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Current Opinion in Insect Science

The functional decoupling of processes in alpine ecosystems under climate change

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Climate change may promote the decoupling of the different above-ground and belowground compartments of high elevation ecosystems. Along elevation gradients, a trade-off between species tolerance to cold climates and metabolic rates dictates that cold adapted organisms display a lower efficiency in decomposition, growth or herbivory. As a consequence, if dispersal or evolution under climate change is systematically faster for agents of one compartment (e.g. insect herbivores, or soil microbes, respectively) compared to others, novel and more efficient functions of lowland organisms will arise in the alpine systems and increase fluxes of elements to and through this compartment. We illustrate this potential decoupling using a mechanistic model, where the efficiency of agents in the compartments follows the metabolic theory. To detect and forecast ecosystem decoupling under climate change, we argue that the current efficiency of agents should be measured systematically along elevation gradients. In addition, future research should investigate the impact of migration and evolution in response to climate change on ecosystem processes.

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Current Opinion in Insect Science 2018, **29**:xx–yy

This review comes from a themed issue on **Global change biology**

Edited by **Oswald Schmitz** and **Adam Rosenblatt**

https://doi.org/10.1016/j.cois.2018.06.004

Introduction

Climate change is not only impacting species distributions worldwide [1,2], but how species interact within food webs [3]. Ecosystem processes are primarily controlled by energy-mediated metabolic efficiency [4•], but they are also limited by the functional composition of species in communities [5•]. Climate change could therefore influence ecosystem processes by: first, modifying temperature and precipitation regimes and subsequent nutrient distribution, second, increasing metabolic efficiency facilitating the fluxes among the different trophic compartments [6,7], or third, modifying the efficiency of the different trophic compartments via the arrival and/or evolution of more efficient novel organisms. Hence, the colonization of previously unsuitable habitats under climate change can form novel biotic interactions [3,8–10,11•], and also induce changes in ecosystem processes [12,13••]. A number of recent models have incorporated biotic interactions for predicting species distribution and abundance under climate change [14,15]. However, those models do not usually include how species turnover and novel interaction or functions might impact ecosystem processes [16]. In contrast, mechanistic, compartment-based, models can produce expectations on how the shifts in available energy or metabolic efficiency influence the fluxes among compartments, or their size, in ecosystems [17–19]. A limitation of these models, however, is that they do not consider how novel functions — arising through the incursion of new agents into an ecosystem or through *in situ* evolution — could reshape ecosystem processes. Forecasting the effect of climate change on ecosystem processes requires considering the direct temperature effect on the metabolism of organisms with the indirect effect of novel species eco-response or evolutionary responses to temperature [3,8,20].

Novel functions in a given ecosystem may arise from two main processes; first, dispersal into the focal ecosystem allowing the colonization of novel habitats from fast niche-tracking species [21,22•], and second, selection and evolution within the focal ecosystem for higher metabolic efficiency [23,24]. Under climate change, more proficient insect herbivores can move into alpine ecosystems, where such trophic interactions are generally weaker [22•,25]. Moreover, given strong novel ecological pressures, standing genetic variation and short generation times, some species (e.g. soil microbes) may evolve new functions over ecological time scales potentially impacting ecosystem processes [26]. Here, we propose that a modified functional efficiency arising in an ecosystem via dispersal and/or evolution might desynchronise fluxes among trophic compartments under climate change. In particular, climate change could modify ecosystem-level dynamics through the decoupling of herbivores or soil microorganisms with the plant compartment. Below, we review the co-variation of biotic and abiotic factors along ecological gradients — elevation in mountain systems — for dissecting the direct effect of temperature increase on decomposition rate, plant productivity, herbivory and elemental cycling from the additional effect of unsynchronised dispersal and evolution among trophic compartments.

Ecosystem structure along elevation gradients

The properties of the different ecosystem compartments vary sharply when moving from low to high elevation [27], and offer the necessary natural variation for providing expectations on the effect of climate change on ecosystems in the near future [28] (Figure 1). Species assemblages along elevation gradients are characterized by strong beta diversity [29,30], culminating in dramatic species turnover at the treeline [e.g. 30–34]. Paralleling compositional turnover, plant functional diversity also varies along elevation, but patterns are much more idiosyncratic and trait specific [35,36]. Functional turnover within different trophic compartments, such as plants [35], herbivores [30] or microorganisms [37], is also reflected in the relative size (energy/matter) of each compartment. Typically, the abundance of herbivores decreases toward the alpine belt [38]. Therefore, it is expected that the role of herbivores — at least for arthropods — on ecosystem functioning in the alpine environment is less pronounced than in warmer and more stable habitats [39]. Because plant–herbivore interactions are reduced at high elevation, it was postulated that plants should also produce lower levels of defences [33], which results in a general increased plant palatability at high elevation [40,41•]. Nonetheless, elevational patterns in plant resistance against insect herbivory vary depending on the type of toxic chemicals produced [25,42].

