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# Warming indirectly increases invasion success in food webs

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1 **Title: Warming indirectly increases invasion success in food webs**

2 **Running title: Warming increases invasions in food webs**

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13

14 **ABSTRACT**

15 Climate warming and biological invasions are key drivers of biodiversity change. Their  
16 combined effects on ecological communities remain largely unexplored. We investigated the  
17 direct and indirect influences of warming on invasion success, and their synergistic effects on  
18 community structure and dynamics. Using size-structured food web models, we found that  
19 warming increased invasion success. The direct physiological effects of warming on invasions  
20 were minimal in comparison to indirect effects mediated by changes on food web structure and  
21 stability. Warmed communities with less connectivity, shortened food chains and reduced  
22 temporal variability were more susceptible to invasions. The directionality and magnitude of  
23 invasions effects on food webs varied across warming regimes. Warmer communities became  
24 smaller, more connected, and with more predator species when invaded than their colder  
25 counterparts. They were also less stable and their species more abundant. Considering food web  
26 structure is crucial to predict invasion success and its impacts under warming.

27

28 **Keywords:** climate change; body size; allometric bio-energetic model; food web structure; food  
29 web stability; temperature dependence; top-down control

30

31

## 32 INTRODUCTION

33 Climate warming and biological invasions constitute two of the most pervasive drivers of global  
34 change (Nelson 2005; Díaz *et al.* 2020). Both drivers strongly impact ecosystems, causing not  
35 only species loss, but also affecting ecological interactions and the structure of interaction  
36 networks (Stachowicz *et al.* 2002; Holzapfel & Vinebrooke 2005; Romanuk *et al.* 2009; Britton  
37 *et al.* 2010; Huang *et al.* 2011; Lurgi *et al.* 2012b; Lu *et al.* 2013; Lurgi *et al.* 2014; Zhang *et al.*  
38 2017). Climate warming and species invasions can act synergistically on ecosystems due to, for  
39 example, impacts of climate change on species niche range dynamics (Thuiller *et al.* 2008; Elith  
40 & Leathwick 2009; Tylianakis & Morris 2017), which differentially influence species' ability to  
41 colonise new habitats and thus invade new communities. Species range shifts affect not only  
42 species composition, but also the structure of species interaction networks creating novel  
43 communities. For example, by promoting species range shifts, climate warming can trigger the  
44 loss of specialised interactions and changes the body size ratio between predator and prey  
45 species, which in turn can influence predator control on prey populations (Lurgi *et al.* 2012b, a).  
46 Yet, we know surprisingly little about how invasions and climate change act together to affect  
47 species and links in ecosystems.

48 Previous studies have shown that warming can enhance invasions by increasing survival and  
49 reproduction of introduced species (Mandrak 1989; Johnson & Evans 1990; Stachowicz *et al.*  
50 2002; Logan *et al.* 2003; Britton *et al.* 2010; Huang *et al.* 2011; Ricciardi *et al.* 2017). However,  
51 warming can also lead to the opposite effect by decreasing the potential for invaders to occupy  
52 new niches (Bradley *et al.* 2010; Bertelsmeier *et al.* 2013). Recent evidence suggests that  
53 warming influence on invasion success may depend on how warming influences trophic  
54 interaction strength and the persistence of native predators or competitors (Holzapfel &

55 Vinebrooke 2005; Lu *et al.* 2013; Seifert *et al.* 2015). On the one hand, warming can prevent  
56 invasions by increasing top-down control on the invader prey (Bradley *et al.* 2010; Lu *et al.*  
57 2013; Lu *et al.* 2016). On the other hand, warming can enhance invasions by releasing top-down  
58 control following predator extinctions (Holzapfel & Vinebrooke 2005). Overall, previous studies  
59 reported various outcomes on the effects of warming on invasions. Our limited understanding of  
60 their causes poses the challenge for gaining a better understanding of the indirect effects of  
61 warming on species and communities. Indirect effects of warming on community structure and  
62 species interactions are often stronger than its direct effects on physiology and demography  
63 (Ockendon *et al.* 2014). This suggests that investigating warming effects on communities and the  
64 complex networks of interactions that structure them is a first step to address this challenge.

65 Ecologists have developed mechanistic frameworks to identify key processes underlying  
66 temperature effects on trophic interactions and networks (Binzer *et al.* 2012; Burnside *et al.*  
67 2014; Fussmann *et al.* 2014; Gilbert *et al.* 2014; Sentis *et al.* 2014). One first important finding is  
68 that, since consumer metabolic rates often increase faster with temperature than their feeding  
69 rates, most consumers become less efficient at processing matter and energy at warmer  
70 temperatures (Vucic-Pestic *et al.* 2011; Fussmann *et al.* 2014; Iles 2014). This reduction of  
71 energetic efficiency lessens energy flow between trophic levels and, if resulting in weakened  
72 interaction strengths, it stabilizes food-web dynamics by reducing population fluctuations (Rip &  
73 McCann 2011; Binzer *et al.* 2012; Gilbert *et al.* 2014). A second important finding is that  
74 elevated temperatures increase consumer extinction risk when metabolic demands exceed  
75 ingestion rates, leading to consumer starvation and extinction (Petchey *et al.* 1999; Rall *et al.*  
76 2010; Sentis *et al.* 2020). Whether these changes would favour invasion success is unclear, as  
77 previous studies exploring the role of community structure and dynamics in preventing or

78 facilitating invasions success have not considered modifications in communities driven by  
79 climate change (e.g. Romanuk *et al.* 2009; Lurgi *et al.* 2014).

