decreased precipitation increased heterogeneity of patch quality is correct, then the benefit of
374 asynchronous dynamics driven by drought conditions would ultimately destabilize the
375 metapopulation: drier years were associated with more extinction events and a decreased

376 proportion of occupied patches that contained fewer caterpillars compared to wetter years. A
377 reduction in the number of suitable patches (i.e., more sinks) and a decreased number of
378 individuals contributing to the following generation will strongly decrease a metapopulation's
379 probability of regional persistence. This work suggests that metapopulations that are largely
380 comprised of drought-sensitive populations existing in low-quality habitat patches are at an
381 increased risk of a network-wide collapse under future climate regimes, when multiyear droughts
382 may become more common

383 Reductions in patch size or complete loss of patches resulting from climate change can
384 produce obvious effects. The effects of altered abiotic conditions on patch quality are more
385 difficult to detect. Johnson (2004) demonstrated that extreme weather events contributing to
386 flooding created strong sink habitat, but only during periods of inundation. At the scale of the
387 plant, a metaanalysis by Huberty & Denno (2004) showed that water stressed plants are of
388 reduced quality, negatively affecting the performance of several insect feeding guilds. Because
389 the field has focused on testing the importance of regional factors on metapopulation dynamics,
390 the interactive effects of weather variability on patch-quality for spatially-structured populations
391 is relatively understudied.

392

409 *Conclusions:*

410 We found that patch quality and precipitation had stronger relative effects than connectivity on
411 all demographic variables of a spatially structured population of an errepid caterpillar that
412 exhibits source-sink metapopulation dynamics. This finding adds to the growing list of studies
413 that have demonstrated the importance of including local factors when predicting occurrence

414 patterns. Our connectivity metric incorporated the natural history of hilltopping species, namely
415 constrained dispersal through mating aggregations at summits. Though less important than quality
416 and precipitation, finding model support for our connectivity metric indicates its potential
417 usefulness for modeling the spatial dynamics of other systems that exhibit hilltopping and
418 analogous mating systems such as lek polygyny in vertebrates (Bradbury and Vehrencamp
419 1977). Detecting a strong influence of precipitation on extinction and colonization dynamics,
420 highlights the importance of incorporating climatic variables in patch-based models to better
421 understand how temperature and precipitation will influence spatially-structured populations in
422 an increasingly variable world.

423 Acknowledgments:

424 We thank Zack Steel for improving the quality of the manuscript and Jennifer Danger Nill for
425 her quantitative assistance. We thank Jackie Sones and Suzanne Olyarnik for facilitating our
426 work at the UC Bodega Marine Reserve. We were supported by NSF-LTREB-0639885 and
427 157538.

428

429 References

430 Alcock J (1987) Leks and hilltopping in insects. *J Nat Hist* 21:319–328. doi:

431 10.1080/00222938700771041

432 Anzures-Dadda A, Manson & RH Patch-and landscape-scale effects on howler monkey

433 distribution and abundance in rainforest fragments. doi: 10.1111/j.1469-1795.2006.00074.x

434 Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using

435 **lme4**. *J Stat Softw* 67:1–48. doi: 10.18637/jss.v067.i01

436 Berg N, Hall A, Berg N, Hall A (2015) Increased Interannual Precipitation Extremes over
437 California under Climate Change. *J Clim* 28:6324–6334. doi: 10.1175/JCLI-D-14-00624.1

438 Bolker BM, Brooks ME, Clark CJ, et al (2009) Generalized linear mixed models: a practical
439 guide for ecology and evolution. *Trends Ecol Evol* 24:127–35. doi:
440 10.1016/j.tree.2008.10.008

441 Boughton D a. (1999) Empirical Evidence for Complex Source-Sink Dynamics with Alternative
442 States in a Butterfly Metapopulation. *Ecology* 80:2727. doi: 10.2307/177253

443 Bradbury JW, Vehrencamp SL (1977) Social organization and foraging in emballonurid bats.
444 *Behav Ecol Sociobiol* 2:1–17. doi: 10.1007/BF00299284

445 Brown JH, Kodric-Brown A (1977) Turnover Rates in Insular Biogeography: Effect of
446 Immigration on Extinction. *Ecology* 58:445–449. doi: 10.2307/1935620

