

Effects of Warming on Intraguild Predator Communities with Ontogenetic Diet Shifts

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Submitted September 22, 2020; Accepted August 3, 2021; Electronically published October 11, 2021

Online enhancements: supplemental PDF.

ABSTRACT: Species interactions mediate how warming affects community composition via individual growth and population size structure. While predictions on how warming affects composition of size- or stage-structured communities have so far focused on linear (food chain) communities, mixed competition-predation interactions, such as intraguild predation, are common. Intraguild predation often results from changes in diet over ontogeny (“ontogenetic diet shifts”) and strongly affects community composition and dynamics. Here, we study how warming affects a community of intraguild predators with ontogenetic diet shifts, consumers, and shared prey by analyzing a stage-structured bioenergetics multispecies model with temperature- and body size-dependent individual-level rates. We find that warming can strengthen competition and decrease predation, leading to a loss of a cultivation mechanism (the feedback between predation on and competition with consumers exerted by predators) and ultimately predator collapse. Furthermore, we show that the effect of warming on community composition depends on the extent of the ontogenetic diet shift and that warming can cause a sequence of community reconfigurations in species with partial diet shifts. Our findings contrast previous predictions concerning individual growth of predators and the mechanisms behind predator loss in warmer environments and highlight how feedbacks between temperature and intraspecific size structure are important for understanding such effects on community composition.

Keywords: temperature, food webs, competition, climate change, cultivation densification, stage structure.

Introduction

The temperature dependence of feeding and metabolic rates govern warming-induced changes in community

composition via species interactions (Kordas et al. 2011; Brose et al. 2012; Gilbert et al. 2014; Reuman et al. 2014). Modeling studies that focus on how interspecific responses in such rates affect community composition via population biomass (Vasseur and McCann 2005; Rall et al. 2009) often neglect population structure and size- or stage-dependent variation in individual responses to temperature (García García et al. 2010; Huss et al. 2019). Intraspecific properties can be critical for understanding both mechanisms and effects of warming on animal communities (Ohlberger et al. 2011; Lindmark et al. 2018; Gårdmark and Huss 2020). Furthermore, predictions of how animal communities respond to warming are, to date, mainly based on linear food chain models (Binzer et al. 2012; Sentis et al. 2017; Lindmark et al. 2019) or complex food webs (O’Gorman et al. 2019). Effects of warming on animal communities depend, however, on the trophic structure (Gilbert et al. 2014; Rudolf and Roman 2018), which differs substantially, for example, between mixed competition-predation communities and linear food chains (Nakazawa 2014), limiting the generality of existing predictions.

An important example of mixed predation-competition communities is intraguild predation systems (IGPs; Polis et al. 1989), where body size- or life stage-dependent ontogenetic diet shifts determine species interactions. Ontogenetic diet shifts often cause predators to shift from competing with to predating on consumer species, resulting in a form of intraguild predation called ontogenetic (or life history) omnivore IGP (Pimm and Rice 1987; Polis et al. 1989; Hin et al. 2011). Such shifts take place either as a diet broadening (e.g., through gape size limitations) or as more complete diet shifts (e.g., through metamorphosis or an ontogenetic change in habitat use; Werner and Gilliam 1984; Mittelbach and Persson 1998). Knowledge of how warming affects such communities is important, as ontogenetic omnivore IGP is common throughout freshwater,

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marine, and terrestrial ecosystems (Polis et al. 1989; Arim and Marquet 2004; Gagnon et al. 2011) and plays a central role in the dynamics and structure of animal communities (Nakazawa 2014; Sanchez-Hernandez et al. 2019).

Composition of ontogenetic omnivore IGP communities depends on the feedback between competition with predator juveniles from intermediate consumers and the predation on those consumers exerted by the adult predators (Hin et al. 2011). Predation on consumers inhibits their competitive impact on juvenile predators, enabling coexistence between consumer and predator. This feedback, termed cultivation, reinforces predator survival and growth as predation suppresses competitors of their own young (Walters and Kitchell 2001). The opposite feedback, termed depensation, occurs when adult predators are too few to reduce interspecific competition, which then instead constrains body growth and development of juvenile predators and thus population growth (Walters and Kitchell 2001; van de Wolfshaar et al. 2006). These reinforcing feedbacks can give rise to three alternative stable states, an IGP state where the species coexist and two states where either consumers or predators are extinct (Hin et al. 2011).

Experiments have shown that warming benefits intraguild predator populations by increased predation rates on the consumer (Frances and McCauley 2018; Rogers et al. 2018). Experimental methods can, however, rarely account for the complexity of how warming could govern the strength of predation in ontogenetic omnivore IGP communities. For example, warming could benefit the competitively superior resource consumers by decreasing resource productivity. This would increase interspecific competition and limit growth and predation rates of intraguild predators on consumers (Holt and Polis 1997; Diehl and Feissel 2001; Savage et al. 2004). Furthermore, the extent of the diet shift (i.e., broadening vs. a complete shift) matters for both predator and consumer responses, as the intraguild predators' dependence or foraging ability on the resource affects predation pressure and therefore coexistence in omnivore IGP communities (van de Wolfshaar et al. 2006; Hin et al. 2011). Both resource productivity and the extent of diet shifts affect the distribution of biomass between species and life stages via the cultivation feedback (van de Wolfshaar et al. 2006; Hin et al. 2011; Rogers et al. 2018). Predictions based on linear food chain models highlight how the prey preference of a predator can influence how warming affects community stability and composition via stage-dependent population processes (Lindmark et al. 2019). Acknowledging that similar relationships likely affect IGP communities, via both direct effects of temperature on, for example, feeding rates and indirect effects and species interactions that depend on the extent of ontogenetic omnivory, would further our understanding of warming effects on animal communities.

Because it affects both population structure and species interactions, the temperature dependence of energetic efficiency (i.e., the ratio between consumption and metabolic rates; Vucic-Pestic et al. 2011) matters for predictions about community responses to warming (Vasseur and McCann 2005; Fussmann et al. 2014; Uszko et al. 2017). Most such predictions, however, stem from models without intraspecific variation in life stage or body size and therefore ignore that optimum growth temperatures within species often decline with size (Björnsson et al. 2007; Morita et al. 2010; Lindmark et al. 2021). Size-dependent declines in energetic efficiency and growth in warmer environments could modify the relative efficiency of different life stages to produce biomass, which affects the strength of species interactions. Consequently, warming could affect competition and predation, as well as the cultivation feedback, in IGP communities not only by affecting interspecific differences in feeding and metabolic rates and inter- or intraspecific resource/prey availability but also by affecting intraspecific size-dependent energetic efficiency.

