

## Letters

## Qualitative differences in tree species distributions along soil chemical gradients give clues to the mechanisms of specialization: why boron may be the most important soil nutrient at Barro Colorado Island

### Introduction

The partitioning of soil resource niches is a potential explanation for the high diversity of tropical forests. Using a combination of habitat filtering that excludes species from soils outside their range of physiological tolerance (Engelbrecht *et al.*, 2007; Laliberté *et al.*, 2014) and trade-offs associated with competitive ability for different soil factors (Tilman, 1982; Chase & Leibold, 2003), ecologists can potentially explain the coexistence of any number of species. However, while a host of recent studies demonstrate that soil resources structure plant communities in tropical forests (Phillips *et al.*, 2003; John *et al.*, 2007; Baldeck *et al.*, 2013), similar investigations into the mechanisms of niche partitioning are rare (Engelbrecht *et al.*, 2007).

Identifying the single environmental axis of most importance in structuring communities can inform the search for causal mechanisms, enhancing the economy of investigation. As a particularly fine example, the discovery that many tropical tree species are restricted to either the dry or wet end of a dry season precipitation gradient (Harms *et al.*, 2001; Pyke *et al.*, 2001) has led to experimental evidence that this specialization is caused by variation in drought tolerance (Engelbrecht *et al.*, 2007). Nevertheless, identifying dominant environmental gradients of specialization does not always lead to corresponding investigations of cause, particularly when extensive studies fail to reinforce longstanding hypotheses of the dominant environmental axes of niche specialization.

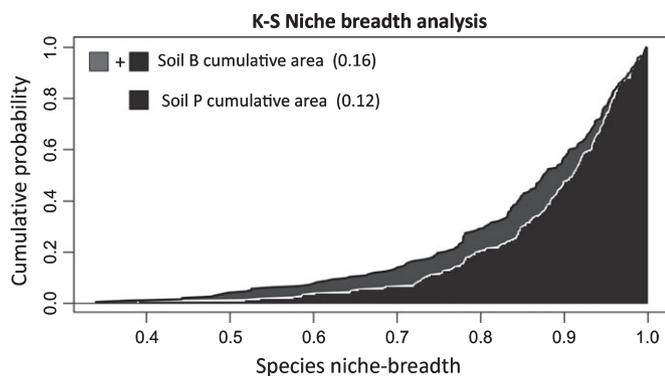
Consider an oft-cited review of the soil chemical gradients responsible for structuring tropical forests (Sollins, 1998), which concluded that the resource/toxin gradients should be (from most to least importance): phosphorus (P), aluminum (Al), base metal cations (e.g. potassium (K) and calcium (Ca)), micronutrients (e.g. soil boron (B) and zinc (Zn)), and soil nitrogen (N). The importance attributed to soil P and Al was based on the fact that productivity in the tropical forests tends to be limited by P

availability (Vitousek, 1984), while soil Al limits agricultural productivity in highly weather, acidic soils (Sanchez, 1976). By contrast, in an extensive study of fine-scale (10 m) tree species distributions and soil nutrient/toxin availabilities in Panama's Barro Colorado Island (BCI), John *et al.* (2007) found that plant species are the most specialized along gradients of soil B, with P and Al having a comparatively minor influence.

Strikingly, the rank order in John *et al.* (2007) is a near-inversion of the one published in Sollins's (1998) review. Moreover, John *et al.* (2007) demonstrate that tree species are the most specialized along a gradient of soil B, the plant essential nutrient considered among plant physiologists and nutritionists to have the narrowest external range between deficient and toxic concentrations (Gupta *et al.*, 1985; Keren & Bingham, 1985; Maas, 1986; Goldberg, 1997). Similarly, in the agricultural literature soil B is known to severely limit worldwide agricultural productivity at both high and low availabilities (Nable & Paull, 1991; Gupta, 1993; Sutton *et al.*, 2007). By contrast, plant ecologists largely ignore soil B. As evidence of ecologists' neglect, consider that John *et al.* (2007) concluded that soil B is the most important soil factor in structuring the world's most intensively studied tropical forest plot, yet none of their more than 250 citations on Web of Science can be found using 'boron' as a search criteria. Here I seek to answer why soil B in particular has a relatively large influence on the distribution of tree species at BCI by contrasting qualitatively different patterns of resource specialization along gradients of soil nutrients and toxins.

