

Changes in forest structure along an elevational gradient cause species-specific stress responses in tree seedlings

Abstract

4 bullet points (1) research conducted + rationale, (2) central methods, (3) key results, (4) main conclusions including key points of discussion.

Introduction

Rapid anthropogenic climate change is causing many species, across a wide range of taxa, to shift their distributions in space (??). ? estimates average latitude and poleward migration rates of NUM and NUM, respectively. For sessile taxa such as trees, range shifts occur as a result of differential recruitment and mortality over space REF. Mean annual temperature and precipitation regime have been identified as important drivers of range shifts in tree species (??), MORE?. It is important to consider however, that range shifts driven by a single environmental variable may cause recruitment of species in suboptimal habitats if range shifts outstrip acclimatory/adaptive potential REF. This may lead to reductions in local and regional species richness (Colwell et al. 2008), ecosystem functioning (Bellard et al. 2012), and ecosystem service provision (Dobson et al. 2011, Isbell et al. 2011). It is therefore important to predict how species will move whether their ranges will contract or expand, and whether species' ranges will shift at similar rates to fully predict impacts of range shifts on ecosystems.

The majority of efforts to predict species range shifts have used bioclimatic envelope models (?). Bioclimatic envelopes are constructed by correlating current species ranges with observed environmental conditions within those boundaries, then projecting spatial climate data into the future under different climate change scenarios to predict how the species boundaries will adjust in response (e.g. ????). (?).

Bioclimatic envelope models have been criticised for making a number of gross simplifications REF, INCLUDE EXAMPLES?. Basic bioclimatic envelope models assume that the breadth of the realised niche (observed spatial range) equals that of the fundamental (bioclimatic envelope) niche (Jump & Peñuelas 2005, Hoffmann & Sgrò 2011). This assumption is challenged by studies which demonstrate that the realised niche is often smaller than the fundamental niche, owing to biotic interactions with other species (Davis et al. 1998, Van der Putten et al. 2010, Ettinger et al. 2011).

Trees have overlapping generations, so the size composition and structure of the adult population will impact the next generation of seedlings.

In this study

Materials and Methods

Study Site

Data collection was conducted across 10 permanent 1 ha closed canopy forest plots in the Kosñipata Valley of Manú National Park, Peru (-13°N, -71°W, Figure ??, Table ??). The Kosñipata Valley has been identified as a potential migration corridor for lowland species to migrate to higher elevations in response to temperature increase (?) and so is an appropriate location to study range shift drivers. Plots are situated between 400 and 3200 m.a.s.l. along this migration corridor (Table ??, Figure ??). The plots form part of a larger plot network established by the Andes Biodiversity and Ecosystem Research Group (ABERG) in 2003 (??).

Study species

We chose nine tree species for comparison from a range of 1635 identified species within the 10 study plots. Species were selected according to their contrasting ranges (Figure ??), differences in genus migratory pattern (?), and because each species makes up a dominant proportion of the biomass in plots across their ranges (ABERG, unpublished data, