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Research

The transient response of ecosystems to climate change is amplified by trophic interactions

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Studies of ecosystem responses to climate change often focus on potential equilibria in species or community distributions, overlooking the transitions to new equilibrium states. Transient phases can however last for decades or centuries, during which both demography and interspecific interactions are expected to play a crucial role. Here, we investigate the response of vegetation to climate warming at high latitudes involving a shift from open vegetation to either boreal (mainly coniferous) or temperate (mainly deciduous) forests. We specifically address how interactions among browsers and vegetation could affect the shift in dominance of vegetation type after climate warming. We characterize the transient dynamics using five measures: 1) asymptotic resilience, i.e. the rate at which equilibrium is restored, 2) initial resilience, the short-term rate of change of the ecosystem after climate change, 3) ecosystem exposure, i.e. the shift of the equilibrium due to climate change, 4) sensitivity, or the time to recover equilibrium, and 5) vulnerability, measured as the cumulative amount of changes in vegetation states during the transient phase. We find that plant–herbivore interactions usually extend the length of the transient period and induce more cumulative changes in vegetation types. This result implies that the consideration of multiple interacting species is necessary to provide robust scenarios of how ecosystems will respond to global changes. We furthermore show that plant–herbivore interactions disrupt the correlation between the five measures characterizing the transient dynamics, highlighting the need for a full multidimensional characterization of transients.

Introduction

Understanding how ecosystems respond to global changes is a major challenge for contemporary ecology. Changes in biodiversity are often not immediate, as they are the consequence of gradual processes such as range shifts or declines in abundance, which can span several years, decades, or longer. Empirical studies (Bertrand et al. 2011, Svenning and Sandel 2013, Savage and Vellend 2014) and simulations

(Dullinger et al. 2012, Boulangeat et al. 2014) have documented situations where species distributions do not match their optimal climate envelope. At the trailing edge of the distribution, some populations may persist for a long time under unfavorable conditions before going extinct. At the leading edge, the colonization of favorable habitats can take a long time because of demographic inertia, community reassembly, or spatial dynamics (Essl et al. 2015). These periods during which ecosystems are in strong disequilibrium with their optimal climate are hereafter referred to as transient phases. Short- and long-term transient dynamics may differ. For example, the state of an ecosystem may slowly change at first and then undergo a sudden shift (Scheffer et al. 2001), or local biodiversity may peak prior to extinctions (Turnbull et al. 2013). Characterizing the length and nature of transient phases is therefore of crucial importance for biodiversity conservation.

Interspecific interactions are expected to influence ecosystem responses to novel environmental conditions and therefore play a major role during transient phases (Van der Putten et al. 2010). Indeed, range shifts are mainly determined by demography and dispersal, both of which are influenced by species interactions (Svenning et al. 2014). Asynchronized range shifts could modify the composition of ecosystems during their transition towards a new equilibrium. For example, the persistence of long-lived trees may delay the extinction of understory species or forest habitat specialists (Vellend et al. 2006). Conversely, abundant consumers may prevent their preferred prey from colonizing new habitats (Brown and Vellend 2014). Interspecific interactions are responsible for positive feedbacks, thereby reducing stability, creating alternative equilibria, or inducing long transient dynamics (Fukami and Nakajima 2011, Lever et al. 2014). For instance, plant–plant competition has been shown to reduce the rate of range expansion during plant migrations (Scheller and Mladenoff 2008). Species interactions could therefore amplify or buffer the response of ecosystems to environmental changes during the transient phase (Zarnetske et al. 2012, Ghedini et al. 2015).

Distributions of biomes are expected to shift higher in altitude or towards the poles in response to climate change (Rizzo and Wiken 1992, Lenoir et al. 2008). Little is known, however, about how species interactions could affect this process. In particular, plant–herbivore interactions are expected to strongly influence the relationship between climate and vegetation distribution (Bond 2005, Holdo et al. 2013, Bakker et al. 2016). Browsing also affects forest succession by favoring or preventing the establishment of different late-successional plants (Côté et al. 2004). In this study, our objective was to investigate how plant–herbivore interactions may mediate the response of vegetation to climate change. We investigated the shifts occurring in northern environments of the Northern Hemisphere, where substantial changes are expected to occur (Gang et al. 2013).

We used simulation models to fully characterize the transient dynamics of ecosystems. Our analyses were based on a spatially-implicit model of transitions between vegetation states across a large climatic gradient, combined with a population dynamics model of a large browser herbivore occurring across the different biomes. We simulated climate warming and investigated the transient dynamics over a temperature gradient in presence and absence of the herbivore. We characterized transient dynamics using five measures: asymptotic and initial resilience, which are respectively defined as the rate at which equilibrium is restored and the reactivity of the ecosystem; ecosystem exposure, which is the final shift in vegetation state due to climate change; sensitivity, i.e. the time for vegetation to reach equilibrium after climate change; and vulnerability, measured as the cumulative amount of changes undergone by the vegetation during the transient phase. We assessed whether plant–herbivore interactions 1) influenced the characteristics of the ecosystem's transient dynamics, and 2) modified the correlation structure between these five different measures. Our simulations and analyses suggested that plant–herbivore interactions could strongly affect how the vegetation respond to climate change. Plant–herbivore interactions also disrupt the correlation structure between different measures of resilience, suggesting that trophic interactions could increase the dimensionality of resilience.