Here, we use a stage-structured bioenergetics model to analyze mechanisms underlying responses to warming of an intraguild predator, a consumer, and their shared prey. We ask what the consequences of warming are on community composition, how this results from how temperature modifies the structuring effects of predation and competition, and how the extent of an ontogenetic diet shift in the predator shapes the community responses to warming. We show how warming leads to a decline in predator biomass that induces a loss of cultivation—the feedback between predation and competition that promotes predator growth—and, subsequently, collapse of the predator population. Furthermore, we show that how temperature affects community composition depends on the extent of an ontogenetic diet shift in the predator population.

Methods

We model the effects of gradual increases in temperature (i.e., warming) in a system consisting of a stage-structured predator ($P_{a,j}$; adults and juveniles) that undergoes an ontogenetic diet shift at maturation, an unstructured intermediate consumer prey (C), and their shared resource (R). We use a bioenergetics approach to model individual-level food-, temperature-, and stage-dependent biomass production and energy allocation (Yodzis and Innes 1992; de Roos et al. 2008). Rates of biomass production are body size-dependent and based on general size-scaling principles of biological rates. The equilibrium biomass densities of these stage-structured models are exact representations of equilibrium conditions of equivalent physiologically

structured population models with continuous size distributions (see de Roos et al. 2008).

Temperature Dependence of Biological Rates

The temperature-dependent biological rates and parameters in our model are resource turnover rate and maximum resource biomass density, intake, maintenance, and mortality rates of predators and consumers. We use the Boltzmann-Arrhenius equation, $r_{i,m,\mu}(T) = e^{E_A(T-T_0)/kTT_0}$, to account for how biological rates increase exponentially with temperature. Here, E_A is the activation energy, T_0 is the reference temperature in kelvins, and k is the Boltzmann constant (Gillooly et al. 2001). This equation predicts an exponential change in relation to the reference temperature and was developed to describe temperature dependence of reaction rates. It thus provides estimates not only of metabolic rates but also of rates dependent on metabolic activity, such as maximum intake and mortality (Brown et al. 2004; Rall et al. 2012; Thorson et al. 2017; Alfonso et al. 2021) within a biologically relevant temperature range (across the full temperature range, consumption rates are, however, unimodal [Englund et al. 2011; Rall et al. 2012]; for details on this assumption, see “Discussion”). Furthermore, we assume that the maximum biomass density of the resource (R_{\max}) decreases and turnover of resource (δ) increases exponentially with temperature. The term R_{\max} declines with temperature (see “Model Parameterization and Analyses”) as metabolic demands increase, and we assume a temperature-independent nutrient supply (Savage et al. 2004; but see Lemoine 2019). The combination of increased metabolism and intake rate and decreased resource production captures reductions in energetic efficiency of food webs via the warming-induced mismatch between respiration and biomass production (O’Connor et al. 2009). Consequently, inter- and intraspecific competition increases over a decreasing resource (or prey) availability with warming, which amplifies interspecific differences in feeding and metabolic rates.

The temperature effect described above does not depend on body size and therefore increases the rates uniformly across life stages and species. However, temperature can affect intraspecific energetic efficiency by reducing the increase in intake rate with size more than for maintenance (Fonds et al. 1992; Lindmark et al. 2021). This results in warming-induced relative declines in the energetic efficiency of large individuals within a population and is in line with the observation that optimum growth temperature declines with size (Björnsson et al. 2007; Morita et al. 2010; Lindmark et al. 2021). We implement a simplistic size-dependent temperature effect by adding a linear scalar of temperature on the maximum intake rate of adult predators that decreases their intake in relation to that of

juveniles and consumers (supplemental PDF [available online], sec. S1). Specifically, with a single parameter ω_b , warming reduces the energetic efficiency of adult predators relative to juveniles and consumers: $\omega(T) = \omega_a + \omega_b(T - T_0)$, where ω_a is the intercept and ω_b the (negative) slope of the scalar. For adult predators, we multiply this temperature effect represented by $\omega(T)$, with the general temperature dependence of maximum intake rates given by the Boltzmann-Arrhenius function $r(T)$, to directly scale the temperature effect on adult (I_{Pa}) versus juvenile (I_{Pj}) intake rates and thus their energetic efficiency. At the reference temperature ($T = T_0$), $\omega(T) = 1$, meaning that there is no difference between the predator life stages in terms of maximum intake rate. Thus, for $\omega(T) = 1$, all differences between adult and juvenile predators can be attributed to the difference in diet (determined by the extent of the ontogenetic diet shift, β ; see below).

Model Formulation

The following set of ordinary differential equations describes the interactions and dynamics of the system:

$$\frac{dR}{dt} = \delta(R_{\max} - R) - I_C(R)C - I_{Pj}(R)P_j - I_{PaR}(R)P_a, \quad (1)$$

$$\frac{dC}{dt} = \nu_C(R)C - \mu_C C - I_{PaC}(C)P_a, \quad (2)$$

$$\frac{dP_j}{dt} = \nu_{Pa}^+(R, C)P_a + \nu_{Pj}(R)P_j - \gamma(\nu_{Pj}^+, \mu_j)P_j - \mu_P P_j, \quad (3)$$

$$\frac{dP_a}{dt} = \gamma(\nu_{Pj}^+, \mu_j)P_j + \nu_{Pa}(R, C)P_a - \nu_{Pa}^+(R, C)P_a - \mu_P P_a. \quad (4)$$

The growth rate of the resource (R) is set by semichemostat dynamics determined by the turnover rate (δ) and the maximum resource biomass density (R_{\max} ; Persson et al. 1998; van der Meer 2016). Resource biomass (eq. [1]) increases with resource growth rate and decreases through predation by the consumer (C), juvenile (P_j), and adult (P_a) predators feeding with a species- and stage-specific intake rate ($I_{C,Pj,a}$) on the resource. Consumer biomass dynamics (eq. [2]) is the difference between biomass production rate (ν_C) and two sources of mortality: background mortality ($\mu_C = d_C r_\mu(T)$, where d is the mass-specific mortality rate) and predation mortality from adult predators ($I_{PaC}P_a$). The biomass of juvenile predators (eq. [3]) increases with reproduction (ν_{Pa}^+) and biomass production (ν_{Pj}) and decreases with maturation (γ) into the adult stage

and temperature-dependent background mortality ($\mu_p = d_p r_\mu(T)$). We assume that adult predators allocate all excess energy available to reproduction rather than somatic growth and that they only reproduce when their energy intake exceeds their maintenance requirements. Therefore, ν_{Pa}^+ is restricted to positive values and is distinguished from ν_{Pa} (i.e., for positive values of ν_{Pa} , $\nu_{Pa}^+ = \nu_{Pa}$, but for negative values of ν_{Pa} , $\nu_{Pa}^+ = 0$). Accordingly, for positive values of adult predator biomass production rate, the difference between juvenile maturation and temperature-dependent adult background mortality rate ($\mu_p = d_p r_\mu(T)$) determines the dynamics of adult predator biomass (eq. [4]).

