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Cite this article: Sentis A, Montoya JM, Lurgi M. 2021 Warming indirectly increases invasion success in food webs. *Proc. R. Soc. B* **288**: 20202622.
https://doi.org/10.1098/rspb.2020.2622

Received: 20 October 2020
Accepted: 22 February 2021

Subject Category:
Global change and conservation

Subject Areas:
ecology, environmental science, theoretical biology

Keywords:
climate change, body size, allometric bio-energetic model, food web structure, temperature dependence, top-down control

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5325020.

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Warming indirectly increases invasion success in food webs

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

1. Introduction

Climate warming and biological invasions constitute two of the most pervasive global change drivers [1]. They cause species loss and alter the structure of interaction networks [2–9]. Climate warming and species invasions can act synergistically due to, for example, impacts of climate change on species niche range dynamics [10], which influence species' ability to colonize new habitats and invade new communities. Species range shifts affect both species composition and the structure of species interaction networks. For example, by promoting species range shifts, warming can trigger the loss of specialized interactions and changes in body size ratio between predators and prey, which in turn can influence predator control on prey populations [3,11]. 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 warmer temperatures can enhance invasions by increasing survival and reproduction of introduced species [6,8,12]. However, warming can also lead to the opposite effect by decreasing the potential for invaders to occupy new niches [13,14]. Recent evidence suggests that warming effects on invasion success may depend on how temperature influences trophic interaction strength and the persistence of native predators or competitors [5,7,15]. On one hand, high temperatures can prevent invasions by increasing top-down control on invasive prey [7,14,16]. On the other hand, warmer temperatures can enhance invasions by releasing top-down control following predator extinctions [5]. It is yet unclear the extent of indirect effects of temperature changes on species and communities. Indirect effects of temperature on community structure and species interactions are often stronger than their direct effects on physiology and demography [17]. To investigate thermal effects on communities and interaction networks is a first step to address this challenge.

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Ecologists have developed mechanistic frameworks to identify key processes underlying temperature effects on trophic interactions and networks [18–20]. Firstly, since consumer metabolic rates often increase faster with temperature than their feeding rates, most consumers become less efficient at processing matter and energy at warmer temperatures [21,22]. This reduction of energetic efficiency lessens energy flow between trophic levels and, if resulting in weakened interaction strengths, it stabilizes food web dynamics by reducing population fluctuations [18,20,23]. Secondly, elevated temperatures increase consumer extinction risk when metabolic demands exceed ingestion rates, leading to consumer starvation and extinction [24–26]. Whether these changes would favour invasion success is unclear, as previous studies exploring the role of community structure and dynamics in preventing or facilitating invasions have not considered modifications in communities driven by temperature [2,4].

In parallel, much effort has been devoted to understanding how invasions impact ecosystems. Several models have unveiled the role of food web structure, such as species richness, complexity or the distribution of feeding links in preventing invasions. These models showed that invasions in food webs tend to decrease species richness and shorten food chains [2,4]. However, a more recent theoretical investigation suggests the opposite, with invasions being instead beneficial for maintaining species richness and ecological functions [9]. We need comprehensive mechanistic frameworks explicitly incorporating both temperature and invasions to better understand and predict their synergistic effects on complex communities.

Here, we explored the combined effects of temperature and invasions on food webs using a theoretical model. Given our understanding of temperature effects on natural communities [18,27,28], and of invasions in food webs [2,4,29], along with previous studies showing a positive influence of weakened top-down control on invasions [5], we expect higher temperatures to increase invasion success if they decrease top-down control or cause predator extinctions. We further expect warmer temperatures to increase connectivity and shorten food chains in response to species loss at higher trophic levels which should in turn destabilize community dynamics [28]. These different observations suggest several hypotheses concerning the synergistic effects of temperature and invasions on food webs. Firstly, we hypothesise that warmer temperatures decrease species richness due to the deterministic loss of top predators [30], which in turn impacts community structure and stability and thus facilitates invasions. A second competing hypothesis is that warmer temperatures first stabilize population fluctuations and reduces community biomass (as in [31]), which impacts community structure and species richness, increasing invasion success. A third, more parsimonious hypothesis is that temperature directly influences all components of community structure and stability which then impacts invasion success. These three first hypotheses only consider the indirect effects of temperature on invasion success. However, warmer temperatures can also directly facilitate invasion if they promote the growth of the invading population. This leads to three additional hypotheses that are similar to those presented above, but they additionally account for the direct effect of temperature on invasion success. By testing these six competing hypotheses, it would be possible to determine the relative importance of the direct and indirect effects of temperature on invasion success.

