Supporting Information

1 Appendix S1

Addition of a single trophic level for a species evolving under climate change reveals a fundamental challenge for ecologists tasked with predicting impacts of climate change, and a challenge for species trying to adapt to a changing climate while being preyed upon. Although our model neglects many processes, it provides a necessary first step in investigating how trophic interactions may affect species ecological and evolutionary responses to climate change and their impacts on ecosystem function. The approach we have developed is promising for future studies.

In particular, both the direct density-mediated effects of the interacting species and the density-driven rate of adaptive trait evolution have impacts on responses to climate change. Species interactions not only can create different outcomes in a constant environment, and hence different initial conditions in a changing environment, but also can create different targets in a changing environment. Thus, they can increase the number of targets and trajectories with climate change so that species may not be evolving to track simply their optimal temperature or thermal niche.

We challenge a recent prediction that predators should aid the adaptation of their prey (Jones, 2008). Although we do not include the potential mechanism of culling of maladapted individuals (Jones, 2008), we do explicitly include strength and direction of selection, and importantly, biomass. The large reduction in biomass of the plant species when the herbivore species is present, has a strong impact on the ability of the plant to adapt to a warming environment.

We focused on the following questions in our study: 1) How does the addition of a herbivore affect the ecological and evolutionary attractors in a static environment?, 2) How does the herbivore affect the ability of the plant to adapt to and persist in a changing environment?, and 3) How do the evolutionary attractors, relative thermal niche widths, and rates of environmental and evolutionary change determine ecosystem responses to warming?

We found the addition of the trophic interaction has a strong negative effect on density and rate of adaptation of the plant. The trophic interaction can create different coevolutionary attractors in a static environment. These attractors are determined by thermal niche widths and create different targets and trajectories in a changing environment. Thermal niche width, coupled with trophic interactions, can either increase or decrease plant and herbivore persistence, depending on the underlying strategy. Shortest persistence times occur at intermediate thermal niche width of the plant, whether herbivores are present or not.

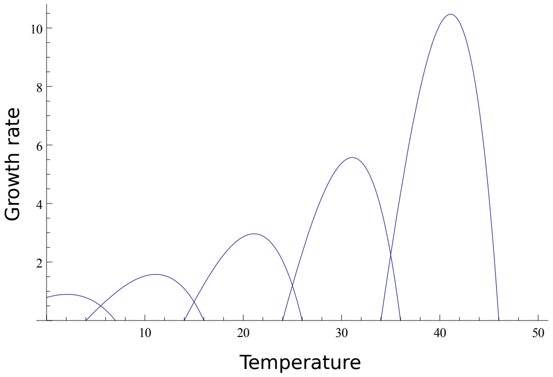

Figure 1: Growth versus temperature curves for species with different thermal optima. The maximum growth rate increases exponentially due to the empirically derived relationship described by Eppley (1972).