Methods

Vegetation dynamics

Our vegetation model represents the development of forest stands from treeless vegetation to boreal or temperate mature forests. We use a state and transition approach (Fig. 1). We consider a large and spatially homogeneous landscape, where spatial units are either treeless, hereafter open vegetation (V), seedlings and saplings, hereafter regeneration (R), mature temperate trees (T), or mature boreal trees (B). The size of the landscape is equal to or larger than the range of the herbivore
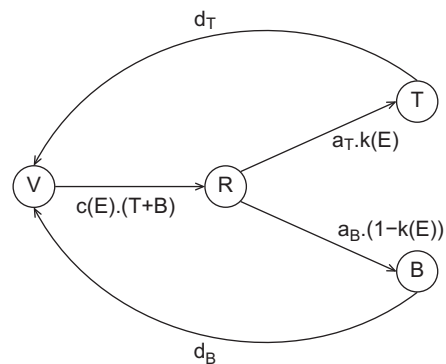

Figure 1. Schematic representation of the state and transition model for vegetation. V = open vegetation; R = seedlings and saplings (forest regeneration); T = mature temperate tree stands; B = mature boreal tree stands. Transition rates involve $c(E)$, the tree colonization rate, a_T, the succession rate of temperate trees, a_B, the succession rate of boreal trees, and $k(E)$, the performance of temperate seedlings relative to boreal seedlings, where E represents the variation along environmental gradients.

population, such that herbivores have access to all available vegetation and are distributed optimally. The model describes transitions between vegetation states. Solving for equilibrium gives the proportion of the landscape occupied by each state.

The following set of differential equations represents the transitions between vegetation states:

$$\begin{cases} \dfrac{dR}{dt} = c(E) \times (B+T) \times V - (a_T \times k(E) + a_B \times (1-k(E))) \times R \\[2mm] \dfrac{dT}{dt} = a_T \times k(E) \times R - d_T \times T \\[2mm] \dfrac{dB}{dt} = a_B \times (1-k(E)) \times R - d_B \times B \end{cases} \quad (1)$$

where $V = 1 - R - T - B$. In our model, mature tree stands can revert back to open vegetation due to natural disturbances such as wind throws, fires and epidemics. Different disturbance rates, d_T and d_B, are considered for temperate and boreal trees, respectively. Open vegetation is colonized by seedlings at a rate $c(E)$ proportional to the amount of mature trees in the landscape. This density dependent effect is based on the metapopulation theory that has been applied to fit vegetation dynamics with empirical data (Talluto et al. 2017). Development towards mature tree stands occurs at rates a_T and a_B for temperate and boreal trees, respectively. An additional parameter $k(E)$ represents the performance of temperate seedlings relative to boreal seedlings (see Table 1 for a list of all model parameters used in this study).

Table 1. Model parameters used in this study.

Parameter	Description	Value	Unit	Source
a_T, a_B	rate of development towards mature tree stands	0.05	year^{-1}	20 years-old trees are considered mature and their consumable biomass becomes inaccessible to browsers
d_T	temperate disturbance rate	0.004	year^{-1}	boreal trees have a smaller average longevity because of regular fires*
d_B	boreal disturbance rate	0.01	year^{-1}	
k	performance of temperate seedlings relative to boreal seedlings	[0.1; 0.8]	year^{-1}	varies with climate
c	tree colonization rate	[0;0.05]	year^{-1}	varies with climate
e_s	summer biomass conversion from vegetation to browser	0.35		kg of vegetation per kg of browser**
e_w	winter biomass conversion from vegetation to browser	0.25		moose digestibility is approximately 25% lower during winter compared to summer***
τ_s	maximum forage intake for summer	3.472	year^{-1}	10 kg per day per individual, for individuals weighing 358 kg on average***. Summer length was set to 124 days†
τ_w	maximum forage intake for winter	6.748	year^{-1}	
ν_s	half saturation of resource intake for summer	34	year^{-1}	rescaled to the season from a value of 100 kg of food per kg of browser per year, which matches observations of production and consumption at Isle Royale†
ν_w	half saturation of resource intake for winter	66	year^{-1}	
γ	maximum reproduction rate	1	year^{-1}	2 offspring per female and a sex ratio of 0.5
m	mortality rate	0.3	year^{-1}	Bertram and Vivion 2002, Patterson et al. 2013
u_B	boreal tree productivity accessible to the herbivore	20 000	kg km^{-2} year^{-1}	Crête 1989, Dussault et al. 2006
u_T	temperate tree productivity accessible to the herbivore	20 000	kg km^{-2} year^{-1}	
u_R	seedlings and saplings productivity accessible to the herbivore	60 000	kg km^{-2} year^{-1}	
f	proportion of leaves in T and S productivity	0.85		Crête and Manseau 1996
r_R, r_T, r_B	smoothing parameter for herbivore impact	10		so that a density of 5 moose per km², i.e. a very high density for moose, such as at Isle Royale†, had a notable effect on vegetation demography (Fig. A4)
h_R, h_T, h_B	pressure levels at which the tree establishment or stand development is reduced by half	0.05		
p	temperate seedlings preference over boreal seedlings	0.8		studies have reported that coniferous species such as *Abies balsamea* were rarely chosen when they were highly available (Crête 1989) or consumed in proportion to their availability when they were less abundant (Belovsky 1981).
p_R	preference of regeneration patches over mature stands at equal biomass production	0.5		the effect of a disproportionate preference of regeneration patches, investigated in Fig. A5.

*Heon et al. 2014; **Belovsky 1981; ***Moen et al. 1997; †Belovsky and Jordan 1978

Although all parameters may be sensitive to the environment E, we focus here on its effect on species interactions only ($c(E)$ and $k(E)$). We thus neglect the variation along the environmental gradient of the development (a_T and a_B) and disturbance rates (d_T and d_B). A sensitivity analysis confirmed that interaction parameters c and k had the largest impacts on the proportion of different vegetation types at equilibrium (Supplementary material Appendix 1 Fig. A1).