To test these hypotheses, we investigated how temperature influences invasions on complex food webs composed of 30 species using a dynamical simulation model. In addition, we investigated the synergistic effects of temperature and invasions on these communities. In contrast to temperature, invasions directly alter community structure by either adding species and links to the system [9] or by promoting species extinctions and decreasing food chain length [2]. Following our first hypothesis, warmer communities are expected to be smaller and thus invasions are expected to cause larger impacts on them because the relative species gain or loss is higher in smaller communities. Our model simulates population dynamics under constant temperature regimes with the aim of gaining a better understanding of (i) temperature effects on invasion success in food webs and (ii) the ecological consequences of invasions on food web structure in warmer communities.

2. Material and methods

We modelled food web dynamics using a size-structured bio-energetic model consisting of a set of ordinary differential equations (ODEs) incorporating the effects of species growth and ecological interactions [32]. The effect of temperature on population dynamics was incorporated into ODEs by introducing thermal dependencies of relevant model parameters. Numerical simulations were executed, with species invasions modelled as the addition of a new species into the community [2]. Simulation results were analysed to assess the effects of temperature on (i) food web properties before invasion, (ii) invasion success, and (iii) the effects of invasions on community structure and stability.

(a) Food web generation

Food webs were generated using the niche model [33]. With only two parameters (number of species (S) and network connectance (C)), this model generates networks that resemble real food web structure [33]. We generated food webs comprising 30 species and with 10% connectance which is representative of empirical food webs [33]. We kept these values fixed across simulations to avoid the confounding effects of variation in species richness and connectance.

(b) Nonlinear model for population dynamics

We simulated species populations biomass dynamics using an allometric bio-energetic model. This model defines predator–prey interaction strengths according to their body mass ratios [32] and has been used to investigate the effects of temperature and invasions on complex food webs [2,34]. The basal resource species grow logistically with an intrinsic growth rate r_i and a carrying capacity K_i (equation (2.1)). Consumers gain biomass according to equation (2.2):

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = r_i B_i\left(1 - \frac{B_i}{K_i}\right) - \sum_m F_{im} B_i \tag{2.1}$$

and

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = \sum_s eF_{si}B_i - \sum_m F_{im}B_m - x_i B_i, \tag{2.2}$$

where B_i is the biomass of species i; e is the assimilation efficiency of predators when ingesting prey (kept constant across consumer–resource species pairs at a value $e = 0.85$ for carnivorous species); x_i is the metabolic rate at which biomass of consumers is lost from the system due to respiration and other metabolic

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processes. F_{ij} describes the functional response between prey i and predator j:

$$F_{ij} = \frac{\alpha_{ij} B_i^q}{1 + \sum_k h_{kj} \alpha_{kj} B_k^q}, \tag{2.3}$$

where α_{ij} represents the elements of the adjacency matrix A, describing the food web obtained according to the procedure explained above, and that represent the attack rates of predator species j on prey species i (equation 2.5*a*). h_{ij} is the handling time, and the shape of the functional response curve is controlled by the parameter q (i.e. the Hill exponent). We kept q constant across interacting species pairs at a value of 1.2 to simulate an intermediate response type between Type II (hyperbolic, $q = 1$) and Type III (sigmoidal, $q = 2$), as in [30,34].

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

$$m_i = m_0 R^{L_i - 1}, \tag{2.4}$$

where m_0 is the body size of basal species and set to $m_0 = 0.01$ g, R is the average predator–prey body mass ratio of all trophic interactions in the food web and was set to $R = 10^2$, L_i is the prey-averaged trophic level of species i [33]. Allometric and thermal dependencies of model parameters were incorporated as in [30]:

$$\alpha_{ij}, h_{ij} = d m_i^b m_j^c e^{E(T_0 - T/kTT_0)} \tag{2.5a}$$

and

$$r_i, x_i = d m_i^b e^{E(T_0 - T/kTT_0)}, \tag{2.5b}$$

where $d = e^I$ is a rate-specific constant calculated for a species with body mass of 1 g and at a reference temperature $T_0 = 20$°C, m_i and m_j are the body masses of species i and j, respectively, b and c are rate-specific allometric exponents. The temperature-dependence term is a version of the Arrhenius equation in which E is the rate-specific activation energy and k is the Boltzmann constant. T is the current temperature of the system in Kelvin. T_0 is the reference temperature at which the rate value is equal to the rate-specific constant d. Values and units for the parameters in equations (2.5*a*) and (2.5*b*) are presented in table 1.