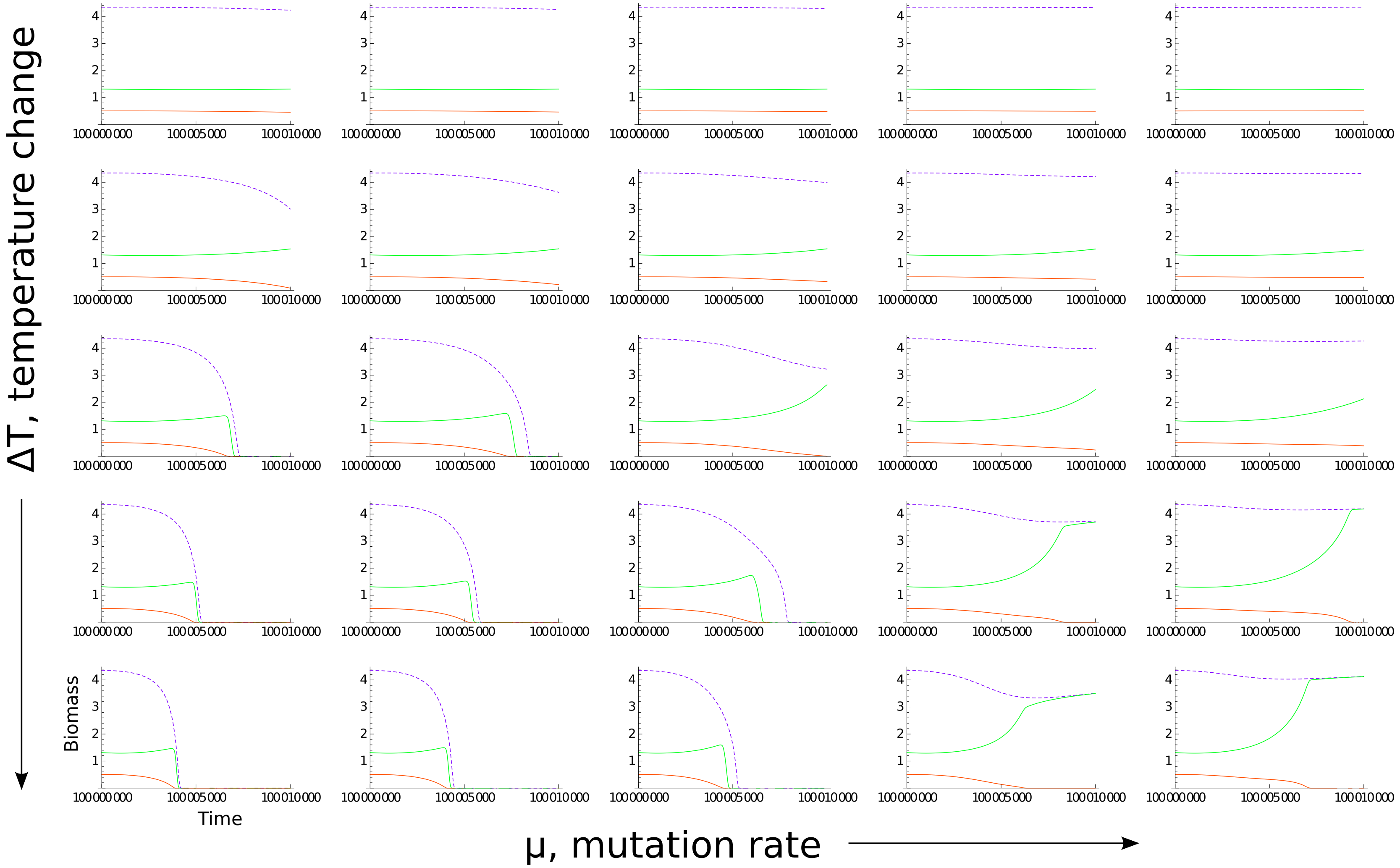

Figure 2: Herbivore biomass (red) and plant biomass with H (green) and without H (dashed purple) through time in a warming environment. Each plot is arrayed across mutation rate and amount of temperature change in the $t = 10^4$ interval of time. For low temperature change and high mutation rate (upper right corner), biomass for both species is relatively constant. For high temperature change and low mutation rate (lower left corner), biomass eventually declines for both species resulting in extinction. Parameters are: $\sigma = 3, w_P = 4, w_H = 8$ and the array values for μ are $10^{-4}, 10^{-3.75}, 10^{-3.5}, 10^{-3.25}, 10^{-3}$ in steps of one order of magnitude and ΔT values are $1, 2, 3, 4, 5$.

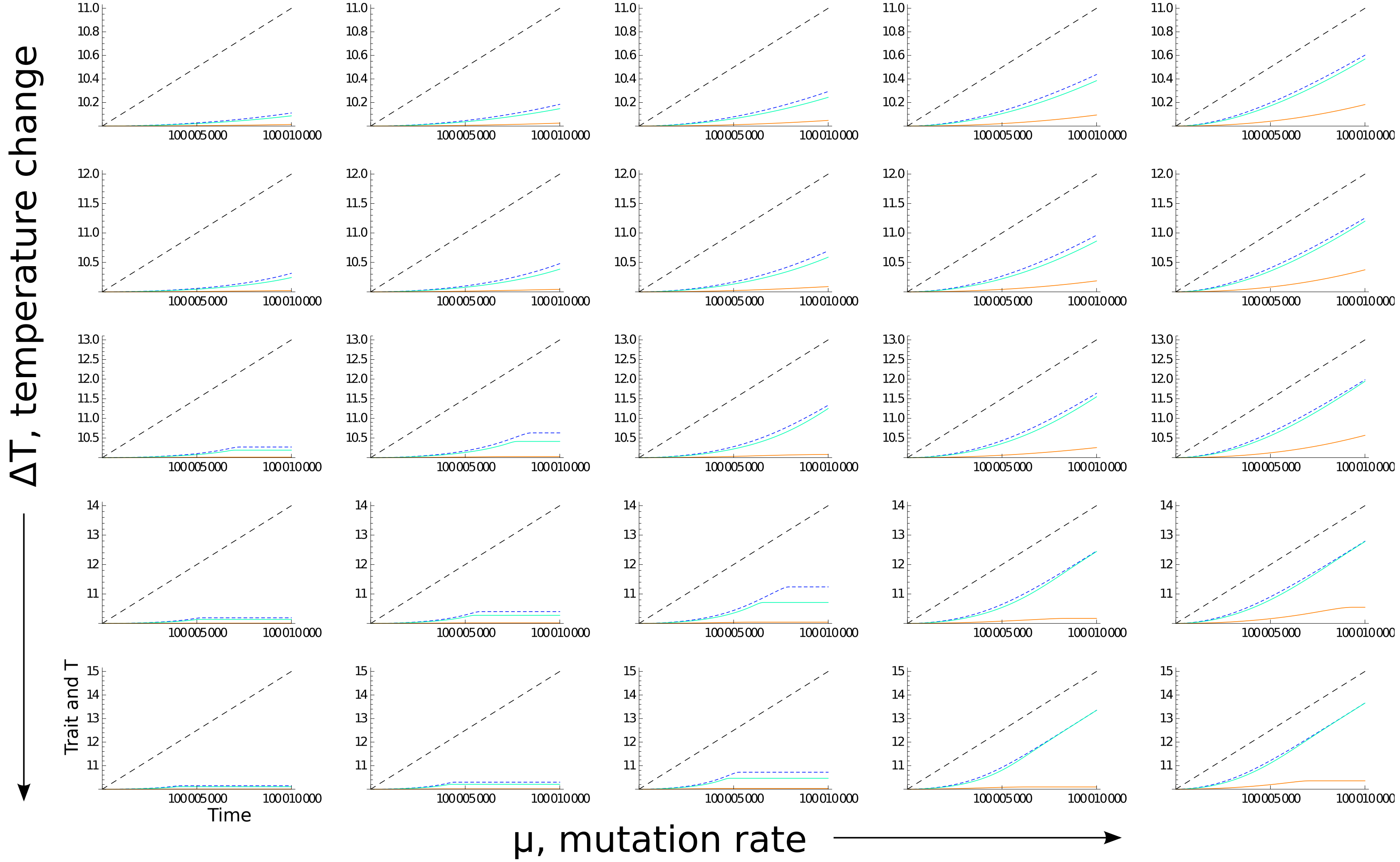

Figure 3: Same as Appendix S1 Figure 2 except for thermal trait and temperature values through time. Black dashed line is temperature, orange is Herbivore trait, light blue is plant trait with H, and dashed dark blue is plant trait without H. For low temperature change and high mutation rate (upper right corner), thermal traits match the moving optimum. For high temperature change and low mutation rate (lower left corner), thermal traits are not able to track the moving optimum resulting in extinction.

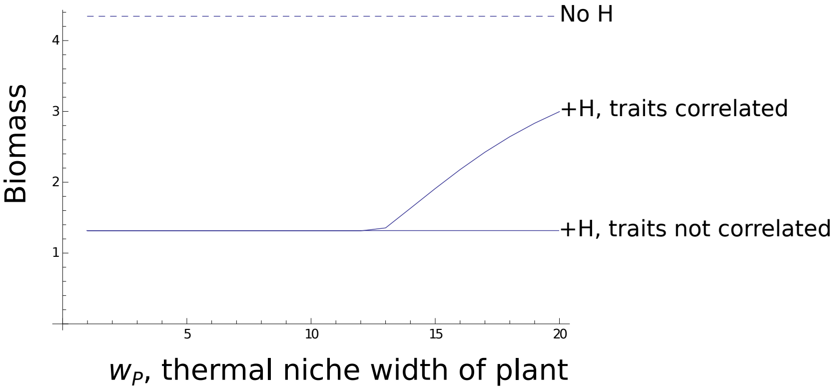

Figure 4: Equilibrium plant biomass versus plant thermal niche width w_P for without the herbivore (dashed line) and with the herbivore (solid lines) for when traits are correlated and not correlated. Parameters are: $\sigma = 3, w_H = 8$.

2 Evolutionary analysis methods

2.1 Adaptive trait evolution

We borrow many of the tools of adaptive dynamics (Dieckmann & Law, 1996; Geritz *et al.*, 1998) to analyze trait evolution.

We define the fitness, $W_{P_{inv}}$, of an invading phenotype of the plant species with traits $s_{P_{inv}}$ and $z_{P_{inv}}$

$$W_{P_{inv}}(s_{P_{inv}}, s_P, z_{P_{inv}}, z_P, s_H, z_H) = \frac{1}{P_{inv}} \frac{dP_{inv}}{dt} \tag{1}$$

Similarly we define the fitness of an invading phenotype of the herbivore species, $W_{H_{inv}}$ with trait $s_{H_{inv}}$ and $z_{H_{inv}}$

$$W_{H_{inv}}(s_{H_{inv}}, s_P, s_H, z_{H_{inv}}, z_H) = \frac{1}{H_{inv}} \frac{dH_{inv}}{dt} \tag{2}$$

and evaluate both fitness equations with the equilibrium environment set by the resident species P and H (refer to the equilibrium above). Hereafter we use the following subscript notation to describe: the $j = P$ plant species and $j = H$ for the herbivore species evolutionary equations involving derivatives of the fitness equations.

2.1.1 Finding the singular strategies

Our goal was to find the evolutionary endpoints for a given static environment and the trajectories in a changing environment. We performed evolutionary simulations. For each simulation, we numerically solved the seven-dimensional system consisting of the three equations for the quantities of the resource, plant, and herbivore (Equations 1, 2, 3) and one equation for each of the trait values of the plants and herbivores (Equation 6). In the evolutionary simulations with

Equation 6, we tested at least two sets of initial conditions and let the traits evolve until no further change was observed.

Following the assumptions of adaptive dynamics, we effectively have a separation of time scales between population dynamics and trait dynamics because we assume a small mutation rate ($\mu = 10^{-3.5}$) for most of our results. We could relax this assumption by increasing mutations μ (Abrams, 2001) to no longer have a separation of ecological and evolutionary time scales, which may be important given recent studies on rapid evolution (Abrams, 2003). Interestingly, this generalized approach usually leads to the same results (Abrams, 2005). Furthermore, although we model mutation limited evolution (Marrow *et al.*, 1996), one may consider μ to include other mechanisms that scale evolutionary rates (Dieckmann & Law, 1996). For example, mutation variance (we assume constant) (Dieckmann & Law, 1996), additive genetic variance (Abrams *et al.*, 1993), or phenotypic variance (Lande, 1976) is also often included in this term (Abrams, 2001), and are also related to population size (Frankham, 1996). Other mechanisms such as heritability (Lande, 1976; Abrams *et al.*, 1993) may be independent of population size, while the assumption of the resident population quickly replaced by a mutant with higher fitness may be opposed by population size. However, we generally assume a small mutation rate and expect there to be adequate time for the mutation to sweep through the population before the next mutation occurs.

2.2 Classifying the singular strategies

To classify the singular strategies, which we denote as s_j^* (for z_j also), we take the second derivative of the invader fitness equation with respect to the invader

$$\left.\frac{\partial^2 W_{j_{inv}}}{\partial s_{j_{inv}}^2}\right|_{s_{j_{inv}} \to s_j \to s_j^*} \qquad \text{for } j = P, H \tag{3}$$

and check that Appendix S1 Eqn 3< 0 for $j = P$ or H, and therefore the singular strategy is an ESS for the plant or herbivore species respectively. To further classify the ESS, we take the second derivative of the fitness equation with respect to the resident

$$\left.\frac{\partial^2 W_{j_{inv}}}{\partial s_j^2}\right|_{s_{j_{inv}} \to s_j \to s_j^*} \qquad \text{for } j = P, H \tag{4}$$

to check if it is convergent stable (Appendix S1 Eqn 4 - Appendix S1 Eqn 3> 0 for $j = P$ or H) and therefore a continuously stable strategy, CSS (Geritz et al.1998) for the plant or herbivore species respectively. We determined the signs of the derivatives numerically by first computing the derivatives of the symbolic expressions and with the parameter values, evaluating the expressions numerically at the ecological and evolutionary steady state as determined by the simulations. Through these methods, we found that the singular strategy *ss* of the plant species can be at a fitness minimum, while the herbivore is always at a CSS under these situations. It is possible that with our no separation of ecological and evolutionary timescales assumption, and under specific parameter combinations, very rapid evolution may turn these fitness minima into branching points (Calcagno *et al.*, 2010) for the plant, although we do not explore this possibility here.

3 Cases descriptions

We use two limiting assumptions regarding our traits to bracket the spectrum of possible scenarios: perfectly correlated traits and completely independent traits. For completely independent traits, the thermally related traits z_P, z_H always matched the temperature T of the environment (Table 1 Trait $z_P = T$) and the traits describing the interaction s_P, s_H are driven by sensitivity to initial conditions.

For correlated traits, the primary distinction of the cases is based on the trait values, which separates the equilibria into four cases: a case where the herbivore is extinct (Case H ext), cases where the traits of both species match the environmental temperature T (Cases T Co-ESS and H-ESS), cases where the traits of both species do not match each other nor T (Cases not T Co-ESS and H-ESS), and a case where the traits undergo coevolutionary cycles (Case Evo-Cyc). The secondary distinction of Co-ESS and H-ESS in Cases T and not T is based on the evolutionary stability of the equilibrium and we found two qualitatively different outcomes in terms of evolutionary stability: if both species are at an evolutionarily stable strategy (ESS), we classify the case as a Co-ESS and if just the herbivore is at an ESS, we classify it as an H ESS, P fitness minimum.

3.1 Assumption 1: Traits correlated

Under this assumption of perfectly correlation, $s_j = z_j$. We will refer to the traits as s_j in notation while considering this assumption.

Case H ext: $s_P = T$, H extinct

Therefore s_P evolves to match T of the environment.

A. s_H too far from s_P initially.

B. Lemmings play (plant takes herbivore to boundary and it goes extinct).

Case T: $s_P = s_H = T$

Equilibrium for the traits of both species is at T, a co-ESS or herbivore ESS and plant fitness minimum.

A. Co-ESS

B. H ESS, P fitness minimum.

Case not T: $s_P \neq s_H \neq T$

Equilibrium above or below T depending on initial conditions, the relative positions of s_P and s_H.

A. Co-ESS

B. H ESS, P fitness minimum.

Case Evo-Cyc: Coevolutionary cycles

In the cycles, the attractor for the plant is changing between a repellor when s_P is closer to T than s_H and an ESS when further.

3.2 Assumption 2: Traits not correlated

For traits not correlated, $z_P = z_H = T$ always if we assume positive biomass for P, H. Therefore in a static environment we focus on s_P, s_H because the stabilizing selection disappears but the interaction between the species remains.

Possible outcomes:

We introduce a quantity x, the location of the singular strategy to illustrate the sensitivity of these cases to initial conditions.

Case x H ext: $s_P = x$, H extinct

where x depends on initial conditions (the relative positions of s_P, s_H) and the extinction rate of H.

Effectively P escapes H.

Case x: $s_P = s_H = x$

A. *H* ESS, *P* fitness minimum

where x depends on initial conditions (the relative positions of s_P, s_H), μ_P, μ_H, σ, and initial values of s_P, s_H.

B. *P* extinct due to overexploitation.

We do not consider this case further.

4 Determinants of Cases in a static environment for correlated traits

We found that the distinct cases and locations depend on the assumption of correlated or uncorrelated traits, relative mutation rates of the two species, relative thermal niche widths of the two species, and the grazing interaction kernel width. The traits not correlated assumption leads to only the grazing trait for each species that shows responses in a static environment since the thermal trait will always match the temperature of the environment T. The grazing trait is a direct result of the initial conditions, the absolute starting positions of traits. Therefore, we present the correlated traits assumption.

When mutation rates are equal between the plant and herbivore species, increasing grazing interaction kernel width increases the regions where the traits of both species match the temperature of the environment T (Appendix S1 Figure 5). In contrast, increasing the thermal niche width of the plant w_P, increases the regions where the traits of both species do not match the temperature of the environment T (Trait $z_P \neq T$ in Table 1 and High ss and Low ss in Figure 2a). In addition, there is an interactive effect of plant thermal niche width and grazing interaction kernel width on the regions of the cases and subcases.

With a higher plant mutation rate, the influence of parameters on cases is modified and the region where evolutionary cycling occurs (Case Evo-Cyc) becomes larger (compare Appendix S1 Figure 5 to Appendix S1 Figure 6).

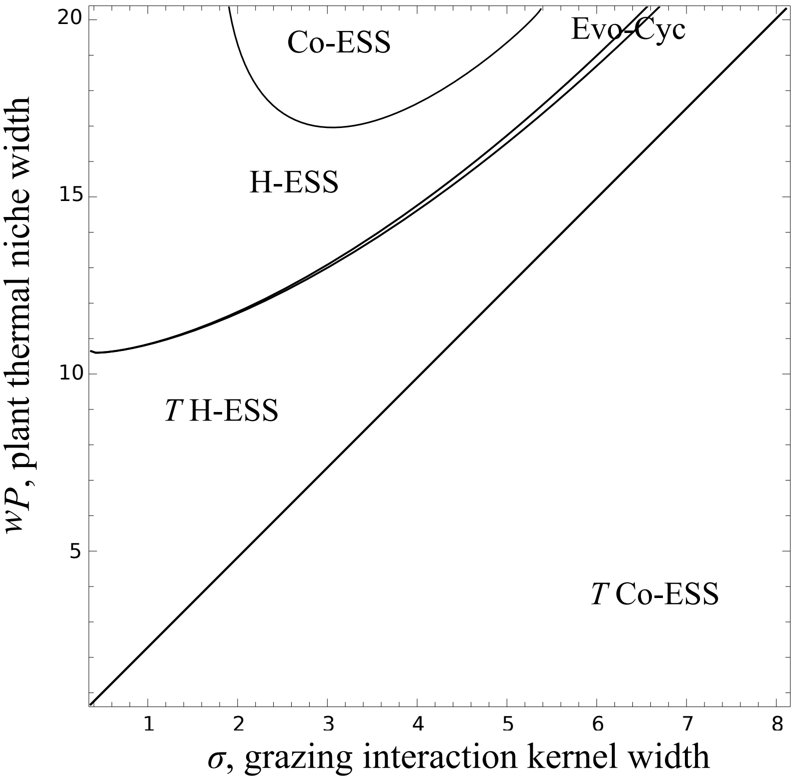

Figure 5: Determinants of Cases and trait values in a static environment for correlated traits. Effect of w_P, the thermal niche width for P and σ, the interaction kernel width on evolutionary attractors (Cases) in a static environment with $\mu_P = \mu_H$. Cases: H ext : $s_P = T$, H extinct, T Co-ESS : $s_P = s_H = T$, Co-ESS, T H-ESS : $s_P = s_H = T$, H ESS, P fitness minimum, Co-ESS : $s_P \neq s_H \neq T$, Co-ESS, H-ESS : $s_P \neq s_H \neq T$, H ESS, P fitness minimum, Evo-Cyc : Coevolutionary cycles. Parameters: $w_H = 8$.

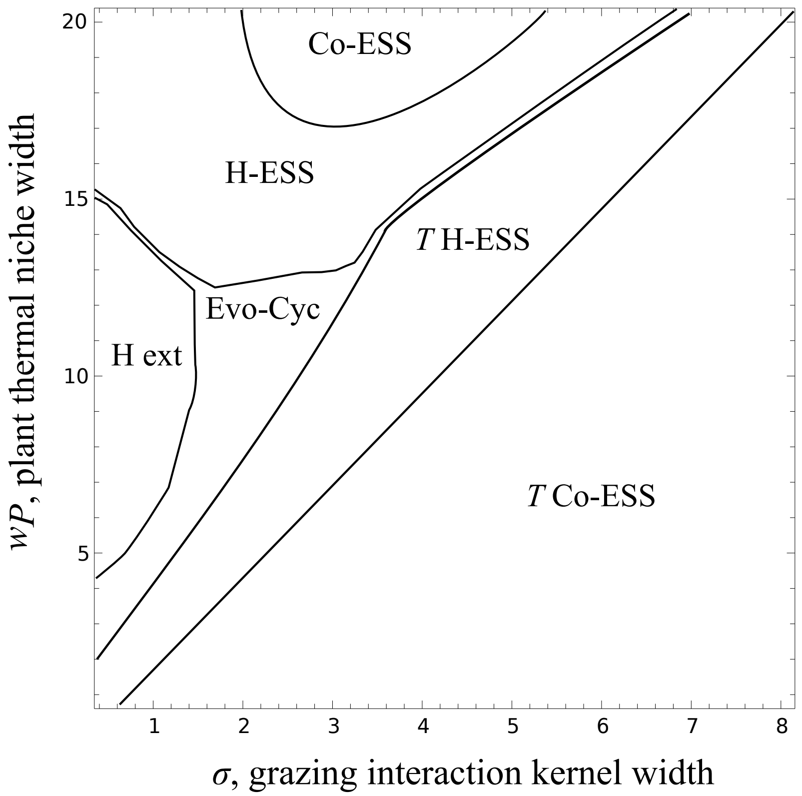

Figure 6: Same as Figure 5 but with $\mu_P > \mu_H$. Effect of w_P, the thermal niche width for P and σ, the interaction kernel width on evolutionary attractors (Cases) for correlated traits in a static environment. Cases: H ext : $s_P = T$, H extinct, T Co-ESS : $s_P = s_H = T$, Co-ESS, T H-ESS : $s_P = s_H = T$, H ESS, P fitness minimum, Co-ESS : $s_P \neq s_H \neq T$, Co-ESS, H-ESS : $s_P \neq s_H \neq T$, H ESS, P fitness minimum, Evo-Cyc : Coevolutionary cycles. Parameters: $w_H = 8$.