80 In parallel to studies focusing on the effects of warming, much effort has been devoted to  
81 understanding how invasions impact ecosystems (Hui & Richardson 2019). Several models have  
82 unveiled the role of food web structure such as species richness, complexity or the heterogeneity  
83 of distribution of interactions in preventing invasions. These models have also suggested that  
84 invasions in food webs tend to decrease species richness and shorten food chains (e.g. Romanuk  
85 *et al.* 2009; Lurgi *et al.* 2014). However, a more recent theoretical investigation suggests the  
86 opposite, with invasions being instead beneficial for maintaining species richness and ecological  
87 functions (Zhang *et al.* (2017). We need comprehensive mechanistic frameworks incorporating  
88 both warming and invasion and their effects on complex communities to better understand and  
89 predict their synergistic effects.

90 Here, we explored the combined effects of warming and invasions on food webs using a  
91 theoretical model. Given our current understanding of the effects of warming on natural  
92 communities on the one hand (Binzer *et al.* 2012; Sentis *et al.* 2017; Boukal *et al.* 2019), and of  
93 the invasion process in complex food webs on the other (Romanuk *et al.* 2009; Lurgi *et al.* 2014;  
94 Hui & Richardson 2019), along with previous studies showing a positive influence of weakened  
95 top-down control on invasions (Holzapfel & Vinebrooke 2005), we hypothesise that warming  
96 increases invasion success if it decreases top-down control or causes predator extinctions. We  
97 further hypothesise warming to increase connectivity and shorten food chains in response to  
98 species loss at higher trophic levels. These effects of warming should in turn destabilise  
99 community dynamics (Boukal *et al.* 2019).

100 To test these hypotheses, we investigated how temperature can influence invasions on complex  
101 food webs comprised of 30 species. Our model simulates population dynamics in food webs  
102 following bio-energetic principles of species life histories and interactions. The model  
103 incorporates the temperature dependency of biological rates allowing the exploration of a wide  
104 range of temperature regimes. We aim at gaining a better understanding of (1) warming effects  
105 on invasion success in food webs and (2) the ecological consequences of invasions on food web  
106 structure in warmed communities.

## 107 **MATERIAL AND METHODS**

108 We modelled community dynamics in complex food webs using a size-structured bio-energetic  
109 community model consisting of a set of ordinary differential equations (ODEs) incorporating the  
110 effects of species growth and ecological interactions (Yodzis & Innes 1992; Brose *et al.* 2006).  
111 Food webs were generated using the niche model (Williams and Martinez 2000). The effect of  
112 temperature on population dynamics was incorporated into ODEs by introducing thermal  
113 dependencies of relevant model parameters. A series of numerical simulations were then  
114 computed and species invasions were modelled as the addition of a new species into the  
115 community (Lurgi *et al.* 2014). Simulation results were analysed to assess the effects of  
116 temperature on (1) food web proprieties (structure, stability and total biomass) before invasion,  
117 (2) invasion success, and (3) the effects of invasions on community structure and stability.

### 118 ***Food web generation***

119 Food webs were generated using the niche model (Williams & Martinez 2000). With only two  
120 parameters (number of species ( $S$ ) and network connectance ( $C$ ), i.e. the fraction of links out of  
121 all possible ones) this model generates networks that resemble real food web structure (Williams

122 & Martinez 2000). We generated food webs comprising 30 species and with 10% connectance.  
123 These values are within the ranges reported for empirical food webs (Williams & Martinez 2000).  
124 We kept these values fixed across experiments to avoid the confounding effects of variation in  
125 species richness and connectance.

### 126 *Non-linear model for population dynamics*

127 To simulate network dynamics of species populations biomass we used an allometric bio-  
128 energetic model adapted from its original formulation by Yodzis and Innes (1992). This model  
129 defines interactions strengths between prey and predator according to their body mass ratios  
130 (Brose *et al.* 2006) and has been used to investigate warming and invasion effects on complex  
131 food webs (Binzer *et al.* 2011; Lurgi *et al.* 2014). Eqn. 1 gives dynamics of basal resource  
132 species. These grow logistically with an intrinsic growth rate  $r_i$  and a carrying capacity  $K_i$ .  
133 Consumers gain biomass according to Eqn. 2:

$$134 \quad \frac{dB_i}{dt} = r_i B_i \left(1 - \frac{B_i}{K_i}\right) - \sum_m F_{im} B_i \quad (1)$$

$$135 \quad \frac{dB_i}{dt} = \sum_s e F_{si} B_i - \sum_m F_{im} B_m - x_i B_i \quad (2)$$

136 where  $B_i$  is the biomass of species  $i$ ;  $e$  is the assimilation efficiency of predators when ingesting  
137 prey (kept constant across consumer-resource species pairs at a value  $e = 0.85$  for carnivorous  
138 species (following Yodzis & Innes 1992));  $x_i$  is the metabolic rate at which biomass of consumers  
139 is lost from the system due to respiration and other metabolic processes.  $F_{ij}$  is a function that  
140 describes the feeding relationship between prey  $i$  and predator  $j$  and is defined by the functional  
141 response:



142 
$$F_{ij} = \frac{\alpha_{ij} B_i^q}{1 + \sum_k h_{kj} \alpha_{kj} B_k^q} \quad (3)$$

