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# Factors limiting montane forest regeneration in bracken-dominated habitats in the tropics

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ABSTRACT

Tropical montane forests are threatened by human-induced fires, resulting in forest patches surrounded by disturbed habitats frequently dominated by bracken fern (*Pteridium* spp.). In most disturbed habitats, natural forest regeneration is principally hindered by (i) seed limitation, due to a lack of seed dispersal, and (ii) establishment limitation, due to harsh abiotic conditions or competition with grasses and weeds. To our knowledge, the combined effect of seed limitation and establishment limitation on the entire regenerating plant community has never been tested in tropical bracken-dominated habitats. We experimentally assessed the effect of bracken fronds on natural seedling establishment in different distances from a tropical montane forest of the Bolivian Andes. At ten sites, we placed 240 m-long transects ranging from the forest interior to the disturbed habitat and installed paired plots at seven distances along each transect. In one plot of each pair, we applied a repeated vegetation removal treatment to assess the effect of bracken fronds on seedling establishment. We analysed the effect of bracken removal on seedling richness, seedling survival and growth of tree and non-tree species. We additionally compared patterns in seedling density and richness from the forest interior towards the disturbed habitat with patterns in seed density and richness in the seed rain and the soil seed bank. Species richness was higher in the forest than in the disturbed habitat. Tree species corresponded to approx. 25% of the species pool in the disturbed habitat and were only present at low densities. Density and species richness of seeds and tree seedlings consistently decreased from the forest edge towards the disturbed habitat, suggesting seed limitation. Seedlings of tree species had high survival probabilities in the disturbed habitat, especially under bracken fronds, suggesting a lack of establishment limitation. Bracken removal in the disturbed habitat did not affect species richness, but significantly reduced seedling survival and growth of tree and non-tree species. Our results suggest that low seed dispersal hinders natural regeneration of bracken-dominated habitats in the tropics and that bracken fronds do not impede seedling establishment. Seed addition of tree species into the bracken vegetation may therefore be a promising strategy to accelerate forest regeneration, but long-term studies and multispecies experiments are needed for assessing the success of this restoration strategy.



## 1. Introduction

Vast areas of tropical montane forests have been deforested by human-induced fires (Cochrane, 2003; Holl, 2012). In many regions, high deforestation has resulted in fragmented landscapes of forest patches surrounded by disturbed vegetation. Forest regeneration in disturbed habitats can be very slow, especially after heavy disturbances like recurrent fires, overgrazing or intensive agriculture (Chazdon, 2003; Hartig and Beck, 2003; Holl, 2002). Deforestation threatens biodiversity and the ecosystem services provided by tropical montane forests, calling for active restoration efforts to accelerate forest regeneration in these areas (FAO, 2012; Holl and Kappelle, 1999). Although many studies have assessed the regeneration of tropical forests and tested restoration strategies in abandoned pastures in lowlands (e.g., Aide and Cavelier, 1994;

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Ganade and Brown, 2002; Holl et al., 2000; Hooper et al., 2005), much less is known about the limiting factors of forest regeneration in fire-disturbed habitats in montane forests (e.g., González-Espinosa et al., 2007; Lippok et al., 2013a; Palomeque, 2012; Slocum et al., 2006).

After fire, bracken fern (*Pteridium* spp.) often colonizes the disturbed habitat and dominates the plant community for long time periods (Kellman, 1980; Marrs et al., 2000), inhibiting or slowing down forest regeneration (Hartig and Beck, 2003; Humphrey and Swaine, 1997; Miatto et al., 2011; Ribeiro et al., 2013). Bracken success has been attributed to its large and deep rhizomes, high frond productivity, deep litter accumulation and chemicals that are supposed to have allelopathic effects on the surrounding vegetation (Gliessman and Muller, 1978; Marrs and Watt, 2006; Marrs et al., 2000). Mainly based on studies in temperate regions, it has been assumed that bracken fronds shade out other species and reduce the diversity of recruiting seedlings and their ability to establish (reviewed by Marrs et al., 2000). Many mechanical and chemical attempts to control bracken have emerged worldwide (e.g., Alday et al., 2013; Milligan et al., 2016; Roos et al., 2010). The most effective treatment to reduce bracken dominance was vegetation removal (i.e., cutting bracken fronds twice per year; Alday et al., 2013; Stewart et al., 2008). Although this treatment did not completely eradicate bracken (Marrs et al., 2000; Roos et al., 2010; but see Aguilar-Dorantes et al., 2014; Douterlungne and Thomas, 2013), it has been shown to increase seedling establishment and species richness of light-demanding species (Alday et al., 2013; Marrs et al., 2000; Milligan et al., 2016; Stewart et al., 2008). In the tropics, most studies that have analysed forest regeneration in bracken-dominated vegetation reported low diversity of tree species (e.g., Günter et al., 2007; Miatto et al., 2011; Ribeiro et al., 2013) and a dominance of non-tree species (Aguilar-Dorantes et al., 2014; Günter et al., 2007; Hartig and Beck, 2003; Palomeque, 2012).

