

KLIMAATVERANDERING EN BIOLOGISCHE INVASIES

CLIMATE CHANGE, TROPHIC INTERACTIONS AND THE RESPONSE OF NATURE TO GLOBAL WARMING

door

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Summary

A central issue in ecology is to understand how species respond to climate change and to predict consequences for community composition and ecosystem functioning. Climate warming causes shifts of species distributions towards the pole, but it is unclear why some species become extremely abundant in new habitats and others not. Plant invasiveness may be caused by a variety of factors. From the perspective of top-down control (the control of abundance by natural enemies), the release from natural enemies and subsequent evolution of increased competitive ability are the most prominent hypotheses to explain invasiveness. Here, I will discuss how human induced global changes can affect the abundance of species, the composition of species communities and the functioning of ecosystems. Current activities focusing on making The Netherlands 'climate warming proof' are mainly aimed at raising dikes and defense against superfluous or limited availability of water. However, climate warming will also have considerable consequences for the abundance of natural species and for their community interactions. For example, climate warming disrupts food chains of trees, caterpillars and the birds that prey on the caterpillars. Climate warming may also enable species to shift their range towards previously cold regions. When a species range shift takes place faster than that of its natural enemy and the new range does not contain a potential enemy, range shifts may lead to a (temporary) outbreak of that species. Therefore, I conclude that climate warming may result into unexpected performance of species, which can either lead to reduced or enhanced local abundance.

Introduction

Across the biosphere terrestrial ecosystems are profoundly affected by a range of human activities that has resulted changes in land use, losses of natural habitats, changes in biogeochemical and hydrological cycles, net primary production, changed atmospheric composition and deposition, climate change, and the release of toxic compounds (Vitousek et al. 1997). These changes have ecological consequences, whether they directly impact upon human society or not, and ecologists are currently facing enormous challenges in order to predict the possible consequences of relatively fast and large-scale environmental changes on biodiversity and the functioning of ecosystems (Schulze and Mooney 1993). Multidisciplinary research programs are carried out across broad geographical ranges assessing effects on individual species, as well as on interactions

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between species from the same and other trophic levels. These interactions between and within trophic levels attracted the attention of ecologists, because they are key to better understand the response of ecosystems to environmental change.

Why looking at trophic interactions?

Trophic interactions between primary producers, first and higher order consumers, are major determinants of the cycling of energy and nutrients within and between ecosystems. Trophic interactions also influence the degree of genetic variability of component species in communities through the process of natural selection (DeAngelis 1992). Species evolve in fluctuating, and sometimes opposing, environmental conditions, but over recent centuries the increasing effect of human activities on the structure of ecosystems and climate have enhanced both the rate and magnitude of environmental changes. Due to different responses of the ecology and evolution of species to changes in their environment, these rapid human-induced changes affect interactions both within and between trophic levels of primary producers and their consumers in a sometimes unexpected and unpredictable fashion (Harrington et al. 1999).

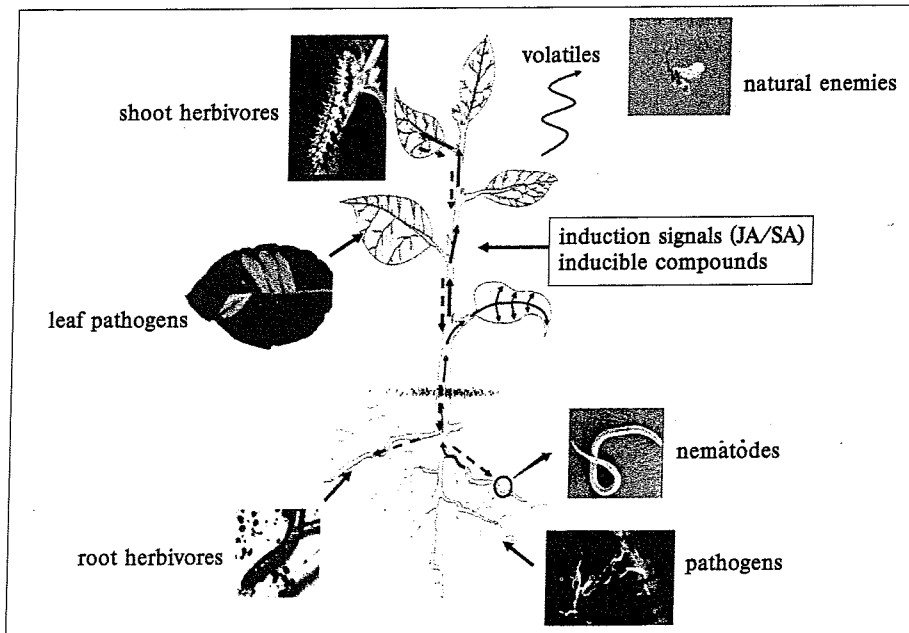


Fig. 1. Above-belowground trophic interactions between a plant, root- and shoot feeders and their natural enemies. Note that belowground plant feeders may induce a defence response above ground and vice versa. Solid arrows indicate that an induction of plant defence in the roots may become expressed in the shoots, whereas dotted arrows indicate defence signals that are induced in the shoots and become effective in the roots. Figure provided by Dr. N.M. van Dam.

Differential responses within and between trophic groups may lead to the re-arrangement of communities through asymmetric changes in competitive, bottom-up and top-down control effects. Consequences in changing biodiversity patterns on ecosystem processes as mediated through trophic interactions have not yet been addressed (Rafaelli

et al. 2002). One of the major challenges of ecology is to understand and predict the consequences of these environmental changes for biodiversity and ecosystem functioning (Loreau et al. 2002). Specifically, we need to improve our understanding of the role of trophic interactions on the levels of genetic variation, community structure, ecosystem functioning and landscape diversity. In this way, concepts, data and theory developed in different ecological sub-disciplines need to be brought together, leading to syntheses, to new perspectives and to innovative approaches in ecology.

The spatial and temporal scales of the system under investigation matters, because many organisms that interact locally exploit their environment differently. This leads to species co-existence within feeding guilds (Ritchie and Olf 1999), but to reduced top-down control of invertebrate herbivores in fragmented habitats (Kruess and Tschamtkke 1994). Landscape studies have been performed mostly with aboveground or easily visible organisms, such as birds, butterflies and plants (Hanski and Gilpin 1997). However, the effects of habitat fragmentation on the dispersal and interactions of soil organisms have been largely overlooked (Wolters et al. 2000).

Another aspect is how trophic interactions determine the stability of communities and ecosystem processes (De Ruiter et al. 1995) and influence evolution in predator-prey systems (Yoshida et al. 2003). Also here it was concluded that a stronger discourse between food web ecology and evolutionary biology may improve our understanding of the role of genetic variation in community and ecosystem stability.

Trophic interactions and the scale of ecosystem response to environmental change

Understanding trophic interactions in relation to global changes requires an understanding of the scales at which the different interacting species operate and at which scale the changes are likely to become manifest. Human-driven processes such as habitat loss and fragmentation of ecosystems may alter the influence of top-down control when the dispersal and host location activity of predators is limited relative to their prey. Habitat fragmentation may reduce the foraging efficiency of parasitoids (Kruess and Tschamtkke 1994), while migratory geese reach disproportionately high densities in the subarctic due to large food availability in their overwintering grounds (Jefferies 2000). Whereas temperatures in tropical Africa have remained fairly constant, spring and night minimum temperatures have increased in northern Europe since 1960, such that tropical migrants like the pied flycatcher may need to migrate further northwards to compensate for changes in the accessibility of caterpillar prey (Both and Visser 2001). Al Gore presented this case study in his movie 'An inconvenient truth' to show how strong effects of climate change already are ('research in the Netherlands has shown...'). These case studies demonstrate that the understanding of local consequences of global changes for trophic interactions requires studies across a range of scales, as well as combining theoretical and empirical approaches. Moreover, vertebrate and invertebrate food chains may respond differently, since species diversity and the degree of specialization in herbivorous and carnivorous invertebrates can be considerably higher than in vertebrate consumers and predators (Duffy 2002).