### Soil B at BCI: a case study of uninvestigated pattern

First, it is necessary to consider the process by which soil B gradient was determined to have a greater influence on specialization relative to other soil nutrient/toxin gradients. John *et al.* (2007) utilized a method called K-S niche-breadth analyses, which ranks environmental gradients according to their distributions of resource specialists vs generalists (see also Feinsinger *et al.*, 1981; Potts *et al.*, 2004). This method defines niche breadth as the proportion of a total resource axis where a species occurs, with generalists occurring across the entire axis (niche breadth *c.* 1) while extreme specialists occur along a narrower subset of the axis (niche breadth *c.* 0). For each resource axis separately, the niche breadths of each species are calculated and then plotted as a cumulative distribution (Fig. 1). Resource axes that are associated with a higher proportion of specialists with low niche-breadth values have a larger area under this cumulative distribution curve than axes associated with a higher proportion of generalists. Thus, by calculating the area under the cumulative niche-breadth curves for each resource using numerical integration, it is possible to rank-order individual gradients in terms of their influence in structuring plant communities, with higher values indicating relatively greater influence (Fig. 1).



**Fig. 1** Cumulative distributions of niche-breadth values for soil phosphorus (P) and boron (B) for 193 tree species at Barro Colorado Island. The soil B gradient has a greater proportion of species with low niche-breadth values than the soil P gradient, resulting in a greater area under the curve. The shading represents that the area under the soil P curve falls entirely within the larger area under the soil B curve.

A crucial limitation of K-S niche-breadth analyses is that it fails to resolve where along a resource axis specialization occurs. In other words, a species that occupies only the bottom 20% of a resource axis has the same niche breadth as another species that occupies only the top 20%. This lack of resolution can complicate the search for testable hypotheses. Trade-off based theories of resources specialization (e.g. Tilman, 1982) suggest that species adapted to environmental extremes develop traits that make them poor competitors in relatively less stressful environments, limiting their realized distributions. Here, extreme refers to those availabilities of the chemical factor at which it primarily limits population growth. Depending on the soil chemical gradient, extreme could mean high availability (particularly with soil Al toxicity) or low availability (e.g. soil P and Ca deficiency). Thus, one would predict qualitative differences in where specialization occurs among gradients (low and high ends of nutrient and toxin availability, respectively), as well as quantitative differences along gradients (increased specialization at extremes). Identifying these regions can elucidate the types of trade-offs that give rise to narrow realized distributions.

In order to compare tree species distributions along different soil chemical gradients, I first had to match fine scale maps of soil nutrient/toxin availability and tree species abundance. To accomplish this, I compared tree census data of all stems  $\geq 1$  cm diameter at breast height across the 50-ha forest plot at BCI (Condit, 1998; Hubbell *et al.*, 1999, 2005) with estimates of soil nutrient availabilities available at  $20\text{ m} \times 20\text{ m}$  blocks intervals (Dalling *et al.*, 2007; see John *et al.*, 2007, for full description of methods). Briefly, estimates of soil nutrient and toxin availability were generated by sampling topsoil from 0 to 10 cm depth at high spatial resolution. Elemental analysis was conducted on Mehlich-III extracts and soil maps at  $20\text{ m} \times 20\text{ m}$  resolution generated using geospatial methods (Cressie, 1991). Combining the soil chemical availabilities and tree species abundance measurements at the  $20\text{ m} \times 20\text{ m}$  scale I was able to calculate the resource distribution of each species.

