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1 **Title:** Observational evidence that maladaptive gene flow reduces patch occupancy in a
2 wild insect metapopulation

3

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26 **Abstract**

27 Theory predicts that dispersal throughout metapopulations has a variety of
28 consequences for the abundance and distribution of species. Immigration is predicted to
29 increase abundance and habitat patch occupancy, but gene flow can have both positive
30 and negative demographic consequences. Here, we address the eco-evolutionary effects
31 of dispersal in a wild metapopulation of the stick insect *Timema cristinae*, which
32 exhibits variable degrees of local adaptation throughout a heterogeneous habitat patch
33 network of two host-plant species. To disentangle the ecological and evolutionary
34 contributions of dispersal to habitat patch occupancy and abundance, we contrasted the
35 effects of connectivity to populations inhabiting conspecific host plants and those
36 inhabiting the alternate host plant. Both types of connectivity should increase patch
37 occupancy and abundance through increased immigration and sharing of beneficial
38 alleles through gene flow. However, connectivity to populations inhabiting the alternate
39 host-plant species may uniquely cause maladaptive gene flow that counters the positive
40 demographic effects of immigration. Supporting these predictions, we find the
41 relationship between patch occupancy and alternate-host connectivity to be
42 significantly smaller in slope than the relationship between patch occupancy and
43 conspecific-host connectivity. Our findings illustrate the ecological and evolutionary
44 roles of dispersal in driving the distribution and abundance of species.

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50 **Introduction**

51 There is now abundant evidence that rapid evolution can play a major role in
52 driving ecological dynamics (Hairston et al. 2005; Schoener 2011), and many sub-
53 disciplines of ecology have seen excellent examples of the unexpectedly far-reaching
54 effects of contemporary evolution (Bailey et al. 2009). For example, studies of
55 population demography (Pelletier et al. 2007; Ozgul et al. 2010; Turcotte et al. 2013),
56 predator-prey cycling (Yoshida et al. 2003; Becks et al. 2010; Hiltunen et al. 2014),
57 community structure (Johnson et al. 2009; Farkas et al. 2013; Urban 2013; Pantel et al.
58 2015), and ecosystem function (Harmon et al. 2009; Bassar et al. 2010; Crutsinger et al.
59 2014) each support how evolution has unanticipated explanatory power in an
60 ecological context.

61 Eco-evolutionary research has for the most part focused on natural selection as
62 the primary evolutionary process of interest, paying less attention to the effects of gene
63 flow, mutation, and genetic drift. This focus has stunted the integration of rapid
64 evolution into ecological subdisciplines for which dispersal is a key feature, such as
65 metapopulation ecology (Hanski 2012), metacommunity ecology (Urban et al. 2008),
66 and island biogeography (Farkas et al. 2015). Although natural selection should feature
67 strongly in how evolution can be important for these subdisciplines (e.g., Farkas et al.
68 2013; Urban 2013), a complete eco-evolutionary approach will necessarily integrate the
69 role of gene flow that results from dispersal.

70 Metapopulation ecology in particular has been hugely successful as a paradigm
71 with which to understand the dynamics of populations across space (Hanski 1998),
72 forming a foundation for modern conservation biology (Hanski and Simberloff 1997).
73 Studies integrating evolution into metapopulation ecology have largely focused on
74 either the evolution of dispersal itself (Van Valen 1971; McPeck and Holt 1992; Ronce

2007; Amarasekare 2016), or on how natural selection and gene flow interact to drive the evolution of functional traits in heterogeneous environments (Hendry et al. 2002; Wynne et al. 2003; Kawecki 2004; Hanski et al. 2010; Hanski and Mononen 2011; Farkas et al. 2013). However, gene flow can either promote or constrain adaptation, depending on degrees of dispersal, habitat heterogeneity, local adaptation, and reproductive isolation (Garant et al. 2007). Therefore, the potential effects of dispersal on metapopulation dynamics as mediated by gene flow are complex, either increasing or decreasing the likelihoods of patch colonization and extinction. This contrasts with much metapopulation theory, which generally predicts dispersal, and population connectivity in particular, to increase patch occupancy through increased colonization of empty habitat and reduced extinction of occupied habitat (Hanski 1994; del Mar Delgado et al. 2011; but see Bowler and Benton 2005 for complexities). Hence, the eco-evolutionary effects of dispersal in metapopulations are complex, but little empirical work has tested a synthetic eco-evolutionary framework (Farkas et al. 2013).

One central but largely untested aspect of eco-evolutionary metapopulation biology is the prediction that gene flow can reduce patch occupancy through increased maladaptation. It is well documented that gene flow can cause maladaptation in nature (Riechert 1993; Storfer and Sih 1998; Moore and Hendry 2005; Postma and van Noordwijk 2005; Bolnick and Nosil 2007; Bolnick et al. 2008; McBride and Singer 2010; Paul et al. 2011; Fedorka et al. 2012; Kovach et al. 2015), but the link from maladaptation to patch occupancy has not been well established empirically. In fact, evidence that maladaptive gene flow can have negative population demographic consequences at all is scarce, with support coming from only a small number of studies (Moore and Hendry 2009; Farkas et al. 2013).

99 In this paper, we offer observational evidence that gene flow between
100 divergently adapted *Timema cristinae* stick insect populations decreases the likelihood
101 of local patch occupancy. In *T. cristinae*, strong selection by avian predators on a highly
102 heritable camouflage polymorphism (striped versus unstriped morphs) drives local
103 adaptation to two morphologically dissimilar host-plant species (Sandoval 1994a; Nosil
104 and Crespi 2006; Comeault et al. 2014; Gompert et al. 2014). However, gene flow
105 between populations inhabiting alternate hosts breaks down local adaptation (Sandoval
106 1994b; Bolnick and Nosil 2007; Nosil 2009), leading to a geographic mosaic of
107 (mal)adaptation (Sandoval 1994b; Bolnick and Nosil 2007). Variation in the local
108 frequency of the poorly camouflaged morph ranges from as low as 1-3% and as high as
109 80%, due to variation in gene flow from populations adapted to the alternate host
110 (Sandoval 1994b; Bolnick and Nosil 2007).