5 Functions and parameters in model

Although many biological and ecological processes are temperature dependent, we incorporate temperature dependence in one growth-related parameter for each species to simplify interpretation. In our model, the nutrient uptake rate (Dell *et al.*, 2011) and grazing rate (Rall *et al.*, 2012; Englund *et al.*, 2011) parameters are temperature dependent but ingestion, metabolism, conversion efficiency, production, and mortality could all have temperature dependencies (Vasseur & McCann, 2005). We obtain the same qualitative results when conversion efficiencies for both species are temperature dependent instead.

We follow recent evidence and suggestions and make temperature relationships unimodal in our model (Dell *et al.*, 2011; Englund *et al.*, 2011), rather than a strictly increasing function such as predicted by the Arrhenius equation to model effects of warming on species interactions in food web models (Mitchell & Angilletta Jr., 2009). The maximum rate of our temperature-related parameters scales (increases) with temperature following Eppley (1972); Bissinger *et al.* (2008); Thomas *et al.* (2012) and the thermodynamic constraints hypothesis (Angilletta *et al.*, 2010). This creates a tradeoff along the temperature axis with colder adapted species relatively disadvantaged in maximum growth rate, not a tradeoff of niche width versus maximum growth rate since we do not model the evolution of niche width. Niche width evolution and a tradeoff of width versus maximum growth rate (Ackermann & Doebeli, 2004) could potentially lead to more diverse patterns in persistence time. We do not assume maximum interaction strength or mortality rates to be a constant proportion of the maximum growth/metabolism rate (Edeline *et al.*, 2013). We used realistic thermal niche widths to describe the unimodal temperature dependence for each species (Sunday *et al.*, 2011). Our grazing rate follows a unimodal relationship with traits following previous theoretical studies (Abrams, 2000; Calcagno *et al.*, 2010) and empirical evidence (Rall *et al.*, 2012) but a one-sided interaction was used in the only other study (Jones, 2008) with trophic interactions evolving under extinction-inducing environmental change.

Our parameter range for mutation rate ($\mu = 10^{-5}$ to 10^{-1}) falls in the previously used ranges of $10^{-2} - 10^{-1}$ for qV (population size scaling factor x genetic variance) (Norberg *et al.*, 2012), 10^{-2} for evolutionary change (Thomas *et al.*, 2012), and $10^{-7} - 10^{-4}$ per capita per time mutation rate (Osmond & de Mazancourt, 2012). Our goal was not to match the value of our mutation rate to an exact value measured empirically on a particular organism, rather to consider a range of values, due to uncertainty in those evolutionary rates and the many mechanisms that create them (Shapiro, 2013) as well as rates of future temperature change. Under our assumption of traits not correlated, we follow a previous study (Loeuille & Leibold, 2008) and split mutations between the two traits, effectively assuming heritably independent mutations with two separate loci, leading to slower adaptation. Parameterizing our model with t timesteps in units of days, leads to approximately 30 years of temperature change, in which we consider 1-4 degrees of temperature change during that time. This range of 1-4 degrees of temperature change (corresponding to about 0.03 to 0.13 degrees change per year) is of the same order of magnitude as previous studies and current predictions (Norberg *et al.*, 2012; IPCC, 2007). Note that outcomes strongly depend on mutation rate, a parameter that has more uncertainty.

Parameter notation follows Hulot & Loreau (2006) and values for resource supply, maximum grazing rate, mortality rates, and conversion efficiencies are similar to values used in (Mellard & Ballantyne IV, 2014; Loeuille *et al.*, 2002; Loeuille & Loreau, 2004) who studied plant-herbivore coevolution in a constant environment. However, we varied these parameters to match natural systems. Most lakes have a heterotrophic to autotrophic biomass ratio of less than 1 and if one compares just the algae and macrozooplankton biomass, one obtains values of similar magnitude (del Giorgio & Gasol, 1995). We use a herbivore to plant biomass ratio of 0.07-0.4. We also used parameters that led to an inversion of the biomass pyramid, up to 100:1 biomass ratio of herbivore to plant biomass, depending on the strategies in a static environment. Although rare, this can occur in some very unproductive aquatic planktonic systems. In such situation, the plant can go extinct before the herbivore, although the herbivore will eventually go extinct without the plant. We recognize that a model that is substantially different from ours in the assumptions could lead to different behavior. However, we leave that for future comparisons.

We speculate that herbivores that are highly specialized on a plant species should have similar thermal optima as the plant species and may also be thermal specialists. If so, then given our results, specialists will start tracking the temperature change sooner than generalist herbivores whom may become more decoupled in their interaction with certain plant species. Although generalists benefit from the insurance multiple species provide, contrary to what we may expect, they may experience lower persistence because they eventually lag too far behind the changing climate. We already observe generalist forest plant species to be lagging more than specialists (Bertrand *et al.*, 2011).

