Forest Ecology and Management 318 (2014) 34–43

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Patterns in understory woody diversity and soil nitrogen across native- and non-native-urban tropical forests

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ARTICLE INFO

Article history:
Received 27 December 2013
Accepted 30 December 2013
Available online 8 February 2014

Keywords:
Invasive plants
Exotic
Soil carbon and nitrogen
Canopy openness
Forest fragmentation
Distance to urban center

ABSTRACT

Urban expansion is accelerating in the tropics, and may promote the spread of introduced plant species into urban-proximate forests. For example, soil disturbance can deplete the naturally high soil nitrogen pools in wet tropical soils, favoring introduced species with nitrogen-fixing capabilities. Also, forest fragmentation and canopy disturbance are likely to favor high-light species over shade-adapted rainforest species. We measured understory woody diversity, the abundance of introduced species, and soil nitrogen and carbon in urban, suburban, and rural secondary forests in Puerto Rico with canopies dominated by (1) native species, (2) introduced Fabaceae (potential nitrogen-fixers), and (3) introduced non-Fabaceae species. We hypothesized that forest stands with introduced Fabaceae in the canopy have higher soil nitrogen levels than stands with other introduced canopy species, and that this higher nitrogen is linked to increased native woody species diversity in the understory. We also predicted that more open canopies and smaller fragment sizes would be positively related with introduced species in the understory, and negatively related with total understory diversity. We found that stands with introduced Fabaceae in the canopy had significantly higher soil nitrogen levels than stands with other non-nitrogen fixing introduced species, and understory woody diversity in Fabaceae stands approached similar diversity levels as stands with native-dominated canopies. As predicted, aboveground stand structure and fragment size were also significantly associated with understory woody diversity across stands. These results suggest that introduced nitrogen-fixing trees may improve recruitment of native woody species in degraded tropical sites where native soil nitrogen is naturally high, particularly as Fabaceae stands mature and canopies close.

1. Introduction

Urban expansion is occurring rapidly in tropical regions (Lambin et al., 2003), with significant potential to affect urban-proximate forests (Kaye et al., 2006; Martinelli et al., 2006), particularly via the spread of introduced plant species (Chytry et al., 2008). Biological invasions are a major driver of global environmental change, endangering native species populations and potentially altering ecosystem structure and function (Vitousek et al., 1996, 1997). Introduced plants may spread from urban centers into nearby forests (Cowie and Werner, 1993; McKinney, 2002, 2008), particularly where unmanaged afforestation is occurring such as on abandoned agricultural sites across Latin America (Lugo, 2004; Grau and Aide, 2008). Investigation of landscape- and ecosystem-scale factors that promote regeneration of native diversity in tropical urban forest fragments has received little attention, despite widespread concern about biodiversity in tropical forests.

Changes in soil properties with urban activity may contribute to the spread of introduced species. For example, localized soil compaction and topsoil removal (e.g. erosion) can increase soil bulk density and decrease the availability of nitrogen (N) and other nutrients in surface soils (Woodward, 1996), contributing to high variability in soil N levels among nearby urban forest stands (Cusack, 2013). Soil N loss in tropical forests can have a negative effect on the establishment of native tropical forest plants (Reiners et al., 1994), likely because native plants are adapted to the relatively high background N availability in highly weathered tropical soils (Walker and Syers, 1976; Chestnut et al., 1999; Martinelli et al., 1999; Hedin et al., 2009). Thus, soil disturbances that deplete naturally high N pools in highly weathered tropical soils can favor introduced species adapted to low soil N (Funk and Vitousek, 2007). This relationship is in contrast to patterns observed in some Northern sites, where N deposition in urban-proximate forests increases N availability in naturally N-poor soils, and can favor the spread of introduced plants that are competitive at higher soil N (Howard et al., 2004). Thus, N depleted soils in urban-proximate tropical forests are likely to promote loss of native plant species,

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http://dx.doi.org/10.1016/j.foreco.2013.12.036
0378-1127/

and the spread of introduced species that have a competitive advantage at low N.

Plants with N-fixing capabilities in the Fabaceae family are highly likely to be successful invaders in N-poor soils (Binggeli, 1996; Pysek, 1998). In tropical areas where native Fabaceae are rare or absent (Allen and Allen, 1981), they can be particularly successful invaders in degraded areas, with the capacity to increase local soil N levels over time via N-fixation (Vitousek et al., 1987). Because of their positive effect on soil N, mature stands of introduced Fabaceae may eventually promote restoration of native understory growth, as has been seen in a dry subtropical forest (Parrotta, 1993). Thus, soil disturbance in urban-proximate tropical forests may deplete N and favor introduced N-fixing species, but these may in turn restore naturally high soil N levels over time.