Species carrying capacity was assumed to be independent of temperature since empirical evidence for its thermal dependency is inconclusive [20,35]. Furthermore, we wanted to avoid biases in the invasion experiments due to the intrinsic limit to community biomass caused by the negative temperature dependence of carrying capacity, which would, in turn, influence invasion success. We thus focused on the effects of temperature on species life-history traits such as reproduction, death and species interactions (i.e. attack rates and handling times) and not on the maximum population density of the basal resources.

(c) Food web structure, community properties and ecological stability

To assess the synergistic effects of temperature and invasions on food webs, we computed food web properties including species richness (S), the number of links (L), connectance ($C = L/S^2$), the average number of links per species (L/S), standard deviation of the generality and vulnerability (*GenSD* and *VulSD*), mean food chain length (*MFCL*), the fraction of basal, intermediate and top predator species (B, I and T), maximum trophic similarity (*MaxSim*), and modularity (Q) (see electronic supplementary material, table S1 and appendix S1 for a full description of properties); before and after invasions, at each temperature. In addition to changes in food web properties, we also assessed community properties such as total community biomass, the average species body size in the community (*AvgBS*) and the average predator:prey body mass ratio (*AvgPPMR*). Lastly, to assess ecological stability, we focused on temporal variability (invariability) of biomass both at the community and population levels. Variabilities, both at the community (i.e. summing across the biomass of all species populations) and at the population level, were calculated as the ratio of the standard deviation to the mean biomass across the last 100 years of the simulations.

Table 1. Parameter values for mass and temperature dependencies of r, α, h and x. Parameters are in biomass units, i.e. per unit of mass of predator or prey. Growth (r in s^{-1}), metabolism (x in s^{-1}), attack rate (α in m^2 s^{-1}) and handling time (h in s). Parameter values are taken from [30] and references therein.

	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

(d) Numerical simulations

Using the food web model specified above (equations (2.1)–(2.5)), we simulated a range of temperature regimes and the addition of new species (i.e. invasions) as follows:

1. 140 niche model food webs were randomly generated ($S = 30$ and $C = 0.1$).
2. Initial biomass densities for basal species were set to their carrying capacity $K \approx 2.75$ following the allometric formulation in equation (2.5*b*) but omitting the temperature-dependence term and assuming an allometric scaling constant and exponent of 10 and 0.28, respectively [30]. Consumer species initial abundances were set to one-eighth of this value.
3. Community dynamics were first simulated for an equivalent of 600 years to reach an equilibrium in the dynamics. Food web, community and stability measures were calculated.
4. After this, an invasion was simulated by introducing a new species into the network. The introduced species were drawn at the beginning of the simulation from the original niche model (step 1) but removed from the community before simulating community dynamics. Since at this time point, some species might have gone extinct (see step 6), rendering the potential introduced species disconnected, we repeated the drawing procedure if necessary, until a connected species was found.
5. After the introduction, we simulated further 600 years of network/community dynamics. We then recorded whether the invasion was successful (i.e. whether the introduced species persisted). Network, community and stability measures were again calculated.
6. A species was considered extinct if at any point during the simulations its biomass fell below 10^{-9} g m^{-2}, at which point its abundance was set to 0.

