



Disentangling the effects of facilitation on restoration of the Atlantic Forest

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Abstract

Facilitation is an important ecological mechanism with potential applications to forest restoration. We hypothesized that different facilitation treatments, distance from the forest edge and time since initiation of the experiment would affect forest restoration on abandoned pastures. Seed and seedling abundance, species richness and composition were recorded monthly during two years under isolated trees, bird perches and in open pasture. Seed arrival and seedling establishment were measured at 10 m and 300 m from the forest edge. We sampled a total of 131,826 seeds from 115 species and 487 seedlings from 46 species. Isolated trees and bird perches increased re-establishment of forest species; however, species richness was higher under isolated trees. Overall, abundance and richness of seeds and seedlings differed between sampling years, but was unaffected by distance from the forest edge. On the other hand, species composition of seeds and seedlings differed among facilitation treatments, distance from the forest edge and between years. Seedling establishment success rate was larger in large-seeded species than medium- and small-seeded species. Our results suggest that isolated trees enhance forest re-establishment, while bird perches provide a complementary effort to restore tree abundance in abandoned pastures. However, the importance of seed arrival facilitation shifts toward establishment facilitation over time. Arriving species may vary depending on the distance from the forest edge and disperser attractors. Efforts to restore tropical forests on abandoned pastures should take into account a combination of both restoration strategies, effects of time and proximity to forest edge to maximize regeneration.

Zusammenfassung

Facilitation ist ein wichtiger ökologischer Mechanismus mit möglichen Anwendungen für die Rekultivierung von Wäldern. Wir vermuteten, dass unterschiedliche Methoden der facilitation, die Entfernung vom Waldrand und die Zeit nach Versuchsbeginn die Waldrekultivierung auf brachliegenden Weiden beeinflussen würden. Die Abundanz von Samen und Sämlingen, Artenreichtum und -zusammensetzung wurden zwei Jahre lang monatlich unter isolierten Bäumen und künstlichen Vogel-sitzwarten (mit facilitation) sowie auf der freien Weide (ohne facilitation) erhoben. Die Ankunft der Samen und Ansiedlung von Sämlingen wurden 10 m und 300 m vom Waldrand entfernt gemessen. Insgesamt sammelten wir 131 826 Samen aus 115 Arten und 487 Sämlinge aus 46 Arten. Isolierte Bäume und Sitzwarten verstärkten die Wiederansiedlung von Waldarten, aber der Artenreichtum war unter isolierten Bäumen höher. Abundanz und Artenreichtum der Samen und Sämlinge waren in den Untersuchungsjahren unterschiedlich, wurden aber von der Entfernung zum Waldrand nicht beeinflusst. Auf der anderen Seite war die

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Artenzusammensetzung je nach facilitation-Methode, Entfernung zum Waldrand und Untersuchungsjahr unterschiedlich. Der Ansiedlungserfolg war bei Arten mit großen Samen höher als bei Arten mit mittleren oder kleinen Samen. Unsere Ergebnisse legen nahe, dass isolierte Bäume die Rekultivierung von Wäldern unterstützen, während künstliche Sitzwarten eine ergänzende Maßnahme zur Rekultivierung von Wäldern auf brachliegenden Weiden ermöglichen. Indessen wechselt die Wichtigkeit der Begünstigung der Ankunft der Samen mit der Zeit hin zur Begünstigung der Ansiedlung. Die ankommenden Arten können mit der Entfernung vom Waldrand und dem Anziehungspunkt für die Ausbreiter variieren. Bei den Anstrengungen zur Rekultivierung von tropischen Wäldern auf brachliegenden Weiden sollten beide Rekultivierungsstrategien und die Effekte von Zeit und Entfernung zum Waldrand Berücksichtigung finden, um die Regeneration zu maximieren.

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Introduction

Deforestation and conversion of forests into agricultural lands and pastures is a common practice in the tropics (Chazdon, 2003). Such anthropogenic pressures lead to biodiversity decline and loss of ecosystem processes and services (Wright, 2005; FAO, 2010). Forest regeneration in degraded lands is limited by a myriad of factors, including exhaustion of seed banks, low rates of seed arrival, long distances to forest edge, seed and seedling predation, unsuitable microclimate conditions, lack of soil nutrients, and competition with exotic pasture grasses (Zimmerman, Pascarella, & Aide, 2000; Hooper, Legendre, & Condit, 2005). Among all of the aforementioned, the low rate of seed arrival and seedling recruitment appear to be a major constraint on restoration of these degraded habitats (Holl, 1999; Cubina & Aide, 2001).

Facilitation has been increasingly recognized as an important process in plant communities, influencing the recovery of forests in degraded lands (Bruno, Stachowicz, & Bertness, 2003; Brooker et al., 2008; Brooker & Callaway, 2009). Isolated trees in abandoned pastures facilitate the establishment of forest species, directly by attracting frugivorous birds, which increases numbers of locally dispersed seeds, and indirectly by outcompeting exotic pasture grasses. Hence, the manipulation of seed dispersal to increase the probability of seed arrival to degraded sites is key in facilitating forest regeneration and competing against encroaching of exotic pasture grasses (Wunderle, 1997; Wenny, 2001). Some studies have monitored seed arrival and seedling establishment in bird perch addition experiments and isolated trees (McClanahan & Wolfe, 1993; Holl, 1998; Toh, Gillespie, & Lamb, 1999; Zanini & Ganade, 2005; Bustamante-Sánchez & Armesto, 2012), but to our knowledge none has compared these restoration approaches directly and disentangled facilitation effects across space and over time to support management practices.

The established plant community that emerges after degradation may be the result of multiple biotic and abiotic filters that determine the species and functional traits that persist (Keddy, 1992; Lortie et al., 2004). Seed size and shade tolerance represent differences in ecological niches and growth/survival trade-offs (Westoby, 1998;

Wright, Muller-Landau, Condit, & Hubbell, 2003). Smaller seeds tend to be dispersed widely, having higher chances of reaching suitable sites, while larger seeds have a greater amount of stored resources, favoring seedling survival and establishment in face of more harsh environments (Kitajima, 2002; Westoby, Falster, Moles, Vesk, & Wright, 2002). Shade tolerance, in turn, enables plant survival in shaded and well-developed secondary forests (Swaine & Whitmore, 1988). Hence, studying how plant functional types persist in communities is an important step toward developing adequate procedures for vegetation management and conservation (Keddy, 1992; Grime, 2006).

We used an *in situ* experimental approach to study facilitation mechanisms affecting arrival and establishment of plants in abandoned pastures over space and time. Furthermore, we assessed abundance, richness and composition of seeds and seedlings, and explored effects of functional traits on seedling establishment. We tested two hypotheses: (1) Isolated trees and bird perches increase abundance and richness of seeds and seedlings arriving to abandoned pastures. (2) Large-seeded and shade-tolerant species have higher establishment success than small- and medium-seeded and shade-intolerant species, given the shaded microenvironment produced by dominant exotic grasses in abandoned pastures. We also investigated how community composition depends on ‘facilitation treatments’ (isolated trees, bird perches and open pasture), distance from the forest edge and time since initiation of the experiment. Our results are discussed regarding processes affecting facilitation during restoration of abandoned pastures.

Materials and methods

Study area and sites

We conducted our field study from May 2004 to April 2006, at the Rio Cachoeira Nature Reserve (25°18'51" S, 48°41'45" W) in the coastal Paraná region, southern Brazil. The regional climate is classified as humid sub-tropical (Köppen's Cfa), with mean annual rainfall of 2600 mm (range: 2500–3000 mm) and absence of a marked dry season. The

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