Although we are not aware of many studies (Jones, 2008; Moya-Laraño *et al.*, 2012; Northfield & Ives, 2013) that have considered trophic interactions in the context of coevolutionary response to environmental change, competition has been shown to help or hinder evolutionary rescue depending on certain conditions (Osmond & de Mazancourt, 2012). Studies on evolutionary rescue typically consider a small, abrupt environmental shift, and derive an analytical expression for the rate of trait change to the new optimum. We however, find out under what conditions all populations can catch a constantly moving optimum.

In addition to steadily increasing temperature (Way & Oren, 2010), abrupt climatic events may affect herbivores very rapidly and shift the ecosystem state (Kurz *et al.*, 2008; Raffa *et al.*, 2008) as well as directly affect plants Charru *et al.* (2010) so it would be interesting to combine these effects in a model along with other possible climate effects. For example, a climate-induced trophic cascade can happen due to size changes rather than extinction of species (Jochum *et al.*, 2012). Higher trophic levels also lead to more changes in the rest of the community if removed (Zarnetske *et al.*, 2012). However, even with these complexities, patterns in biotic interactions have emerged repeatedly in the past, patterns which may be used to bolster our predictions for the future (Blois *et al.*, 2013).

Table 1: Parameter values unless noted otherwise.

Variable or Parameter [Dimension]	Definition	Value (Range)
R [Quantity of nutrient]	inorganic nutrient quantity	state variable
P [Quantity of biomass]	plant species biomass	state variable
H [Quantity of biomass]	herbivore species biomass	state variable
z_P [Dimensionless]	plant thermal trait	evolves
z_H [Dimensionless]	herbivore thermal trait	evolves
s_P [Dimensionless]	plant grazing interaction trait	evolves
s_H [Dimensionless]	herbivore grazing interaction trait	evolves
I [nutrient (time)$^{-1}$]	inorganic nutrient input	0.5 (0.5-5)
q [time^{-1}]	inorganic nutrient loss rate	1
k [(producer biomass x time)$^{-1}$]	per unit biomass uptake rate	function of s_P
l [producer biomass (nutrient)$^{-1}$]	conversion of nutrients into plants	1
m [time^{-1}]	loss rate of plant biomass	0.1
a [(consumer biomass x time)$^{-1}$]	per unit biomass consumption rate of herbivores on plants	function of s_P, s_H, z_H
b [consumer biomass (producer biomass)$^{-1}$]	conversion of plants into herbivores	1
d [time^{-1}]	loss rate of herbivore biomass	0.4 (0.1-0.4)
w_P [temperature]	plant thermal niche width	1-30
w_H [temperature]	herbivore thermal niche width	8-12
σ [Dimensionless]	interaction kernel width	0.1-8
a_{max} [Dimensionless]	maximum grazing rate	0.2 (0.2-0.5)
α_j [Dimensionless]	Eppley curve coefficient for species j	0.81
β_j [Dimensionless]	Eppley curve exponent for species j	0.0631
$\mu_{P,H}$ [biomass^{-1}]	per unit biomass mutation size	$10^{-5} - 10^{-1}$
ΔT [temperature]	amount of temperature change [C]	0-10

6 Ecological Equilibrium

For our analysis, let $\hat{R}, \hat{P}, \hat{H}$ represent equilibrium quantities of resource, plants, and herbivores respectively so that,

$$\begin{aligned} \hat{R} &= \frac{Iab}{qab+dk}, && (5) \\ \hat{P} &= \frac{d}{ab}, && (6) \\ \hat{H} &= \frac{Iabkl-qabm-dkm}{a(qab+dk)}, && (7) \end{aligned}$$

is the equilibrium with the plant and the herbivore present. The existence of this interior equilibrium with $\hat{H} > 0$ is possible when $I > \frac{dm}{bal} + \frac{mq}{kl}$.

The equilibrium without the herbivore is

$$\begin{aligned} \hat{R} &= \frac{m}{kl}, && (8) \\ \hat{P} &= \frac{Ikl-qm}{km}. && (9) \end{aligned}$$

7 Shift from equilibrium under warming

We compare the adaptation of the plant with and without the herbivore to see under what conditions the herbivore can help adaptation of the plant to a warming environment. We use analytical methods to examine how the addition of a herbivore to the system affects the ecological equilibrium and the different eco-evolutionary pathways it acts through such as the direction of selection, strength of selection, rate of adaptation, and evolutionary endpoints.

In general, the addition of a herbivore can affect the plant adaptation through the following mechanisms:

0) Abundance

1) Direction of selection First set of criteria

2) Strength of selection Second set of criteria

3) Abundance relative to selection Third set of criteria

4) Starting location (can be $\neq T$, the temperature of the environment)

The criteria listed next to the mechanisms follow Osmond and de Mazancourt (2012) reasoning. All must be met for the addition of the interacting species (herbivore) to help adaptation of the focal species (plant).

7.1 Adaptation without the herbivore

We consider the evolutionary equation for rate of trait change for the plant, $\frac{dz}{dt} = \mu P \frac{\partial W}{\partial z}$. At equilibrium, we can treat R and P as constant. Without the herbivore in the system, the fitness gradient is then $\frac{dW}{dz_P} = lR\left(\frac{\partial k}{\partial z_P}\right)$. Therefore, our equation for rate of trait change becomes

$$\frac{dz}{dt} = \mu \hat{P}_{\mathrm{no}H} l \hat{R}_{\mathrm{no}H} \frac{\partial k}{\partial z_P} \tag{10}$$

with $\hat{P}_{\mathrm{no}H}$ and $\hat{R}_{\mathrm{no}H}$ defined in Appendix S1 Equations 8 and 9.