447 Coumou D, Rahmstorf S (2012) A decade of weather extremes. *Nat Clim Chang* 2:491. doi:
448 10.1038/nclimate1452

449 Fleishman E, Ray C, Sjögren-gulve P, et al (2002) Assessing the Roles of Patch Quality, Area,
450 and Isolation in Predicting Metapopulation Dynamics. *Conserv Biol* 16:706–716

451 Franzén M, Nilsson SG (2010) Both population size and patch quality affect local extinctions
452 and colonizations. *Proceedings Biol Sci* 277:79–85. doi: 10.1098/rspb.2009.1584

453 Gelman A (2008) Scaling regression inputs by dividing by two standard deviations. *Stat Med*
454 *Stat Med* 27:2865–2873. doi: 10.1002/sim.3107

455 Grainger TN, Germain RM, Jones NT, Gilbert B (2017) Predators modify biogeographic

456 constraints on species distributions in an insect metacommunity. *Ecology* 98:851–860. doi:
457 10.1002/ecy.1712

458 Gripenberg S, Roslin T, Gripenberg S, Roslin T (2007) Up or down in space? Uniting the
459 bottom-up versus top-down paradigm and spatial ecology. *Res Oikos* 116:181–188. doi:
460 10.1

461 Grof-Tisza P, Steel Z, Cole EM, et al (2017) Testing predictions of movement behaviour in a
462 hilltopping moth. *Anim Behav* 133:161–168. doi: 10.1016/j.anbehav.2017.08.028

463 Grof-Tisza P, Steel Z, Karban R (2016) The Spatial Distribution and Oviposition Preference of
464 the Ranchman’s Tiger Moth, *Platyprepia virginalis* (Lepidoptera: Erebidae). *J Lepid Soc*
465 71:16–19. doi: 10.18473/lepi.v71i1.a4

466 Hall LS, Krausman PR, Morrison ML (1997) The Habitat Concept and a Plea for Standard
467 Terminology. *Wildl. Soc. Bull.* 25:173–182

468 Hanski I (1994) Patch-occupancy dynamics in fragmented landscapes. *Trends Ecol Evol* 9:131–
469 135. doi: 10.1016/0169-5347(94)90177-5

470 Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49. doi: 10.1038/23876

471 Hanski I, Moilanen A, Pakkala T, Kuussaari M (1996) The quantitative incidence function model
472 and persistence of an endangered butterfly metapopulation. 10:578–590

473 Hanski I, Thomas CD (1994) Metapopulation dynamics and conservation: A spatially explicit
474 model applied to butterflies. *Biol Conserv* 68:167–180. doi: 10.1016/0006-3207(94)90348-
475 4

476 Harrison S (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biol J*
477 *Linn Soc* 42:73–88. doi: 10.1111/j.1095-8312.1991.tb00552.x

478 Harrison S, Quinn JF (1989) Nordic Society Oikos Correlated Environments and the Persistence
479 of Metapopulations. Source: *Oikos* 56:293–298

480 Huberty AF, Denno RF (2004) Plant water stress and its consequences for herbivorous insects: a
481 new synthesis. *Ecology* 85:1383–1398

482 Huey RB, Kingsolver JG (1989) Evolution of thermal sensitivity of ectotherm performance.
483 *Trends Ecol Evol* 4:131–135. doi: 10.1016/0169-5347(89)90211-5

484 Hunter MD, Price PW (1992) Playing Chutes and Ladders: Heterogeneity and the Relative Roles
485 of Bottom-Up and Top-Down Forces in Natural Communities. *Ecology* 73:724–732. doi:
486 10.2307/1940152

487 Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? *Glob Ecol*
488 *Biogeogr* 24:52–63. doi: 10.1111/geb.12233

489 Johnson DM (2004) Source-Sink dynamics in a temporally heterogeneous environment. *Ecology*
490 85:2037–2045. doi: 10.1890/03-0508

491 Kahilainen A, van Nouhuys S, Schulz T, Saastamoinen M (2018) Metapopulation dynamics in a
492 changing climate: Increasing spatial synchrony in weather conditions drives metapopulation
493 synchrony of a butterfly inhabiting a fragmented landscape. *Glob Chang Biol*. doi:
494 10.1111/gcb.14280

495 Karban R, de Valpine P (2010) Population dynamics of an Arctiid caterpillar-tachinid parasitoid
496 system using state-space models. *J Anim Ecol* 79:650–61. doi: 10.1111/j.1365-