Browser population dynamics

The vegetation model is coupled to a model of population dynamics for a large browsing mammal such as moose *Alces* sp., elk *Cervus canadensis*, or red deer *C. elaphus*, which leave at the transition between boreal and temperate biomes. The model is also possible to calibrate for mixed-feeding animals that graze and browse, such as *Capreolus capreolus* or *Odocoileus virginianus*, with two additional parameters to describe the herbivore impact on vegetation (see Eq. 11 and Supplementary material Appendix 2). For simplicity, we modeled a closed population without emigration or immigration. This approximation should be valid when the size of the region considered is large enough to encompass all available habitat, or when the population is geographically constrained by natural or anthropogenic barriers. Our model allows the proportion of available vegetation types to influence the browser dynamics through consumer–resource interactions. We distinguish summer and winter dynamics, however, because of reported differences in resource use between seasons. We use a metaphysiological approach where the age structure and sex ratio of the herbivore population is implicit and the only state variable is the total biomass of browser, H (Owen-Smith 2002). We finally consider the seasonality of recruitment. The browser dynamics is given by:

$$dh/dt = G_s(R,T,H) + G_w(R,T,B,H) - M(H) \qquad (2)$$

where G_S is the net gain in browser biomass during summer (when deciduous tree leaves are available) from resource intake and limited by reproduction, G_W is the gain in browser biomass during winter from resource intake, and M represents the loss of browser biomass due to natural mortality. No hunting is considered in this model. Resource intake is modeled using a non-linear, ratio-dependent functional response (Eq. 3, 4), which represents intraspecific competition (Neill et al. 2009). This functional response reflects that, at high browser density, the average consumption rate of the population decreases because the amount of resources available to each individual is reduced and the search time is increased. It also reflects that, at high resource density, physiological constraints such as the capacity of the digestive organs limit the consumption rate. Net gains are computed as follows:

$$G_s(R,T,H) = H \times \min\left(\gamma, e_s \times \frac{\tau_s \times F_s(R,T)/H}{\nu_s + F_s(R,T)/H}\right) \qquad (3)$$

$$G_w(R,T,B,H) = H \times e_w \frac{\tau_w \times F_w(R,T,B)/H}{\nu_w + F_w(R,T,B)/H} \qquad (4)$$

where e_s and e_w are the biomass conversion factors from vegetation to browser, τ_s and τ_w are the maximum intake of vegetation biomass per unit of herbivore biomass for the length of the summer and winter, respectively, and ν_s and ν_w are the half-saturation resource intakes rescaled to the corresponding season. Summer accumulation of browser biomass is limited by the maximum possible reproduction γ when resources are unlimited. The summer and winter resources F_s and F_w are a mixture of different vegetation types. During summer, the diet of browsers is mainly composed of deciduous leaves (Crête and Manseau 1996). Although mature boreal forests also provide deciduous leaves, we consider that summer diet is mainly supported by R and T vegetation types. F_s is therefore computed as a proportion f of resources from R and T. In winter, the diet is restricted to twigs of deciduous trees, i.e. the complementary part of resources from R and T, and the foliage of coniferous trees (resources from B). Each vegetation type contributes to winter or summer resources relative to their proportion in the landscape and their productivity (accessible to the herbivore). The resources are computed as follows:

$$F_s = \left(u_R \times R + u_T \times T\right) \times f \qquad (5)$$

$$F_w = \left(u_R \times R + u_T \times T\right) \times \left(1 - f\right) + u_B \times B \qquad (6)$$

where u_R, u_T and u_B represent the amount of biomass (kg) accessible to browsers in a uniform landscape of R, T and B, respectively.

To account for additional grazing during summer, Eq. 5 is completed with an additional term including resources from open vegetation F_{sG}:

$$F_{sG} = \min\left(u_G \times V, p_G \times F_s\right) \qquad (7)$$

where u_G is the amount of grass biomass in a landscape where $V = 1$, and p_G is the maximum proportion of grazed resources compared to browsed resources in the summer diet.

Finally, mortality is proportional to population biomass:

$$M(H) = m \times H \qquad (8)$$

where m is the annual mortality rate.

Herbivory

The feedback of herbivores on vegetation is modeled through their impacts on transition rates. We consider first that the main impact of browsers occurs through feeding upon seedlings and saplings, which affects both a and $c(E)$ because browsing slows down successional rates (Franklin and Harper 2016). Second, we distinguish the effects of browsers on

temperate and boreal stand development because of their preference for deciduous trees (mainly occurring in temperate stands) over coniferous trees (mainly occurring in boreal stands) (Côté et al. 2004, Long et al. 2007, Bakker et al. 2016). Finally, browsers have a limited effect at low density and a saturating effect at high density. Transition rates are influenced as follows:

$$c(E) = c_0(E) \frac{1}{1 + e^{r_R \times (P_R - h_R)}} \tag{9}$$

$$a_T = a_{T_0} \frac{1}{1 + e^{r_T \times (P_T - h_T)}} \tag{10}$$

$$a_B = a_{B_0} \frac{1}{1 + e^{r_B \times (P_B - h_B)}} \tag{11}$$

where P_R is the total herbivory pressure on vegetation type R, and P_T and P_B are the specific pressures on temperate and boreal regeneration. r_R, r_T and r_B are smoothing parameters, and h_R, h_T and h_B are pressure levels at which tree establishment (Eq. 9) or stand development (Eq. 10 and 11) are reduced by half.

Herbivory pressure is computed as the ratio between the amount of biomass consumed (Eq. 3 and 4) and the available biomass (Eq. 5 and 6). We only consider pressure on regeneration (R), making the assumption that few mature trees die from herbivory because only a small part of their biomass is available and consumed by browsers (Bakker et al. 2016). The model does not account for other potential impacts of herbivores such as debarking or trampling.

To account for preference of temperate resources over boreal resources within the vegetation state R, we use a parameter p which gives the proportion of temperate resources used by browsers when both T and B are present in equal proportions. This emulates active foraging, where the preference for a particular resource increases with its availability (similar to a functional response in resource selection; Bjørneraas et al. 2012). The differential impact of browsers on regeneration state R compared to mature stands T (during summer) directly depends on the relative biomass production that is available (i.e. $u_R \times R$ versus $u_T \times T$). Because regenerating patches are more productive, they are proportionally more heavily browsed than mature stands. Details on the calculation of herbivore impacts can be found in the Supplementary material Appendix 2.

Model parameterization

We parameterized the model to represent succession in temperate and boreal ecosystems up to the tree line. The variation of the relative competitive ability of temperate seedlings over boreal seedlings is difficult to parameterize from empirical data. We therefore reasoned as follows. The fundamental niche of a species represents the locations where its per capita intrinsic growth rate is positive (Godsoe et al. 2017).