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

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Table 2. Structural equation model comparisons. Different hypotheses regarding the effects of temperature and network/community structure on invasion success were tested. Each hypothesis corresponded to a specific model formulation (see electronic supplementary material, appendix S2 for model descriptions). Models were compared using the Akaike information criterion (AIC). Fisher's C was calculated as a measure of goodness of fit. d.f., degrees of freedom. Models are ordered by AIC scores.

model	Fisher's C	d.f.	*p*-value	AIC
only temperature indirect effects	20.58	18	0.301	162.58
direct and indirect effects of temperature	20.58	18	0.301	164.58
deterministic interactions most important	40.08	28	0.065	182.08
deterministic and indirect effects of temperature	22.67	20	0.305	190.67
instability and productivity are most important	10.68	8	0.221	190.68
biomass, stability and temperature	3.875	4	0.423	207.88

(e) Statistical analyses

The relationship between temperature and food web structure, stability and community properties (i.e. total biomass, *AvgBS* and *AvgPPMR*) and their corresponding effects on invasion success were analysed using piecewise structural equation models (SEMs). We computed SEMs considering invasion success (i.e. whether the invasive species established after introduction) as a response variable, with temperature affecting it directly and indirectly via network and community properties. In particular, we compared six different SEM structures to test the hypotheses presented in the Introduction (see electronic supplementary material, appendix S2 for full SEMs details). The six SEMs were compared using the Akaike information criterion (AIC) and Fisher's C was calculated as a measure of goodness of fit.

To assess invasion effects on food web structure, stability and community properties, we calculated the log ratio of values after versus before invasion for food web (electronic supplementary material, table S1) and community properties, and stability. To disentangle the direct and indirect effects of temperature on these ratios, we performed another SEM following the same rationale as above and using the log ratio of the effects as a response variable (i.e. effect size). We included species richness before invasion as a latent variable to determine whether the effects of the invasion on community structure and stability were modulated by the original effect of temperature on the number of species. We additionally assessed the differences between communities vulnerable versus resistant to invasions in terms of these effects by comparing after/before log ratios of each property between invaded and non-invaded communities using Mann–Whitney *U*-tests.

All simulations and analyses were performed in R language and environment for statistical computing [36]. Numerical simulations were computed using the deSolve package [37]. Food web analyses were conducted with cheddar [38]. Modularity was computed using the cluster_louvain function from the igraph package [31]. Piecewise SEMs were performed using the piecewiseSEM [39] package. Computer code developed to run model simulations and analysed outputs are available from the following repository: https://github.com/mlurgi/temperature-dependent-invasions.

3. Results

We focus on (i) the influence of temperature on invasion success and (ii) the community-wide consequences of invasions. Effects of temperature on food webs before invasion are detailed in electronic supplementary material, appendix S3. In line with previous findings [30], we found that warmer communities harbour less species than their colder counterparts, particularly at high trophic levels, which in turn translates into higher connectance. These structural changes prompt an increase in both community biomass and stability in warmer environments (electronic supplementary material, appendix S3).

(a) How does temperature influence invasion success?

SEMs comparison based on AIC revealed that the effects of temperature on invasion success were best predicted by our first hypothesis (i.e. only indirect effects of temperature) where temperature affects community structure and stability which then affect invasion success (table 2). We found that communities exposed to warmer temperatures were more susceptible to invasions and these thermal effects were mostly indirect (figure 1 and electronic supplementary material, table S2). Species richness (S), the number of links (*L*), the average number of links per species (L/S), mean food chain length (*MFCL*) and the fraction of basal and intermediate species (*B* and *I*, respectively) had a strong and significant influence on invasion success (figure 1; electronic supplementary material, table S2).

Even though temperature had a direct significant effect on most network properties (electronic supplementary material, table S2 and figures S1–S3), only a few of them affected invasion success. In particular, we found that communities with longer food chains (*MFCL*) were more resistant to invasion. In addition, communities with more links (*L*) and greater proportions of basal (*B*) and intermediate (*I*) species were more prompt to invasion (figure 1). Communities harbouring more specialized species (i.e. small L/S) also were more susceptible to invasion.

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

(b) Ecological consequences of invasions along the temperature gradient

In general, invasions strongly decreased species richness (figures 2*a* and 3), which, in turn, affected several network properties (figure 3). Moreover, we found that the magnitude