497 2656.2010.01664.x

498 Karban R, Grof-Tisza P, Holyoak M (2017) Wet years have more caterpillars: interacting roles
499 of plant litter and predation by ants. *Ecology* 98:2370–2378. doi: 10.1002/ecy.1917

500 Karban R, Grof-Tisza P, Maron JL, Holyoak M (2012) The importance of host plant limitation
501 for caterpillars of an arctiid moth (*Platyprepia virginalis*) varies spatially. *Ecology* 93:2216–
502 2226

503 Karban R, Grof-Tisza P, Mcmmunn M, et al (2015) Caterpillars escape predation in habitat and
504 thermal refuges. *Ecol Entomol* 40:725–731. doi: 10.1111/een.12243

505 Karban R, Mata TM, Grof-Tisza P, et al (2013) Non-trophic effects of litter reduce ant predation
506 and determine caterpillar survival and distribution. *Oikos* 122:1362–1370

507 Kneitel JM, Miller TE (2003) Dispersal Rates Affect Species Composition in Metacommunities
508 of *Sarracenia purpurea* Inquilines. *Am Nat* 162:165–171. doi: 10.1086/376585

509 Liebhold A, Koenig WD, Bjørnstad ON (2004) Spatial Synchrony in Population Dynamics.
510 *Annu Rev Ecol Evol Syst* 35:467–490. doi: 10.1146/annurev.ecolsys.34.011802.132516

511 Moilanen A (1999) Patch Occupancy Models of Metapopulation Dynamics: Efficient Parameter
512 Estimation Using Implicit Statistical Inference. *Ecology* 80:1031. doi: 10.2307/177036

513 Moilanen A, Hanski I (1998) Metapopulation dynamics: effects of habitat quality and landscape
514 structure. *Ecology* 79:2503–2515. doi: 10.1890/0012-
515 9658(1998)079[2503:MDEOHQ]2.0.CO;2

516 Mortelliti A, Amori G, Boitani L (2010) The role of habitat quality in fragmented landscapes: a

517 conceptual overview and prospectus for future research. *Oecologia* 163:535–47. doi:
518 10.1007/s00442-010-1623-3

519 Pachauri RK, Meyer, A. L (2014) Climate change 2014: Synthesis report. Contribution of
520 working groups I, II and III to the fifth assessment report of the intergovernmental panel on
521 climate change. IPCC

522 Painter KJ (2014) Multiscale models for movement in oriented environments and their
523 application to hilltopping in butterflies. *Theor Ecol* 7:53–75. doi: 10.1007/s12080-013-
524 0198-0

525 Pardikes NA, Shapiro AM, Dyer LA, Forister ML (2015) Global weather and local butterflies:
526 Variable responses to a large-scale climate pattern along an elevational gradient. *Ecology*
527 96:2891–2901. doi: 10.1890/15-0661.1.sm

528 Pe'er G, Saltz D, Münkemüller T, et al (2013) Simple rules for complex landscapes: the case of
529 hilltopping movements and topography. *Oikos* no-no. doi: 10.1111/j.1600-
530 0706.2013.00198.x

531 Pe'er G, Saltz D, Thulke H-H, Motro U (2004) Response to topography in a hilltopping butterfly
532 and implications for modelling nonrandom dispersal. *Anim Behav* 68:825–839. doi:
533 10.1016/J.ANBEHAV.2004.02.006

534 Pepi A, Grof-Tisza P, Holyoak M, Karban R (2018) As temperature increases, predator attack
535 rate is more important to survival than a smaller window of prey vulnerability. *Ecology*.
536 doi: 10.1002/ecy.2356

537 Powell JA, Opler PA (2009) *Moths of Western North America*. University of California Press

538 Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on
539 fragmented animal populations. *Proc Natl Acad Sci U S A* 105:20770–5. doi:
540 10.1073/pnas.0806080105

541 R Development Core Team R (2011) R: A Language and Environment for Statistical Computing.
542 R Found. Stat. Comput. 1:409

543 Rabasa SG, Gutiérrez D, Escudero A (2008) Relative importance of host plant patch geometry
544 and habitat quality on the patterns of occupancy, extinction and density of the monophagous
545 butterfly *Iolana iolas*. *Oecologia* 156:491–503. doi: 10.1007/s00442-008-1008-z