It is often represented using a Gaussian response curve, with the optimum of temperate trees found under warmer temperatures than boreal trees. We thus define $f_T(E)$ and $f_B(E)$, the respective fitness functions of temperate and boreal trees (Supplementary material Appendix 3 Fig. A3). We modeled variation of colonization of open vegetation by seedlings (c(E)) as a linear combination of $f_T(E)$ and $f_B(E)$ (Fig. A3), and the variation of competitive ability of temperate seedlings over boreal seedlings (k(E)) as $f_T(E) / (f_T(E) + f_B(E))$. We parameterized these functions following the frequency of key boreal and temperate species in a dataset combining Forest Inventories provided by the US Forest Service and Québec (Canada) forest inventories (Vissault 2016). This parameterization was also consistent with observations over a restricted gradient around the transition between temperate and boreal forests (3 to 5.5°C; Fisichelli et al. 2012, Fig. A3c). A sensitivity analysis on vegetation model parameters showed that, in addition to c(E) and k(E), the ratio of d_T over d_B also influenced whether boreal or temperate mature stands dominates the landscape (Fig. A1).

We included realistic ranges of parameters for a typical population of a large browser. To do so, we mostly compiled data published on moose (Table 1), as they are common in the boreal-temperate ecosystems across the Holarctic, including North America (*Alces americanus*) and Eurasia (*A. alces*). The impact of herbivores was calibrated using data accumulated at Isle Royale (Belovsky and Jordan 1978, Supplementary material Appendix 4).

Equilibrium and transient analysis along the climatic gradient

We divided the increasing temperature gradient into 50 increments of 0.2°C. We then simulated a change in climate for each increment, where initial conditions were set as the equilibrium, and parameter values corresponded to a 0.2°C warmer climate. We characterized the transient dynamics for each interval using five complementary measures. We performed the analysis both in presence and absence of browsers, focusing on the dynamics of the vegetation.

We used two complementary measures of local stability defined in Arnoldi et al. (2016). First, the asymptotic resilience (R_∞, Fig. 2) quantifies the rate at which the equilibrium is approached. Second, the initial resilience ($-R_0$, Fig. 2) is the mathematical opposite of the reactivity, i.e. the strongest initial amplification of a displacement. It describes whether a disturbance of a stable system smoothly disappears (positive values) or is initially amplified (negative values). We use three additional measures to complete the characterization of the transient response of the ecosystem to climate change. Following Pacifici (2015), the exposure of the ecosystem at specific environmental conditions (ΔN, Fig. 2) is defined as the shift of the ecosystem equilibrium between the pre- and post-climate change. The return time (Δt, Fig. 2) is defined as the length of the transient phase, and informs on the sensitivity of the ecosystem (De Keersmaecker et al. 2015). Finally, we propose a new measure: the cumulative amount of
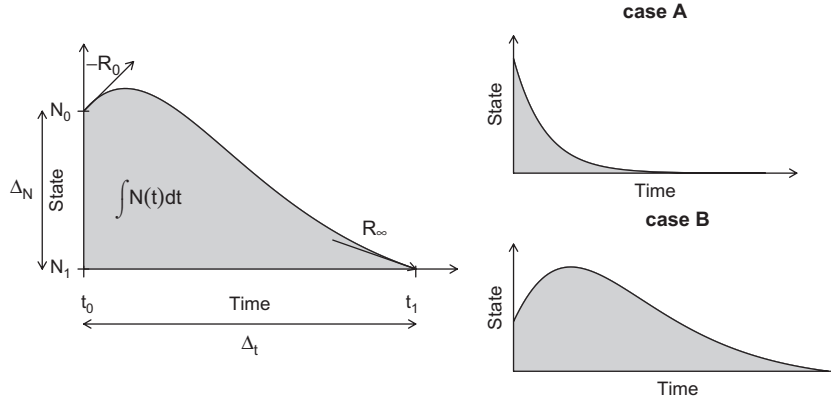
Figure 2. The five measures describing the transient phase. The system is moving from the equilibrium state N_0 at t_0 to the equilibrium state N_1 reached at t_1 in response to a change in environmental conditions. Five measures describe the transient phase: 1) R_∞, the asymptotic resilience, is given by the real part of the leading eigenvalue computed after linearization of the dynamical system at the new equilibrium. R_∞ is positive for a stable system and negative in case of instability. 2) $-R_0$, the initial resilience, is the opposite of the reactivity. It is negative if the system is reactive. 3) the exposure is the shift in state ΔN, computed as the difference between N_0 and N_1 for one unit of the environmental gradient, 4) The sensitivity is the return time Δt, and 5) the cumulative changes in state during the transient phase $\int N(t)dt$. The transient phase could have different shapes. Two examples are given in the right panel. In case A, the reaction is not amplified (positive resilience R_0) and the final equilibrium is reached slowly (small asymptotic resilience R_∞), although the exposure is greater than in case B. In the latter, the system is very reactive (large negative resilience R_0) and the final equilibrium is reached faster (larger R_∞), although the exposure is less than in case A. The cumulative changes are greater in case B.

changes in vegetation states undergone during the transient phase. It is defined by the integral of the variation in the system state over the duration of the transient phase ($\int N(t)dt$, Fig. 2), and may be seen as an integrated measure of ecosystem vulnerability.

We computed the two measures of local stability from the Jacobian matrix J at the new equilibrium (post-climate change). We excluded the dimension of the Jacobian related to the browser state variable, as we focused only on vegetation. We computed the asymptotic resilience as the opposite of the real part of the dominant eigenvalue of J. We measured initial resilience as the leading eigenvalue of the following matrix:

$$M = \frac{-J + J^T}{2} \qquad (12)$$

where J^T is the transpose matrix of J. We used the rootsolve package (Soetaert 2009) in R ver. 3.2.2 (www.r-project.org>) to compute the Jacobian matrices numerically. The exposure was measured as the difference between the two equilibrium states of the interval, using Euclidean distances between vegetation proportions. We computed the distance to the final equilibrium at each time step as the Euclidean distance between vegetation states. We then considered that the new equilibrium was reached when the Euclidean distance was lower than 1×10^{-10} for 10 consecutive time steps. We used the first of these time steps to evaluate the return time. We summed the Euclidean distances of each time step for the length of the return time to compute the cumulative changes in vegetation states (i.e. how much the vegetation changes during the transient phase).