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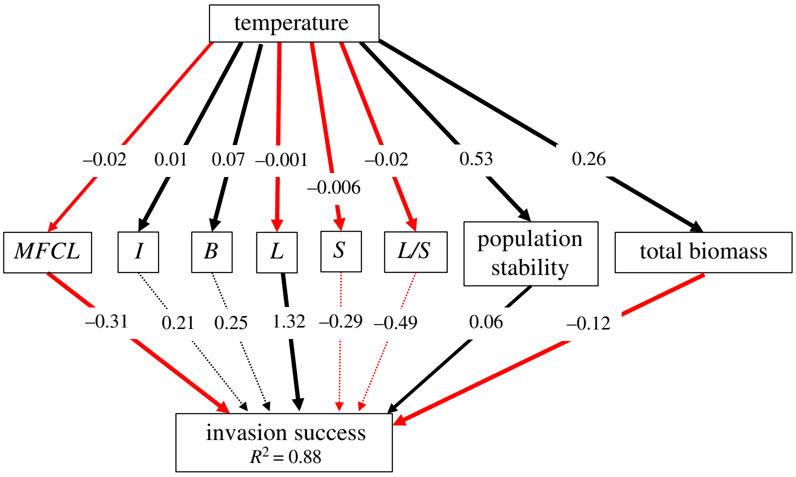

Figure 1. Indirect effects of temperature on invasion success in complex food webs. Path diagram describing the results of structural equation models (SEMs). Arrows indicate the direct effects of the predictor on response variables. Only predictors having a statistically significant effect (i.e. p-value < 0.05) on invasion success are shown (see electronic supplementary material, table S2 for more details). Black and red arrows represent positive and negative effects, respectively. Solid and dotted arrow styles represent strongly (p-value < 0.001) and marginally (p-value < 0.05) statistically significant effects, respectively. (Online version in colour.)

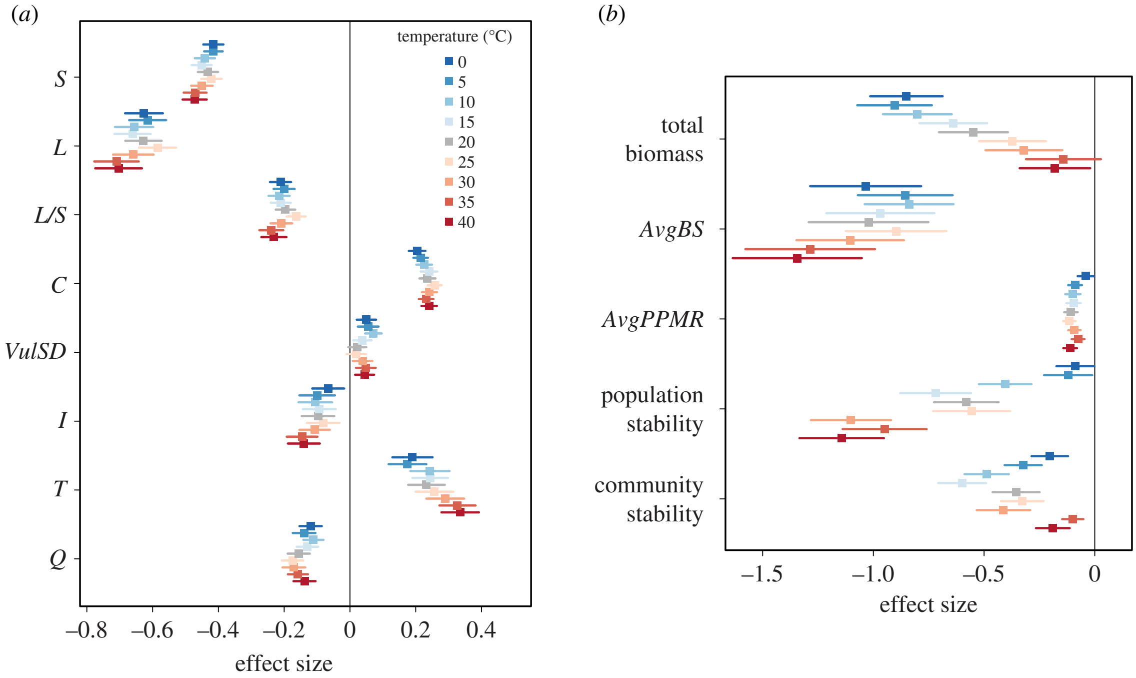

Figure 2. Effect of successful invasions on complex food webs across temperature regimes on network (*a*) and community (*b*) properties. Effect sizes (mean ± s.d.) were quantified as the log ratio between the values of the network/community property after species introduction versus before introduction. Negative values thus indicate negative effects of the invasion on the community (i.e. the value after the invader's establishment is smaller than before the introduction). Only effects on properties identified by SEMs as being significantly influenced by temperature (electronic supplementary material, table S3) are shown. Only a subset of temperature regimes is shown to ease the visualization of the results. (Online version in colour.)

of the change of community properties driven by invasions often depended on temperature (figure 3 and electronic supplementary material, table S3). In particular, warmer communities lose more species and interactions when invaded than their colder counterparts. This translates into more connected communities (figure 2*a*). Interestingly, SEMs revealed that these thermal effects were mainly mediated by the indirect effect of temperature on species richness before invasion and on the change of species richness induced by invasion (figure 3).