111 Recently, Farkas et al. (2013) reported results concerning two central
112 predictions of eco-evolutionary metapopulation theory. First, they showed
113 experimentally that camouflage maladaptation reduces *T. cristinae* abundance due to
114 increased bird predation. Natural observations offered corroboration, showing that
115 maladaptation negatively correlated with abundance. Second, they tested for an
116 influence of gene flow on maladaptation by correlating the morph frequency in host-
117 plant patches with the expected morph frequency of immigrants. They did not find an
118 association, suggesting that gene flow did not play a role in structuring phenotypic
119 variation across the landscape (Farkas et al. 2013). This finding was surprising given
120 strong and diverse evidence for detectable effects of gene flow across multiple spatial
121 scales in past work (Sandoval 1994b; Nosil et al. 2003, 2012; Nosil 2009). A third
122 prediction – that maladaptive gene flow can reduce patch occupancy – remains untested
123 empirically, although Farkas et al. (2013) used an eco-evolutionary metapopulation

124 model (Hanski et al. 2010) to demonstrate how maladaptation in *T. cristinae* should in
125 principle reduce habitat patch occupancy through increased local extinctions.

126 Here, we use the observational data from Farkas et al. (2013) to test this third
127 prediction. To do so, we use the concept of population connectivity, which integrates
128 the geographical distance to populations and abundance in those populations (see
129 Supplemental Information) to measure the expected amount of immigration to any
130 given habitat patch (Hanski 1994). For every habitat patch, whether occupied or
131 unoccupied, we can calculate population connectivity, and can calculate more derived
132 and specific measures of population connectivity by excluding a subset of populations
133 based on arbitrary criteria such as patch size or habitat type. Here, for each host-plant
134 patch in the natural landscape of interest, we sub-divide the total population
135 connectivity by calculating two, non-overlapping measures of connectivity based on
136 host-plant species. "Alternate-host connectivity" measures population connectivity only
137 to populations of *T. cristinae* living on the alternate host-plant species. "Conspecific-host
138 connectivity" measures connectivity only to populations of *T. cristinae* living on the
139 same (conspecific) host-plant species. For example, for all *A. fasciculatum* patches,
140 conspecific-host connectivity measures population connectivity using only *T. cristinae*
141 populations inhabiting other *A. fasciculatum* patches, whereas alternate-host
142 connectivity measures populations connectivity only using *T. cristinae* populations
143 inhabiting *C. spinosus* patches.

144 Metapopulation theory predicts increasing connectivity to increase patch
145 occupancy due to ecological mass effects (i.e., direct increases in abundance through
146 immigration), by increasing colonisation and reducing the likelihood of extinction
147 (Hanski 1998). However, evolutionary models predict more complex effects of
148 connectivity for populations, especially in heterogeneous landscapes (Garant et al.

149 2007). On the one hand, gene flow can increase fitness as it promotes adaptation by
150 increasing genetic variance (Barton 2001; Swindell and Bouzat 2006), facilitates the
151 spread of beneficial mutations (Peck et al. 1998; Feder et al. 2003; Morjan and
152 Rieseberg 2004), reduces genetic drift by increasing neighbourhood size (Alleaume-
153 Benharira et al. 2006), and reduces inbreeding depression (Ingvarsson and Whitlock
154 2000; Keller and Waller 2002). On the other hand, gene flow between alternate habitats
155 may reduce mean population fitness and constrain adaptation by driving the
156 phenotypic mean away from the optimum (Sandoval 1994b; Bolnick and Nosil 2007;
157 Nosil 2009) and introducing a variance load as the distribution of phenotypes spreads
158 away from the mean (Bridle et al. 2010). The positive fitness and demographic effects of
159 gene flow and mass effects should be roughly equal for alternate- and conspecific-host
160 connectivity, but we predict the negative effects to be larger for alternate- than
161 conspecific-host connectivity (Figure 1, inset).

162 Following the above-predicted mechanisms, we evaluate the influence of
163 maladaptive gene flow by testing for a difference between the effects of alternate- and
164 conspecific-host connectivity on patch occupancy and abundance (see Sexton et al. 2011
165 for similar approach). Because of the potentially negative effects of maladaptive gene
166 flow on patch occupancy, eco-evolutionary metapopulation theory predicts the
167 relationship between patch occupancy/abundance and alternate-host connectivity to be
168 smaller in slope (i.e., **less positive**) than the relationship with conspecific-host
169 connectivity (Figure 1). The magnitude of difference in the slopes will be determined a
170 balance of positive and negative effects. Although we might predict both slopes to be
171 positive in sign, the sign of the slopes could differ if the effects of maladaptive gene flow
172 are so strong that alternate-host connectivity has a net negative influence on patch
173 occupancy, despite the positive role of mass effects and beneficial gene flow. In this

174 context, conspecific-host connectivity serves as control against which we compare the
175 effect of alternate-host connectivity, allowing us to isolate the effects of maladaptive
176 gene flow on patch occupancy and abundance.

177

178 **Methods**

179 *Study system*

180 *Timema cristinae* is a sexual, univoltine, flightless stick insect (Phasmida:
181 Timematodea) endemic to a ~30-km² region of chaparral habitats outside Santa
182 Barbara, California, where it is the only resident species in the genus *Timema*. They feed
183 predominantly on the perennial shrubs *Adenostoma fasciculatum* (Rosaceae) and
184 *Ceanothus spinosus* (Rhamnaceae), which are dominant plants in the chaparral of this
185 region. The plant species differ substantially in leaf morphology, with *A. fasciculatum*
186 having fascicled, needle-like leaves and *C. spinosus* having broad, ovate leaves. Divergent
187 natural selection from bird predators has led to the evolution of two morphs that are
188 each best camouflaged on one of the host-plant species: a striped morph with a
189 prominent white dorsal stripe is best camouflaged on *A. fasciculatum*, and an unstriped,
190 solid-green morph is best camouflaged on *C. spinosus* (Sandoval 1994a; Nosil and Crespi
191 2006). In addition, body shape, size, and hue are all under divergent selection from
192 predators between the two host-plant species, and thus contribute to the ability of
193 ecotypes to achieve good crypsis (Nosil and Crespi 2004, 2006). Mark-recapture studies
194 demonstrate that many or even most *T. cristinae* individuals remain on a single host
195 plant individual for extended periods, with the average weekly dispersal distance being
196 ~2m, the maximum ~8m, and the per-generation dispersal estimated at ~12m
197 (Sandoval 2000). When the host-plant species are in proximity to one another, this
198 dispersal can lead to substantial degrees of maladaptation, depending on the relative

199 abundance of each host species in the landscape (Sandoval 1994b; Bolnick and Nosil
200 2007).

