Ecological Indicators 83 (2017) 249–259

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Research paper

Tree growth indicates resource quality for foliage-feeding insects: Pattern and structure of herbivore diversity in response to productivity

Tim Mark Ziesche

Forest Research Institute, Department of Development and Monitoring, Forest Ecology, Alfred-Möller Str. 1, 16225 Eberswalde, Germany

ARTICLE INFO

Keywords:
Biodiversity patterns
Community assembly
Environmental change
Plant-herbivore interactions
Species-energy relationship
Species turnover

ABSTRACT

In forests, local site conditions can affect both trees and herbivores and hence site-related factors act indirectly on herbivores mediated by tree growth rates. Here, tree foliage represents a fundamental prerequisite for insect herbivore development providing energy in the form of plant tissue quality. Resource-based theories, on the other hand, assume that the synthesis of defensive compounds is a trade-off with growth and peaks at low resource availability. However, the extent to which plant tissue quality in response to site productivity is relevant in the species-energy relationship is unknown. Therefore, we aimed at a better understanding of the form and structure of the species-energy relationship in forest insects. We used census data of foliage-feeding insects along a productivity gradient of Scots pine forests defined by relative growth rates of trees (RGR). As a result, diversity monotonically increases with decreasing RGR (as a proxy for energy) during almost two decades of sampling. Herbivore assemblages become more similar with available energy as species turnover linearly decreases and proportions of sites occupied by individual species rise. The results suggest that tree growth rate influences herbivore dynamics in this system by altering the chemical composition of needles, without necessarily affecting the form in the relationship. The site-specific resource availability requires trees to adjust their allocation to synthesis of carbon-based secondary metabolites or growth, which then results in fundamental differences in herbivore dynamics at low vs. lowest RGR (regular cycles (dominance) vs. dampened cycles (evenness)). However, these differences inevitably demonstrate that species richness is not necessarily a result of more individuals and implicate that different mechanisms are involved (facilitation vs. competition/temporal heterogeneity). The resulting pattern and structure of foliage-feeding insects advance our understanding of herbivore dynamics in response to site quality and tree growth, which may ultimately improve our knowledge of plant-insect interactions in the face of environmental change.

1. Introduction

Energy, in the form of resources, is one of the strongest determinants of species persistence in natural systems (Tilman and Pacala, 1993). In forests, those resources are provided by plant tissues for foliage-feeding insects and their quality widely responds to stand growth dynamics modified by site quality and environmental conditions recently shifting with anthropogenic global warming (Pretzsch et al., 2014). Studies have already demonstrated changes in ecological interactions and ecosystem function that are associated with recent global warming (Harrington et al., 1999) and predicted increased herbivory (Williams and Liebhold, 1995). Hence, there is growing concern that climatic and land-use changes could negatively affect ecosystem stability and resilience, and the role of environmental energy in determining community species richness has, to our knowledge, rarely been addressed in the face of environmental change. Generally, the relationship between tree growth rate and community structure of forest insects may constitute an important component of tree growth dynamics. Therefore, how species diversity changes with energy in nature and how individual species are affected across energy gradients might be substantial in the interpretation of current and future environmental changes.

The availability of energy in a habitat has already been of interest in the theory of island biogeography proposed by MacArthur and Wilson (1967). Subsequently Wright (1983) demonstrated that energy explains diversity better than area, because richness increases faster with mean energy availability than it does with area, known as the species-energy relationship. The relationship is a well described pattern in ecological theory and has been widely recognized to be fundamental to an understanding of spatial community dynamics (Rosenzweig, 1995; Gaston, 2000). Both hypotheses assume a strong link between species richness and species abundance that came to be known as the ‘more individuals hypothesis’ (MIH; Wright, 1983; Rosenzweig and Abramsky, 1993), however, the generality of the MIH and a generalizable scale-dependend form of the species-energy relationship has

E-mail address: zieschet@outlook.de.

http://dx.doi.org/10.1016/j.ecolind.2017.07.053
Received 30 March 2017; Received in revised form 22 July 2017; Accepted 27 July 2017

recently been questioned (Storch et al., 2005; Gillman and Wright, 2006; Hurlbert and Jetz, 2010).

In terms of plant-insect interactions, the resource or energy is basically provided by nutritional quality of plant tissues with insect herbivores when relevant climate variables correspond (Kimmins, 1997). Plant tissue quality is a key determinant of the fecundity and performance of herbivorous insects (Awmack and Leather, 2002) and describes the inherent components such as the levels of nitrogen, carbon, or trace elements (Mattson, 1980; Tilman, 1987). The prevailing mineral composition of the tree foliage on the other hand is known to reflect the nutrient status of the soil (Chen et al., 1998) and depends widely on site quality, e.g. soil fertility (Aerts and Chapin, 2000). Site quality determines long-term productivity in forests and site-related factors also act indirectly on herbivores mediated by tree growth rates (Scriber and Slansky, 1981; Mattson and Scriber, 1987). Hence, plant tissue quality vs. tree growth inevitably affects population persistence in a habitat presumably leading to higher species richness, however, the way how resources change with productivity determines the structure in species richness. For instance, both a greater amount of resources, capable of supporting larger populations (Brown, 1981), and a greater variety of resource types, supporting populations of a greater variety of species (Carrara and Vázquez, 2010), have been suspect of the species-energy theory.