In addition to soil disturbance, forest fragmentation and canopy disturbance are common in tropical forests (McGrath et al., 2001; Geist and Lambin, 2002; Sodhi et al., 2010), particularly around urban areas (Huston, 2005), and are also linked to the spread of introduced plants (Cowie and Werner, 1993; Charbonneau and Fahrig, 2004; Groffman et al., 2006). For example, forest fragmentation in Brazil decreased species number and stem abundance (Benítez-Malvido and Martínez-Ramos, 2003), with urban fragments particularly susceptible to establishment of introduced plants (da Fonseca and Carvalho, 2012). Increased canopy openness has been linked to the success of shade intolerant introduced plants, particularly in wet tropical forests where mature forest canopies are dense and native understory plants are adapted to low light (Murphy et al., 2008; Siddique et al., 2008). Introduced Fabaceae can have a strong competitive advantage where disturbed canopies create high light understory conditions (Wolfe and Van Bloem, 2012). Thus, disturbances to both soil and aboveground forest structure in urbanized tropical areas are likely to favor the spread of introduced Fabaceae species.

Colonization of disturbed urban-proximate forests by introduced species could alter successional pathways. First, if introduced plants are established as successful invaders reaching the canopy, they may persist and dominate species assemblages in the long-term, especially if they are shade tolerant with high survival and growth under the canopy (Murphy et al., 2008). Alternately, initial cohorts of introduced plants may facilitate the regeneration of native species if they improve site conditions, resulting in novel species assemblages (Lugo and Helmer, 2004), or restoration of native species compositions eventually.

Here, we examined distributions of introduced Fabaceae, introduced non-Fabaceae, and native trees in the canopies and understories of eight forest stands in an urban-suburban watershed, and three stands in a rural watershed in subtropical secondary forests in Puerto Rico. We explored relationships for understory woody plant diversity with soil and aboveground characteristics to address the following hypotheses: (1) forest stands with introduced Fabaceae in the canopy have higher soil N levels than stands with non-Fabaceae introduced canopy species, approaching the high background soil N levels found in native tropical forests; (2) stands with Fabaceae in the canopy have greater native understory plant diversity than stands with non-Fabaceae introduced canopy species, indicating improved recruitment of native species in high N soils; (3) disturbances that allow more light into the understory are negatively associated with total native woody species diversity, and positively associated with the abundance of introduced plants in the understory.

2. Materials and methods

2.1. Study sites

The main site for this study was an urban-suburban watershed in Puerto Rico, with additional sites in a rural watershed (Fig. 1). Eight urban and suburban forest stands were located in the Río Piedras watershed within the San Juan Urban Long Term Research Area (ULTRA-Ex). The 8 stands represented the major forested areas of the urban-suburban (hereafter "urban") watershed, spanning from the low-elevation urban core, to higher elevation suburban areas (Table 1). The urban watershed is in the subtropical moist forest life zone (sensu Holdridge et al., 1971), ranges in elevation from 0 to 220 m above sea level (masl), has mean annual precipitation (MAP) of 1750 mm, and mean annual temperature (MAT) of 25.7 °C. Rural sites were located in secondary forests in the USFS Cubuy Annex (18°16′N, 65°52′W), which is also in the

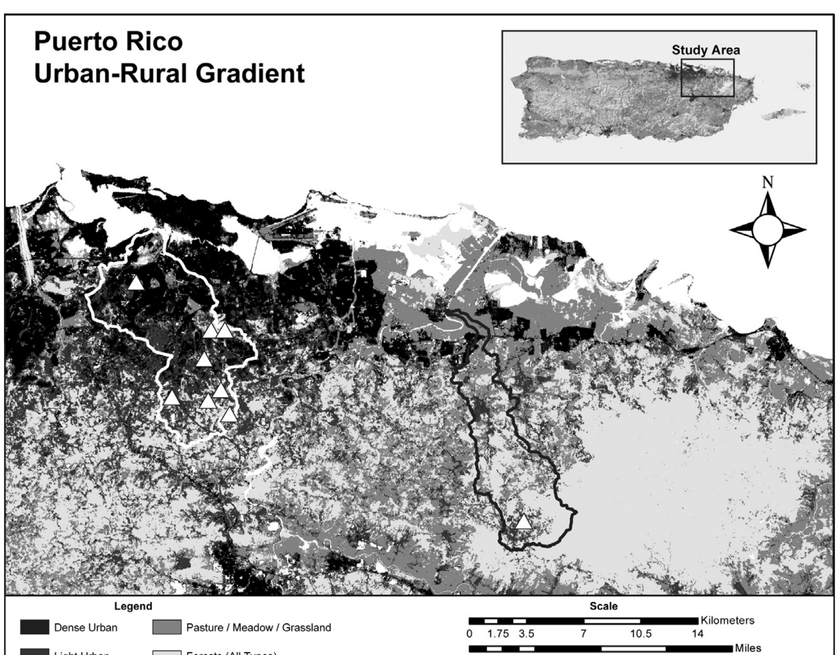

Fig. 1. Map showing the locations of 8 forest fragments (white triangles) within the urban Río Piedras watershed in Puerto Rico (white outline), and three sites in a rural forest watershed (black line) within the USFS Cubuy Annex (white triangle). Cover types have been modified from (Kennaway and Helmer, 2007).