201

202 *Sampling protocol*

203 Between the 1st and 5th of April 2011, we sampled all *Adenostoma fasciculatum*
204 (N = 117) and *Ceanothus spinosus* (N = 69) patches in a 30 x 60 meter area (Figure 2;
205 N34.513297, W-119.800065, elevation: 850m) by vigorously shaking all branches and
206 catching fallen *T. cristinae* in a sweep net. Individual plants of the same species were
207 determined to be part of the same patch if they were within 30 cm of one another. One
208 of us (P.N.) phenotyped all *Timema* as striped or unstriped, recording morph
209 frequencies and population sizes in each patch. Because melanic (brown, red, or grey)
210 *Timema* individuals are relatively rare and are not host-associated (Comeault et al.
211 2015), records of melanic individuals were not included in calculations of abundance or
212 phenotype frequency. We manually mapped the geographic location and measured the
213 physical dimensions of each host-plant patch (Figure 2), and patch size was calculated
214 as rectangular solid. Further details of the sampling protocol are found in Farkas et al.
215 (2013).

216

217 *Data Analysis*

218 The core test of our hypothesis involves testing for a difference between the
219 effects of alternate- and conspecific-host connectivity on patch occupancy (occupied
220 versus unoccupied) and *Timema* abundance. We did this by combining generalized
221 linear models with linear hypothesis testing (Fox and Weisberg 2011), comparing
222 parameter estimates within the models. This approach is akin to testing for an
223 interaction between the degree of connectivity and the type of connectivity (alternate

224 vs. conspecific). However, each habitat patch has a measure of each type of connectivity,
225 precluding the use of a two-way analytical approach. Alternate- and conspecific-host
226 connectivity were calculated as connectivity to populations inhabiting the alternate
227 versus conspecific host-plant species, the sum of which equals the total population
228 connectivity (see Supporting Information for details of how these indices were
229 estimated). Thus, alternate-host connectivity equals the connectivity to *T. cristinae*
230 populations inhabiting *C. spinosus* for *A. fasciculatum* patches and *A. fasciculatum* for *C.*
231 *spinosus* patches, whereas conspecific-host connectivity equals connectivity to *T.*
232 *cristinae* populations inhabiting *A. fasciculatum* for *A. fasciculatum* patches and *C.*
233 *spinosus* for *C. spinosus* patches.

234 For the analysis of both patch occupancy and abundance, we used a single hurdle
235 model for zero-inflated and overdispersed count data (R package *pscl*; Zeileis et al.
236 2008) because it is a holistic approach that simultaneously analyzes occupancy and
237 abundance data, and because our abundance data were both overdispersed and zero-
238 inflated, such that purely Poisson-error models were inappropriate (Supporting
239 Information). The censored component of the model (zero vs. non-zero) used a
240 binomial distribution with logit link function (analogous to a binomial GLM) and
241 effectively modelled patch occupancy, whereas the zero-truncated component used a
242 Poisson distribution and effectively modelled *T. cristinae* abundance, not including zero
243 values.

244 In addition to considering the effects of connectivity on patch occupancy and
245 abundance, we test for an influence of alternate- and conspecific-host connectivity on
246 the degree of maladaptation, predicting a positive relationship with alternate-host
247 connectivity, a negative relationship with conspecific-host connectivity, and a difference
248 between the slopes of those relationships. We fit a generalized linear mixed model using

249 Penalized Quasi-Likelihood with Bernoulli error (MASS package in R), coding *Timema* as
250 either adapted or maladapted, according to the match between their morph (striped
251 versus unstriped) and host-plant species, again employing linear hypothesis testing
252 (Fox and Weisberg 2011) to compare slopes. Host-plant patch ID was included as a
253 random factor ($n = 136$) to account for non-independence among individuals collected
254 from the same bush, but this factor explained negligible variance (intraclass correlation
255 coefficient = 2.7×10^{-8}).

256 In both models (and both components of the hurdle model), we included
257 alternate-host connectivity, conspecific-host connectivity, host-plant species, and ln-
258 transformed host-plant patch volume ("patch size") as independent variables. Following
259 initial model fitting, we tested whether the parameter estimates for alternate-host
260 connectivity and conspecific-host connectivity (1) differed from one another, and (2) as
261 a sum were significantly different than zero, using Wald Chi-square comparisons in both
262 cases (Fox and Weisberg 2011). The former tests the prediction that the effects of
263 alternate-host connectivity on patch occupancy, abundance, and local adaptation is
264 smaller than the effect of conspecific-host connectivity. The latter tests the predictions
265 that total connectivity increases patch occupancy and abundance, but will have no effect
266 on local maladaptation.

267 To check for a potential influence of spatial autocorrelation, which could violate
268 the assumption of non-independence and spuriously inflate power, we compared
269 generalized linear models to penalized-quasilikelihood generalized linear mixed models
270 incorporating spatial correlation structure for patch occupancy, *Timema* abundance,
271 and maladaptation (Dormann et al. 2007). Results of PQL-GLMMs did not differ from
272 those of GLMMs (see Supporting Information), indicating a lack of substantial spatial
273 autocorrelation among residuals in our models. Accordingly, variograms showed no

274 signature of autocorrelation for patch occupancy, and only slight autocorrelation at very
275 small distances for abundance (see Supporting Information).

276

277 **Results**

278 *Patch occupancy and Timema abundance*

279 As predicted, the effects of alternate-host connectivity on both patch occupancy
280 and *Timema* abundance were significantly smaller than those of conspecific-host
281 connectivity (Figure 3; occupancy: $\chi^2 = 11.91, p < 0.001$; abundance: $\chi^2 = 4.21, p =$
282 0.040). Patch occupancy significantly increased with conspecific host-connectivity, and
283 showed a non-significant, negative trend with alternate-host connectivity (Table 1,
284 Figure 3A). *Timema* abundance increased with conspecific-connectivity and showed a
285 non-significant positive trend with alternate-host connectivity (Table 1, Figure 3B). It is
286 important to highlight that the non-significance of alternate-host connectivity for patch
287 occupancy and *Timema* abundance (Table 1) does not constitute evidence against a role
288 for maladaptive gene flow. Effects of gene flow on occupancy and abundance simply
289 predict a significantly lower slope for alternate- than conspecific-host connectivity, as
290 we observed (Figure 1, “Discussion”). Patch occupancy increased marginally with total
291 population connectivity ($\chi^2 = 3.31, p = 0.070$), and *Timema* abundance increased
292 significantly with total connectivity ($\chi^2 = 10.43, p = 0.001$). Both patch occupancy and
293 *Timema* abundance increased with patch size, but neither differed between host-plant
294 species (Table 1).

295

296 *Maladaptation*

297 There were no significant effects of alternate- or conspecific-host connectivity on
298 maladaptation (Table 1), no significant difference between effects of alternate- and

299 conspecific-host connectivity on maladaptation ($\chi^2 = 0.22, p = 0.638$), and no significant
300 effect of total population connectivity ($\chi^2 = 0.23, p = 0.629$). Maladaptation was not
301 influenced by patch size, but *C. spinosus* plants harboured significantly more
302 maladaptation than *A. fasciculatum* plants (Table 1).

