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Same but different: Diversity and complexity of an arthropod trophic network and comparative seed viability of an invasive and a native legume species

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ABSTRACT

Exotic species are species established outside of their natural range and include invasive species, which are the second most important cause of biodiversity loss worldwide and a high risk factor for fragile ecosystems. The exotic species *Leucaena leucocephala*, a high-risk invasive species, has been introduced to Andean tropical dry forests of Colombia. Here, we compare the complexity and structure of the arthropod trophic networks of the seeds of two legume species, *Senegalia riparia* (native) and *L. leucocephala* (exotic), and also evaluate seed germination potential after Bruchinae emergence in comparison with that of undamaged seeds. We found 16 species of arthropods associated with both legume seeds, but the native species had more parasitoids, causing its network to be more dense and complex than that of the exotic species. Four arthropod species connected the two networks. The native species seeds already used for beetle development had the lowest germination percentage, whereas those of the exotic species exhibited the highest. Comparing the structure of seed feeder communities and their effects on germination in exotic and native legumes is essential for understanding how exotic species relate to native communities and how anthropogenic changes affect species diversity, ecosystem dynamics, and community structure and interactions.

1. Introduction

Human use of natural landscapes has modified natural habitats and altered the dynamics and structure of natural ecosystems and communities worldwide (Foley et al., 2005). Among these practices, the introduction of exotic species is one of the major causes of ecosystem degradation and biodiversity loss (McNeely et al., 2001). The successful establishment of exotic plant species in an ecosystem depends on the type and amount of interactions that the species develop with native herbivores and organisms from different guilds, such as predators, competitors and parasitoids. Exotic species affect hydrological cycles, fire regimes, nutrient cycles, ecosystem structure and function (Pauchard et al., 2008; Richardson and Rejmánek, 2011; Schüttler and Karez, 2008), and species composition and interactions (Aragón et al., 2014).

It has previously been demonstrated that exotic plant species sustain lower herbivore diversity than natives because of the short evolutionary history of interactions between the exotic plant and the native herbivores and natural enemies (Bezemer et al., 2014 and references therein). Few studies have explored whether this reduction in biodiversity due to exotic species affects the amount and type of tritrophic interactions (McCary et al., 2016), and to the best of our knowledge, no previous study has analyzed and compared the structure, complexity and characteristics of the trophic networks associated with exotic and native plants. Ecological network analysis might be a very effective tool for understanding such differences. Species interactions can be thought of as a network that shows the connections among species that develop and evolve together and which constitute an important agent of diversification (Thompson, 1994). Such interactions can be mutualistic or antagonistic and may vary among species and ecosystems (Thompson, 2006) and this affects the structure and complexity of the ecological networks involving both native and invasive plant species. Another important factor that can regulate the establishment of exotic species in a new ecosystem is seed germination success, which can be influenced by abiotic factors such as soil type, soil humidity, temperature, and drainage (among others) and by

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biotic factors such as seed predation and fungal and bacterial decay.

In Colombia, the invasive legume *Leucaena leucocephala* is broadly distributed throughout the tropical dry forest biome. It was initially introduced to provide shade for cattle in pastures and for use in living fences around pastures and crops, but its highly invasive behavior has enabled it to disperse into a large range of ecosystems from well-preserved dry forests to highly transformed systems. Throughout its distribution, *L. leucocephala* co-occurs with approximately 20 species of native legume trees, thus providing an excellent opportunity to study how exotic species interact with native species and become part of novel ecosystems. This species is also considered one of the 100 worst invasive species worldwide (Lowe et al., 2000).

Bruchinae beetles are one of the very few subfamilies of insects that feed on legume seeds. Females deposit their eggs on the seed pod or directly on the seed coat, and larval development typically occurs inside a single seed. Some studies have shown that seed feeding by these insects on legumes can reduce the probability of germination by between 90 and 100% (Orozco-Almanza et al., 2003). However, if seeds are hard and waterproof, holes made by insects could favor germination by facilitating increased water intake (Takakura, 2002).

