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Variation in seed dispersal along an elevational gradient in Great Smoky Mountains National Park

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ABSTRACT

Seed dispersal by ants is ecologically important and geographically widespread as 20–50% of all herbaceous species in eastern deciduous forests are dispersed by ants, but we know little about how or why such interactions vary geographically. In this paper, we examined variation in seed dispersal by ants along an extensive elevational gradient (256–2025 m) in the Great Smoky Mountains National Park, USA. Specifically, we asked whether variation in ant community composition affected seed removals and seed dispersal distance of *Trillium undulatum* and *Hexastylis arifolia*, two common understory herbs found throughout the southern Appalachian Mountains. We also examined variation in myrmecochore abundance, specifically *Trillium* spp. and *H. arifolia*, along the same elevational gradient. Measures of ant community and climate variables strongly covaried with elevation, while *Trillium* species richness and abundance did not. We found that seed removals decreased with elevation, but seed dispersal distance did not depend on elevation. The most important variables predicting seed removals were average annual temperature and the abundance of *Aphaenogaster rudis*, both of which varied along the elevational gradient. Seed dispersal by ants did not depend on ant community composition, but was dominated by one species, *A. rudis,* which occurred at every site and removed the vast majority of all observed seeds in this study. Though the ant fauna in the Great Smoky Mountains National Park is diverse, dispersal of *T. undulatum* and *H. arifolia*, and likely other myrmecochores, is driven by one ant species, *A. rudis*.

1. Introduction

Ant–seed interactions are ecologically important and geographically widespread (Giladi, 2006; Rico-Gray and Oliveira, 2007). Ants collect and transport seeds to ant nests, where they consume the nutritional reward and discard the seed virtually unharmed; the seed can subsequently germinate (Beattie and Culver, 1981). It has been estimated that ants disperse plant species from over 80 plant families (Beattie, 1985) and within the monocots, myrmecochory has evolved tens of times independently (Dunn et al., 2007a). Interactions between ants and seeds are very important to the maintenance of natural plant communities (Giladi, 2006; Kalisz et al., 1999) as seed dispersal establishes the initial template for seedling

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distribution. Though ant–seed mutualisms are ecologically important, most studies to date have focused on interactions among seeds and ants in a single location, or perhaps a few locations within a region. However, a growing number of studies have indicated that a variety of interspecific interactions can vary geographically (MacArthur, 1972; Jeanne, 1979; Bertness et al., 1981; Pennings et al., 2001). While geographic variation in certain species interactions, such as herbivory (Pennings et al., 2001; Goranson et al., 2004; Andrew and Hughes, 2005; Novotny et al., 2006; Dyer et al., 2007), seed predation (Louda, 1982; Moles and Westoby, 2003), and pollination (Thompson, 1994; Aras et al., 1996; Arroyo et al., 2005; Devoto et al., 2005), has received considerable attention, few studies to date have examined geographic variation in seed dispersal mutualisms (but see Gove et al., 2007; Manzaneda et al., 2007).

Ant–seed dispersal mutualisms might vary geographically for at least three reasons. First, the density and diversity of ant seed dispersers might vary (Gove et al., 2007; Parr et al., 2007). Second, plant density, composition, or diversity might vary, thereby influencing the relative abundance or availability of seeds to dispersers (Gorb and Gorb, 2003; Heithaus et al., 2005). Third, climatic conditions might vary and indirectly limit interactions between seeds and their ant dispersers. A critical step in understanding spatial variation in species interactions is to examine how such interactions vary along known gradients in plant or animal communities or varying climatic conditions. Elevational gradients provide an ideal context for such a study because they condense both variation in plant and animal communities and variation in climate onto a small geographic space (Fukami and Wardle, 2005). In this study, our goal was to use an elevational gradient in the southern Appalachian Mountains, where ant communities are well-characterized (Cole, 1940; Mitchell et al., 2002; Dunn et al., 2007b; Sanders et al., 2007), to understand geographic variation in ant–seed dispersal mutualisms. In particular, we examined seed removal rates and seed dispersal distance along an elevational gradient in the Great Smoky Mountains National Park, USA. By experimentally putting out seeds, we reduced the potential effects of variation in the plant community and the abundance of seed resources in order to focus on consequences of variation in the seed-dispersing ant community.