Van de Koppel et al. (2006) provide a simple framework in order to explain how the dynamics of trophic interactions depend on the scales at which resources are distributed and consumers utilize the resources. They conclude that apparent discrepancies between theoretical and empirical studies may be due to an uncoupling of the population dynamics of the resource species and the consumer species where these are tightly linked. On the other hand, when consumers are spatially subsidized, they may overexploit resources in connected patches. This could be a negative side effect when linking isolated habitat fragments leading to species loss, while connections were restored aiming at increasing survival changes of isolated populations of species. Nature conservation may benefit from theoretical insight into how to broaden the resource basis to con-

sumers on the one hand, while concomitantly preventing extinction of resources as a result of outbreaks of consumer populations on the other.

Spatial approaches have been rarely applied to communities of soil organisms (Ettema and Wardle 2002). Hedlund et al. (2004) show that dispersal is a major factor in maintaining a diverse range of trophic interactions in disturbed systems. The dispersal of soil organisms, however, has been largely overlooked and soil biota have not been employed at all as model systems for testing metapopulation theory. Soil food webs can be studied in the context of resource use incorporating both spatial and temporal dimensions by separating the bacterial and fungal decomposition pathways, because the size and range of resource use within these two pathways vary considerably (Hedlund et al. 2004). Spatial scales are smallest in the lower trophic layers of the bacterial pathway, even though temporal dynamics are highest there. Passive dispersal of soil microorganisms could balance the spatial and temporal differences between the bacterial and fungal decomposition pathways. Still, it is important to determine whether dispersal or establishment is the most constraining factor following, for example, changes in land use. Soil food webs respond much slower, or idiosyncratically, to land use changes than above-ground organisms (Hedlund et al. 2003) and information on how to increase soil community development may help nature conservation programs that aim to restore former species rich communities after exposure to former types of land use.

Trophic interactions, natural selection and the stability of community structure and ecosystem functioning

Changing environmental conditions influence interactions between species through the number and strength of the interactions themselves. Whereas food web ecologists often ignore the process of natural selection in their models, evolutionary ecologists assume that genetic variation is an important prerequisite that enables species to defend themselves from their own antagonists while accruing sufficient resources for reproduction and survival (Clay and Koover 1996). For example, defensive mechanisms in plants can be expressed directly or indirectly, and both defensive strategies are subject to natural selection (Price et al. 1980). Indirect plant defence strategies are not quantified in food web models, but they can affect the stability of food webs (Vos et al. 2001). Similarly, pathogens play an important role in the evolution of host life histories (Burdon 1987), while the direct contribution of pathogens to flows of nutrients and energy is so minimal that these are normally not considered in food web models (Marcogliese and Cone 1997).

The discussion on the role of biodiversity for ecosystem processes and food web stability has focussed mainly on the redundancy of species in soil food webs. Some studies have observed considerable redundancy in soil food webs (Wardle 2002), so it is debatable how the loss of genetic variability may affect the relationship between species diversity and ecosystem processes, or food web stability. However, it is intriguing that interaction strength remains the basis for both food web (in)stability and natural selection, further suggesting that besides loop length and indirect interactions the amount of genetic variation may also be a force stabilising food web structure and ecosystem process rates.