Forest regeneration in disturbed habitats depends on the establishment of tree species already present at a site or colonizing from adjacent source habitats (Holl, 2012). At sites with a low intensity of degradation, forest vegetation may regenerate from resprouting and the soil seed bank (Holl, 2012). However, studies on the soil seed bank in bracken-dominated areas usually report small amounts of seeds of tree species, suggesting a low potential for natural regeneration from the seed bank (Aguirre, 2007; Da Silva and Silva Matos, 2006; Lippok et al., 2013b; Xavier et al., 2016). Regeneration of forest species from an adjacent source habitat can be hindered by (i) seed limitation (i.e., dispersal limitation *sensu* Münzbergová and Herben, 2005), due to low seed dispersal from source habitats, and (ii) establishment limitation (i.e., habitat limitation *sensu* Münzbergová and Herben, 2005), due to harsh abiotic conditions or competition with established vegetation that can inhibit germination and/or seedling survival (reviewed by Holl, 2002). First, most tropical tree species depend on animals for seed dispersal (Howe and Smallwood, 1982). Most seed dispersers avoid disturbed habitats because of the lack of perching structures, food resources and a high predation risk (Wunderle, 1997), resulting in low seed dispersal into disturbed habitats (Holl, 1999; Holl et al., 2000; Wijdeven and Kuzee, 2000). Second, harsh abiotic conditions (i.e., high temperatures and low humidity) may limit forest regeneration in open habitats by reducing seedling performance in terms of survival and growth (e.g., Gunaratne et al., 2010; Holl, 2002; Sady et al., 2010). Abiotic effects can be exacerbated by strong competitive effects of grasses and ferns on establishing seedlings (Wilson, 1998; Hooper et al., 2002, 2005). However, in a few cases, it has been proven that early successional grasses and ferns ameliorate abiotic conditions and increase the probability of seed germination (e.g., Aide and Cavelier, 1994; Gould et al., 2013; Holl, 1999; Zimmerman et al., 2000). To our knowledge, the combined effects of seed limitation and establishment limitation on forest regeneration have never been tested experimentally in bracken-dominated habitats in the tropics.

In this study, we experimentally tested the effect of bracken on natural seedling establishment of tree and non-tree species in a disturbed tropical montane forest in Bolivia over two years. We installed a total of 140 plots at 10 sites in transects ranging from the forest interior to the disturbed habitat. In half of the plots, we implemented a vegetation removal treatment, cutting the vegetation taller than 1 m in the forest and all bracken fronds in the disturbed habitat twice per year, while the other plots were left as a control. The treatment aimed to remove bracken fronds in the disturbed habitat because bracken comprises more than 70% of the vegetation there. We investigated the effects of vegetation removal and habitat type on species richness, seedling survival and seedling growth of tree and non-tree species. Additionally, we assessed changes in density and species richness of seeds and seedlings along the gradient from the forest interior towards the disturbed habitat by comparing seedling data to corresponding studies on the seed rain and soil seed bank at the same sites (Lippok et al., 2013b; Saavedra et al., 2015). We aimed to determine if forest regeneration in the bracken-dominated habitat is hindered by seed limitation and/or establishment limitation. Therefore, we tested the following hypotheses: (i) if seed limitation in bracken-dominated habitats is constrained by the distance to the forest, we expect higher density and species richness of seeds and seedlings of tree species in plots in the forest and close to the forest edge; (ii) if bracken-dominated habitats are establishment limited, we expect low seedling survival and growth of seedlings of tree species in the disturbed habitat; (iii) if bracken fronds impede tree seedling establishment, we expect lower seedling survival and growth when bracken fronds are present, while the opposite effect would indicate facilitative effects of bracken fronds on tree seedlings.

## 2. Methods

### 2.1. Study area

The study was conducted between 2010 and 2013 on the eastern slopes of the Bolivian Andes, in the vicinity of Chulumani village about 120 km from La Paz city (16°24′ S, 67°31′W). The study area is located in the montane forests of the Yungas region between 1900 and 2500 m asl. Mean annual temperature is 20.8 °C and mean annual precipitation is 1459 mm (Molina-Carpio, 2005). The forests in the area have been highly fragmented, due to uncontrolled human-induced fires and the extension of coca (*Erythroxylum coca* Lam.) plantations (Killeen et al., 2005, 2008). Only two relicts of mature continuous forest, each comprising ca. 3000 ha, remain in the area. These relicts are surrounded by fire-disturbed vegetation dominated by the bracken fern *Pteridium arachnoideum* (Kaulf.) Maxon and successional shrubs (Gallegos et al., 2015; Lippok et al., 2013a).

### 2.2. Experimental design

At ten sites situated between 1900 and 2500 m of elevation, separated by at least 1 km from each other, we installed a 240 m-long transect perpendicular to the forest edge. To assess the effect of distance to the forest edge on seedling recruitment, we selected seven distances along each transect, three in the forest interior (at 160, 40 and 20 m from the forest edge) and four in the disturbed habitat (at 5, 20, 40 and 80 m from the forest edge; Fig. A.1, Supplementary material). At each distance, we set one block comprising two 1 $m^2$ plots. To start the experiment with similar conditions in all plots, we initially removed the vegetation