Ants are important seed dispersers in eastern deciduous forest ecosystems (Beattie and Culver, 1981; Gunther and Lanza, 1989; Heithaus and Humes, 2003; Ness, 2004), where they disperse 20 to 50% of the total herbaceous flora (Handel et al., 1981; Gaddy, 1986). Both ant communities (Sanders et al., 2007) and the abundance and diversity of ant-dispersed plants are known to vary strongly in space within this region (Mitchell et al., 2002; Webster and Jenkins, 2008). Similar to other elevational diversity gradients (Botes et al., 2006; Rahbek, 2005), both ant diversity and abundance decrease with elevation in the southern Appalachian Mountains, largely because temperature decreases with elevation (Sanders et al., 2007).

In this context, we explore two inter-related hypotheses regarding the effects of variation in the ant community on seed removals, namely that seed removal is a function of ant abundance and ant diversity. In addition, we ask whether seed dispersal distance varies along the elevational gradient and if it does, whether that variation is a function of the ant community. If seed dispersal by ants is a diffuse mutualism, in which any of a variety of partners might suffice, then seed dispersal should track variation in ant abundance or diversity. Alternatively, if seed dispersal by ants depends on one of a few keystone mutualists, seed dispersal rates might be more closely correlated with the abundance or activity of particular ant species (Gove et al., 2007). We also examine how the presence and abundance of ant-dispersed flora vary along the same gradient.

2. Materials and methods

2.1. Site description

We carried out this study at 11 sites distributed across an elevational gradient in the Great Smoky Mountains National Park (GSMNP) in eastern Tennessee and western North Carolina, USA, in June–August 2005–2007. Approximately 80% of GSMNP is comprised of deciduous forests (Whittaker, 1956). Elevation in GSMNP ranges from 256 to 2025 m. Temperature and precipitation, as well as the number and abundance of ant species, vary systematically with elevation in this system. Moreover, there appears to be little variation among individual mountains in the GSMNP in the relationships among temperature, precipitation, and ant community composition (Dunn et al., 2007b; Sanders et al., 2007). Therefore, we treated the sites as if they occurred along a single elevational gradient, which is a common practice in many elevational gradient studies, in this system and others (e.g. Sanders, 2002; Dunn et al., 2007b; Rahbek, 2005).

We focused our study on the removal and dispersal of seeds of two common understory myrmecochores (ant-dispersed plants), *Trillium undulatum* (Willd). and *Hexastylis arifolia* (Michx.) (Berg, 1958, 1972; Gunther and Lanza, 1989; Zettler et al., 2001). We used *T. undulatum* seeds for all seed removal experiments. However, due to a late season frost and a severe regional drought in 2007, we were unable to collect any *Trillium* seeds within GSMNP. As a result, we used seeds from *H. arifolia*, a myrmecochore species with seeds morphologically similar to those of *T. undulatum* (Zettler et al., 2001), to track seed dispersal distance. Because we are interested in whether interactions between ants and seeds vary along the elevational gradient and not the details of particular plant species, such a substitution is warranted. Additionally, we compared three sites where we used both *H. arifolia* and *T. undulatum* seeds and there were no differences in seed dispersal distance between the two species ($F = 0.07$, $df = 1, 37$, $P = 0.8$). We carried out all seed removal experiments and seed dispersal observations in July and August, when ants are active throughout the elevational gradient and when *Trillium* species are fruiting at higher elevations (personal observations). While *Trillium* and *Hexastylis* are not all still fruiting at lower elevations in July and August, the high seed removal rates we report suggest that ants still remove seeds at these sites, despite the fact that natural plant populations are no longer fruiting.