Intake rates of consumers and juvenile predators feeding on the resource (eq. [5]) and of adult predators feeding on the resource (eq. [6]) and on consumers (eq. [7]) are functional responses of the respective prey density. The general temperature dependence term of the intake rate, $r_i(T)$, scales the functional responses of all species, and the linear scalar of temperature on the maximum intake rate, $\omega(T)$, scales the adult predator's (supplemental PDF, sec. S1). We assume the functional response follows a Monod (1949) function with half-saturation constant H and a maximum intake rate $I_{\max,C,P}$:

$$I_{C,P_j}(R) = \frac{I_{\max,C,P}R}{H + R} r_i(T), \quad (5)$$

$$I_{PaR}(R) = \frac{I_{\max,P}\beta R}{H + \beta R + (1 - \beta)C} r_i(T)\omega(T), \quad (6)$$

$$I_{PaC}(C) = \frac{I_{\max,P}(1 - \beta)C}{H + \beta R + (1 - \beta)C} r_i(T)\omega(T). \quad (7)$$

The parameter β affects the extent of the ontogenetic diet shift and is the proportion of resource relative to consumer in the adult predators diet, representing their feeding preference; $\beta = 0$ corresponds to a complete diet shift at maturation (i.e., adults feed exclusively on consumers), and $\beta = 1$ corresponds to full resource competition between predator and its prey (the consumer) and thus absence of predation and of an ontogenetic diet shift.

Biomass production rate is the difference in biomass assimilation rate (intake rate scaled with an assimilation efficiency, α) and maintenance rate ($M_{C,P}$) scaled with the temperature dependence of maintenance rate, $r_M(T)$:

$$\nu_{C,P_j} = \alpha I_{C,P_j}(R) - M_{C,P} r_M(T), \quad (8)$$

$$\nu_{Pa} = \alpha(I_{PaC}(C) + I_{PaR}(R)) - M_P r_M(T). \quad (9)$$

The maturation rate of juveniles (γ) increases with their biomass production rate ($\nu_{P_j}^+$) and depends on the ratio (z) between body size when entering and leaving the juvenile stage, and it decreases with mortality rate (μ_p). Furthermore, juveniles mature only when they can cover maintenance costs, and therefore maturation is restricted to positive values:

$$\gamma(\nu_{P_j}^+, \mu_p) = \frac{\nu_{P_j}^+ - \mu_p}{1 - z^{(1 - \mu_p/\nu_p^+)}}. \quad (10)$$

Model Parameterization and Analyses

We parameterized the model following the original model used by de Roos et al. (2008) and its community extension with a predator with ontogenetic diet shifts in Hin et al. (2011; see sec. S2 of the supplemental PDF for a summary of parameter values), to which we added temperature dependencies (see table 1 for corresponding parameters). As in those temperature-independent models, we used the maintenance rate (at the reference temperature, expressed in $\text{Mass}(\text{Mass} \times \text{Time})^{-1}$) of consumers (M_c) to scale the time variable in the model (see sec. S2 of the supplemental PDF for a more detailed description). Therefore, $M_{c,T_0} = 1$ (de Roos et al. 2008; Hin et al. 2011), and all other rates scale relative to M_{c,T_0} . The maximum intake rate of consumers is assumed to be 10 times that of maintenance (de Roos et al. 2008). Mass-specific maintenance, maximum intake, and mortality rates scale with adult body size as $\text{Mass}^{-0.25}$, with a proportionality constant of 0.01 for maintenance and 0.001 for mortality, such that $d_c = 0.1$ (de Roos et al.

Table 1: Parameters used for temperature-dependent processes

Parameter	Value	Unit	Description	Reference
k	8.617332×10^{-5}	eVK ⁻¹	Boltzmann constant	...
$E_{A\delta}$.4	eV	Activation energy of resource turnover rate	Lindmark et al. 2019
$E_{AR_{\max}}$	-.4	eV	Activation energy of maximum resource biomass density	Lindmark et al. 2019
E_A	.6	eV	Activation energy of maintenance, maximum ingestion, and mortality rate	Brown et al. 2004
T_0	292	K	Reference temperature (equivalent to 19°C)	Lindmark et al. 2019
ΔT	Varied	K	Change in temperature in relation to T_0	...
ω_a	1	...	Intercept, linear temperature effect on maximum intake rate of P_a	...
ω_b	-.05	...	Slope, linear temperature effect on maximum intake rate of P_a	...

2008). We assume that predators are 100 times the size of consumers (Jennings et al. 2002; Hin et al. 2011). The mass-specific body size scaling of biological rates results in $M_p = 0.3$, $I_{\max p} = 3$, and $d_p = 0.03$. However, ontogenetic omnivory often trades off for efficiency in resource use (Werner and Gilliam 1984; Vance-Chalcraft et al. 2007). Accordingly, intraguild predators are often inferior to intraguild consumers in competition for shared resources (Holt and Polis 1997; Vance-Chalcraft et al. 2007). Therefore, based on calculations of the minimum resource requirements needed to meet metabolic demand (Hin et al. 2011), the maximum intake rate of predators ($I_{\max p}$) at the reference temperature is set to 2.5 instead of 3. Given the allometric scaling and the size difference between predators and consumers, this corresponds to a consumer maximum intake ($I_{\max c}$) of 10 (Hin et al. 2011).

Resource turnover rate (δ) equals 1 (Hin et al. 2011) and maximum resource biomass density (R_{\max}) equals 2.5, which allows for coexistence between consumer and predators at the reference temperature given default parameters.