Figure 1

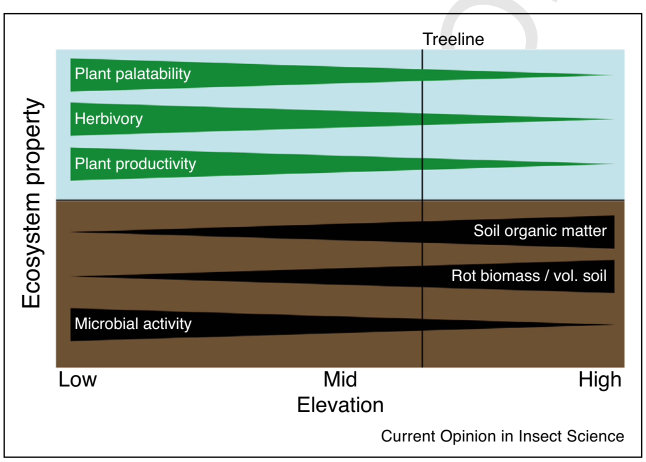

Illustration of compartment variation above and below the treeline. The depicted trends are based on multiple syntheses of ecosystem processes along elevation gradients [e.g. 25,37,39,41•,44,75].

Soil-related properties and processes also vary along elevation gradients [37,43] (Figure 1). Particularly, across the treeline boundary drastic changes appear, largely mediated by temperature-driven variation in carbon and nitrogen stocks and microbial activity in the soil [27]. Soil depth, nutritive value and microbial diversity all decreases, but carbon, nitrogen and root biomass per volume of soil tend to be higher at high elevation [44,45•], indicating slower organic matter decomposition, slower mineralization rate, higher carbon sequestration [28] and lower efficiency of cold-adapted decomposers [46] at higher elevation. To summarize, plant productivity at the species and community level [47], insect herbivory [48], decomposition from soil organisms [49] all decrease with elevation, while organic matter and carbon storage increases. As a consequence, the size of the different compartments [28], but also the speed of the processes [50], largely varies below compared to above the treeline. The overall functioning of the alpine ecosystem is slower than at low elevation [51•,52], since it is expected to be largely mediated by physiological tradeoffs. As species evolved to tolerate cold and harsh environments, they are constrained to reduce their overall metabolism [38,44,53,54].

Climate change and the decoupling of plant–soil–herbivore dynamics

As a consequence of climate change, the processes at high elevation may slowly tend toward those of low elevation, but additional ecological and evolutionary effects might accelerate this dynamic by; first, directly increasing metabolic activity under warmer temperatures, or second, indirectly decoupling the efficiency between compartments. More specifically, a rapid migration of herbivores toward higher elevation following climate warming could increase herbivory rates resulting in reduced plant biomass [20]. Similarly, soil warming could stimulate decomposition and nutrient cycling if the activity of decomposers is directly under the influence of temperature [55•]. Moreover, higher temperatures might select for micro-organisms that are more efficient under the new temperature conditions [26], further increasing decomposition rates. If warming increases soil nutrient availability, it may indirectly enhance plant nutritional status, in turn affecting aboveground plant–insect–enemy interactions, depending on the feeding mode and diet breadth of the insects, as well as on how plant endogenous defenses themselves respond to warming [9].

We illustrate the direct and indirect effect of temperature increase on ecosystem functioning in an alpine system using a mechanistic model involving soil microbe decomposers, plants and herbivores inspired from [56,57]. In addition to previous work focusing on the functioning of the ecosystem [58], we here explore how climate change might influence ecosystem functioning directly, or indirectly via a shift in the parameters of the metabolic

Please cite this article in press as: Pellissier L, Rasmann S: The functional decoupling of processes in alpine ecosystems under climate change, Curr Opin Insect Sci (2018), https://doi.org/10.1016/j.cois.2018.07.005