303

304 **Discussion**

305 For *T. cristinae* metapopulations, conspecific- versus alternate-host plant
306 connectivities represent degrees of immigration from similar versus divergent habitat
307 types. Coupled with local adaptation to those different habitats (Farkas et al. 2013), we
308 predicted the demographic effects of alternate- and conspecific-host connectivity to
309 differ due to a difference in the degree of maladaptive gene flow associated with
310 immigration (Figure 1). We show here that alternate-host connectivity has an effect on
311 patch occupancy that is significantly smaller than that of conspecific-host connectivity
312 ($p < 0.001$). This result helps fill a gap in eco-evolutionary metapopulation biology by
313 providing evidence consistent with maladaptive gene flow reducing patch occupancy
314 throughout a wild metapopulation.

315 As stressed above, significance of the negative correlation between alternate-
316 host connectivity and patch is neither necessary nor sufficient to support the
317 hypothesis. It is not sufficient evidence because the relationship between conspecific-
318 host connectivity and occupancy could itself be negative, which would call into question
319 the interpretation of a negative slope for alternate-host connectivity as supportive of
320 maladaptive gene flow. It is not necessary evidence because immigration from *Timema*
321 populations on the alternate host should have both a positive demographic effect of
322 increased population size and beneficial gene flow, as well as a negative demographic
323 effect of maladaptive gene flow (Figure 1). It is possible (and apparently true in this

324 system) that the balance between positive and negative effects weighs in favour of
325 positive effects and leads to a significantly positive slope, but that would not in itself
326 suggest that maladaptive gene flow plays no role in structuring patch occupancy. To test
327 for a role of maladaptive gene flow in driving patterns of patch occupancy, it is both
328 necessary and sufficient to test for a difference between the slopes of these two
329 measures of connectivity, where conspecific-host connectivity serves as a control
330 against which to compare the effect of alternate-host connectivity (Figure 1). A similar
331 comparative analytical approach was used to demonstrate negative fitness
332 consequences of maladaptive gene flow in *Mimulus laciniatus*, where experimentally
333 induced gene flow from the species range core into the range margin increased fitness
334 less strongly than gene flow between marginal populations (Sexton et al. 2011).

335 Evidence that maladaptive gene flow can reduce abundance is another
336 prediction of eco-evolutionary metapopulation biology that has received little empirical
337 support. Farkas et al. (2013) added support by showing that populations of *T. cristinae*
338 harbouring maladapted morphs have lower abundances than well-adapted populations
339 (see also Moore and Hendry 2009 for an example with stickleback). Here we use a
340 stronger set of explanatory variables to confirm this result, finding a smaller effect of
341 alternate-host connectivity on abundance than conspecific-host connectivity, paralleling
342 the results for patch occupancy (Table 1, Figure 3).

343 A third prediction is that gene flow can yield maladaptation. However, we found
344 no relationship between either alternate- or conspecific-host connectivity and
345 maladaptation (Table 1), and no significant difference between their effects. One
346 possibility is that in our study network, gene flow is effective at a distance large enough
347 relative to the spatial grain of heterogeneity that morph frequencies are smoothed or
348 homogenised across large parts of the network. This process would result in some

349 evidence for local adaptation at the scale of the entire network (Farkas et al. 2013), but
350 could make effects of gene flow undetectable through a correlation of morph frequency
351 and host-specific connectivity based on individual plants (Sandoval 1994b). However,
352 because the demographic changes shown to be associated with host-specific
353 connectivity in this study are in theory mediated by morph frequency, this explanation
354 demands another mechanism for the link between connectivity and demography.
355 Instead, we suggest that gene flow does indeed cause maladaptation, but that
356 differences in the temporal scale over which morph frequency, demography, and
357 connectivity change leads to incongruent correlations. Maladaptation within *T. cristinae*
358 populations can change rapidly throughout a season, on the order of days and weeks
359 (Nosil et al. 2003; Nosil and Crespi 2006; Farkas et al. 2013; Gompert et al. 2014),
360 whereas population connectivity values will be driven by the spatial occurrence, species
361 identity, and volume of host plants (related to *Timema* abundance), which are relatively
362 stable through time. Hence, the signal of maladaptive gene flow in morph frequencies
363 should become quickly eroded as natural selection removes maladapted individuals
364 from the population. This hypothesis explains why we would nevertheless expect to see
365 lower population size and occupancy on patches experiencing high maladaptive gene
366 flow – hard natural selection by avian predators removes many maladapted individuals,
367 leaving populations better adapted, but with lower abundance.

368 Another possibility stems from range margin literature that shows how gene
369 flow between divergently adapted populations along an environmental cline can lead to
370 population collapse in the absence of a cline in local (mal)adaptation (Bridle et al. 2010;
371 Polechová and Barton 2015). These studies show that the sharing of alleles for
372 quantitative traits can lead to ubiquitous adaptation by increasing adaptive potential
373 through increased genetic variance (Barton 2001). In these models, the demographic

374 load associated with increased variance can reduce population sizes such that drift can
375 overcome selection and lead to local extinction. The stripe (presence/absence or size)
376 in *T. cristinae* is largely, but not completely, controlled by a few loci of large effect
377 (Comeault et al. 2014, 2015), so this body of theory could perhaps help to explain our
378 findings. However, the largely major-locus control of the stripe likely limits the
379 usefulness of these models, which assume selection is distributed evenly across
380 multiple loci, such that per locus selection is weak. With a trait driven by a few loci of
381 major effect, gene flow between divergently adapted populations is less able to share
382 beneficial alleles, and drift is less able to overcome selection when population sizes are
383 low. Empirical findings that gene flow between divergently adapted populations causes
384 maladaptation further suggest the sharing of beneficial alleles plays little role in
385 promoting good camouflage (Sandoval 1994b; Bolnick and Nosil 2007; Nosil 2009).

386 A final possibility is that alternate-host connectivity causes maladaptive gene
387 flow in traits that we did not measure in this study, and that are important enough to
388 show a clear influence on abundance and occupancy. For example, body size and shape
389 are known to be important for crypsis in addition to the dorsal stripe (Nosil and Crespi
390 2006), were not measured in this study, and may have been influenced by population
391 connectivity. However, this hypothesis still leaves many things to be explained. First,
392 the fact that morph frequency is not influenced by connectivity remains enigmatic,
393 given extremely strong support for the effects of gene flow on morph frequency in
394 nature (Sandoval 1994b; Bolnick and Nosil 2007; Nosil 2009). Second, previous analysis
395 shows that maladaptation correlates with *T. cristinae* abundance in this metapopulation
396 (Farkas et al. 2013), so a revised hypothesis suggests that gene flow is a driver of
397 demographic patterns acting through multiple traits simultaneously. Future research is

398 needed to evaluate the potential role of maladaptation in traits other than the dorsal
399 stripe, and to explain the why connectivity fails to predict morph frequencies.