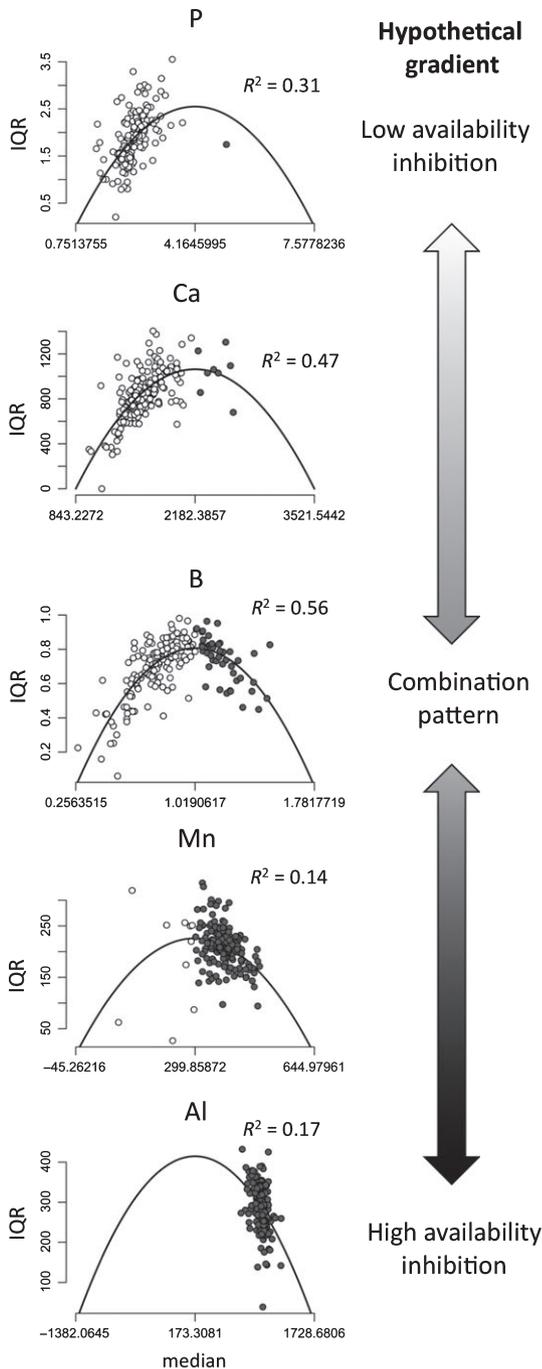
I determined where specialization occurs in different gradients by plotting the center (median) vs the breadth (interquartile range,

IQR) of species' resource distributions (Supporting Information Methods S1). To stay consistent with the original analysis of John *et al.* (2007), I excluded all species with fewer than 50 occurrences. Each point in the regression represents one species ( $n = 193$ ), where the median value ( $x$ -axis) splits the occurrences in two, such that half of all occurrences fall above and half below that concentration of the soil factor. Similarly, IQR ( $y$ -axis) is calculated by taking the difference between the third and first quartiles of resource concentrations where a species occurs (encompassing 50% of occurrences around the median). IQR is the most robust measure of scale, measuring the width of species' resource distributions while remaining relatively insensitive to extreme outliers.

Using the hypothesis that resource specialization increases at environmental extremes, I predicted that species with realized distributions centered at low ends of nutrient gradients (e.g. soil P) and high ends of soil toxins (soil Al) should have relatively narrower breadths. In order to represent a sample of chemical gradients with different qualitative effects that are known to play important roles in tropical forests (Sollins, 1998; John *et al.*, 2007; Condit *et al.*, 2013), I analyzed species distributions along the nutrients soil P, Ca and B, and the toxins soil manganese (Mn) and Al (see Schreeg *et al.*, 2010 for potential Mn toxicity at BCI). For each regression in Fig. 2, a first-order quadratic equation accounted for equal to or markedly greater variation in IQR relative to a linear regression (not shown). Further, each regression line exhibits a similar shape, with a peak in the predicted IQR at intermediate median values and declines as the species' medians either increase or decrease. I additionally conducted regressions using abundance data rarefied to the least abundant species (50 occurrences); however, as both the rarefied (Fig. S1) and original data (Fig. 2) exhibit the same qualitative patterns among soil resource gradients, I restrict my discussion here to the original data.

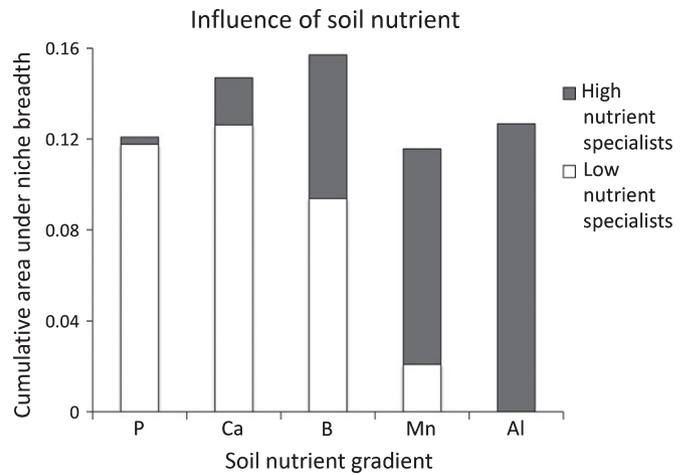
The patterns in Fig. 2 are shown using the full breadths of the quadratic regression line along the  $x$ -axis in order to highlight qualitative differences among the chemical gradients. Strikingly, Fig. 2 confirms the predicted relationship between specialization (decreased IQR) and environmental extremes. For the soil nutrients P and Ca, species with distributions centered at low availabilities have narrower distributions (lesser IQRs) than those centered at higher availabilities. By contrast, the opposite pattern is observed for gradients of potentially toxic soil factors (Mn and Al), with the narrowest distributions being associated with the highest availabilities. The soil B gradient exhibits a combination pattern, with species' centered at either end of the concentration gradient exhibiting relatively narrow distributions. Further, this pattern contributes to, but is not anticipated from, conclusions drawn from the original K-S niche-breadth analysis of soil nutrient gradients at BCI (John *et al.*, 2007).