143 where  $\alpha_{ij}$ 's are the elements of a quantitative version of the adjacency matrix  $A$ , describing the  
144 food web obtained according to the procedure explained above (*Food web generation*), and that  
145 represent the attack rates of predator species  $j$  on prey species  $i$  (Eqn. 5a).  $h_{ij}$  is the handling  
146 time, i.e. the average time spent by an individual of predator species  $i$  handling and digesting an  
147 individual of prey species  $i$ . The shape of the functional response curve is controlled by the  
148 parameter  $q$  (i.e. the Hill exponent). We kept  $q$  constant across interacting species pairs at a value  
149 of 1.2 to simulate an intermediate response type between Type II (hyperbolic,  $q = 1$ ) and Type III  
150 (sigmoidal,  $q = 2$ ), as in (Binzer et al. 2011, 2016).

151 Growth, metabolic, attack rates, and handling times are functions of species body masses and  
152 temperature. Body mass of species  $i$  scales according to its position in the food web:

153 
$$m_i = m_0 R^{L_i - 1} \quad (4)$$

154 where  $m_0$  is the body size of basal species in the food web and set here to  $m_0 = 0.01\text{g}$ ,  $R$  is the  
155 average predator-prey body mass ratio of all trophic interactions in the food web and was set here  
156 to  $R = 10^2$ ,  $L_i$  is the prey-averaged trophic level of species  $i$  (Williams & Martinez 2004).  
157 Allometric and thermal dependencies of model parameters were incorporated as follows (Binzer  
158 et al. 2016):

159 
$$\alpha_{ij}, h_{ij} = d m_i^b m_j^c e^{\frac{E(T_0 - T)}{k T T_0}} \quad (5a)$$

160 
$$r_i, x_i = d m_i^b e^{\frac{E(T_0 - T)}{k T T_0}} \quad (5b)$$

161 where  $d = e^J$  is a rate-specific constant calculated for a species with body mass of 1g and at a  
162 reference temperature  $T_0 = 20^\circ\text{C}$  (293.15K),  $m_i$  and  $m_j$  are the body masses of species  $i$  and  $j$ ,  
163 respectively,  $b$  and  $c$  are rate-specific allometric exponents. The temperature dependence term is  
164 a version of the Arrhenius equation in which  $E$  is the rate-specific activation energy and  $k$  is the  
165 Boltzmann constant.  $T$  is the current temperature of the system in Kelvin.  $T_0$  is the reference  
166 temperature at which the rate value is equal to the rate-specific constant  $d$ . Values and units for  
167 the parameters in Eqns. 5a and 5b are presented in Table 1.

168 Species carrying capacity was assumed to be independent of temperature since empirical  
169 evidence for the thermal dependency of carrying capacity is inconclusive (Fussmann *et al.* 2014;  
170 Gilbert *et al.* 2014; Uszko *et al.* 2017; Bernhardt *et al.* 2018). Furthermore, we wanted to avoid  
171 biases in the invasion experiments due to the intrinsic limit to community biomass caused by the  
172 negative temperature dependence of carrying capacity, which would, in turn, influence invasion  
173 success. We thus focused on the effects of temperature on species life-history traits such as  
174 reproduction, death and species interactions (i.e. attack rates and handling times) and not on the  
175 maximum population density of the basal resources.

### 176 ***Food web structure, community properties and ecological stability***

177 To assess the synergistic effects of temperature and invasions on food webs, we measured a set of  
178 statistical food web properties (Table 2), before and after invasions, across a range of  
179 temperatures. In addition to changes in food web properties we also assessed community  
180 properties such as total community biomass, the average species body size in the community  
181 (*AvgBS*), and the average ratio of predator vs. prey body masses (*AvgPPMR*). Lastly, to assess  
182 ecological stability, we focused on temporal variability of biomass both at the community and

183 population levels. We quantified stability using two measures: (1) community invariability,  
184 measured as the inverse of total community biomass variability and (2) population invariability,  
185 as the inverse of average population-level biomass variability (Haegeman et al. 2016).  
186 Variabilities, both at the community (i.e. summing across the biomass of all species populations)  
187 and at the population level, were calculated as the ratio of the standard deviation to the mean  
188 biomass across the last 100 years of the simulations.

### 189 *Numerical simulations*

190 Using the food web model specified above (Eqns. 1-5) we simulated a range of temperature  
191 regimes and the addition of new species (i.e. invasions) as follows:

- 192 1. 140 niche model food webs were randomly generated ( $S = 30$  and  $C = 0.1$ ).
- 193 2. Initial biomass densities for basal species were set to their carrying capacity  $K \approx 2.75$   
194 following the allometric formulation in Eqn. 5b but omitting the temperature dependent  
195 term and assuming an allometric scaling constant and exponents of 10 and 0.28  
196 respectively (Binzer *et al.* 2016). Consumer species initial abundances were set to 1/8 of  
197 this value as in Binzer *et al.* (2016).
- 198 3. Community dynamics were first simulated for an equivalent of 600 years ( $18.9216 \times 10^9$   
199 seconds) to achieve persistence (i.e. no further species extinctions) after initial transient  
200 dynamics. After these first 600 years, an equilibrium was reached and food web and  
201 community properties were calculated. The objective here was to quantify the direct  
202 effects of temperature on community structure before invasion. Resulting community  
203 features, and their relationship to temperature values, can then be related to invasion  
204 success.