In the main analysis (figs. 1–4), we set the activation energy of resource turnover rate (δ) to 0.4 and that of R_{\max} to -0.4 (Lindmark et al. 2019). While these parameter values are uncertain, our choice allows us to capture reductions in energetic efficiency of food webs via the warming-induced mismatch between respiration and biomass production (O'Connor et al. 2009). We also consider a range of combinations of temperature effects on R and resource turnover rate to study the effect of resource dynamics on

our results concerning temperature responses (supplemental PDF, sec. S3). In the main analysis, the activation energy for maintenance, maximum ingestion, and mortality rate are all set to 0.6, as in Lindmark et al. (2019), which corresponds to an average prediction by the metabolic theory of ecology (Brown et al. 2004), to control for effects arising from differences in temperature sensitivities between these rates. We account for such temperature-dependent shifts in intraspecific energetic efficiency only in adult predators, via the linear temperature effect on maximum intake rate ($\omega(T)$). Furthermore, in section S4 of the supplemental PDF we analyze how an increase in the consumer intake rate relative to the predator's influences how warming affects community composition, and in section S5 of the supplemental PDF we analyze the effect of warming on composition and predator extinction temperature in a community with a warm-adapted predator.

In the main analyses, we model warming as gradual increases in temperature T and vary the predator resource preference β (using $\beta = 0$ as a baseline scenario before we cover the full $\beta = 0$ –1 range) to study temperature effects on equilibrium biomass densities, coexistence between species, and mechanisms underlying these effects. We explore temperature ranges in relation to T_0 , in which changes in community composition relevant for our study occur, and present our results for this temperature difference ΔT (in kelvins) from T_0 . We used continuation analyses in the MATLAB extension MatCont (Dhooge et al. 2008) to determine biomass density equilibria, limit cycles, and bifurcations.

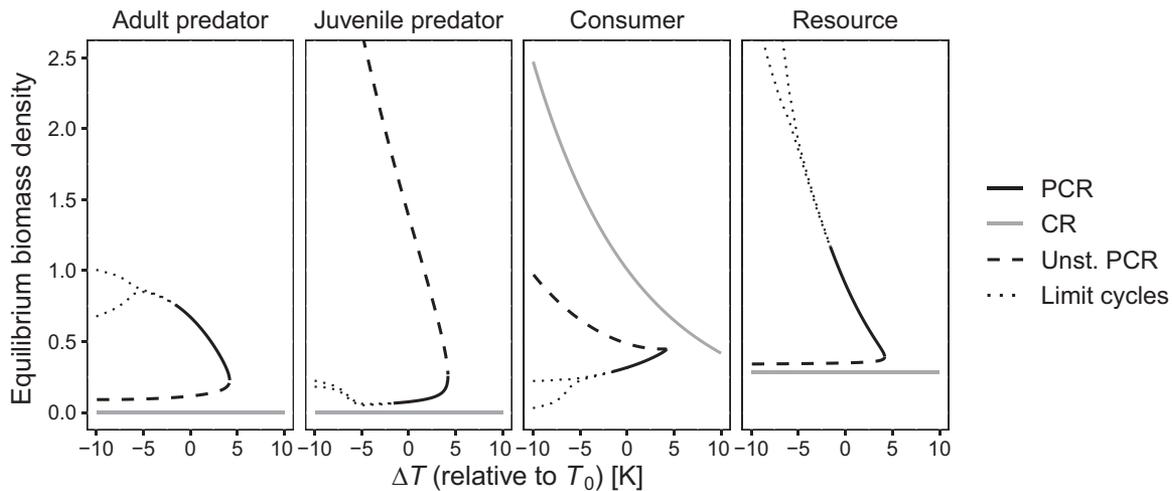


Figure 1: Equilibrium biomass density of adult and juvenile predators (P_a and P_j , respectively), consumers (C), and their shared resource (R) over temperature change (ΔT) when the predator completely shifts diet from a shared resource to consumers at maturation (i.e., $\beta = 0$). Black solid lines represent the stable PCR state, black dotted lines represent the minimum and maximum values of limit cycles (i.e., amplitudes) in the PCR state, black dashed lines represent the unstable PCR state, and solid dark gray lines represent the stable CR state.

Results

Below we first present the community composition and feedbacks at the reference temperature, followed by how they depend on warming, and finally how community responses to warming vary with type of ontogenetic omnivory. We present all results for temperature change (ΔT) in relation to T_0 .

Composition of the IGP Community with a Diet-Shifting Ontogenetic Omnivore

At the reference temperature and in a large part of the analyzed temperature range, two alternative stable states exist in the IGP community, with predators either present or extinct (fig. 1). A cultivation-feedback mechanism between predation and competition with consumers enables predator persistence. In this coexistence state of predator and consumer (hereafter, “PCR state”), the resource and adult predator biomass densities are high, creating an en-

vironment that supports a high mass-specific biomass production rate (i.e., high energetic efficiency) of juvenile predators and consumers (fig. 2D). This high biomass production is due to the high predation pressure that the adults exert, which reduces interspecific competition (i.e., a cultivation effect). Predation thus favors growth of juvenile predators but leads to low juvenile biomass density because of a high maturation rate out of the juvenile life stage. Because of low prey availability among adults relative to juveniles (compare consumer and resource biomass densities in fig. 1), juvenile biomass production rate (and therefore maturation rate) is higher than adult biomass production rate (reproduction rate; fig. 2A, 2C). This results in low juvenile biomass and high adult predator biomass (fig. 1). Consequently, reproduction limits predator population growth, as shown by the difference between population reproduction rate and maturation rate in figure 2C (which the large adult-to-juvenile biomass ratio also reflects; fig. 1).