To gain a better understanding of how exotic species integrate into their recipient communities and the complexity of their interactions, and to understand the different associations between plants and seed feeders, we compared the taxonomic and functional diversity as well as the complexity and structure of the arthropod trophic networks associated with the seeds of a native legume, *Senegalia riparia*, and the exotic *L. leucocephala*. In addition, we evaluated the degree to which the damage produced by the development of Bruchinae beetles inside the seeds of both species affects germination. We expected that (1) the richness of spiders and insects would be lower in the exotic species; (2) the trophic network associated with the exotic legume would be less diverse and complex; and (3) irrespective of the species, seeds subject to beetle development would show decreased viability compared to undamaged seeds.

2. Materials and methods

2.1. Sampling area

The sampling for this study was performed in a pasture containing legume trees dispersed within and around a cattle pasture. The area covers 115,500 m^2 and is located adjacent to the Sumapaz River and along the highway that connects the municipalities of Melgar and El Espinal (Department of Tolima, Colombia: 4°15′06″N, 74°44′56″O; 323 m in altitude). The area corresponds to a Tropical Dry Forest biome, and the legume tree species include *Pithecellobium dulce, Pseudosamanea guachapele, Parkinsonia aculeata*, *S. riparia* and *L. leucocephala*. The native species used in this study, *S. riparia*, was found among the vegetation separating the river from the pasture, while *L. leucocephala*, the exotic species, was found along the fence that surrounded the pasture next to the highway. We chose *S. riparia* and *L. leucocephala* because their seeds are very similar in shape, color and size (Fig. 1) and because there are two periods during the year when the seeds of both species are available to beetles: June–August and December–January.

2.2. Study species

Leguminosae is the most diverse family of plants inhabiting the tropical dry forests of Colombia. *L. leucocephala*, an invasive species, and *S. riparia*, a native species, are two legumes that coexist in large areas of tropical dry forest in the central Andes, with *S. riparia* producing large amounts of seeds in synchrony with *L. leucocephala* around the month of June.

Fig. 1. Seeds of *Leucaena leucocephala* (left) and *Senegalia riparia* (right) collected from a Colombian tropical dry forest.

Leucaena leucocephala (Lam) is a member of the Mimosoideae (Fabaceae) family that is native to Guatemala, Honduras, El Salvador and Southern Mexico. Globally, it has successfully adapted to a large variety of lowlands, being naturalized in approximately 105 countries in the subtropics and tropics and on all continents, except Antarctica (Walton, 2003). *Leucaena leucocephala* is widespread and considered a weed in 25 of those countries. Indeed, it is considered by Hughes and Jones (1998) as the worst weed globally, and by the IUCN's Invasive Species Specialist Group (2015) as one of the 100 worst invasive organisms (Lowe et al., 2000). *Leucaena leucocephala* was introduced to Colombian tropical dry forests (Baptiste et al., 2010) for use as living fences and cattle feed (CATIE, 1991). It is classified as a high-risk invasive species due to its ability to rapidly disperse (Baptiste et al., 2010). Although the date of first introduction in Colombia is unclear, the species is believed to have been in the country for approximately 80 years. *L. leucocephala* is a legume tree with a rounded canopy that ranges from 3 to 12 m in height. The seeds are enclosed in large, dry, laterally compressed, and leather-like seed pods, each of which contains between 15 and 30 oval, dark brown seeds that are 5–10 mm long and 3–6 mm wide (Fig. 1). The seeds are covered by wax, which makes water absorption during germination difficult (Zárate, 1987). The species is very abundant alongside roads, in living fences and inside pastures, where it provides shade to cattle.

Senegalia riparia (Kunth) is also a member of the Mimosoideae (Fabaceae) family that is native to Colombia but distributed from Mexico to South America. It can be up to 10 m in height, and its cylindrical branches have small but very sharp spines that are 1–3 mm long. The seed pods are long, small, laterally compressed, and contain 3 to 15 oval, brown and laterally compressed seeds. Each seed is 5–10 mm long and 3–5 mm wide (Fig. 1). The species is found along dirt roads and river banks in tropical dry forests.

2.3. Data collection, experimental design and analyses

During June 2013, we collected seed pods from at least five different trees of each legume species, filling at least five hermetically-sealed bags with a capacity of 3.7 L each. By collecting the same amount of samples from each legume species, we avoided the confounding effect that seed abundance in the field could have