400 The lack of geographical signal on morph frequencies reported here and in
401 Farkas et al. (2013) remains enigmatic, and begs the question of whether alternate-host
402 connectivity leads to gene flow *per se*, or whether it simply leads to the movement and
403 change of phenotypes across space, without any genetic mixing between morphs
404 through sexual reproduction. Although we do not have direct data showing that
405 connectivity in the metapopulation studied here leads to genetic mixing, the existence of
406 maladaptive gene flow in the *T. cristinae* system is well established in previous work
407 examining a range of spatial scales in other populations. For example, genomic studies
408 show that differentiation between populations is consistently greater (and linkage
409 disequilibrium within populations lower) for populations geographically isolated from
410 the alternative host, relative to populations adjacent to the alternate host (Nosil et al.
411 2003, 2012; Nosil 2007). In fact, genetic differentiation between adjacent populations is
412 very weak (mean genome wide $F_{ST} \sim 0.01$; Nosil et al. 2012; Soria-Carrasco et al. 2014).
413 Genomic data aside, classical genetic crosses within populations regularly segregate for
414 both striped and unstriped morphs, consistent with a long history of gene flow at this
415 locus between populations (Sandoval 1993; Comeault 2014; Comeault et al. 2015).
416 Finally, levels of maladaptation are so high (e.g., over 80% of the maladapted morph) in
417 some populations that it seems unlikely recurrent dispersal (without gene flow) could
418 create them, year after year (Bolnick and Nosil 2007). A recent study in this system
419 furthermore shows that the third, melanic *T. cristinae* morph might facilitate gene flow
420 between populations inhabiting different host-plant species by preventing the
421 expression of striped/unstriped phenotypes and thereby reducing selection pressure
422 against maladapted genotypes (Comeault et al. 2015). Hence, substantial levels of gene

423 flow in the metapopulation studied here are very likely to be contributing to the
424 reported findings.

425 Our data provide insight into why studies might not always show a strong
426 relationship between total population connectivity and patch occupancy, despite the
427 strong prediction of metapopulation theory (Hanski 1998). Specifically, separately
428 evaluating the effects of conspecific- and alternate-host connectivity demonstrated the
429 value of considering the evolutionary importance of population connectivity in
430 heterogeneous environments. We showed that alternate-host connectivity does not
431 correlate with either patch occupancy or *Timema* abundance, whereas conspecific-
432 connectivity does so strongly in both cases (Figure 2, Table 1). Hence, evaluating the
433 relative roles of connectivity on ecology and evolution can be important because they
434 might have contrasting effects on the ecological properties of populations, and could
435 have downstream effects that influence community structure or ecosystem processes
436 (Farkas et al. 2015). In this study, the net effect of connectivity is to increase patch
437 occupancy and population size (but note that the effect on patch occupancy is only
438 marginally significant). However, if a greater proportion of total connectivity were due
439 to populations on the alternate host-plant species, or the effect of that connectivity were
440 larger, the scales could be tipped such that the beneficial effects of connectivity might be
441 nullified or even inverted. Increasing total connectivity could, in theory, reduce patch
442 occupancy and population size due to maladaptive effects of gene flow (Farkas et al.
443 2015).

444 In addition to supporting major predictions of eco-evolutionary metapopulation
445 biology, our results have potential relevance to the study of species range margins. A
446 classic eco-evolutionary hypothesis in this discipline suggests that asymmetrical gene
447 flow **into species range margins from range cores with greater abundance** constrains

448 adaptation to novel environmental conditions at the margins, leading to failed marginal
449 establishment and increased marginal extinction (Haldane 1956; Mayr 1963;
450 Kirkpatrick and Barton 1997; Kubisch et al. 2014). Evidence supporting a role for gene
451 flow in constraining species ranges shows either that gene flow may be asymmetric and
452 hence flow from core to margin (Moeller et al. 2011; Paul et al. 2011), or that gene flow
453 homogenizes phenotypes across environmental clines (Bridle et al. 2009; Emery et al.
454 2011; Fedorka et al. 2012). Until now, direct empirical evidence that maladaptive gene
455 flow can prevent establishment or increase local extinction has been largely lacking
456 from the range margin literature. However, in *T. cristinae*, local adaptation to host-
457 plants in terms of crypsis exists outside the context of core-margin dynamics. Instead,
458 the asymmetrical gene flow required by population genetics models predicting range
459 boundaries (Kirkpatrick and Barton 1997) is determined externally by the size and
460 spatial configuration of host-plant patches, rather than higher abundance at the species
461 range core. Nevertheless, our results inform the range margin debate by modelling
462 patch occupancy as a function of population connectivity, a measure that is largely a
463 function of abundance.

464

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472

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694 **Figure Legends**

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696 **Figure 1.** Predictions for effects of conspecific- and alternate-host connectivity on
697 occupancy. The relationship between alternate-host connectivity and patch occupancy
698 (blue, lower line) is expected to be smaller in slope than the relationship between
699 conspecific-host connectivity and patch occupancy (red, upper line). Inset table shows
700 demographic effects of processes associated with connectivity in heterogeneous
701 landscapes. The solid arrows indicate positive demographic effects of immigration and
702 beneficial gene flow, whereas the dashed arrow demonstrates negative demographic
703 consequences of maladaptive gene flow. Relationships are drawn as linear for
704 convenience, and are not meant to imply theoretically linear relationships.

705

706 **Figure 2.** Map of host-plant patches inhabited by *T. cristinae* metapopulation. Blue
707 (dark grey): *A. fasciculatum*, orange (light grey): *C. spinosus*, filled: occupied, unfilled:
708 unoccupied. Circle sizes are scaled to ln-transformed patch volume, calculated as a
709 rectangular solid.