Considering this, the relationship between available energy and productivity in long-lived plants may be obscured by the production of secondary compounds against herbivores. The presence of toxic metabolites in plants is known to affect fitness in specialist insects (Bernays, 1998) and theories of plant defense emphasise that plant defenses are determined by the resources available in the local habitat (Coley et al., 1985; Gulmon and Mooney, 1986). The growth-differentiation balance hypothesis (GDBH) provides a framework that predicts a trade-off between costs of secondary metabolites relative to the demand for photosynthate by growth (Herms and Mattson, 1992) and suggests a humped interaction of secondary compounds and resource availability (with maximum defense at lower resources, Fig. 1). Consequently, if plant defense affects insect herbivores non-linear along the productivity gradient, this should be reflected in species densities and thus richness according to the MIH.

The overall aim of this study was to investigate the relationship between tree growth rates, forest insect diversity and community structure in a landscape of planted and widely even-aged Scots pine forests (*Pinus sylvestris* L.). Therefore, we describe the form and structure of insect diversity along a productivity gradient to test for the relevance of the species-energy relationship, using site specific tree growth rates (RGR – as a proxy for energy). Foliage-feeding insect assemblages (butterflies and sawflies) are used as a case study on a naturally occurring productivity gradient of the north-eastern German lowland (Fig. 2), for which extremely detailed census data and forest inventories are available (3248 ± 382 sampled sites per year). Here, the resource can be depicted as a one-dimensional continuum and is given by pine needles, though variable in nutrition or palatability of subsequent needle age classes (1–4 year-old shoots) relative to site quality (i.e. nutrient or soil water availability).

The purposes of our examination were to (i) test and specify the pattern of species diversity along the productivity gradient and to (ii) prove if the pattern prevails over time in a community of highly varying population densities and recent increase in anthropogenic impact such as nitrogen deposition or climate change. Each single species contributes to the overall diversity pattern with (iii) effects on the density and range in response to environmental energy. Hence, we test the 'more individuals hypothesis' as a mechanism for the positive association between energy availability and species richness, because most large-scale richness studies lack data on abundance to test assumptions of the MIH. Finally, changes (iv) in a community along the productivity gradient are demonstrated using diversity indices such as the species turnover ($ß_{sim}$), evenness (E), and diversity structure (Shannon-index) compared with (v) defoliation measures.

We hypothesize that growth rate of Scots pine is negatively associated with the density of their herbivores. As expected this would translate into increase in diversity (MIH) challenging effects of the GDBH in pine forests. To verify whether the relationship between growth rates and insect diversity is affected over time, we analyse whether and how the distribution and density of individual species changes along the energy gradient between 1995 and 2013, a period of recently dampened population cycles.

2. Materials and methods

2.1. Study area

The research area (29479 km^2) is predominantly covered by pine forests, homogeneous in structure and stand age due to extensive harvesting around the middle of the 20th century. One third of the area (37%) is covered by forest (~1.1 million ha) consisting of planted Scots

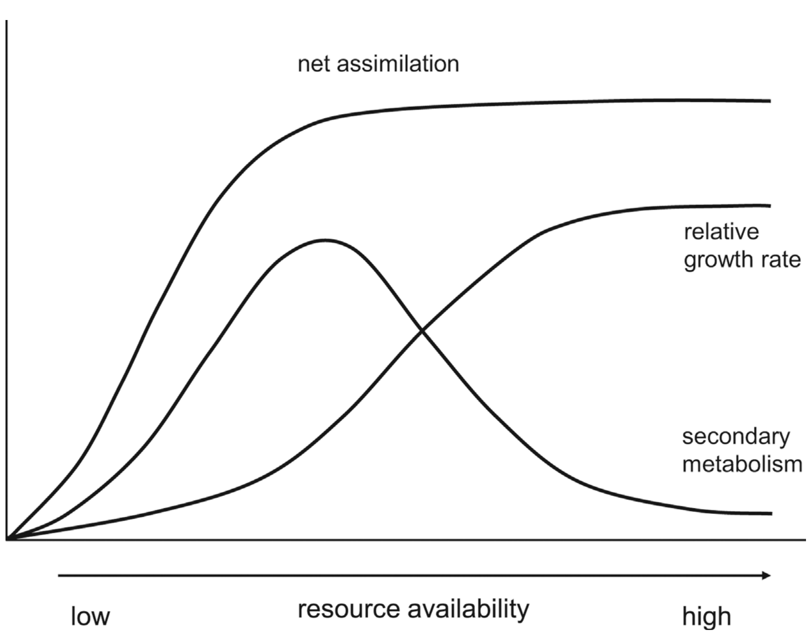

Fig. 1. The plant defense pattern in response to productivity measures (GDBH) might be crucial in the determination of the form of the species-energy relationship in forest foliage: norms of reaction for net assimilation rate, relative growth, and secondary metabolism along a gradient of changing resource (water/nutrients) availability (from Herms and Mattson, 1992).