Finally, we analyzed how the five different measures correlated and how these correlations varied with the inclusion of plant–herbivore interactions. We used non-parametric Spearman's rank correlations because the five measures had different frequency distributions.

Results

The preference for regenerating patches over mature stands when both areas have equal biomass available to the herbivore (i.e. active foraging, when p is above 0.5) amplifies the effects of herbivores on vegetation dynamics, but the results are qualitatively similar when this preference is removed (Supplementary material Appendix 5). We thus present our results using a more parsimonious, neutral preference. The impacts of a mixed-feeder population on the transient dynamics of the vegetation are very similar to the impacts of strict browsers (Supplementary material Appendix 6), thus only the latter are presented here.

As expected, vegetation dominance changed along the climatic gradient from open vegetation to boreal trees and then to temperate trees, whether plant–herbivore interactions were present or not (Fig. 3a–b). The maximum browser biomass was observed when mature boreal trees (state B) dominated and seedlings and saplings (state R) were at their highest proportions (Fig. 3b–c). When plant–herbivore interactions were included, transitions between dominant vegetation types occurred at higher temperatures (Fig. 3), and the proportion of mature trees (B and T combined) was reduced (Fig. 3, 4a), to the benefit of regeneration state R (Fig. 3). The total biomass of browsers was larger when we considered
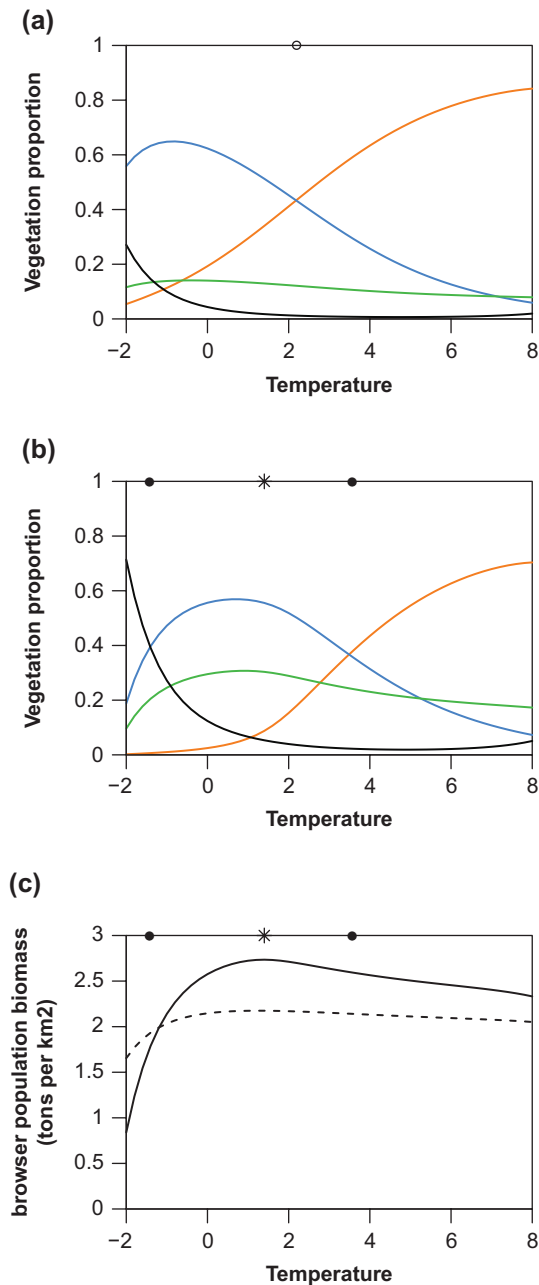
(a)

(b)

(c)

Figure 3. Changes in ecosystem state at equilibrium along the temperature gradient. Proportion of open vegetation V (black), mature boreal tree stands B (blue), mature temperate tree stands T (orange), and seedlings and saplings R (green). (a) Changes in vegetation proportions without plant–herbivore interactions in the system. (b) Changes in vegetation proportions with plant-herbivore interactions. (c) Changes in browser biomass. An asterisk indicates where the browser biomass reaches its maximum population biomass. The dashed line indicates the carrying capacity for the browser population in absence of feedback on the vegetation. The open (no browsers) and closed (with browsers) circles indicate transitions in vegetation type dominance from open (V) to boreal (B) and then from boreal (B) to temperate (T).

their influence on vegetation, except at the coldest temperatures, where accounting for plant–herbivore interactions reduced browser biomass at equilibrium (Fig. 3c).

The transient response of the vegetation to changes in climate was impacted by plant–herbivore interactions. Asymptotic resilience increased towards temperate-dominated ecosystems (Fig. 4b). The presence of plant–herbivore interactions, however, decreased the asymptotic resilience across the whole gradient, with a larger effect when the browser abundance was at its maximum (Fig. 4b). Initial resilience reached its minimum in the temperate-dominated portion of the gradient (Fig. 4c), where tree colonization rate, $c(E)$, was maximal (Fig. A2). Plant–herbivore interactions increased the initial resilience of the vegetation along most of the temperature gradient except in the coldest extreme of the gradient where vegetation was more reactive (Fig. 4c). The exposure of the vegetation increased in the temperature ranges where open/boreal and boreal/temperate transitions occurred. Plant–herbivore interactions amplified and shifted the shape of the exposure response towards warmer temperatures (Fig. 4d). The sensitivity (i.e. the time to reach a new equilibrium) decreased monotonically with increasing temperature in absence of browsers (Fig. 4e). Plant–herbivore interactions slowed down the return to equilibrium. This effect was non-linear, peaking at maximum browser population biomass. Finally, plant–herbivore interactions considerably increased the cumulative changes undergone by the vegetation in response to climate warming (Fig. 4f). Different trajectories illustrate the different transient dynamics that may occur (Fig. 5).