546 Resetarits WJ, Bohenek JR, Breech T, Pintar MR (2018) Predation risk and patch size jointly
547 determine perceived patch quality in ovipositing treefrogs, *Hyla chrysoscelis*. *Ecology*. doi:
548 10.1002/ecy.2130

549 Robles H, Ciudad C (2012) Influence of Habitat Quality, Population Size, Patch Size, and
550 Connectivity on Patch-Occupancy Dynamics of the Middle Spotted Woodpecker. *Conserv*
551 *Biol* 26:284–293. doi: 10.1111/j.1523-1739.2011.01816.x

552 Schooley RL, Branch LC (2009) Enhancing the area-isolation paradigm: habitat heterogeneity
553 and metapopulation dynamics of a rare wetland mammal. *Ecol Appl* 19:1708–22

554 Shapiro A (1979) Weather and the liability of breeding populations of the checkered white
555 butterfly, *Pieris protodice*. *J Res Lepid* 17:1–23

556 Shields O (1967) Hilltopping: an ecological study of summit congregation behavior of butterflies
557 on a southern California hill. *J Res Lepid* 6:69–178

558 Shurin JB (2001) Interactive effects of predation and dispersal on zooplankton communities.

559 Ecology 82:3404–3416. doi: 10.1890/0012-9658(2001)082[3404:IEOPAD]2.0.CO;2

560 Tack AJM, Mononen T, Hanski I (2015) Increasing frequency of low summer precipitation
561 synchronizes dynamics and compromises metapopulation stability in the Glanville fritillary
562 butterfly. *Proceedings Biol Sci* 282:20150173. doi: 10.1098/rspb.2015.0173

563 Thomas CD, Harrison S (1992) Spatial dynamics of a patchily distributed butterfly species.
564 61:437–446

565 Thomas CD, Thomas JA, Warren MS (1992) Distributions of occupied and vacant butterfly
566 habitats in fragmented landscapes. *Oecologia* 92:563–567

567 Thomas JA, Bourn NA, Clarke RT, et al (2001) The quality and isolation of habitat patches both
568 determine where butterflies persist in fragmented landscapes. *Proceedings Biol Sci*
569 268:1791–6. doi: 10.1098/rspb.2001.1693

570 van Nouhuys S, Hanski I (2002) Colonization rates and distances of a host butterfly and two
571 specific parasitoids in a fragmented landscape. *J Anim Ecol* 71:639–650. doi:
572 10.1046/j.1365-2656.2002.00627.x

573 Ver Hoef JM, Boveng PL (2007) QUASI-POISSON VS. NEGATIVE BINOMIAL
574 REGRESSION: HOW SHOULD WE MODEL OVERDISPersed COUNT DATA?
575 *Ecology* 88:2766–2772. doi: 10.1890/07-0043.1

576 Weisser WW (2000) Metapopulation dynamics in an aphid-parasitoid system. *Entomol Exp Appl*
577 97:83–92. doi: 10.1046/j.1570-7458.2000.00719.x

578

579

580

581

582

Table 1: Annual mean and standard deviation of *Arctia virginalis* caterpillar abundance, proportion of occupied patches, proportion of patch turnover, and the number extinction and colonization events across 6* marsh and 7 prairie habitat patches.

Year	Total t-1 precipitation	High-quality (marsh) habitat				Low-quality (prairie) habitat			
		Abundance (mean±SD)	Occupancy	Extinction	Colonization	Abundance (mean±SD)	Occupancy	Extinction	Colonization
2007	124.2	31.7±23.0	1			38.1±72.2	0.86		
2008	64.8	35.2±28.5	1	0	0	13.7±10.2	0.86	0	0
2009	72.2	13.2±18.6	0.83	1	0	0.6±0.5	0.57	3	1
2010	53.9	9.7±6.3	1	0	1	0.3±0.5	0.29	4	2
2011	103.4	29.2±15.14	1	0	0	3.7±5.3	0.71	0	3
2012	111.3	67±19.6	1	0	0	33.7±40.4	1	0	2
2013	63.3	3.4±2.5	1	0	0	23.1±50.3	0.71	2	0
2014	74.9	6.8±2.4	1	0	0	1.9±1.6	0.71	1	1
2015	54.5	6.3±6.1	0.75	1	0	1.6±3.7	0.29	3	0
2016	70.6	6.8±6.8	1	0	1	0.1±0.4	0.14	1	0
2007-16 (mean±SD)	79.3±24.7	21.7±23.9	0.96±0.1	0.22±0.4	0.22±0.4	11.7±32.1	0.61±0.5	1.56±1.5	0.90±1.1