- 205 4. After the first 600 years, an invasion was simulated by introducing a new species into the  
206 network. The introduced species was randomly drawn as an additional species from the  
207 original niche model network (i.e. ensuring it was different from all species originally  
208 present in the network). Since at this time point some species might have gone extinct  
209 (see step 6), rendering the potential introduced species disconnected, we repeated the  
210 drawing procedure if necessary until a connected species was found. This procedure  
211 avoided introducing an invasive species with no interactions.
- 212 5. After the introduction, we simulated further 600 years of network/community dynamics.  
213 We then recorded whether the invasion was successful (i.e. whether the introduced  
214 species persisted). Structural network and community properties were calculated again to  
215 assess community structure after the introduced species became invasive (i.e. established  
216 itself successfully in the community) or went extinct.
- 217 6. A species was considered extinct if at any point during the simulations its biomass fell  
218 below  $10^{-9}$  g.m<sup>-2</sup>, at which point its abundance was set to 0.

219 For each of the 140 food webs, this procedure (i.e. steps 2 to 6 above) was repeated for each of 41  
220 constant temperature regimes ranging from 0 to 40°C at 1°C intervals, yielding a total of 5740  
221 numerical simulations. We used the same unique food webs for each temperature treatment to  
222 avoid confounding effects caused by initial differences in food web structure.

### 223 *Statistical analyses*

224 The relationship between temperature and food web structure, stability and community properties  
225 - i.e. total biomass, *AvgBS*, and *AvgPPMR* -, and their corresponding effects on invasion success  
226 were analysed using piecewise structural equation models (SEMs). We computed SEMs

227 considering invasion success (i.e. whether the invasive species established after introduction) as a  
228 response variable, with temperature affecting it directly and indirectly via network and  
229 community properties. The effect of species richness on food web and community properties was  
230 also incorporated into the SEMs, accounting thus for the indirect effect of temperature on  
231 network and community properties via  $S$  (see Appendix S2 for full SEM details).

232 To assess invasion effects on food web structure, stability and community properties, we  
233 calculated the ratio of values after (i.e. at the end of the simulations) vs. before (i.e. after initial  
234 transient dynamics) invasion for food web (Table 2) and community properties, as well as  
235 stability measures. To disentangle the direct and indirect effects (manifested via species richness)  
236 of temperature on these ratios, we performed another SEM following the same rationale as above  
237 and using the ratio of the effects as a response variable (i.e. effect size). We additionally assessed  
238 the differences between communities vulnerable vs. resistant to invasions in terms of these  
239 effects by comparing after/before ratios of each property between invaded and non-invaded  
240 communities using Mann-Whitney U tests.

241 All simulations and analyses were performed in R -language and environment for statistical  
242 computing (R Development Core Team 2017)-. Numerical simulations of ODEs were computed  
243 using the ode function of the deSolve package (Soetaert et al. 2010). Food web analyses were  
244 conducted with cheddar (Hudson et al. 2013). Modularity ( $Q$ ) was computed using the  
245 cluster\_louvain function from the igraph package (Csardi & Nepusz 2006). Piecewise SEMs and  
246 models within were performed using the piecewiseSEM (Lefcheck 2016) and the lme4 (Bates et  
247 al. 2015) packages respectively. Computer code developed to run model simulations and analyse  
248 outputs is available from the following repository: [https://github.com/mlurgi/temperature-](https://github.com/mlurgi/temperature-dependent-invasions)  
249 [dependent-invasions](https://github.com/mlurgi/temperature-dependent-invasions).

250 **RESULTS**

251 We focus on (i) the influence of warming on invasion success and (ii) the community-wide  
252 consequences of invasions. Effects of warming on food webs before invasion are detailed in  
253 Appendix S3. In line with previous findings (Binzer *et al.* 2016), we found that warmer  
254 communities harbour less species than their colder counterparts, particularly at high trophic  
255 levels, which in turn translates into higher connectance. These structural changes prompt an  
256 increase in both community biomass and stability in warmer environments (Appendix S3).

257 ***How does warming influence invasion success?***

258 Communities exposed to warmer temperatures were more prompt to invasions. Temperature had  
259 a direct positive effect on invasion success, although this effect was very weak (Fig. 1 and Table  
260 S1). This result holds even after accounting for temperature effects on species richness and other  
261 community and network properties (Table S1). Temperature influenced invasion success  
262 indirectly by modifying community properties, thus making communities more susceptible to  
263 invasions. Direct effects of network properties on invasion success were about an order of  
264 magnitude larger than the direct effect of temperature (compare arrow weights -i.e. standardised  
265 coefficients- on Fig. 1). In particular, the number of links ( $L$ ), the average number of links per  
266 species ( $L/S$ ), mean food chain length ( $MFCL$ ) and the fraction of basal and intermediate species  
267 ( $B$  and  $I$  respectively) had a strong and significant influence on invasion success (Fig. 1 and Table  
268 S1). Surprisingly, we found no direct effect of species richness on invasion success (Table S1)  
269 which is likely due to the small variability in species richness in our communities after the initial  
270 transient dynamics (Fig. S1a and Appendix S3).