In the absence of browsers, the asymptotic and initial resilience were negatively correlated (Fig. 6). Return time was positively correlated with initial resilience and exposure, and negatively correlated with asymptotic resilience. The cumulative amount of changes was negatively correlated with the asymptotic resilience, and positively correlated with exposure as well as return time. When plant–herbivore interactions were considered, these correlations were altered, reduced, or lost statistical significance (Fig. 6). This disruption was even bigger when considering active foraging of regeneration patches over mature stands by browsers in summer (Fig. A5b).

Discussion

In a context where substantial range shifts are expected for both the temperate and boreal biomes, there is a pressing need to investigate how fast the vegetation could react and how trophic interactions could modify its transient response. Our study reveals that plant–herbivore interactions are likely to amplify the response of vegetation to climate change by lengthening the transient phase and increasing the vegetation changes accumulated during this period. Furthermore, we showed that trophic interactions induced more complexity to predicting the resilience of ecosystems. The original approach
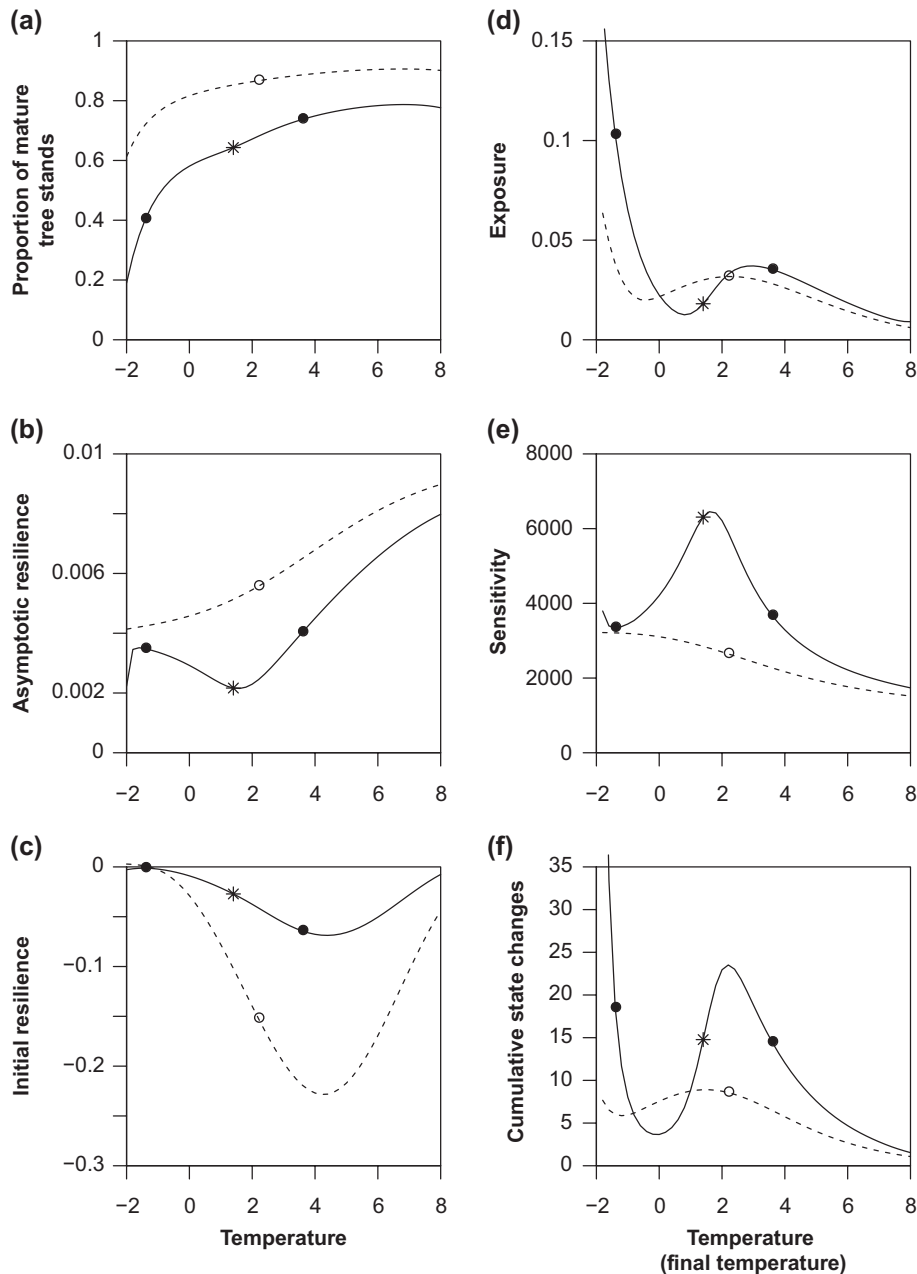
Figure 4. Ecosystem responses along the increasing temperature gradient, with or without plant–herbivore interactions. (a) Proportion of mature tree stands at equilibrium along the increasing temperature gradient, (b) asymptotic resilience R_∞ (c) initial resilience $-R_0$, (d) exposure ΔN (e) sensitivity Δt, and (f) cumulative changes in vegetation state during the transient period $\int N(t)\,dt$. For the five measures (b – f), dashed lines indicate values without browsers, and solid lines indicate values when including plant–herbivore interactions. The circles, solid when herbivores are included and open otherwise, indicate the change in dominant vegetation type from open (V) to boreal (B) and then from boreal (B) to temperate (T). The asterisk indicates climatic conditions with maximum herbivore population biomass.

we used could be applied to any simulation model, from the simplest theoretical models to the more complex ecosystem models. For instance, the same analytical framework could be applied to dynamic range models (Pagel and Schurr 2012) or dynamic vegetation models (Snell et al. 2014). The model could also be applied to the altitudinal transition between deciduous and coniferous forests in temperate mountains,

although parameter values would need to be adapted to this context.