Emmerson et al. (2004) analysed the strength of trophic interactions in relation to the stability of communities. Interaction strengths describe the pathways and transfer of energy through an ecosystem whereas the patterning of interaction strengths determines community stability and ecosystem processes (De Ruiter et al. 1995). Strong interactions may destabilize food webs, and the way in which they are organised in trophic loops seems to influence the way in which food webs respond to environmental change (Neutel et al. 2002). Interestingly, empirical data show a strong skew towards weak interactions, and global change scenarios of increased atmospheric levels of CO₂ level may affect the patterning of interaction strengths of plant-herbivore interactions. The change can have a straightforward effect on primary productivity, but it can also affect the qual-

ity of the resources for herbivores. When primary production increases, food quality often decreases (for example, due to increased C/N ratio's), such that the average population size of consumers will likely decline. As a consequence, species populations will become more variable and (environmental or anthropogenic) perturbations will require longer recovery periods. As a result of these joint changes, communities are likely to become less stable, owing to reduced resilience, component species will experience smaller and more variable population sizes, and thus will become more prone to extinction. Natural selection and co-evolution drive species towards specialization, unless environmental disturbances relax selection pressures (Hoffmeister et al. 2004). Specialization can be an evolutionary penalty in unpredictable environments, so that human induced environmental changes may result into communities dominated by generalist species. Case studies on invasive species show that their abundance can be strongly controlled by natural enemies and escape can transmogrify subordinate species into dominants (Keane and Crawley 2001). Habitat fragmentation is in some cases known to have a disproportionately detrimental effect upon higher trophic levels (predators, parasitoids), than lower trophic levels (plants, herbivores), which are more abundant (Kruess 2003). The loss of higher trophic levels is almost certain to increase the interaction strength between plants and herbivores, which could contribute to rapid extinction that can be observed in disturbed landscapes.

Such extinction cascades have been suggested by Janzen (1974), but these have thus far received very little empirical attention. On the other hand, genetic variation allows species to adapt to new environmental circumstances. There are some examples of rapid selection processes that maintain the stability of predator-prey interactions (Yoshida et al. 2003), and more examples are known from studies on pathogen-host interactions (Kover and Clay 1996). However, whether such processes of rapid evolutionary change also allow many other natural species to keep up with environmental change is still an open question. Ultimately, the crux of the problem lies in the fact that anthropogenic disturbance may reduce numbers of populations of species, thus reducing the ability of species to adapt to rapidly changing circumstances, a runaway effect that may accelerate extinction rates (Hughes et al. 1997).

Above-belowground trophic linkages in a changing world

Above and belowground communities influence each other through a variety of direct and indirect interactions (Wardle 2002). Time lags in the response of belowground organisms to change leads to different selection pressures, for example as exerted by above and belowground herbivores and pathogens (Van der Putten et al. 2001). Above and belowground systems interact through primary plant products (carbohydrates, proteins) and secondary plant chemicals. Soil ecosystem processes will be relatively insensitive to changes in primary compounds, but information exchanged through secondary compounds (especially plant defence chemicals) is more immediate (van Dam et al. 2003, Bezemer et al. 2003) and might be more susceptible to environmental change. Above-belowground interactions are not well-incorporated into ecosystem models and they explore possibilities to do so by discussing these interactions at scales that range from local to global (Schröter et al. 2004). At all scales, the number of possible interactions is simply overwhelming. Above-belowground models for plant species or communities and their associated above and belowground herbivores might differ when focussing on primary or on secondary plant metabolites. Functional shifts in soils, for example from a fungal-based decomposition pathway to a bacterial-based decomposition pathway when land use intensifies, are expected to cause significant, non-linear changes that might affect the accuracy and applicability of ecosystem models. Models may also be used to test which trophic interactions are most sensitive to the consequences of global change, as well as to determine the consequences of differences in above and belowground time lags for community composition and ecosystem processes.

Research programme

In my research programme, I study how plant abundance can be controlled by both above- and belowground enemies. Climate warming causes shifts of species distributions towards the pole, but it is unclear why some species become abundant in new habitats and others not. Plant invasiveness may be caused by a variety of factors, for example habitat disturbance, hybridization with other species, enhanced benefits from symbionts in the new habitat, or loss of natural enemies. However, enemy release and evolution of invasive plants have been rarely, if ever, considered from a combined above-belowground approach. In my VICI-study, I examine how release from above- and belowground enemies influences the evolution and invasiveness of plant species that expand their range from warm into previously cold climate regions. My general hypothesis is that differences in plant abundances between southern species in their new habitats, as well as between southern species in new and original habitats, are caused by differences in mobility between plants, their natural enemies and the predators of the enemies.