An unstable PCR state separates the stable PCR state from a stable consumer-resource state (hereafter, “CR

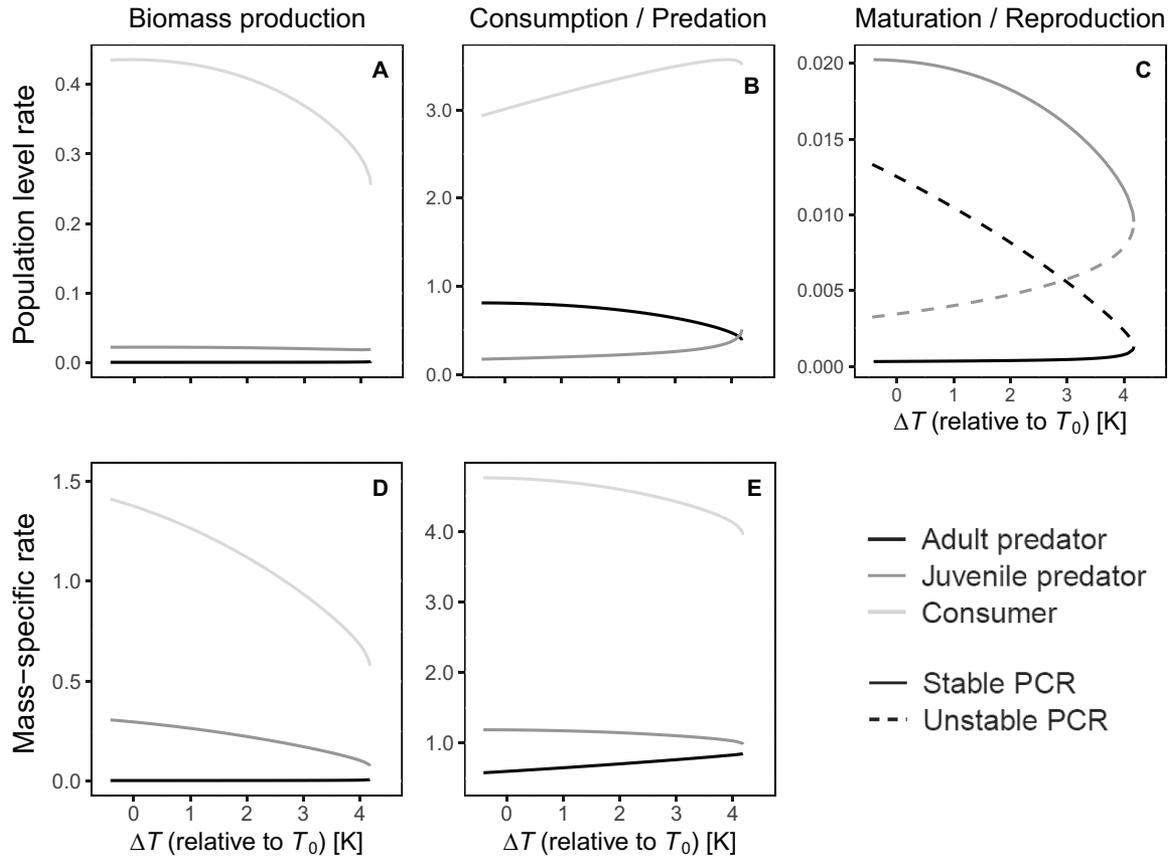


Figure 2: Population-level (A–C; expressed in $\text{Mass} \times \text{Time}^{-1}$) and mass-specific (D, E; expressed in $\text{Mass}(\text{Mass} \times \text{Time}^{-1})^{-1}$) biomass production rates (A, D) and equilibrium consumption/predation rates (B, E) for adult predators (black lines), juvenile predators (dark gray lines), and consumers (light gray lines) over change in temperature (ΔT) in the stable PCR state and population-level maturation (dark gray lines) and reproduction rate (black lines) in the stable (solid lines) and unstable (dashed lines) PCR state (C).

state”) in which the predator is extinct (fig. 1). In contrast to the stable PCR state, high reproduction rate (fig. 2C), high juvenile and consumer biomass, and low adult biomass (fig. 1) characterize the unstable PCR state. Here, high interspecific competition causes a low maturation rate (fig. 2C), low adult biomass, and predation pressure on consumers, such that the cultivation effect is lost. Predator invasion into the CR state is possible only with cultivation, which requires a large enough biomass of invading adult predators (exceeding adult predator biomass in the unstable state) to exert top-down control and suppress competition from consumers.

Effects of Warming on Community Composition

Warming decreases predation pressure on the consumer (figs. 1, 2) and increases competition for the resource between the juvenile predator and the consumer (compare figs. 2B and 1). Thereby, warming induces a loss of the cultivation effect and a negative feedback that eventually causes a collapse of the predator population (fig. 1). Furthermore, limit cycles that are present at lower temperatures ($\Delta T < -1.6$ K) decrease in amplitude and eventually change to fixed-point dynamics with warming (fig. 1).

Competition for resources increases in the community because population-level consumption rates by juvenile predators and consumers increase (fig. 2B), while resource turnover rate (δ) increases at a lower rate and maximum resource biomass density (R_{\max}) instead decreases with warming. Equilibrium resource levels therefore decrease with warming (fig. 1; see analyses of separate temperature effects in sec. S3 of the supplemental PDF). Because warming leads to lower adult predator and resource biomasses, total community biomass also decreases.

In contrast, consumer and to some extent juvenile predator (for $\Delta T > -5$ K) biomass densities increase with warming (fig. 1). For juvenile predators, the mass-specific biomass production rate decreases in the stable PCR state as warming reduces resource availability. This reduces maturation rate of juvenile predators (fig. 2C), causing biomass to accumulate in the juvenile predator stage (fig. 1). The unstructured consumer biomass density increases because its population-level consumption (and thus biomass production) increases in relation to predation (fig. 2A, 2B). This occurs because the size-dependent warming effect on energetic efficiency decreases the predation rate (see the supplemental PDF, sec. S3). Ultimately, the increased interspecific competition with warming decreases the predator maturation rate to such an extent that the predator population collapses (at $\Delta T = 1$ K; figs. 1, 2C).

Warming decreases adult biomass density (or average biomass density for limit cycles; fig. 1) partly through a warming-induced increase in mortality, but mainly (for

$\Delta T > 0$) because the maturation rate decreases (fig. 2C). This reduces the flow of biomass to the adult stage. Furthermore, the size-dependent warming effect on energetic efficiency (i.e., via $\omega(T)$) restricts the increase in energetic efficiency of adults that an increased prey density (the consumer) otherwise would cause. This limits potential increases in the predator reproduction rate, which, in turn, has negative effects on the biomass production of juvenile predators. However, there is still a positive (but small) effect on the mass-specific biomass production rate of adult predators with warming in the stable PCR state. For any increase in temperature above the reference temperature ($\Delta T > 0$), warming-induced loss of predator biomass decreases the population-level predation rate in relation to the consumer population biomass production rate (fig. 2A, 2B). Warming thereby impedes the effect of predation in the community and ultimately leads to loss of the cultivation effect and, finally, predator exclusion (at $\Delta T = 4$ K). Above this point, a single equilibrium state in which predators are extinct replaces the two alternative stable states, and only consumers and the resource exist (fig. 1).