This study first highlights the potential role of browsers in determining the proportion of temperate and boreal biomes at equilibrium. Herbivory, similar to fire, has already been suggested as being a determinant driver of vegetation distribution (Bond 2005). Measures of sapling growth at the
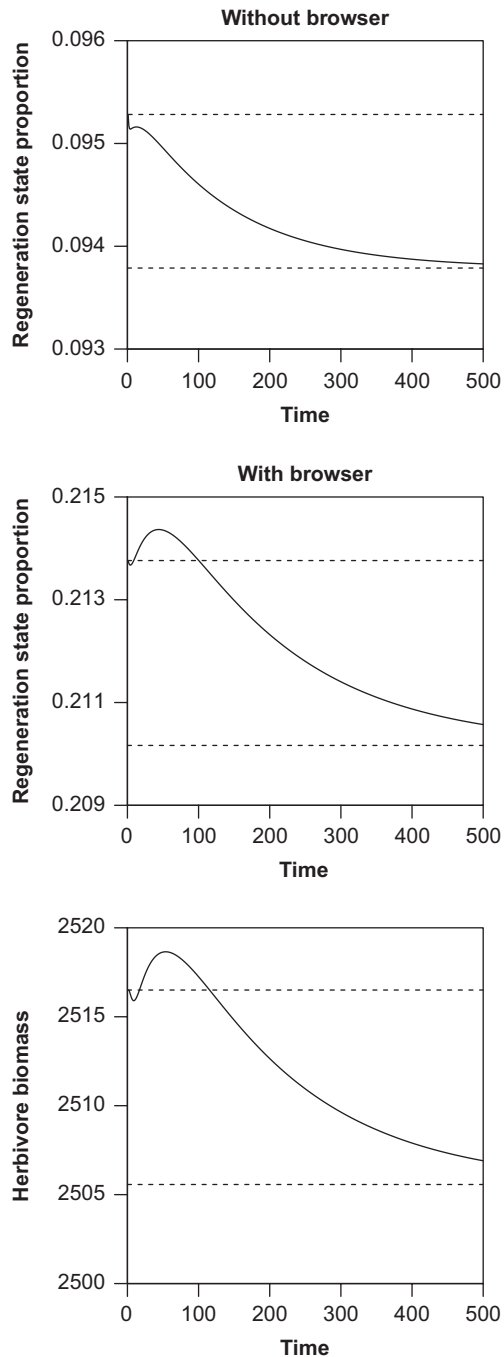
Figure. 5 Example of univariate trajectories of the ecosystem response to climate change. For the interval [5; 5.02]°C, the response of the vegetation (proportion of regeneration state) and herbivore (population biomass) to simulated climate warming are plotted over time (annual time steps). The dashed lines correspond to the state values at the starting and final equilibria. The upper and lower panels show trajectories without and with browsers, respectively.

transition between temperate and boreal forests previously showed that browsing can induce a shift of 1.5°C (summer temperature) for species range limits (Fisichelli et al. 2012).

Here, the model reveals that the shift in vegetation dominance (from open vegetation to boreal forest to temperate forest) is slightly shifted towards warmer temperatures when the reciprocal feedback between vegetation and herbivore is taken into consideration. Furthermore, our results suggest that ecosystem exposure is amplified in the presence of plant–herbivore interactions. This means that herbivory makes range limits sharper. Transitional landscapes with mixed boreal and temperate forests are considered particularly sensitive to climate change (Guerin et al. 2013). A more abrupt transition in vegetation type dominance induced by plant–herbivore interactions could increase their exposition. Such abrupt range edges have previously been reported in a theoretical analysis on the consequences of resource–consumer interactions (Holt and Barfield 2009).

Beyond their impacts on plant distributions at equilibrium, our results suggest that large browsers may have a substantial influence on range dynamics following climate change. Our local stability analysis showed that primary consumers could either promote or limit resilience according to the different measures, as previously proposed by Donohue et al. (2013). Plant–herbivore interactions reduced the asymptotic resilience of the system, decreasing the rate at which the new equilibrium was approached. This is because browsers increase the proportion of open vegetation, making systems more unstable compared to regions with a higher proportion of mature trees. Conversely, plant–herbivore interactions increased the initial resilience of the vegetation (i.e. vegetation was less reactive), delaying the short-term response of the ecosystem to climate change. This is likely because browsers reduce the colonization rate of open vegetation by trees through their consumption of tree sprouts.

Like several studies before us (reviewed by Bakker et al. 2016), we found that plant–herbivore interactions increased the sensitivity of ecosystems (return time). The length of the response of an ecosystem to environmental change is difficult to predict because it is driven by a multitude of factors (Essl et al. 2015). Return time is partly determined by age at maturity and mortality rates of trees, with long-lived species having delayed responses (Vellend et al. 2006). Although vegetation demography is not explicit in our model, we divided the vegetation into age groups (seedlings versus mature trees), which accounted for response delays originating from demography. Moreover, in response to environmental change, interacting species continuously affect the dynamics of each other, which may induce additional lags (Scheller and Mladenoff 2008, Hossack et al. 2013, Essl et al. 2015). The population of browsers, for instance, may respond rapidly to an increase in temperate tree seedling availability, thereby limiting the succession towards mature forests. This, in turn, reduces the production of new seedlings, potentially reducing the browser population and allowing succession to happen.

