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Post-industrial areas as successional habitats: Long-term changes of functional diversity in beetle communities

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Abstract

Understanding succession is one of the main goals in ecosystem ecology, but very few studies regarding arthropods have actually examined this topic in sufficient detail. Missing are studies that examine the long-term trend of primary succession of arthropods in post-industrial habitats and also the functional consequences of primary succession on arthropods. We used epigeic beetles as a model group to investigate the process of primary succession of arthropods on spoil heaps for about 30 years of spontaneous development. For carabid beetles, we calculated indices of functional diversity (functional evenness, functional richness and functional divergence). To quantify functional diversity we used these functional traits: wing morphology, habitat preference and humidity dependence. Our results reveal that the main environmental factor determining the structure of beetle communities is spoil heap age, which is itself correlated with forest cover. The descriptive rank-abundance models that best fit our community structure were Gambin and Zipf – Mandelbrot. Abundances of brachypterous and forest species were positively correlated with successional age. Our results provide evidence that primary succession in post-industrial habitats differs from that in more natural habitats due to the rapid rate of successional changes and their attributes. In particular, abiotic factors are constitutive in comparison to interspecific competition during succession. The canonical correspondence analysis model identified that irregular disturbances are another important phenomenon of succession in post-industrial habitats. We assume that constant indices of functional evenness and richness reflect rapid colonization from surrounding habitats. Functional divergence was significantly correlated with increasing proportion of forest species.

Zusammenfassung

Sukzessionen zu verstehen ist eines der Hauptziele der Ökosystemökologie, aber nur wenige Untersuchungen an Arthropoden haben dieses Thema tatsächlich mit genügender Genauigkeit betrachtet. Es fehlen Untersuchungen, die den langfristigen Trend der Primärsukzession bei Arthropoden in Industriefolgehabitaten und die funktionalen Konsequenzen der Primärsukzession für Arthropoden erforschen. Wir wählten epigäische Käfer als Modellgruppe, um die Primärsukzession von Arthropoden auf

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Abraumhalden über 30 Jahre spontaner Entwicklung hinweg zu untersuchen. Für die Laufkäfer kalkulierten wir Indizes der funktionalen Diversität (funktionale Evenness, funktionaler Reichtum und funktionale Divergenz), wobei wir die folgenden funktionalen Merkmale benutzten: Flügelmorphologie, Habitatpräferenz und Feuchteabhängigkeit. Unsere Ergebnisse zeigten, dass das Alter der Abraumhalde der wichtigste die Struktur der Käfergemeinschaft bestimmende Umweltfaktor war, wobei das Alter mit der Waldbedeckung korreliert ist. Die deskriptiven Rang-Abundanz-Modelle, die die Gemeinschaftsstruktur am besten beschrieben, waren Gambin und Zipf-Mandelbrot. Die Abundanzen der kurzflügeligen Arten und der Waldarten waren positiv mit dem Sukzessionsalter korreliert. Unsere Ergebnisse belegen, dass sich die Primärsukzession in Industriefolgehabitaten von der in naturnäheren Habitaten unterscheidet, was auf die Geschwindigkeit der Sukzessionsänderungen und ihrer Merkmale zurückgeht. Insbesondere sind abiotische Faktoren bestimmend im Vergleich zu interspezifischer Konkurrenz während der Sukzession. Eine kanonische Korrespondenzanalyse zeigte, dass unregelmäßige Störungen ein weiteres wichtiges Phänomen bei der Sukzession in Industriefolgehabitaten ist. Wir nehmen an, dass konstante Werte von funktionaler Evenness und funktionalem Reichtum die schnelle Besiedelung aus Habitaten in der Umgebung widerspiegelt. Die funktionale Divergenz war signifikant mit der Zunahme von Waldarten korreliert.

Keywords: Carabids; Environmental factors; Functional traits; Landscape restoration; Rank-abundance models; Species turnover; Spoil heaps

Introduction

The replacement of species in an environment over time is typical for ecosystem development. Successional processes are traditionally divided into primary and secondary successions (Miles, 1979). Primary succession is ecosystem development in situations where no previously developed soil exists. Species which *de novo* colonize this environment create and modify it by their presence (Dobson, Bradshaw, & Baker, 1997; Vitousek, Matson, & Cleve, 1989). Unlike cases of secondary successions, in the initial stages of primary successions random processes are of significant importance and species change is determined mainly by abiotic environmental factors (Majer, 1989; Walker & Moral, 2003). Urbanized areas today cover approximately 1 – 6% of land (Alberti et al., 2003), and more than 50% of people live in them (Millennium Ecosystem Assessment, 2005). Some urbanized and post-industrial locations present examples of new primary successional habitats. The spoil heaps are such unique anthropic ecosystems, since they lack a soil profile with diaspores and have specific microclimate (Ash, Gemmell, & Bradshaw, 1994; Majer, 1989). Urban and post-industrial ecosystems can become a refuge for species and can increase the biological richness of cultural landscape (Tropek et al., 2010). That makes them among the most important ecosystems on Earth. Moreover, various mining activities have affected about 1% of the Earth's terrestrial surface and occur in most countries of the world (Walker, 2012). Therefore, there are increasing numbers of studies highlighting the succession of post-industrial habitats, including in the context of restoration ecology and conservation biology (Harabis, Tichanek, & Tropek, 2013; Lundholm & Richardson, 2010; Walker & Moral, 2003). The most common studies focusing on organisms colonizing such places relate to vegetation (Ash et al., 1994; Kovar, 2004; Prach et al., 2013; Song, Shu, Wang, & Liu, 2014). There are several papers focusing on primary succession of arthropods in post-industrial habitats, however, they focus mainly on specific topics e.g. importance of the survival of endangered species (Tropek et al., 2010; Tropek, Cerna, Straka, Cizek, & Konvicka, 2013) or changes of species diversity in time (Schwerk & Szyszko, 2011; Schwerk, 2014). Long-term trends in arthropod succession and studies based on functional diversity (FD) are missing entirely, although arthropods can often indicate changes in an environment in a more comprehensive and sensitive manner than changes on a vegetation or vertebrate level (Gerlach, Samways, & Pryke, 2013; Hodkinson, Webb, & Coulson, 2002; Kremen et al., 1993; Samways, McGeoch, & New, 2010).

During primary succession, species associated with newly created habitats (pioneer species) will increase in number over time as a result of colonization processes. The colonization of new habitats is determined mainly by (a) accumulation of resources, (b) species pool, (c) edge effect and (d) the species – area relationship (MacArthur & Wilson, 1967; Walker & Moral, 2003). Such effects determining the structure of temperate ecosystems can be expected in forest species. These species will respond to an alteration in the environment during primary successional seres by increased abundance and species richness. Species which are not associated with forest habitats show the opposite trend. Such trends are usually documented in terms of species diversity (Stenbacka, Hjältén, Hilszczański, & Dynesius, 2010). However, guilds or functional groups of arthropods can respond to the availability of specific resources and environmental factors, which may change in the course of succession. Functional roles may thus be a key factor in diversity responses to habitat succession (Gibb, Johansson, Stenbacka, & Hjältén, 2013). FD provides a new concept for the interpretation of successional changes. Alteration of vegetation structure over time determines distribution of animals in time and space and their life-history traits (Lytle & Poff, 2004, Renöfält, Nilsson & Jansson 2005). Functional characteristics of organisms contribute to fitness, because functional characteristics