Generalizing Temperature Effects: Warming-Induced Loss of Cultivation

Each of the main drivers of warming effects on community composition—decreasing maximum resource biomass density that intensifies competition, mortality, and intraspecific changes in energetic efficiency ($\omega(T)$) of the predator—contributes to predator exclusion at high temperatures through a warming-induced loss of cultivation. Disregarding any single process still results in very similar changes in community composition leading to predator exclusion. We show this by testing possible combinations of the temperature-dependent resource turnover rate ($E_{A\delta}$), maximum resource biomass density (R_{\max}), mortality ($r_H(T)$), and the intraspecific effect of warming on energetic efficiency (ω_b ; see the supplemental PDF, sec. S3). When warming does not reduce the maximum resource biomass density ($E_{AR_{\max}} = 0$), does not change intraspecific energetic efficiency in the predator ($\omega_b = 0$), and increases the resource turnover rate to the same degree as it increases intake rates ($E_{A\delta} = E_A = 0.6$), biomass densities of the different species and stages do not change over temperature, as all rates increase equally with warming (fig. S3.1; figs. S1–S4 are available online). However, when there is an unequal effect of temperature on any of these rates, the decrease in maturation rate and loss of adult predator biomass are consistent, independent of which single temperature-dependent process is in effect (figs. S3.1, S3.2). Consequently, our finding of warming-induced predator collapse via loss of cultivation is robust to the single

temperature effects caused by changes in resource dynamics and changes in biological rates of consumers and predators.

Temperature Effects on Community Composition Vary with Type of Ontogenetic Omnivory

Because community composition in the IGP community depends on how warming modulates the relative strength of competition and predation, the extent to which the predator exhibits a partial rather than a complete ontogenetic diet shift affects how the community changes with temperature. If predators broaden their diet on maturation (i.e., $\beta > 0$), such that adults split their time feeding on consumers and the resource, predation on consumers decreases and competition for the resource increases compared with that under complete diet shifts. Consequently, the temperature at which predator extinction occurs decreases with predator resource preference (β ; predator extinction point $Ext_p = 3.9$ for $\beta = 0.15$ and $Ext_p = 4.2$ for $\beta = 0$; figs. 1, 3).

Predator diet broadening (to a sufficient extent, indicated by the predator invasion point Inv_p in fig. 4) enables predators to also survive in the absence of consumers (in a predator-resource, or PR, state), as adult predators then have access to an additional energy source (the resource). Because warming increases metabolic demands, it also increases the resources necessary (β value at Inv_p) to meet minimal energy requirements for predators (fig. 4). In the lower temperature range, adult predators can sustain high biomass production and predation by feeding on the resource. At low temperatures, this leads to consumer exclu-

sion (figs. 3, 4). The temperature at which this occurs coincides with the consumer invasion point (Inv_c , i.e., the set of parameter values that enables predators to outcompete consumers but also consumers to invade the PR state; e.g., for $\beta = 0.15$, $Inv_c = -2$ K; fig. 3). The possibility for consumer exclusion therefore enables both warming-induced consumer invasion and predator exclusion, that is, a shift from a predator- to a consumer-dominated community. Moreover, limit cycles observed for $\beta = 0$ disappear for β values that allow adult predators to persist in the absence of consumer prey. As in communities with predators exhibiting a complete diet shift ($\beta = 0$), a stable CR state is a possible alternative state to the PCR state (for $Inv_c < \Delta T < Ext_p$; fig. 3). However, a CR state is also an alternative to the PR state if initial biomass density of consumers is sufficiently high to exclude predators by competition. Therefore, a temperature range with bistability with either a stable PR or a stable CR state replaces the bistable PCR/CR for temperatures below the consumer invasion point ($Inv_c = -2$ K for $\beta = 0.15$ in fig. 3; light gray area in fig. 4).

An increasing β (i.e., a higher predator resource preference) opens up for several combinations of alternative states over temperature (fig. 4) and decreases the temperature range for which coexistence is possible (i.e., of the PCR state; dark gray area in fig. 4). For $\Delta T = 1.5$ K and $0.27 < \beta < 0.53$, there is a small region where the PCR state is possible but where predators can also exclude consumers, making a PR, a CR, or a PCR state possible (black area in fig. 4). For $\beta > 0.53$, the exclusion of either predators or consumers depends on whether predation or competition, determined by temperature and initial

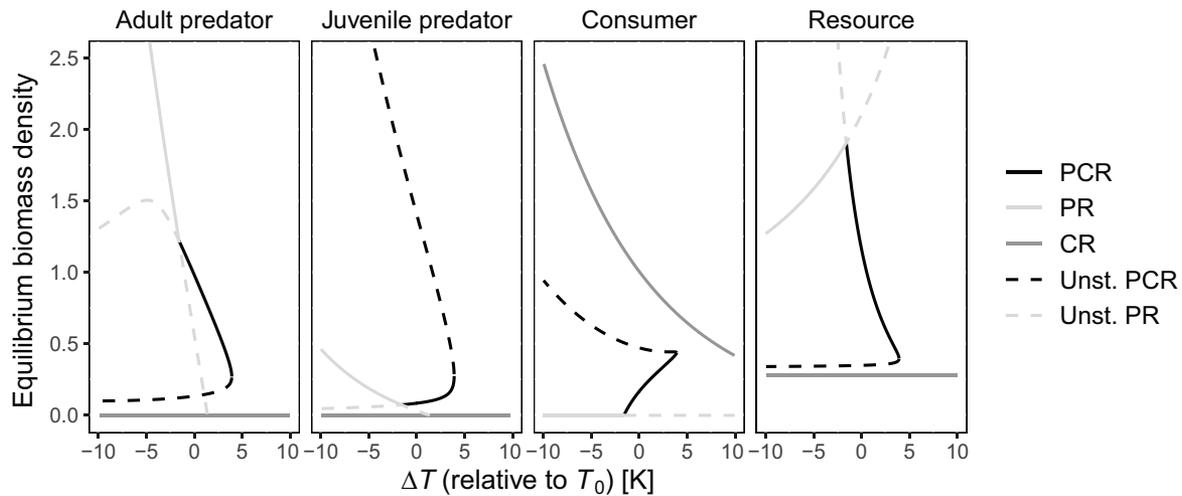


Figure 3: Equilibrium biomass density of adult and juvenile predators (P_a and P_j , respectively), consumers (C), and their shared resource (R) over temperature change (ΔT) for a community where adult predators feed on both the resource and consumers ($\beta = 0.15$). Black solid lines represent the stable PCR state, black dashed lines represent the unstable PCR state, solid dark gray lines represent the CR state, solid light gray lines represent the stable PR state, and dashed light gray lines represent the unstable PR state.