Warmer temperatures prompted a stronger decrease in the proportion of intermediate species (I) when invaded whereas the proportion of top species increased under invasion, and this effect was magnified by warmer temperature (figure 2). The proportion of basal species (B) was not influenced by invasion or temperature (electronic supplementary material, table S3). This suggests that intermediate species became top predators when their predators disappeared in invaded communities, yielding a lower fraction of intermediates while increasing the fraction of top predator species. Finally, the impact of invasion on modularity (Q) and vulnerability ($VulSD$) were weakly influenced by temperature, with warmer temperatures reducing the impact of invasion on these two community properties.

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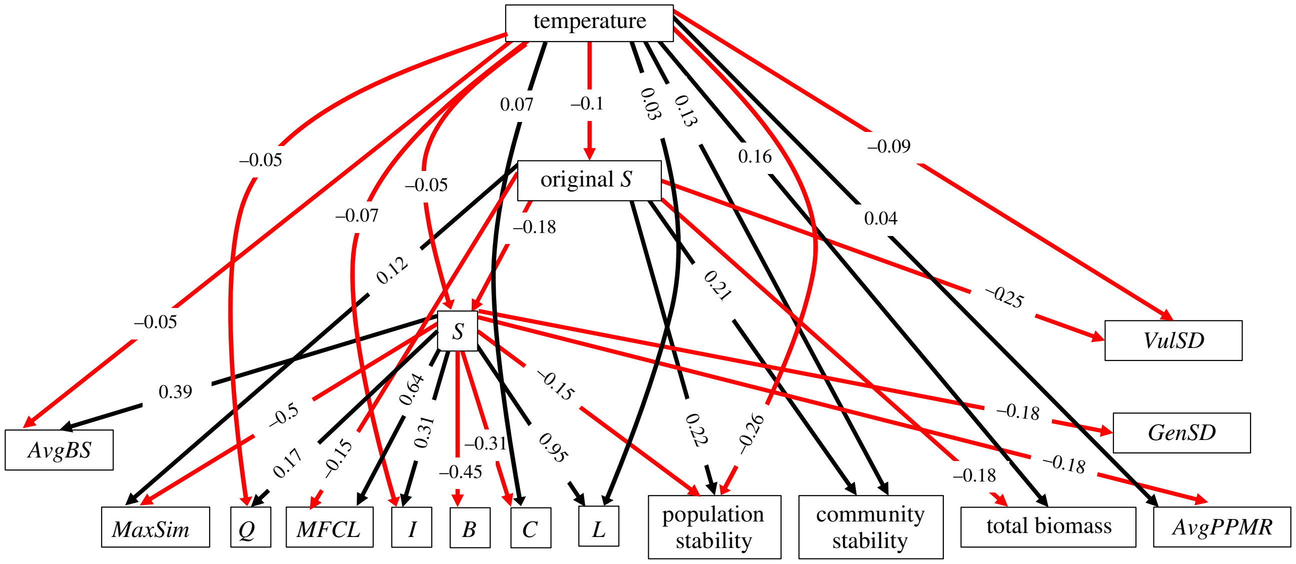

Figure 3. The influence of temperature on the effects of invasions on complex communities. A schematic representation of the outcome of structural equation models (SEMs) describing the direct and indirect (via original species richness in the community and changes in S) effects of temperature on the changes of community and network properties due to invasions. Network and community properties refer to the effect of invasions on them (measured as the log ratio between the property values after versus before invasion), except for original S, which refer to the actual values of the number of species before invasion. Arrows indicate the direct effects of the predictor on response variables. Numbers overlain on the arrows indicate relative magnitudes of the effects. To improve visualization, only predictors with very strong statistically significant effect (i.e. p-value < 0.001) on response variables are shown (see electronic supplementary material, table S3 for a full set of effects). The average links per species (L/S) and the fraction of top species (T) are not shown to improve clarity of the picture, but the effects on these are equivalent to those on connectance (C) and the fraction of intermediate species (I), respectively. Black and red arrows represent positive and negative effects, respectively. (Online version in colour.)