271 Even though warming had a direct significant effect on most network properties (Table S1, Figs.  
272 S1-S3), only a few of them affected invasion success. In particular, we found that communities  
273 with longer food chains (*MFCL*) were more resistant to invasion. In addition, communities with  
274 more links (*L*) and greater proportions of basal (*B*) and intermediate (*I*) species were more prompt  
275 to invasion (Fig. 1). Communities harbouring more specialised species (i.e. small *L/S*) also were  
276 more susceptible to invasion.

277 Changes in population stability and total community biomass also affected invasion success  
278 under warming. Whereas larger total community biomass conferred resistance against invasions,  
279 communities with higher population stability were easier to invade (Fig. 1). Overall our results  
280 show that indirect effects of temperature on invasion success, mediated by changes in network  
281 and community properties and dynamics, were stronger than direct ones.

### 282 ***Ecological consequences of invasions along the temperature gradient***

283 Overall, invasions strongly decreased species richness (Fig. 2a), which, in turn, affected several  
284 network properties. Moreover, we found that the magnitude of the change of food web and  
285 community properties driven by invasions often depended on temperature (Fig. 2 & Table S2). In  
286 particular, warmer communities loose more species and interactions when invaded than their  
287 colder counterparts. This translates into more connected communities (Fig. 2a). Higher  
288 connectance (*C*) was accompanied by a larger heterogeneity in the distribution of predators  
289 among prey species (*VulSD*) and a stronger increase in the fraction of top predators (*T*). On the  
290 other hand, warming prompted a stronger decrease in the proportion of intermediate species (*I*)  
291 when invaded. The proportion of basal species (*B*) was not influenced by invasion or temperature  
292 (Table S2). This suggests that intermediate species became top predators when their predators

293 disappeared in invaded communities, yielding a lower fraction of intermediates while increasing  
294 the fraction of top predator species. Warming also lead to a stronger decrease in modularity ( $Q$ )  
295 which is explained by the presence of a larger fraction of top consumers and a higher  
296 connectance.

297 Community properties and stability were affected more heterogeneously by invasions across  
298 temperature regimes than network structure (Fig. 2). Total community biomass increased in  
299 warm invaded communities relative to their pre-invasion state (positive effect sizes), whereas it  
300 decreased under colder conditions (Fig. 2b, negative effect sizes). Similarly, population stability  
301 increased in colder communities (at 0 and 5°C) but decreased in warmer ones (although the effect  
302 was weak at 35°C). In addition, invasions always decreased community stability (Fig. 2b),  
303 although this effect was weaker in colder environments compared to warmer ones. Overall, we  
304 found that warm invaded communities have less species, with these species fluctuating more over  
305 time (i.e. reduced stability) than cold invaded communities.

306 Lastly, the average body size ( $AvgBS$ ) of species in the community remains mostly unaffected by  
307 invasions except at very low temperatures where invasions decreased average body size. On the  
308 other hand, the average predator:prey body size ratio ( $AvgPPMR$ ) was negatively impacted by  
309 invasion and this effect was more pronounced when temperature increased (Fig. 2b). The  
310 decrease in body size ratio, along with the considerable increase in the fraction of top predator  
311 species (Fig. 2a), while the fraction of basal species was unaffected by invasion or warming  
312 reinforces the observation that top predators were lost and replaced by consumers further down  
313 the food web. Interestingly, this replacement appeared to be stronger in warmer communities that  
314 also lost more species than colder ones.



315 The effects of unsuccessful invasions (i.e. when the introduced species went extinct) on food  
316 webs were more homogeneous across the temperature gradient than those caused by successful  
317 invasions, mainly affecting species numbers, connectivity ( $L$  and  $L/S$ ), and the fraction of  
318 intermediate species (Appendix S4).

## 319 **DISCUSSION**

320 Global warming and biological invasions affect communities simultaneously. It is fundamental to  
321 better understand their synergistic effects on biodiversity (Bradley *et al.* 2010). Using dynamical  
322 models we have investigated the interactive effects of warming and invasions on the structure and  
323 dynamics of complex food webs. We showed that warming has two overall effects on invasions  
324 and on invaded communities. First, it modified key aspects of community structure and dynamics  
325 that in turn facilitated invasions by introduced species. Secondly, warming mostly amplified the  
326 impacts of invasions on the structure and organisation of communities. Importantly, the  
327 directionality of the effects of invasions on recipient communities changed across the temperature  
328 gradient for community biomass and population stability. Further, our results suggest that the  
329 direct effects of temperature on invasion success are weaker to those mediated by changes in  
330 community structure and stability.

331 Previous attempts to understand and predict the combined effects of warming and invasions have  
332 been based mainly on bioclimatic envelop models, relying on temperature thresholds for survival  
333 and reproduction of the invasive species (Stachowicz *et al.* 2002; Walther *et al.* 2009; Sorte *et al.*  
334 2010; Kent *et al.* 2018). Such phenomenological approaches, even though informative, lack a  
335 mechanistic understanding of how warming mediates invasions and how both can synergistically  
336 affect ecological communities. Here, we have provided a first step towards a better understanding

337 of the synergistic effects of warming and invasions on complex ecological communities. Our  
338 efforts complement recent attempts to better understand how warming modulates the effects of  
339 invasions on natural communities (Zhang et al. 2017).

#### 340 ***Warming effects on invasion success***

341 We found that, before invasion, warming increased food web stability but decreased the  
342 persistence of top predators, as reported in previous studies (Fussmann *et al.* 2014; Binzer *et al.*  
343 2016; Sentis *et al.* 2017). This increased stability is likely explained by average trophic  
344 interaction strength decreasing and by consumers being less efficient at feeding relative to their  
345 metabolic losses (Boukal *et al.* 2019). Warmer communities thus contained less species, but  
346 network connectance increased. Whether these warming-induced changes influence invasion  
347 success remains an open question.

348 Previous theoretical models showed that more connected food webs are generally better at  
349 repelling invaders (Romanuk *et al.* 2009). In contrast, Lurgi *et al.* (2014) showed that, when  
350 controlling for the number of species, less connected food webs are more resistant to invasions.  
351 Here, we found that invasions are more successful in warmer communities, which are more  
352 connected but poorer in species richness than colder ones. Invasion success was strongly  
353 mediated by the indirect effects of temperature on network and community properties and  
354 stability, with these effects only weakly mediated by species richness. Temperature had an impact  
355 on the composition of species across trophic levels, influencing greatly the proportion of top  
356 predators. This, in turn, made communities more susceptible to invasions by reducing mean food  
357 chain length. We also found that warming directly increased invasion success. Nevertheless, the  
358 direct effect of warming on invasion success was much weaker than its indirect effects.

359 Our results are in line with empirical studies reporting that the influence of warming on invasion  
360 success may depend on how warming affects the strength of trophic interactions and the  
361 persistence of local predators or competitors (Holzapfel & Vinebrooke 2005; Lu *et al.* 2013;  
362 Seifert *et al.* 2015). Warming can prevent invasions by increasing top-down control on  
363 introduced species (Lu *et al.* 2013; Lu *et al.* 2016). On the other hand, Holzapfel and Vinebrooke  
364 (2005) showed that warming can enhance invasions by removing top-down control on the  
365 invader following predator extinctions. Our model results suggest that the loss of top predators,  
366 which in turn reduces mean food chain length, is a driving mechanism of invasion success. This  
367 highlights the importance of species loss at high trophic levels on facilitating invasions under  
368 warming.

### 369 ***Ecological consequences of invasions along a temperature gradient***

370 Our results are in line with previous studies showing that invasions decrease species richness and,  
371 as a consequence, impact strongly community structure (Hui & Richardson 2019). However,  
372 recent theoretical studies have suggested that warming is predicted to have an opposite effect on  
373 invasions, by enhancing species richness and ecosystem functioning (Zhang *et al.* 2017). We  
374 found that temperature can modulate the consequences of invasions for community structure.  
375 Warmer communities tend to lose more species and interactions when invaded, which translates  
376 into more connected communities compared to colder ones. This intensification in the effects of  
377 invasions across the temperature range highlights the importance of considering a full spectrum  
378 of temperature treatments to fully understand the effects of warming on invaded communities.

379 The proportion of top predator species in our model food webs increased as a consequence of  
380 invasion, especially in warmer environments. This result apparently contradicts the loss of top

381 predators following invasions that we observed. Both observations are reconciled by a third  
382 result: invasions shorten food chains. In short, when top predators go extinct they are replaced by  
383 consumers further down the food web, which in turn become top predators. This switch decreases  
384 the proportion of intermediate species while increasing the proportion of top species, ultimately  
385 shortening food chain length. Invasions thus exacerbate the previously observed effect of  
386 warming on top predator species, and corroborates previous empirical findings of higher trophic  
387 levels being most vulnerable to climate change (Voigt *et al.* 2003). We should thus expect  
388 warmer and invaded communities being even more susceptible to invasions, entering a positive  
389 feedback loop via the loss of predator species.

390 As any modelling study, ours relies on a set of assumptions that can influence model predictions.  
391 For instance, we did not account for temperature fluctuations, evolutionary change or differences  
392 in the thermal traits of the invasive species (e.g. the invasive species may have thermal traits  
393 better adapted to warmer climate) that can also influence invasion success and species persistence  
394 (Vasseur *et al.* 2014; Zhang *et al.* 2017). The assumption of invasive species possessing similar  
395 thermal performance than resident species is supported by the observation that most invasive  
396 species are introduced by human transport and their invasion success is not proven to be strongly  
397 related to the climate in their native environment (Gippet *et al.* 2019). Additionally, in our model,  
398 introduced species, and their biotic interactions, have been defined following the same heuristics  
399 as the rest of the species in the recipient community (i.e. they are drawn from the niche model),  
400 whereas in natural communities invasive species tend to be generalists, both in terms of habitats  
401 and interactions (Elton 1958). We decided to define introduced species in this way to be as  
402 parsimonious as possible in our experiments and avoid the confounding effects of over-generalist  
403 species in modelled communities. It would be interesting to extend the results presented here

404 using invasive species with more realistic traits. Despite these limitations, our model provides a  
405 first step in the exploration of the consequences of warming and invasions in species-rich  
406 communities.

## 407 **CONCLUSION**

408 Research on the effects of temperature on biological invasions has traditionally focused on the  
409 species level and have not explicitly considered species interactions, usually not taking into  
410 account the way temperature can affect food web and community properties prior to invasions.  
411 Understanding the joint effects of warming and invasions at the community level constitutes a  
412 pressing challenge to unveil the full consequences of global change on natural communities. Here  
413 we addressed this challenge and showed that temperature's direct effects on invasion success are  
414 weaker than its indirect effects mediated by changes in food web structure, community properties  
415 and stability. Moreover, we showed that the impact of invasions depend on the temperature  
416 experienced by the invaded communities. Warmer food webs lose more species and interactions  
417 when invaded than their colder counterparts. These changes are accompanied by an increase in  
418 the fraction of top predator species, enhanced total community biomass and decreased stability.  
419 Overall, our study suggest that both warming and invasion act synergistically to fasten species  
420 loss creating smaller and more connected networks. It paves way for a better understanding of the  
421 causes and consequences of invasions in a warming world.

