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

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

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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

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INTRODUCTION

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

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

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

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

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:

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

143   where α_{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:

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

154   where m_0 is the body size of basal species in the food web and set here to $m_0 = 0.01$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):

$$159 \qquad \alpha_{ij}, h_{ij} \; = \; dm_i{}^b m_j{}^c e^{E\frac{T_0 - T}{kTT_0}} \qquad\qquad (5a)$$

$$160 \qquad r_i, x_i \; = \; dm_i{}^b e^{E\frac{T_0 - T}{kTT_0}} \qquad\qquad (5b)$$

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161 where $d = e^I$ is a rate-specific constant calculated for a species with body mass of 1g and at a

162 reference temperature $T_0 = 20$ºC (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.

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

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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 (18.9216×10^9

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.

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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^{-2}, 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 40ºC at 1ºC 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

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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-

249   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).

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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 (V*ulSD*) 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

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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.

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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

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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

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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

19

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.

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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607

608   **Tables**

609   **Table 1.** *Parameter values for mass and temperature dependencies of r, α, 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 (α in [m^2 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	α_{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.

Property	*Abbrev.*	*Description*
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

31

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, $MxSim = \frac{1}{S}\sum_{i=1}^{S} max_{\forall i \neq j}(s_{ij})$
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).

617
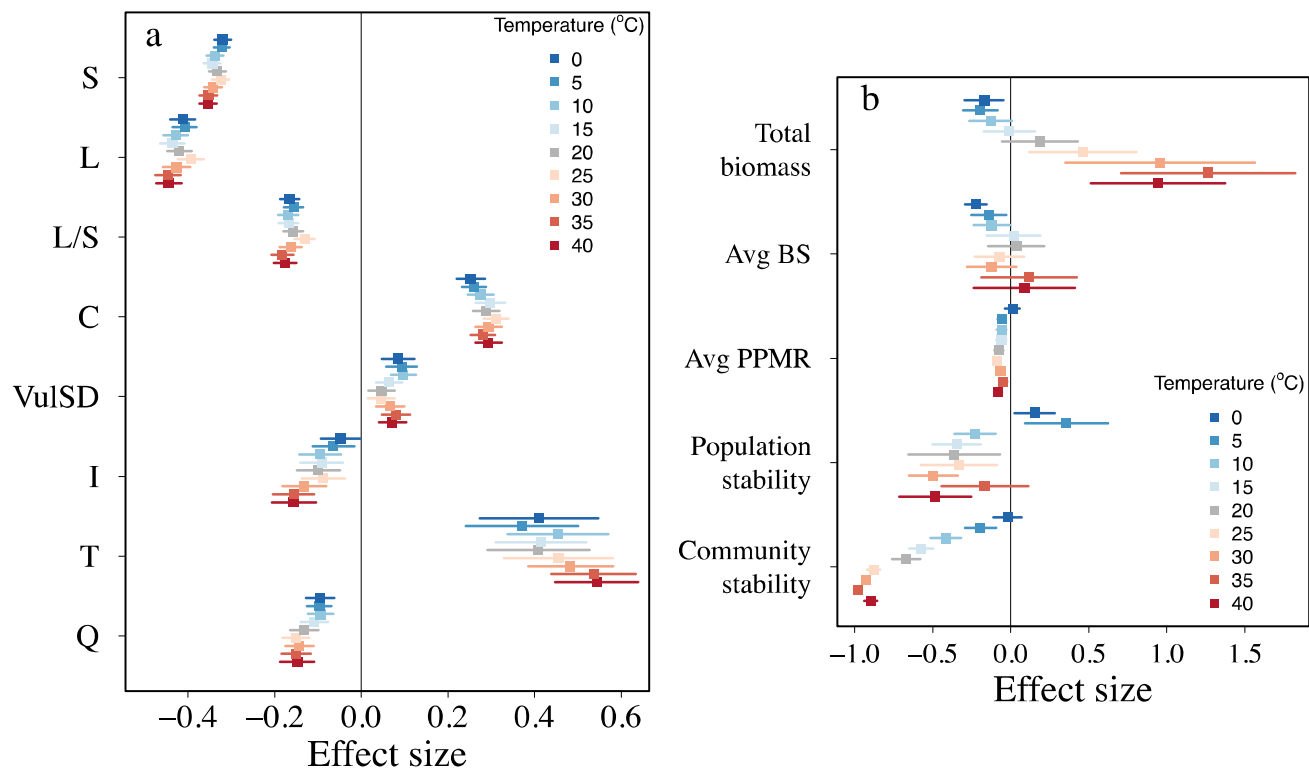
618 **Figures**

619 **Figure 1.**
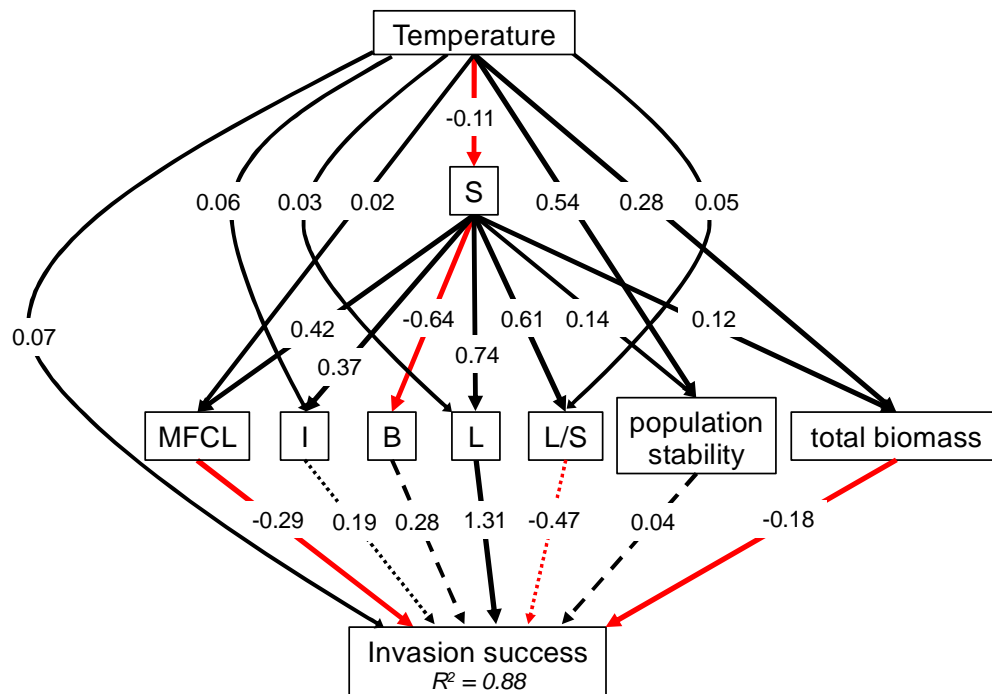
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622

623 **Figure 2.**

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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 ± 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