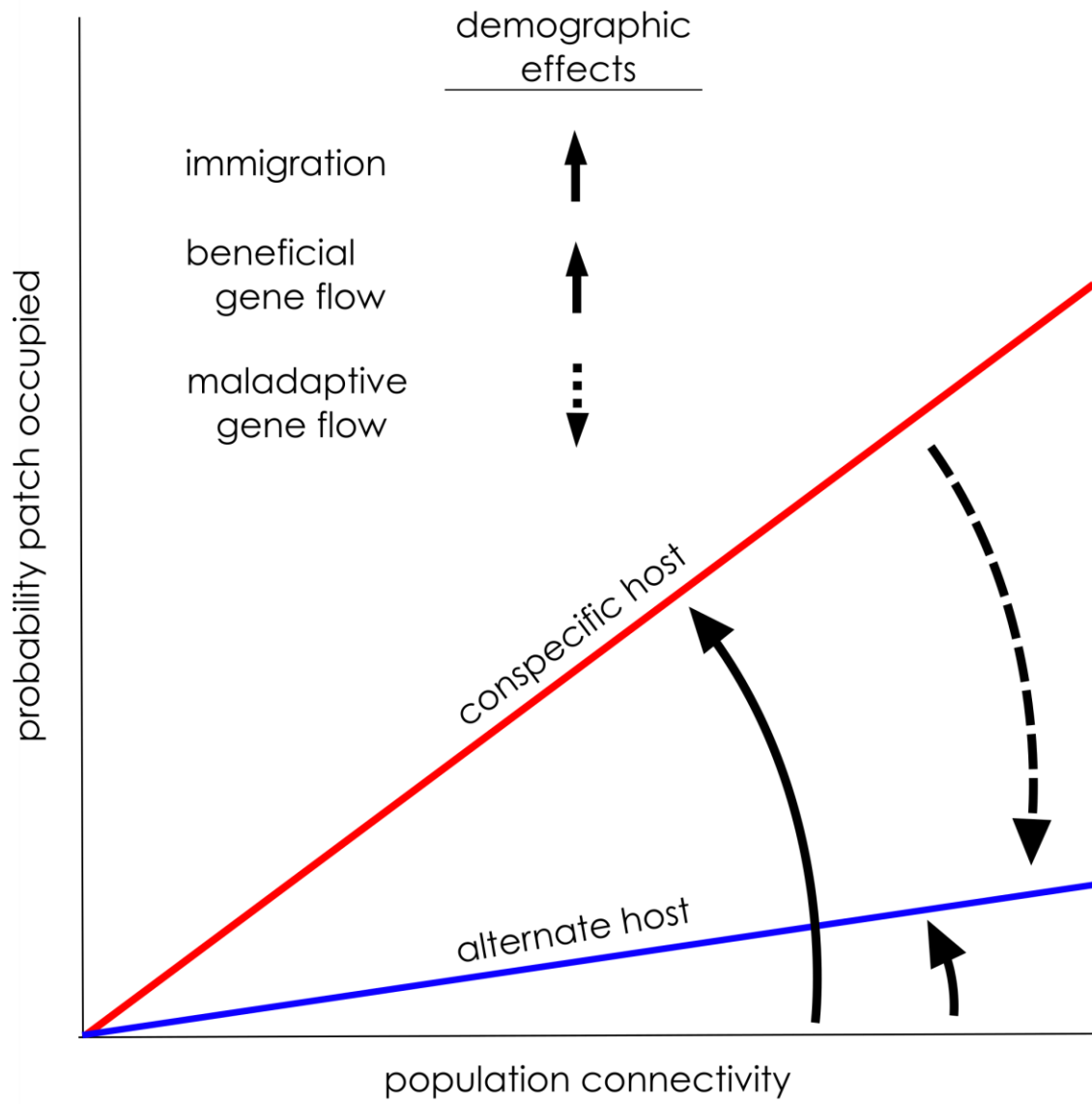
710

711 **Figure 3.** Relationships between connectivity and (a) patch occupancy and (b) *Timema*
712 abundance. (a, b) Curves are predicted values for relationships between alternate-host
713 connectivity (blue, dashed) and conspecific-host connectivity (red, solid), and shaded
714 areas show 1 standard error. (a) Histograms show raw counts of occupied (top) and
715 unoccupied (bottom) patches across levels of connectivity to alternate hosts (light blue)
716 and conspecific hosts (dark red). (b) Points are raw, unconditional data for abundance
717 and alternate host connectivity (blue triangles) and conspecific-host connectivity (red
718 circles). Predictions and errors are from generalized linear models of patch occupancy
719 and *Timema* abundance (see Supporting Information).

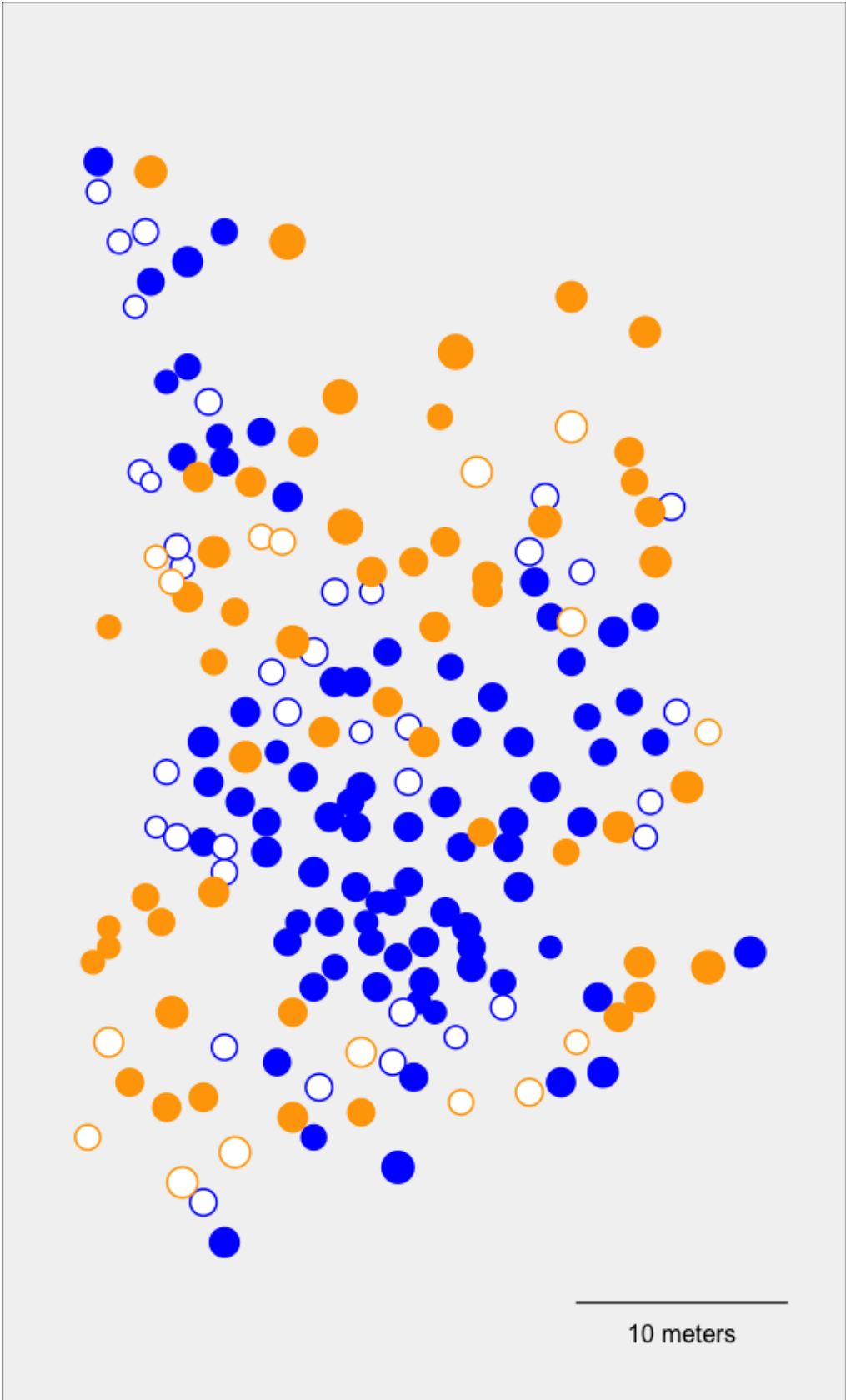
720 **Table 1:** Effects of conspecific-host connectivity (Con-Host), alternate-host connectivity (Alt-Host), ln-transformed patch volume (Ln-
721 Size), and host plant species (Host spp.) on patch occupancy (zero component in hurdle model), *Timema* abundance (count component
722 of hurdle model), and maladaptation (Bernoulli GLMM).
723