7.2 Adaptation with the herbivore

7.2.1 Traits not correlated

Now we consider the situation with the herbivore in the ecosystem and traits not correlated. We only have to consider the thermal trait z because only it relates to adaptation to temperature change. This also means that the herbivore affects plant adaptation only through density effects so we only have to consider one mechanism, Abundance. We modify Appendix S1 Equation 10 with the following notation:

$$\frac{dz}{dt} = \mu \hat{P}_H l \hat{R}_H \frac{\partial k}{\partial z_P} \tag{11}$$

with $\hat{P}_H$ and $\hat{R}_H$ defined in Appendix S1 Equations 5 and 6.

We know in general that $\hat{P}_{\mathrm{no}H} > \hat{P}_H$ but also that $\hat{R}_{\mathrm{no}H} < \hat{R}_H$. For the herbivore to never help the plant adapt when traits are not correlated, we have to show that $\hat{P}_{\mathrm{no}H}\hat{R}_{\mathrm{no}H} > \hat{P}_H\hat{R}_H$. We are not aware that this relationship has been shown before so are uncertain if it is always true. However, we can see it is always true for the parameter values we explored in our model.

Furthermore, by imposing our system constraint in the form of the feasibility criteria for H, $I \geq \frac{dm}{bal} + \frac{mq}{kl}$, we can show analytically that for (+) parameter values, as long as $qab < 1$, the herbivore never helps the plant adapt.

7.2.2 Traits correlated

For correlated traits, we have more complicated expressions and we see other possibilities for the herbivore to help the plant adapt, specifically by increasing the strength of selection in the direction of environmental change.

The fitness gradient for the plant with correlated traits ($s_P = z_P$ and $s_H = z_H$) is:

$$\frac{dW}{dz_P} = lR\left(\frac{\partial k}{\partial z_P}\right) - H\left(\frac{\partial a}{\partial z_P}\right). \tag{12}$$

To satisfy the first set of criteria, Direction of selection,

$$\left(\frac{\partial}{\partial z}\right)k \qquad \text{and} \qquad \left(\frac{\partial}{\partial \mathrm{z}}\right)\mathrm{a} \tag{13}$$

must be of the same sign to have the grazing select in the same direction as the environment for the plant.

To satisfy the second set of criteria, Strength of selection,

$$\left|\left(\frac{\partial}{\partial z}\right)(k-a)\right| \quad > \quad \left|\left(\frac{\partial}{\partial z}\right)k\right| \tag{14}$$

must be true for grazing to increase the strength of selection. This will always will be true if $\frac{\partial k}{\partial z}$ and $\frac{\partial a}{\partial z}$ are of different signs.

To satisfy the third set of criteria, Abundance relative to selection, we have to compare the grazing effect on abundance relative to selection. Thus we will have grazing increasing the rate of adaptation iff

$$\hat{P}_H \left| l\hat{R}_H \left(\frac{\partial}{\partial z}\right) k - \hat{H} \left(\frac{\partial}{\partial z}\right) a \right| > \hat{P}_{\text{no}H}\hat{R}_{\text{no}H} \left| \left(\frac{\partial}{\partial z}\right) k \right|, \tag{15}$$

where $\hat{H} > 0$.

If $T > z_H > z_P$, the herbivore will slow evolution down. When grazing selects in the opposite direction as the environment and has a stronger selective effect, $\left|\frac{\partial a}{\partial z}\right| > \left|\frac{\partial l}{\partial z}\right|$, it reverses direction of selection and the population evolves away from T. However, satisfying the first criteria, if $T > z_P > z_H$, the herbivore could potentially speed up evolution.

These analyses show what must happen for the herbivore to help the plant adapt from its equilibrium when first departing from a static environment. Once the environment changes sufficiently, transient dynamics can make these criteria less stringent. When the environment has changed sufficiently, the equilibrium population equations are no longer valid so the third criteria cannot be evaluated. Traits can switch relative positions so the first criteria may not be valid, the second criteria also. We never find the herbivore to aid the adaptation of the plant when we parameterize our model with realistic values, the exception being that we find the herbivore to help when it creates a head-start for the plant through coevolution in a static environment, therefore acting through the fourth mechanism, Starting location.

8 Conclusions

Trophic interactions create different responses of the thermal traits and biomass of species to a warming climate and, in general, have a negative impact on persistence of species. Species thermal traits do not always match the environmental temperature and as the environmental temperature changes, may track an evolutionary attractor some distance from it. Although the trophic interaction acts through a number of mechanisms in our model, amount of biomass strongly affects species persistence. In addition, we show that the dynamics, persistence, and biomass can be contingent on the evolutionary endpoint (attractor) in a constant environment. The amount of biomass and evolutionary endpoint in a static environment and adaptation in a changing environment are strongly influenced by a key parameter in our model, the thermal niche width, regularly measured in empirical studies. Future studies should identify for particular ecosystems, the thermal niche widths of both plants and their herbivores, in order to increase the predictive ability of modeling in the context of climate change that includes species interactions.

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