Community properties and stability were always negatively affected by invasions (figure 2). Invasion decreased total community biomass and warming dampened this negative effect (figure 2*b*). Invasions also decrease population stability, but this effect was more pronounced in warmer than in colder communities (figure 2). Overall, we found that warm invaded communities are composed of less species compared with their colder counterparts, with these species fluctuating more over time than cold invaded communities. The SEM analysis indicated that these effects were linked to both the direct and indirect effects of temperature mediated by changes in species richness before invasion and due to invasion (figure 3).

Lastly, the average body size (*AvgBS*) was negatively impacted by invasion and this effect was more pronounced when temperature increased (figure 2*b*). The decrease in average body size, along with the considerable increase in the fraction of top predator species (figure 2*a*), while the fraction of basal species was unaffected by invasion or temperature, reinforces the observation that top predators were lost and replaced by consumers further down the food web. This replacement appeared to be stronger in warmer communities that also lost more species than colder ones. Once again, these thermal effects were mainly mediated by the indirect effect of temperature on the impact of invasion on species richness (figure 3). This highlights that changes in community properties are mainly linked to interactions between temperature and invasion on species richness.

The effects of unsuccessful invasions on food webs were more homogeneous across the temperature gradient than those caused by successful invasions, mainly affecting species numbers, connectivity (L and L/S) and the fraction of intermediate species (electronic supplementary material, appendix S4).

4. Discussion

Global warming and biological invasions affect communities simultaneously. We investigated the interactive effects of temperature and invasions on food web structure and dynamics. We showed that temperature has two overall effects on invasions and on invaded communities. Firstly, warmer temperatures modified community structure and dynamics, which in turn facilitated invasions. Secondly, warmer temperatures mostly amplified the impacts of invasions on communities. Further, we found that temperature effects on invasions are mostly indirect and mediated by changes in community structure and stability.

Previous attempts to predict the combined effects of warming and invasions have been based mainly on bioclimatic envelop models, relying on temperature thresholds for survival and reproduction of the invasive species [8,40–42]. Such phenomenological approaches lack a mechanistic understanding of how temperature mediates invasions and how both can synergistically affect ecological communities. Here, we have provided a first step towards a better understanding of the synergistic effects of temperature and invasions on communities, which complement recent empirical attempts to discern how temperature modulates invasion effects [9].

(a) Temperature effects on invasion success

We found that, before invasion, warmer temperatures increased food web stability but decreased the persistence of top predators, as reported earlier [15,25,27,30]. This increased stability is probably explained by average trophic interaction strength decreasing and by consumers being less efficient at feeding relative to their metabolic losses [28]. Warmer communities thus contained less species, but network connectance increased.

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These results agree with empirical evidence showing that warming decreases species richness and leads to simpler and more connected communities, especially in closed or isolated systems [25,43–45]. Whether these warming-induced changes influence invasion success remains an open question.

Previous theory showed that more connected food webs are generally better at repelling invaders [4]. By contrast, Lurgi *et al.* [2] showed that less connected food webs are more resistant to invasions. The classical biotic resistance hypothesis [46] stresses that speciose communities are harder to invade [47,48]. Assuming connectance increases as species richness decreases [49], our results agree with empirical observations of the biotic resistance hypothesis [6]. We found that invasions are more successful in warmer communities, which are more connected but poorer in species richness than colder ones. Invasion success was strongly mediated by the indirect effects of temperature on network and community properties and stability, with these effects only weakly mediated by species richness. Temperature changed the proportion of top predators, which made communities more susceptible to invasions by reducing mean food chain length. Overall, our results show that the direct effects of temperature on invasion success were much weaker than its indirect effects.

Our results agree with empirical studies where temperature effects on invasion success depend on how temperature affects interaction strength and the persistence of local predators or competitors [5,7,15]. Warming can prevent invasions by increasing top-down control on introduced species [7,16]. For instance, Seifert *et al.* [15] conducted a warming and invasion microcosm experiment in tri-trophic planktonic food chains and found that warming increased predatory interaction strength which prevented invasions by herbivores. Holzapfel & Vinebrooke [5] showed that warming can enhance invasions by removing top-down control on the invader following predator extinctions. Our model generalizes these empirical results and highlights the importance of species loss at high trophic levels on facilitating invasions under warming.