To quantify this, I separated species into two groups depending on whether their median was less than or greater than the mid-point of the quadratic regression line (indicating lower niche breadths associated with low or high resource availabilities, respectively). Next, I calculated the contribution of low and high resource specialists to the total area under the cumulative niche-breadth curve. The patterns in Fig. 3 suggest that the cumulative areas for soil P and Ca are driven almost exclusively by low nutrient



**Fig. 2** Median vs interquartile range (IQR) for multiple soil chemical gradients at Barro Colorado Island. Each point represents one species ( $n = 193$ ). Points that fall on the left tail are open (low nutrient specialists), while points that fall on the right are closed (high nutrient specialists). Soil nutrient gradients show a pattern of increasing tree species' IQR with median resource availability, while the potential toxins manganese (Mn) and aluminum (Al) have the opposite pattern. Soil B gradients exhibit a combination of both patterns. Each plot displays the full breadth of a first-order quadratic regression line with an associated  $R^2$  value.

specialists, while the opposite is true for soil Mn and Al. Soil B exhibits an intermediate pattern, with high resource specialists contributing *c.* 40% of the area under the cumulative niche-breadth curve (compared to 2% and 9% for P and Ca, respectively). In fact,

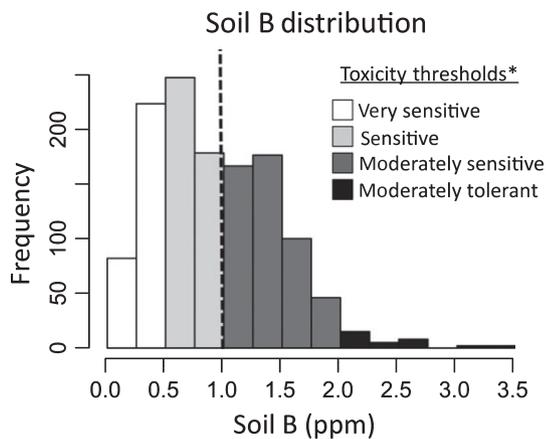


**Fig. 3** Cumulative area under the niche breadth curves broken down into whether they are from high or low-nutrient specialists. Note that soil boron (B) again appears to have a combination pattern. If soil B was limited to its low nutrient-specialists, it would have a lower influence than soil phosphorus (P), suggesting its unique pattern is indispensable in considering its influence relative to other soil gradients.

if high resource-specialists were removed from the analysis, soil B would have a lower influence than soil P or Ca.

John *et al.* (2007) hypothesized that soil B may be an important axis of specialization at BCI due to its pervasive scarcity. However, the patterns in Figs 2 and 3 indicate that low resource-specialization along soil B gradients is barely more than half the story. A literal interpretation for the combined pattern in Fig. 2 is that soil B gradients have sufficient breadth to limit plant vital rates with deficiency at its lowest concentrations and toxicity at its highest concentrations. As soil B is also the nutrient with the narrowest range between concentrations that are deficient and toxic to plants (Gupta *et al.*, 1985; Keren & Bingham, 1985; Maas, 1986; Goldberg, 1997), the next question is whether soil B availabilities at BCI reach concentrations high enough to be toxic to plants.

The credibility of soil B inhibiting plants at its highest availabilities can be assessed by comparing the soil B distribution at BCI with published thresholds of toxicity. While these threshold values are not available for tree species at BCI, it is common practice to infer the potential role of a soil toxin in natural systems via analogy with agriculture ones where data is available—in fact, this is precisely why soil Al and Mn are suspected to be toxic in tropical forests (e.g. Sollins, 1998; Schreeg *et al.*, 2010). The most extensive dataset on B toxicity thresholds have been published by Maas (1986), who conducted a meta-analysis of experiments aimed at determining levels of soil B in hydroponic feed solution that cause significant yield reduction in agricultural and ornamental plants. Maas (1986) found that the plants could be separated into functional groups depending on their tolerance to B toxicity, with the most sensitive functional group inhibited at concentrations as low as 0.5 ppm. The histogram in Fig. 4 shows the distribution of soil B values at BCI range from nearly 0 to > 3.5 ppm, which would span the toxicity thresholds of four functional groups of plants from Maas (1986).