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608 **Tables**

609 **Table 1. Parameter values for mass and temperature dependencies of  $r$ ,  $\alpha$ ,  $h$  and  $x$ .** Parameters  
610 are in biomass units, i.e. per unit of mass of predator or prey. Parameters extracted / calculated  
611 from: growth ( $r$  in [1/s], (Savage et al., 2004)), metabolism ( $x$  in [1/s], (Ehnes et al., 2011)),  
612 attack rate ( $\alpha$  in [ $\text{m}^2 \text{s}^{-1}$ ]) and handling time ( $h$  in [s]), both calculated from (Rall et al., 2012).  
613 Metabolic rates were calculated using the conversion factor from Peters (1983).

	$r_i$	$\alpha_{ij}$	$h_{ij}$	$x_i$
Intercept (I)	-15.68	-13.1	9.66	-16.54
Body mass scaling species $i$ ( $b$ )	-0.25	0.25	-0.45	-0.31
Body mass scaling predator ( $c$ )		-0.8	0.47	
Activation energy ( $K$ )	-0.84	-0.38	0.26	-0.69

614

615 **Table 2. Network structural properties used in this study to quantify the structure of simulated**  
 616 **food webs.** The name of the properties, their abbreviations and a brief description are presented.

<i>Property</i>	<i>Abbrev.</i>	<i>Description</i>
Species richness	$S$	Number of species in the community.
Number of links	$L$	Total number of trophic interactions in the food web.
Links per species	$L/S$	Average number of links (i.e. interactions) per species.
Connectance	$C$	Fraction of realised links out of all the possible links in the food web. Calculated as: $C = L/S^2$
Standard deviation of generality	$GenSD$	Quantifies the variability of species' normalised number of prey (or their generality) $G_j = \frac{1}{L/S} \sum_{i=1}^S a_{ij}$ , where $a_{ij}$ are the elements of A, the adjacency matrix representing the food web and in which if $a_{ij} = 1$ there is a trophic interaction between prey $i$ and predator $j$ .
Standard deviation of vulnerability	$VulSD$	Quantifies the variability of species' normalised number of predators (or their vulnerability) $G_i = \frac{1}{L/S} \sum_{j=1}^S a_{ij}$
Mean food chain length	$MFCL$	Average length (i.e. number of links) of all the paths (food chains) running from each basal species to each top predator species in the food web.
Fraction of basal species	$B$	Fraction of basal species, out of the total number of

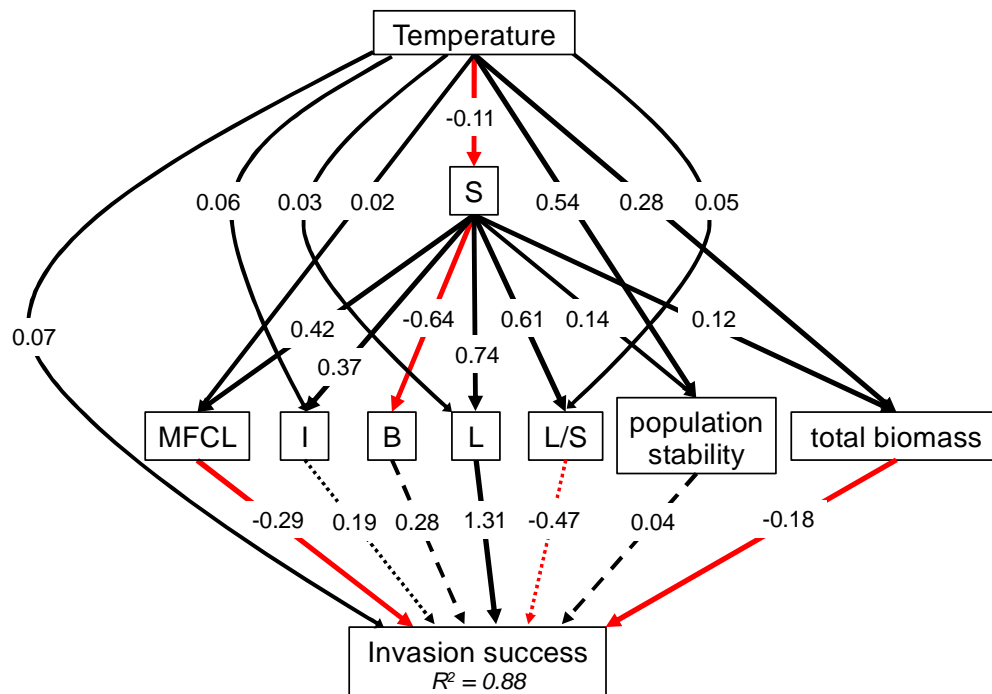


species, in the food web. Basal species are those with no prey (i.e. no incoming links).