* In 2012-14 and 2015-16, 5 and 4 marsh patches were surveyed, respectively, as a result of patch destruction and lupine senesce

Table 2. Parameters (q, patch quality; c, connectivity; p, t-1 precipitation) and model comparisons (Akaike statistics corrected for sample size) for response variables (Patch-level caterpillar abundance and probabilities of patch occupancy, colonization, and extinction) for a spatially structured population of *A. virginalis*, in a 10-year study. An $\alpha = 0.3$ km was used to calculate connectivity. All models included “patch” as a random effect to account for a repeated measures experimental design. Models with strong support ($\Delta AIC_c < 2$) are shown in boldface.

Model no.	Parameters	Abundance		Occupancy		Colonization		Extinction	
		ΔAIC_c	AICc weight	ΔAIC_c	AICc weight	ΔAIC_c	AICc weight	ΔAIC_c	AICc weight
1	~ q x c + q x p + p x c	2.7	0.04	6.2	0.01	1.6	0.10	5.3	0.02
2	~ q x c + q x p	2.4	0.05	4.4	0.03	4.9	0.02	5.9	0.02
3	~ q x c + p x c	0.5	0.12	4	0.04	5.8	0.01	3.8	0.05
4	~ q x p + p x c	2.2	0.05	3.9	0.04	0	0.22	3.2	0.07
5	~ q x c + p	0.1	0.15	2.2	0.09	6.1	0.01	3.8	0.05
6	~ q x p + c	2.1	0.06	2.2	0.09	2.8	0.06	3.9	0.05
7	~ p x c + q	0.1	0.16	1.8	0.11	3.5	0.04	1.7	0.14
8	~ q x c	18.7	<0.001	12.2	<0.001	6.2	0.01	12.9	<0.001
9	~ q x p	2.6	0.04	2.4	0.08	0.6	0.16	2.1	0.11
10	~ p x c	5.1	0.01	15.4	<0.001	4.4	0.02	6.5	0.01
11	~ q + c + p	0	0.16	0	0.27	4	0.03	1.8	0.13
12	~ q + c	19.6	<0.001	10	0.00	4.2	0.03	10.9	0.00
13	~ c + p	5	0.01	13.4	<0.001	4.6	0.02	6.3	0.01
14	~ q + p	0.7	0.12	0.3	0.23	1.9	0.08	0	0.32
15	~ q	24	<0.001	10.4	0.00	2.1	0.08	9.1	0.00
16	~ c	27.5	<0.001	23.9	<0.001	4.7	0.02	15.1	<0.001
17	~ p	3.1	0.03	11.3	<0.001	3.2	0.04	6.3	0.01
18	~ intercept	26.4	<0.001	21.9	<0.001	3.3	0.04	15	<0.001

Notes: ‘Abundance’ was modeled using a negative binomial error distribution; the other response variables were modeled using a binomial error distribution. Akaike weight (AICc weight) is the probability that a given model is best among all candidate models, given the data

Table 3. Parameter estimates and standard error for the most parsimonious models ($AIC_{c_{min}}$) determined through AICc model comparison for the four dependent variables of interest; for these best performing models, we used backwards step deletion (1 degree of freedom) from the full model (i.e., maximum number of parameters in $AIC_{c_{min}}$) and likelihood ratio tests (LRT) to determine the contribution of each parameter to overall model fit.

Response variable and fixed effect	Standardized effect size	SE	X^2 df	LRT	P value
Caterpillar Abundance					
Quality	1.47	0.50	1	4.62	0.03
Connectivity	0.86	0.49	1	2.86	0.09
Precipitation	1.33	0.27	1	25.47	<0.001
Probability of patch occupancy					
Quality	3.36	0.88	1	13.57	<0.001
Connectivity	0.98	0.60	1	2.5	0.11
Precipitation	2.04	0.69	1	12.2	<0.001
Probability of patch colonization					
Quality	-2.01	1.50	1	3.30	0.07
Connectivity	-0.14	0.82	1	0.08	0.78
Precipitation	2.33	0.98	1	2.33	0.13
Quality \times Precipitation	-5.94	3.47	1	5.79	0.06
Connectivity \times Precipitation	-3.73	1.99	1	2.75	0.10
Probability of patch extinction					
Quality	-1.99	0.81	1	7.96	0.01
Precipitation	-3.60	1.42	1	11.27	<0.001