Variable	Patch Occupancy (Zero Model)				Abundance (Count Model)				Maladaptation			
	<i>b</i>	<i>se</i>	<i>z</i>	<i>p</i>	<i>b</i>	<i>se</i>	<i>z</i>	<i>p</i>	<i>b</i>	<i>se</i>	<i>z</i>	<i>p</i>
Con-Host	2.239	0.578	3.875	< 0.001	1.122	0.232	4.836	< 0.001	0.414	0.492	0.844	0.402
Alt-Host	-0.290	0.713	-0.406	0.685	0.475	0.344	1.382	0.167	0.071	0.730	0.097	0.923
Ln-Size	1.180	0.231	5.115	< 0.001	1.204	0.097	12.443	< 0.001	0.126	0.192	0.654	0.514
Host sp.	0.060	0.257	0.232	0.816	0.158	0.105	1.498	0.134	0.584	0.230	2.542	0.012

724 Note: *b* = parameter estimate, *se* = standard error, *z* = z-value, *p* = p-value. Effects significant at $\alpha = 0.05$ are highlighted in boldface text.
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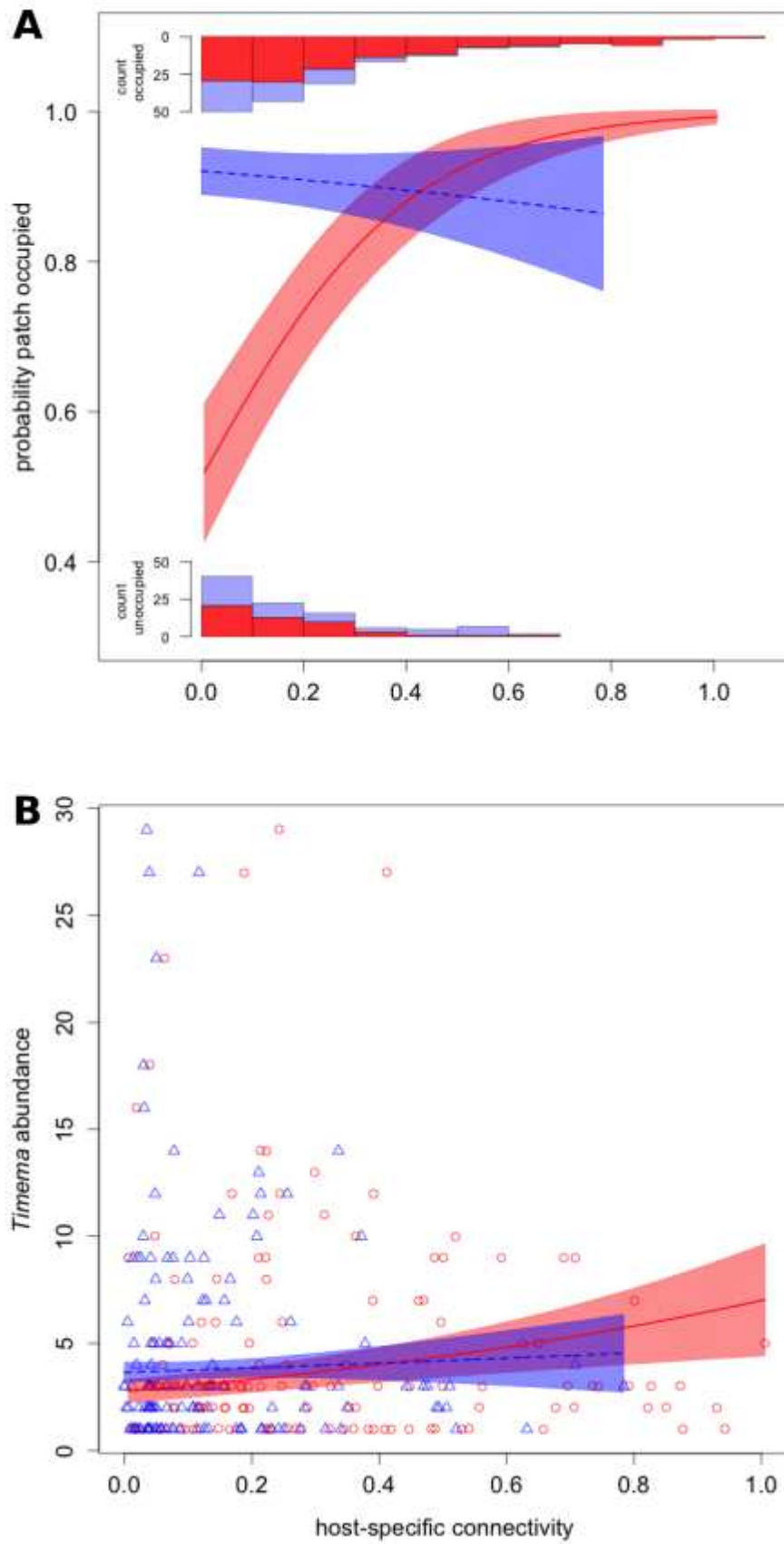