(b) Ecological consequences of invasions along a temperature gradient

Our results agree with previous studies showing that invasions decrease species richness and, as a consequence, impact strongly community structure [29]. However, recent theory has suggested that warming is predicted to have an opposite effect on invasions, by enhancing species richness and ecosystem functioning [9]. We found that warmer communities tend to lose more species and interactions when invaded, which translates into more connected communities compared to colder ones. These predictions are in line with experimental results showing that the negative impact of invasions on species richness and connectance in aquatic communities is stronger under warmer temperatures [5,50].

The proportion of top predator species in our model food webs increased as a consequence of invasion, especially in warmer environments. This result apparently contradicts the loss of top predators following invasions that we observed. Both observations are reconciled by a third result: invasions shortened food chains. In short, when top predators go extinct, they are replaced by consumers further down the food web, which in turn become top predators. This switch decreases the proportion of intermediate species while increasing the proportion of top species, ultimately shortening food chain length. Invasions thus exacerbate the previously observed effect of warmer temperatures on top predator species, and corroborate previous empirical findings of higher trophic levels being most vulnerable to climate change [51]. We should thus expect warmer and invaded communities being even more susceptible to invasions, entering a negative feedback loop via the loss of predator species.

Our model relies on a set of assumptions that can influence model predictions. For instance, we did not account for temperature fluctuations, evolutionary change, or differences in the thermal traits of the invasive species (e.g. invasives may have warm-adapted thermal traits) that can also influence invasion success [9]. The assumption of similarity in thermal traits between invasive and resident species is supported by the observation that most invasive species are introduced by human transport and their invasion success is not strongly related to their native climate [40]. It would be interesting to extend the results presented here using invasive species with more realistic traits. Finally, we only considered constant temperatures and did not simulate the gradual increase in temperature that characterizes climate change. We expect that, for a given final temperature, a gradual and a non-gradual increase in temperature should produce similar results for the extinction of species not being able to cope with high temperatures (i.e. when their metabolic costs outweigh, their energetic gains), as the extinction thermal threshold is driven by physiology and not by population dynamics. However, the timing of the invasion might be important as the probability of invasions and their ecological consequences are temperature-dependent. Based on our results at a constant temperature, we hypothesize that the likelihood of invasions and their consequences would be weaker at the initial stage of warming when temperature starts to rise.

5. Conclusion

Understanding the joint effects of temperature and invasions at the community level constitutes a pressing challenge. Here, we showed that temperature's direct effects on invasion success are weaker than its indirect effects mediated by changes in food web structure, community properties and stability. Moreover, we showed that the impact of invasions depend on the temperature experienced by the invaded communities. Warmer food webs lose more species and interactions when invaded than their colder counterparts. These changes are accompanied by an increase in the fraction of top predator species, enhanced total community biomass and decreased stability. Overall, our study suggests that both temperature and invasion act synergistically to increase the rate of species loss creating smaller and more connected networks. It paves way for a better understanding of the causes and consequences of invasions in a warmer world.

Data accessibility. The R code developed as part of this study to implement and execute numerical simulations of food web dynamics and to run the statistical analyses are provided in the GitHub repository: https://github.com/mlurgi/temperature-dependent-invasions.

Authors' contributions. A.S. and M.L. conceived research. All authors designed research. M.L. performed modelling work. M.L. and A.S. analysed output data. J.M.M. financially managed the project and obtained the funding. A.S. and M.L. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Competing interests. The authors declare no competing interests.

Funding. This work was funded by the FRAGCLIM Consolidator grant (no. 726176) from the European Research Council under the European Union's Horizon 2020 Research and Innovation Program. M.L. was additionally supported by the 'Laboratoires d'Excellences (LABEX)' TULIP (ANR-10-LABX-41) and by a Region Midi-Pyrénées Project (CNRS 121090) to J.M.M. A.S. was additionally supported by the ANR project EcoTeBo (ANR-19-CE02-0001-01) from the French National Research Agency (ANR).

Acknowledgements. We thank two anonymous reviewers for comments and suggestions that substantially improved the quality of this manuscript.

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