Figure legends:

Figure 1. The relationship between log abundance of caterpillars and standardized precipitation (left panel) and standardized connectivity (right panel). Center lines represent best fit from statistical models and outer lines represent the 95% confidence interval. Blue and red lines associated with dashed and solid confidence intervals represent high- and low-quality patches, respectively. White and black circles represent the raw data for high- and low-quality sites, respectively.

Figure 2. The relationship between the probability of patch occupancy and standardized precipitation (left panel) and standardized connectivity (right panel). Center lines represent best fit from statistical models and outer lines represent the 95% confidence interval. Blue and red lines associated with dashed and solid confidence intervals represent high- and low-quality patches, respectively.

Figure 3. The relationship between the probability of patch colonization and standardized precipitation. Center lines represent best fit from statistical models and outer lines represent the 95% confidence interval. Blue and red lines associated with dashed and solid confidence intervals represent high- and low-quality patches, respectively (Left panel). The relationship between the probability of patch colonization and the interaction of standardized connectivity and precipitation (Right panel).

Figure 4. The relationship between the probability of patch extinction and standardized precipitation. Center lines represent best fit from statistical models and outer lines represent the 95% confidence interval. Blue and red lines associated with dashed and solid confidence intervals represent high- and low-quality patches, respectively.

Figure 1.