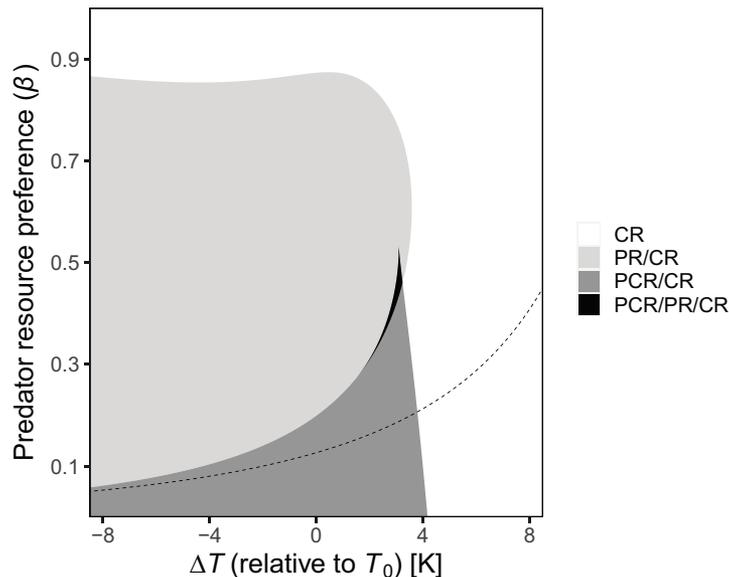


Figure 4: The possible states of intraguild predator community composition with a consumer (C), its intraguild predator (P), and their shared resource (R) depend on the resource preference (β) in the predator (the extent of the diet shift; i.e., the proportion time adult predators spend feeding on the resource vs. on the consumer) and the change in temperature (ΔT) relative to T_0 . Shading indicates different stable community states, and the dashed line indicates the predator invasion point Inv_p that marks the point where predators can invade a resource-only state.

biomass densities of the system, controls community composition (fig. 4). When the predator mainly feeds on the resource (i.e., β values above the upper Inv_C ; fig. 4), predators can no longer eliminate the consumer. Instead, predators then become extinct and a CR state is the only possible state (white area in fig. 4).

Increasing the strength of competition from the consumer on the predator (i.e., by increasing the relative maximum intake rate of consumers, I_{maxC}) increases the ability of the consumer to outcompete the predator. Therefore, the parameter space (range of β and temperature change) where the CR state is the only possibility increases at the expense of the PCR and PR states (see the supplemental PDF, sec. S4). Furthermore, our results could depend on the potential for species to adapt to different temperature regimes. If we change model assumptions such that predator energetic efficiency increases with warming to the extent that the predator can outcompete the consumer, temperature-dependent coexistence and consumer or predator dominance can be affected (supplemental PDF, sec. S5).

Discussion

We studied temperature effects on communities characterized by intraguild predation, resulting from ontogenetic diet shifts, to make predictions about how warming affects

mixed competition-predation interactions and community composition. In line with previous studies of linear food chains (Binzer et al. 2012; Sentis et al. 2017; Lindmark et al. 2019), we find that predators can also become extinct with warming in intraguild predator communities. We show, however, that this occurs as a collapse and via a different mechanism: warming-induced loss of cultivation. Warming increases competition between consumers and juvenile predators for their shared resource. This hampers the juvenile growth rate and therefore maturation into adult predators, and predation by adults on consumers subsequently declines. This reinforces the poor growth of predator juveniles because it releases consumers from predation, which further increases competition. This contrasts with the warming-induced effect of predators in food chains (Binzer et al. 2012; Lindmark et al. 2019), as warming-induced loss of cultivation increases (albeit a little) the energetic efficiency of the intraguild predatory (adult) stage (reflected in their biomass production rate; fig. 2D). The cultivation-dependent bistability in intraguild predator communities thus makes a gradual rise in temperature cause a collapse of the predator population. We also show that the extent of the predator's ontogenetic diet shift determines how community composition varies with temperature. Partial diet shifts of intraguild predators narrow the temperature range of predator-consumer coexistence; as a result, warming can lead to a sequence of community reconfigurations.

We predict a warming-induced shift in the dominant interaction in the community from predation to competition, inducing the loss of predator cultivation and ultimately predator extinction. Two temperature-dependent processes mainly enabled this shift: reduced predation in relation to consumer biomass (as the consumer population increases while population-level predation rate does not) and a warming-driven decline in resource availability (through increasing feeding rates, increasing maintenance costs, and decreasing maximum resource biomass density levels). This is in contrast to what has been found in empirical studies (Frances and McCauley 2018) and system-specific, experiment-coupled modeling studies (Rogers et al. 2018) of IGP communities that suggest that the intraguild predator can benefit from warming and cause consumer extinction. Experiments on dragonfly IGP communities by Frances and McCauley (2018) showed consumer exclusion through increased predation rates. Similarly, warming experiments by Rogers et al. (2018) showed that their intraguild predator (large blue crabs) increased predation on the consumer (green crab), which should contribute to consumer exclusion in warmer environments (however, the blue crabs were also superior in feeding on their shared prey, in contrast to our intraguild predator, which is an inferior competitor). Comparable to these studies, “individual” predation (i.e., the mass-specific predation rate) also increases with warming in our intraguild predatory stage (fig. 2E). At high temperatures, however, a competition-induced decrease in maturation rate, and consequently low biomass of predators, outweighs this mass-specific biomass increase in predation rate. As experimental studies often are done under nonequilibrium conditions within single generations, they can generally not capture effects of competition on maturation and reproduction rates. Importantly, as Rogers et al. (2018) pointed out, in their model (originally proposed by Mylius et al. [2001]) based on mesocosm experiments maturation rate is not a dynamic function of food availability and therefore cannot capture how warming-induced competition affects maturation rate (van de Wolfshaar et al. 2006). In all animals, growth and development requires energy. We find that accounting for such an energy-dependent rate of reaching maturation was critical for understanding how temperature affects community composition, as temperature- and food-dependent rates of biomass transfer between juvenile (competitors) and predatory adults alter predation and competition.

