Acta Oecologica 61 (2014) 32–40

Contents lists available at ScienceDirect

Acta Oecologica

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

Original article

Ant community structure during forest succession in a subtropical forest in South-East China

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ARTICLE INFO

Article history:
Received 18 August 2014
Received in revised form
13 October 2014
Accepted 14 October 2014
Available online

Keywords:
BEF-China
Biodiversity
Conservation
Ecosystem functioning
Formicidae
Gutianshan National Nature Reserve

ABSTRACT

Understanding how communities respond to environmental gradients is critical to predict responses of species to changing habitat conditions such as in regenerating secondary habitats after human land use. In this study, ground-living ants were sampled with pitfall traps in 27 plots in a heterogeneous and diverse subtropical forest to test if and how a broad set of environmental variables including elevation, successional age, and tree species richness influence ant diversity and community composition. In total, 13,441 ant individuals belonging to 71 species were found. Ant abundance was unrelated to all environmental variables. Rarefied ant species richness was negatively related to elevation, and Shannon diversity decreased with shrub cover. There was considerable variation in ant species amongst plots, associated with elevation, successional age, and variables related to succession such as shrub cover. It is shown that younger secondary forests may support a species-rich and diverse community of ants in subtropical forests even though the species composition between younger and older forests is markedly different. These findings confirm the conservation value of secondary subtropical forests, which is critical because subtropical forests have been heavily exploited by human activities globally. However, the findings also confirm that old-growth forest should have priority in conservation as it supports a distinct ant community. Our study identifies a set of ant species which are associated with successional age and may thus potentially assist local conservation planning.

1. Introduction

Across taxa and trophic levels, tropical and subtropical forests support the highest species diversity on Earth (e.g. Basset et al., 2012; Gaston, 2000; Primack and Corlett, 2005). However, a steadily increasing human population, together with new agricultural practices, has caused large-scale exploitation and habitat conversion of these forests (e.g. Gibbs et al., 2010; Hansen et al., 2013). Human disturbance results in a change of species composition, and in general, in declining diversity of forest organisms (Barlow et al., 2007; Gibson et al., 2011).

As land-use pressure on primary forest is predicted to persist (e.g. Hansen et al., 2013; Miettinen et al., 2011), secondary forests that regenerate from logging or abandoned agriculture will become even more important as habitats for forest organisms. Thus it is critical to assess if such secondary forests can conserve native forest organisms (Dunn, 2004), and which environmental conditions explain the diversity and community composition of organisms in secondary forests, particularly in areas like subtropical South-East China where virtually none of the original species-rich primary forests remained after the 1950s Great Leap Forward (López-Pujol et al., 2006).

Ants (Hymenoptera: Formicidae) are ideal target organisms for these questions. As a taxonomic group they have a long history as biological indicators (Alonso, 2000; Andersen and Majer, 2004), because they are reliably and easily sampled, and show ecologically

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http://dx.doi.org/10.1016/j.actao.2014.10.003
1146-609X/

interpretable responses to disturbance (Gerlach et al., 2013; Hoffmann and Andersen, 2003). By being key-stone organisms as e.g. predators, seed dispersers, and partners in countless mutualisms they directly influence ecosystem processes (reviewed in Del-Toro et al., 2012; Folgarait, 1998), especially in tropical and subtropical forests where ants are dominant arthropods greatly contributing to total animal abundance and biomass.

Many studies have investigated the responses of ant communities to land use in tropical forests but there are less studies in subtropical forests. As a general trend, ongoing forest recovery and succession tended to increase ant species richness and diversity, and over time ant communities became more similar to old-growth forest communities (e.g. Bihn et al., 2008; Floren and Linsenmair, 2005; Vasconcelos, 1999).

Ground-living ant communities in forests are also known to be responsive to a wide range of environmental variables such as elevation (e.g. Brühl et al., 1999), soil moisture (e.g. Kaspari and Weiser, 2000), litter cover (e.g. McGlynn et al., 2009) or understory vegetation cover (e.g. Gunawardene et al., 2012). It is therefore crucial to include a wide range of potentially confounding biotic and abiotic variables when studying ground-living ant communities in diverse and heterogeneous forest ecosystems, particularly when habitats change along environmental gradients such as forest succession. Understanding how individual species and entire communities respond to such gradients will help to better predict responses to future conditions, e.g. along elevation gradients in the light of likely up-slope shifts of species with ongoing global warming (Lenoir et al., 2008).

A further as yet unresolved question is whether producer diversity has an impact on ant diversity, as there is usually a direct relationship between plant and arthropod species (sensu Haddad et al., 2009; Scherber et al., 2010). However, studies correlating tree diversity with ground-living ant diversity are scarce. The few studies conducted so far found no influence of tree diversity on ground-living ants (Donoso et al., 2010; Gunawardene et al., 2012), but are not representative to reject cross-group diversity relationships between trees and ants.

We tested if and how the abundance, species richness, Shannon diversity, and community composition of ground-living ants are influenced by forest succession and a comprehensive set of environmental variables, including tree species richness and elevation, in a diverse subtropical forest in South-East China. In particular, we hypothesized (1) that the richness and diversity of the overall ground-living ant community is, as indicated for example by Gunawardene et al. (2012), not or only marginally influenced by tree species richness but instead driven by forest succession or environmental variables; (2) that there is pronounced species variation along environmental gradients and during forest succession. Finally, we aimed to identify ant species that are associated with a certain successional age and might potentially support the diagnosis of successional age.

2. Material and methods

2.1. Study site

Our study was conducted in the Gutianshan National Nature Reserve (GNNR, 29°08′–29°17′ N, 118°27′–118°11′ E), Zhejiang Province, in South-East China. Along an elevation gradient of 250–1260 m asl, the GNNR protects 8000 ha of a diverse mixed evergreen broad-leaved forest. About half of the naturally occurring tree species are deciduous, but evergreen species numerically dominate in old-growth forest. Common canopy tree species are *Castanopsis eyrei* (Fagaceae), *Cyclobalanopsis glauca* (Fagaceae), and *Schima superba* (Thecaceae) (Bruelheide et al., 2011; Legendre et al., 2009).

As almost everywhere in South-East China (López-Pujol et al., 2006), most of the area in and around the GNNR has been heavily logged or converted to agricultural land. However, slopes steeper than 30° were often left relatively undisturbed because they were inappropriate for agriculture. The GNNR is now one of the most prominent semi-natural forest remnants in South-East China. The reserve consists of a mosaic of secondary forests in different successional stages, ranging from <20 years to >80 years recovery time since the last clear-cut logging activities or the abandonment of former agriculture. Outside the protected areas, forests are dominated by two commercial coniferous plantation species, *Cunninghamia lanceolata* (Cupressaceae) and *Pinus massoniana* (Pinaceae). Apart from anthropogenic disturbance, occasional heavy ice storms are the main drivers of succession (Du et al., 2012). The area is located in a typical subtropical summer monsoon climate. Mean annual precipitation is 1964 mm, with the strongest rainfalls from May to July and a short dry period from October to December (Geissler et al., 2012).

In 2008, 27 plots (30 × 30 m) were established in the GNNR as part of the newly founded 'Biodiversity-Ecosystem Functioning (BEF) China' project (Bruelheide et al., 2011, 2014) (Fig. 1). Plots were selected along gradients of tree species richness and successional age, and were randomly distributed over the entire reserve excluding areas that were inaccessible or had steep slopes >50°. The minimum distance between two neighboring plots was at least 200 m, which is larger than the maximum foraging distances even of most large ant species. In total, 147 species of trees were recorded, ranging from 25 to 69 species per plot (Table 1). Plots were classified into five successional stages (numbered 1–5) based on local knowledge on former agriculture and forestry: <20 yrs (5 plots), <40 yrs (4), <60 yrs (5), <80 yrs (6), and >80 yrs (7) post

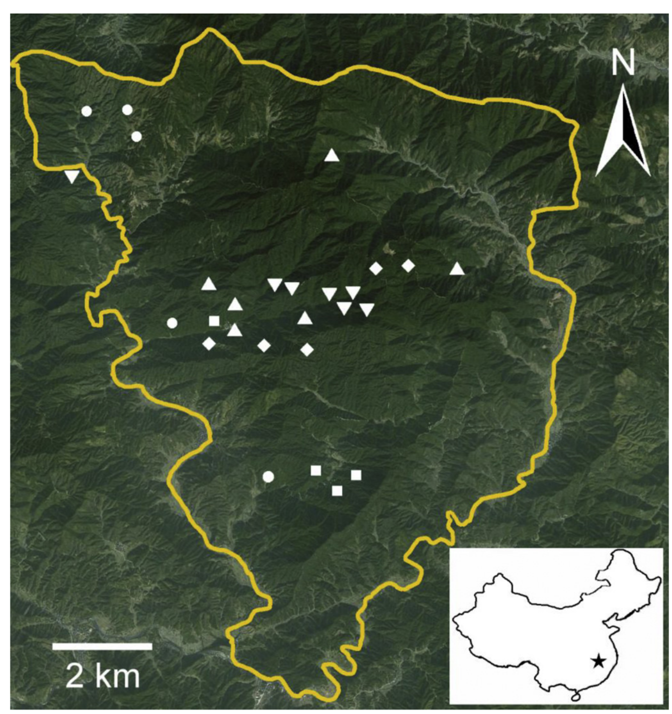

Fig. 1. The Gutianshan National Nature Reserve (GNNR) in subtropical South-East China. Overview map (based on Google™ Earth) of the GNNR showing the boundary of the reserve, the location of study plots, and the location inside the P.R. China (embedded picture). Circles refer to successional stage 1, squares to stage 2, diamonds to stage 3, up-facing triangles to stage 4, and down-facing triangles to stage 5.