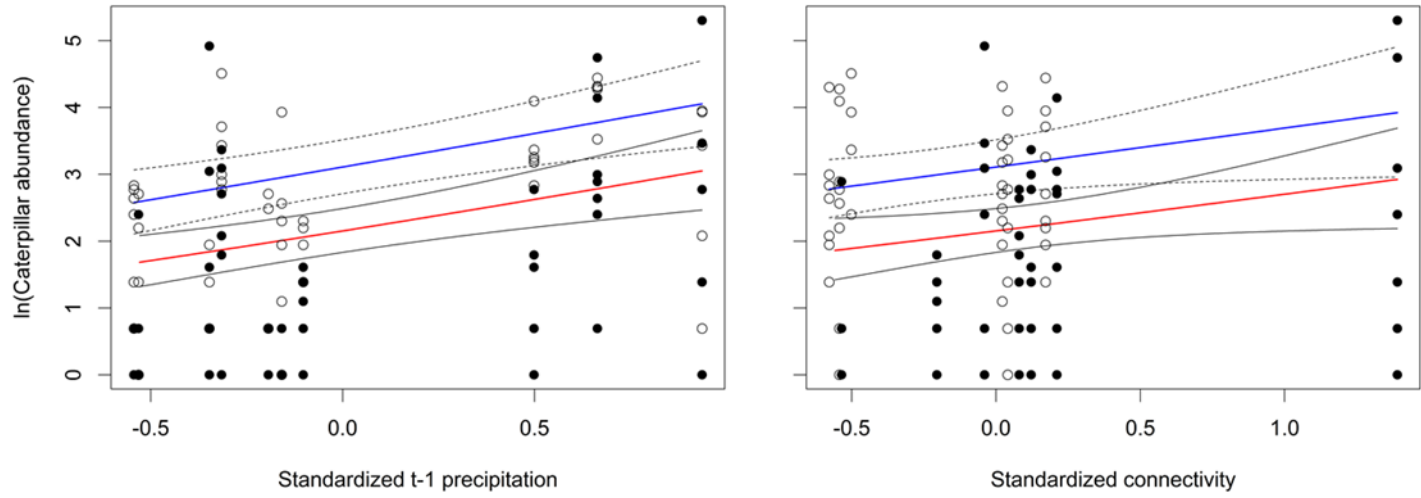


Figure 2

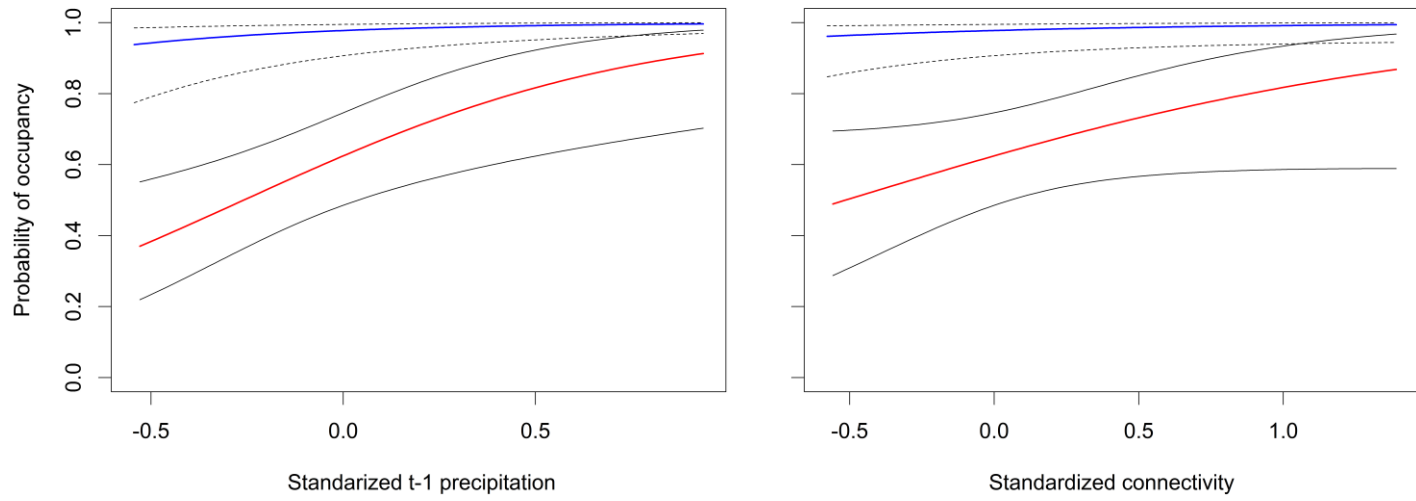


Figure 3

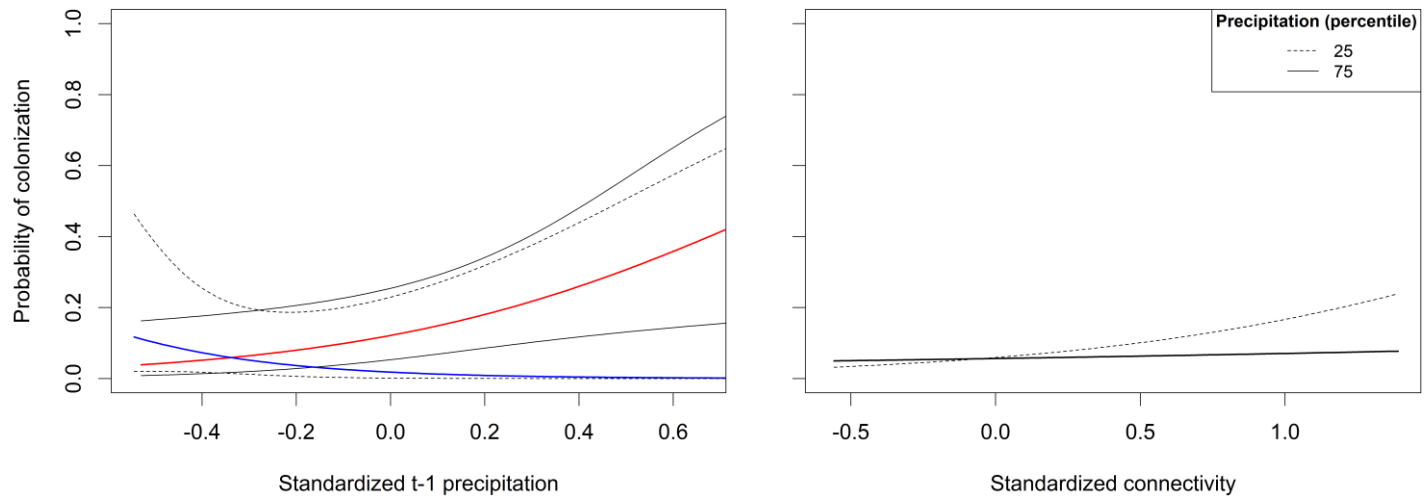


Figure 4