Using an integrated measure of transient dynamics, we showed that herbivory could increase the cumulative proportion of the landscape undergoing a change in vegetation before reaching a new equilibrium. This is consistent with
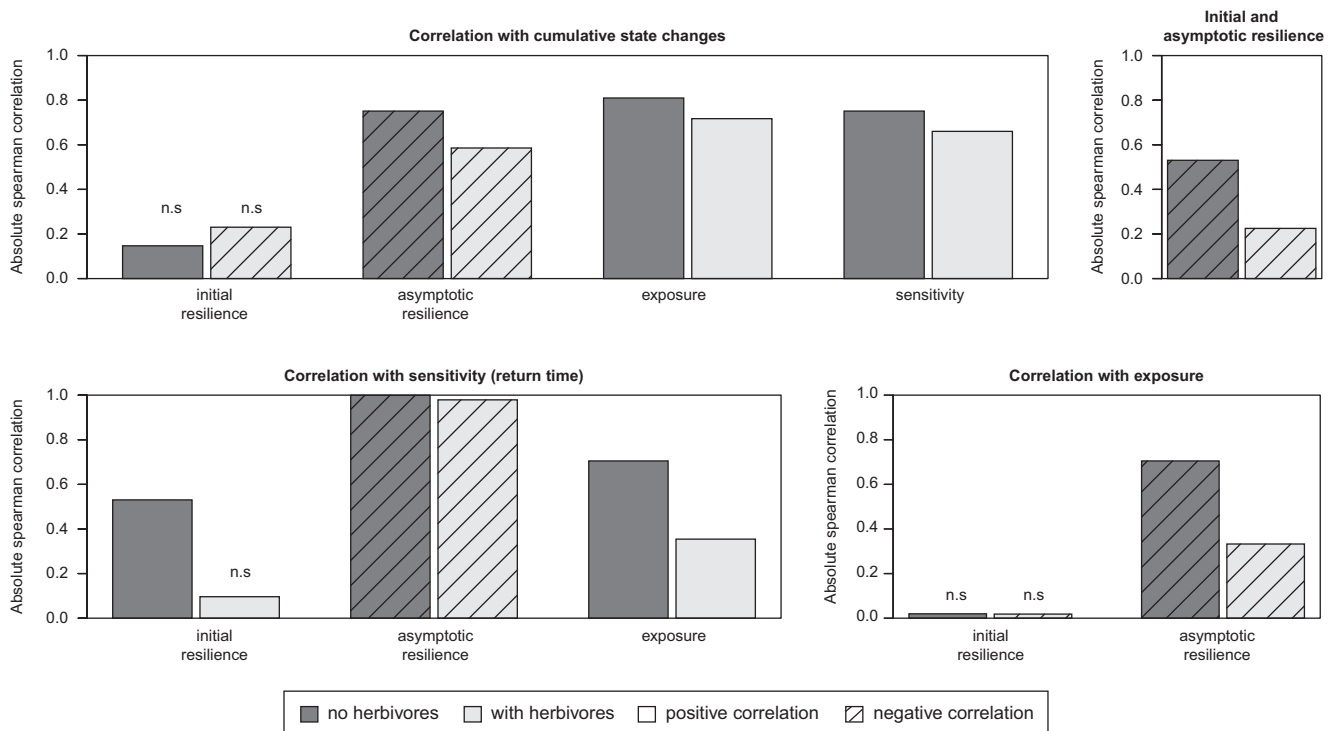
Figure 6. Correlations among descriptors, in presence and absence of browsers. Spearman rank correlations were computed from all values along the climatic gradient. Dark grey and light grey bars indicate correlations in absence and presence of browsers, respectively. Stripped bars indicate negative correlations. Not statistically significant correlations (p-values >0.05) are labeled 'n.s'.

previous studies suggesting that top–down trophic interactions may multiply climate change effects on ecosystems (Zarnetske et al. 2012). Measuring vulnerability using the cumulative amount of changes in state is novel, however, and has the benefit of integrating the different dimensions of transient dynamics.

Although some measures of transient dynamics of ecosystems were correlated when considering plants only, relationships weakened or disappeared in presence of browsers. We thus reach a similar conclusion to Donohue et al. (2013), which is that ecosystem stability and dynamics have increasing dimensionalities with increasing species interactions and trophic levels. It is therefore beneficial to use several complementary measures when studying the resilience and transient dynamics of ecosystems in general.

In this study, we did not consider that browser population dynamics could be directly affected by climate change, nor that the impacts of herbivory on vegetation could be mitigated by climate. A deeper investigation would be necessary to evaluate the relative importance of these mechanisms. However, a variation of selected parameters relating to these mechanisms showed that they should not change our general conclusions. Including the variation of selected parameters led to similar impacts of plant–herbivore interactions on the transient vegetation for the five transient state measures (Supplementary material Appendix 7).

Most of the forest as well as the herbivores that live in boreal and temperate regions are under active management,

and their population dynamics are therefore controlled. Further analysis should focus on how different hunting or forest harvesting scenarios could affect the response to climate change. This would require additional developments to integrate local management strategies into a finer regional context than what we used in this study.

Several other factors could also modify the response of vegetation to climate change, such as wildfires (Staver et al. 2011) or the presence of other interacting herbivores (Kaarlejärvi and Olofsson 2014). Grazing, in addition to browsing, may reduce competition of seedlings with grasses and offset the effect of browsers (Bakker et al. 2016, Supplementary material Appendix 6). Interactions with abiotic components could also influence ecosystem dynamics and their response to climate change. For example, interactions between plants and soil have been shown to generate various equilibrium topologies for different sets of parameters, potentially inducing transient responses with sudden shifts (Burg et al. 2014). Finally, in addition to demography and species interactions, we suspect that spatially explicit dynamics could contribute to delays in the response of ecosystems to climate change (Essl et al. 2015). The spatial context, through source–sink or metapopulation dynamics, could create situations where access to new suitable sites would be limited by dispersal (immigration credit), or where local sink populations would persist for a long time, inducing additional lags in the response of the ecosystem to climate change (Essl et al. 2015).

Transient dynamics are likely more common than equilibria in ecological systems (Fukami and Nakajima 2011, Svenning and Sandel 2013), and are particularly important at the broad scale at which conservation decisions are taken. Anthropogenic warming has already pushed many ecosystems into transient phases, which will likely persist during the next century and beyond (Svenning and Sandel 2013). Focusing on plant–herbivore interactions, we suggest that the response of vegetation to climate change would be difficult to forecast without considering the effects of other trophic levels. More studies integrating multiple trophic levels and temporal dynamics are therefore needed to improve our understanding of species distribution and how they will respond to global changes. Such modeling approaches would also be useful to anticipate the effects of wildlife management in the context of climate change.

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