We predict that effects of warming-induced predator extinctions in IGP communities may be advanced when predators broaden, instead of completely shift, their diet over ontogeny. Diet broadening means less predation on the consumer relative to the shared resource and higher competition with consumers than if adults are specialist

predators, and therefore the temperature at which predators become extinct decreases. Diet broadening also results in a smaller range of coexistence, as predators can exclude consumers at low temperatures (corresponding to high resource levels) when they can survive on the resource alone. This means that how warming constrains predator dominance depends on the extent of its diet shift. Increased growth rates often follow from diet shifts, implying a better food resource (e.g., shifting from an invertebrate to a vertebrate prey) or simply more food if the diet broadens rather than shifts (Sanchez-Hernandez et al. 2019). We disregarded such factors (i.e., assuming equal energy content of the resource and consumers through equal assimilation efficiencies) that may affect the extent of diet shifts as well as system-specific factors (e.g., prey mobility; Sih and Christensen 2001). Nevertheless, our results suggest that ontogenetic diet broadening in IGP predators should confine coexistence with consumers in nature to more narrow temperature ranges than for IGP predators with complete ontogenetic diet shifts. This also suggests increased sensitivity to warming and seasonal variability in temperature for predators with partial diet shifts.

We show how temperature enhances competition and drives the cultivation mechanism through the stage-dependent growth rate of predators. Hin et al. (2011) also pointed out the importance of stage-dependent growth rate for community composition and stability in intraguild predator communities. Using a stage-structured biomass model, they demonstrated that in IGP communities, low resource levels increase interspecific competition for the predator juvenile stage. This imposes a bottleneck that restricts maturation of IGP predators, which leads to loss of predation and eventually to predator extinction. This is an example of how ontogenetic asymmetry (de Roos 2020) in relative resource availability of each life stage of a predator with an ontogenetic diet shift governs population regulation and therefore stage-specific biomass (Osenberg et al. 1992; Reichstein et al. 2015). Studies of natural populations of predators with ontogenetic diet shifts suggest that the feedback between loss of predation and increased competition is an important mechanism governing community composition (Byström et al. 1998; Casini et al. 2009; Gårdmark et al. 2015). In this study, temperature enhances competition, as resource levels increase less with warming than do intake and maintenance rates of consumers and predators. Interspecific competition reduces the predator maturation rate and causes biomass to accumulate in their juvenile stage (i.e., a juvenile bottleneck). Myrvold and Kennedy (2015) showed empirically that warming increases intraspecific competition and causes juvenile bottlenecks in their study of wild steelhead, and Watz et al. (2019) found support for temperature effects on growth via interspecific competition in

two species of charr. However, to our knowledge no studies have until now linked juvenile bottlenecks to temperature-dependent predation and interspecific competition and the resulting effects of warming on the composition of intraguild predation communities. Consequently, the temperature dependence of cultivation that we identify in this study is a novel process by which predators with ontogenetic diet shifts could suffer from warming.

We used the Boltzmann-Arrhenius function to describe temperature dependence of biological rates and resource dynamics. While this response function should be appropriate for maintenance and mortality rates, the relationship between temperature and functional response is hump shaped (i.e., has an optimum; Englund et al. 2011; Uszko et al. 2017). Thus, the Boltzmann-Arrhenius function is suitable only for studying warming effects on functional responses at temperatures below the optimum (Englund et al. 2011). Including optimum-type temperature responses in community models requires assumptions about the location of species-specific optima and their distance to arbitrary reference temperatures, adding complexity without necessarily providing generality (Dee et al. 2020). We find that the processes important for changes in community composition with warming hold for a large part of an optimum-type temperature response curve (i.e., below the optimum) and that these processes take place in a small range above the reference temperature because of strong effects of warming on predation and competition. Despite disregarding species-specific optima, we show that if the predator is warm adapted such that it gains energetically from warming compared with the consumer, the outcome of warming on composition in the intraguild predator community can change (supplemental PDF, sec. S5). Generalizing and identifying key processes in how species-specific adaptations affect IGP community composition changes with warming is therefore an important avenue for future work.

We conclude that interspecific interactions, which often vary over ontogeny, shape temperature responses of both populations and communities as they modulate flows in bioenergetic pathways in animal communities. Both intraguild predation and ontogenetic diet shifts are common characteristics of natural communities (Polis et al. 1989; Arim and Marquet 2004; Finke and Denno 2005; Gagnon et al. 2011). Therefore, the novel mechanism of warming-induced loss of cultivation presented here, by which such predator populations can collapse under warming, may be important to account for. Our results are thus relevant for studies attempting to identify patterns in, or make general predictions about, how community composition changes with temperature in time and space. It is particularly important to consider our findings when assessing warming effects in systems that humans rely

on for resources and for which functioning depends on intraguild predation and ontogenetic diet shifts. Examples include intraguild predation for biological control in agricultural systems (Müller and Brodeur 2002) and cultivation for fished predator populations (Walters and Kitchell 2001). Considering our findings in light of the fact that humans often exert additional mortality on such predator populations has implications for predicting their responses to warming but also their conservation. With mean temperatures increasing globally (IPCC 2014), warming-induced loss of cultivation suggests possible steep declines and abrupt loss of intraguild predator species and biodiversity and changes in species composition.

Acknowledgments

We thank two anonymous reviewers for their knowledgeable and rewarding comments, which greatly helped in improving the manuscript. This work was supported by grants from the Swedish Research Council (2015-03752 to A.G.) and the Swedish Research Council Formas (217-2014-474 to M.H.).

Statement of Authorship

A.G. conceived the study. V.T. led and all authors contributed to study design and model development. V.T. and A.G. parameterized the model, and V.T. performed analyses. V.T. led the writing, and all authors contributed to the revision of the manuscript.

Data and Code Availability

MatCont model code, output data, and R code for figures are available via https://github.com/VThunell/Warming_IGP_communities and <https://doi.org/10.5281/zenodo.5172298> (Thunell et al. 2021).

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Associate Editor: Axel G. Rossberg
 Editor: Jennifer A. Lau