733
 734 **Figure 1**
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Figure 2



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Figure 3

741 Supplemental Information*742 Use of a hurdle model*

743 Hurdle models are useful for the analysis of count data that fail to conform to a Poisson
744 distribution by having overdispersion or more zero counts than expected (Zeileis et al.
745 2008). They are mixture models that are comprise of two components, one that models
746 zero values versus non-zero values, and a second that models count values greater than
747 zero. For the purposes of this paper, they can thus simultaneously model patch
748 occupancy and abundance excluding zeros, assuming binomial and Poisson
749 distributions, respectively, for the two model components. Calculating the
750 overdispersion parameter for a GLM with Poisson error for abundances greater than
751 zero demonstrate strong overdispersion in these data ($\Phi = 3.40$). Setting both hurdle
752 model components to be evaluated assuming a Poisson distribution, we can test for the
753 necessity of a hurdle by evaluating pairwise equality between all coefficients from the
754 two components using Wald linear hypothesis testing (Zeileis et al. 2008; Fox and
755 Weisberg 2011). A test for the necessity of a hurdle strongly rejected the null model (χ^2
756 = 35.85, $p < 0.001$), indicating a hurdle model was appropriate for the analysis of our
757 data.

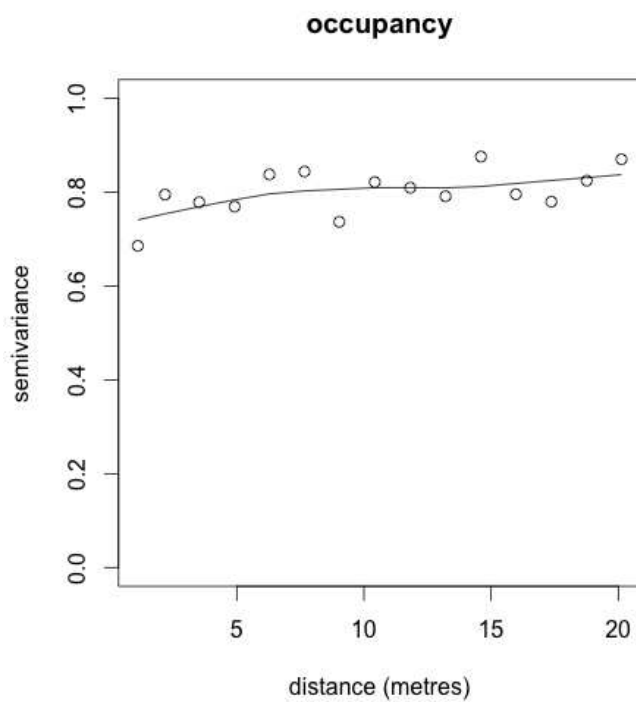
758

759 Spatial autocorrelation

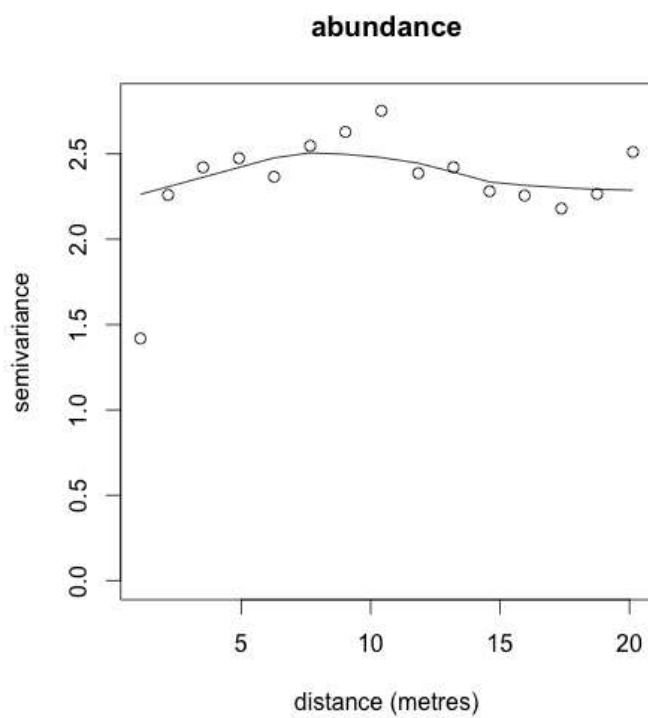
760 To evaluate whether spatial autocorrelation could account for our observations, we
761 performed independent quasi-binomial and quasi-Poisson GLMs and examined
762 variograms of the residuals, which showed low levels of autocorrelation (Figures S1 and
763 S2). In addition, we compared these GLM models to penalized-quasilikelihood
764 generalized mixed models (PQGLMMs) that incorporated spatial structure (Dormann et
765 al. 2007). Parameter estimates and standard errors were not substantially influenced by
766 the inclusion of spatial structure (Table S1), and in some cases increased parameter
767 estimates, suggesting the method not including autocorrelation is conservative.

Table S1. Comparison of quasilielihood GLM and penalized quasilielihood GLMM for patch occupancy (1) and *Timema abundance* (2). b = parameter estimate, se = standard error, t = t-value, p = p-value. Con-Host = connectivity to conspecific host, Alt-Host = connectivity to alternate host, Ln-Size = log_e-transformed patch volume, Host spp. = host plant species (dummy coded: *A. fasciculatum* = 0).

	GLM				PQGLMM			
(1) Patch occupancy								
	b	se	t	p	b	se	t	p
Con-Host	4.851	1.343	3.612	< 0.001	4.851	1.343	3.612	< 0.001
Alt-Host	-0.770	1.149	-0.670	0.504	-0.770	1.149	-0.670	0.504
Ln-Size	2.091	0.416	5.032	< 0.001	2.091	0.416	5.032	< 0.001
Host spp.	0.267	0.467	0.572	0.568	0.267	0.467	0.572	0.568
(2) Abundance								
	b	se	t	p	b	se	t	p
Con-Host	0.933	0.394	2.366	0.019	1.434	0.426	3.367	< 0.001
Alt-Host	0.279	0.590	0.474	0.636	0.025	0.664	0.038	0.970
Ln-Size	1.069	0.160	6.698	< 0.001	1.379	0.161	8.579	< 0.001
Host spp.	0.157	0.183	0.857	0.393	0.161	0.198	0.811	0.419



231



232

233 Figure S1. Variogram showing spatial autocorrelation among errors from
234 GLMs for patch occupancy (a) and *Timema* abundance (b). Solid lines are LOWESS
235 smoothers.