**Fig. 4** A histogram of soil boron (B) values from Barro Colorado Island. The different colors represent B toxicity thresholds for four functional groups of plants. The results of the regression between median and interquartile range (IQR) values are consistent with tree species with medians < 1 ppm being adapted to soil B as a limiting soil nutrient, while species adapted to medians > 1 ppm are adapted to soil B as a soil toxin. \*Toxicity thresholds are reproduced from a meta-analysis by Maas (1986).

The patterns of resource specialization in Fig. 2 suggest that some tree species are specialized at relatively low concentrations of soil B, while others are specialized at relatively high concentrations of soil B. This type of specialization could be explained if a trade-off exists between traits that confer tolerance to B deficiency and toxicity. Consistent with this, Marschner (1995, p. 395) notes that there is a direct positive correlation between a species' critical thresholds for B deficiency and toxicity, such that low B specialists have relatively lower toxicity thresholds, and vice versa. Similarly, research on the physiological traits of B toxicity and deficiency tolerance document a trade-off between traits that either enhance B uptake and mobility (deficiency tolerance) or B efflux and internal complexation (toxicity tolerance) (e.g. Dell & Huang, 1997; Brown *et al.*, 2002; Sutton *et al.*, 2007; Camacho-Cristobal *et al.*, 2008). The quadratic regression in Fig. 2 demonstrates that tree species distributions become increasingly narrow at median B levels above 1 ppm, suggesting that tree species specialized along regions of B availability that cause inhibition in the 'moderately sensitive' functional group (Maas, 1986) may be adapted to B as a toxic, rather than deficient, growth limiting factor.

## Conclusions

The function of niche theory should be to provide an eco-evolutionary understanding of the extent and mechanisms of specialization, wherever it occurs. The search of the extent of environmental specialization is often the entry along this path, but only establishes the margin beyond a null-model that niches exist. This brings about the second step – the search for the dominant axes of specialization among individual gradients (e.g. using K-S niche-breadth analysis). These methods allow investigators to single out ecologically important gradients, but ignore qualitative differences among the gradients, as evidenced in the inability of K-S niche-breadth analyses to discriminate qualitative differences in where specialization occurs in soil nutrients and toxin gradients (Figs 2, 3).

The third step involves using a description of pattern to form hypotheses about the mechanisms of niche specialization.

The method of using quadratic regression between the median and IQR of species resource distributions can help investigators form hypotheses about the mechanisms of resource specialization. In the case of soil B, it suggested a unique pattern of resource specialization at both ends of a concentration gradient may be responsible for the greater proportion of specialists along soil B gradients relative to other soil nutrients and toxins. Specifically, the data are consistent with the hypotheses that tree species at BCI adapted to the lowest median levels of soil B availability are directly inhibited at the highest soil B concentrations found within their communities, and vice versa. This hypothesis could not be generated by the original K-S niche-breadth analysis. Further, the regressions in Fig. 2 suggest an ecologically important threshold at which trade-offs between tolerance to B toxicity and the breadth of a distribution may occur. This trade-off falls within published toxicity thresholds in agriculture and ornamental reference species (Maas, 1986), corroborating the hypotheses for toxicity effects at the highest soil B availabilities at BCI. The search for mechanism can be further guided by physiological literature on functional trade-offs between traits that confer tolerance to deficiency and toxicity.

The conclusions presented here are based on correlations and are subject to several potential sources of error. For example, tree species both respond to and influence the availability of chemical factors in the soil via the deposition of leaf litter and root exudates (Finzi *et al.*, 1998; Reed *et al.*, 2008; Van Haren *et al.*, 2010; but see Powers *et al.*, 2004). Further, the soil measurements used in my analysis were limited to a depth of 10 cm and thus may not indicate the availability of soil nutrients and toxins experienced by more deeply rooted tree species. However, while the patterns of resource specialization described here do not demonstrate causality, they provide new hypotheses for a phenomenon the ecological community has ignored. Time and experiments will tell if these hypotheses are valid.

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**Supporting Information**

Additional supporting information may be found in the online version of this article.

**Fig. S1** Median vs interquartile range (IQR) for multiple soil chemical gradients at Barro Colorado Island using data rarefied to the least abundant species (50 occurrences).

**Methods S1** Details on how regressions between median and interquartile range with both the original and rarefied data on species resource distributions were conducted.

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**Key words:** niche breadth, nutrient toxicity, resource gradients, soil boron, tropical forest.