Fraction of intermediate species	$I$	Fraction of species in the food web having both prey and predators (i.e. sitting in the ‘middle’ of the food web).
Fraction of top species	$T$	Fraction of top consumers in the food web (i.e. species that do not have predators).
Maximum similarity	$MxSim$	The average maximum trophic similarity across species in the network. Trophic similarity ( $s_{ij}$ ) of a pair of species is the number of common prey and predator species divided by the pair’s total number of predator and prey species. Thus, $MxSim = \frac{1}{S} \sum_{i=1}^S \max_{v_{i \neq j}}(s_{ij})$
Modularity	$Q$	A measure that quantifies the extent to which species within the same compartment share more interactions among themselves than with species in other compartments (see Appendix S1 in Supporting Information for details on modularity calculation).

618 **Figures**

619 **Figure 1.**

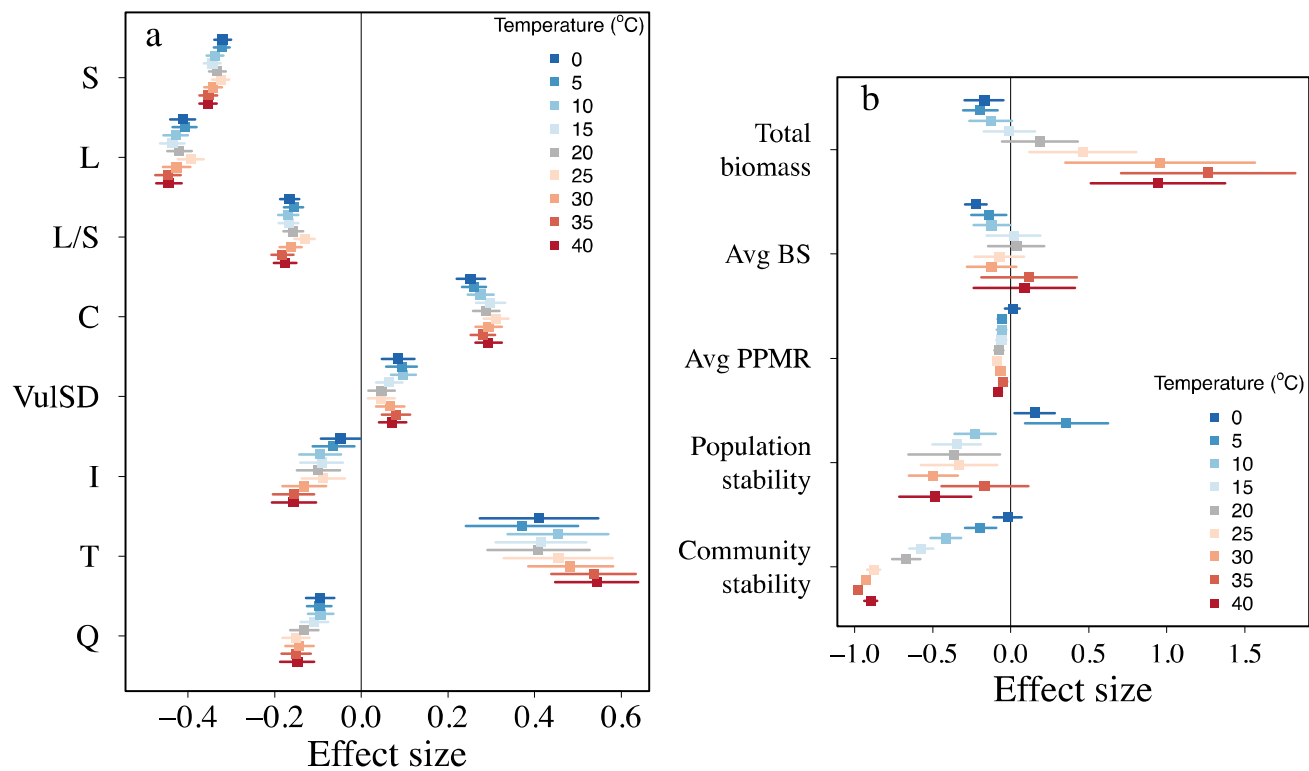


620

621

622

623 **Figure 2.**



624

625

626 **Figure legends**

627 **Figure 1. Structural equation model (SEM) describing the direct and indirect effects of**  
628 **temperature on invasion success in complex food webs.** Arrows indicate the direct effects of  
629 predictor on response variables. Only predictors having a statistically significant effect (i.e. p-  
630 value < 0.05) on invasion success are shown (see Table S1 for more details). Black and red  
631 arrows represent positive and negative effects respectively. Solid, dashed, and dotted arrow styles  
632 represent strongly (p-value < 0.001), intermediate (p-value < 0.01), and marginally (p-value <  
633 0.05) statistically significant effects respectively. Model fit: Fisher's C = 22.67, p-value = 0.305,  
634 degrees of freedom = 20.

635

636 **Figure 2. Effect sizes (mean  $\pm$  s.d.) of successful invasions on complex food webs across**  
637 **temperature regimes on network (a) and community (b) properties.** Effect sizes were quantified  
638 as the ratio between the values of the network/community property after species introduction vs.  
639 before introduction, minus unity. Negative values thus indicate negative effects of the invasion  
640 on the community (i.e. the value after the invader's establishment is smaller than before the  
641 introduction). Only effects on properties identified by SEMs as being significantly influenced by  
642 temperature (Table S2) are shown. Only a subset of temperature regimes is shown to ease the  
643 visualisation of the results.

644