In order to test this hypothesis I relate plant traits of successful and non-successful invaders from southern Europe into The Netherlands to metabolic costs invested in growth and defence in both the original and new habitats. The invaders are compared with related plant species that are not invasive and with related plant species that are native in the invaded habitats. Furthermore, spatially explicit models need to be developed to test spatio-temporal dynamics of plant release from above- or belowground enemies, and their consequences for plant invasiveness in the new habitats. This approach enables to explain and predict plant invasions due to climate warming.

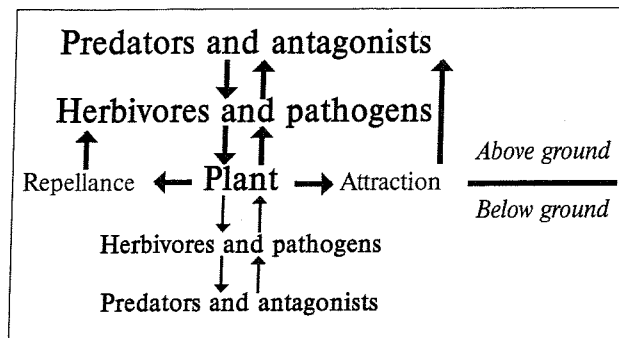
The first results show that non-native plant species, which have invaded The Netherlands recently by range expansion from southern to Northern Europe, indeed are less exposed to growth reducing soil organisms than comparable native plant species (Van Grunsven et al., manuscript accepted). This will mean that the non-native plant species have an advantage, for example in competition with other plant species, when compared with the native relatives. The control of plant abundance by natural soil-borne enemies has been demonstrated for *Prunus serotina* (black cherry), which is one of the six major invasive pests in The Netherlands. When plants moving into The Netherlands due to climate warming have a chance to escape from their native soil-borne enemies, this will have potential consequences for vegetation management and for the composition of natural vegetation. Especially when exotic species become unnaturally dominant.

Current work in my group focuses on the response of exotic plants to both below and aboveground enemies. We compare exotic plants from warm climate regions with related native plants in their response to development of pathogenic activity in the soil, as well as aboveground herbivores. The question is how the feedback-interactions with soil organisms relate to aboveground interactions with herbivores and other their natural enemies. One possibility is that below ground other rules are active than above ground. The alternative is that above and belowground the same rules are active, which would enhance our capacity to generalize and to make predictions. Such ecological effects are important to be incorporated into nature management scenarios in order to predict the future of nature in temperate regions of the world.

Concluding remarks

Multitrophic interactions play a central role in the response of ecosystems to environmental change appearing in processes at all levels of ecological organisation. They may determine biological diversity ranging from within species to entire landscapes. They also link sub-components of ecosystems, such as above- and below ground. As trophic interactions determine the fitness of almost all species, they govern processes such as ecosystem development and stability, and other key processes. This research area con-

Fig. 2. This scheme shows how plants are the link between above- and belowground multitrophic interactions. The relatively small size of the letters of belowground herbivores, pathogens and their natural enemies illustrates my working hypothesis that plants moving from the south to the north due to climate warming, may be released from their relatively immobile natural soil-borne enemies, rather than from the more mobile aboveground enemies. Figure re-drawn and converted after Van der Putten et al. (2001).



tributes to the understanding of trophic interactions in a changing world and requires bridging between isolated subdisciplines in ecology. My long-term goal is to encourage new research programs across the various disciplines and levels of ecological organisation in order to enhance our capacity to predict and manage consequences of complex global changes both induced or not induced by human activities.

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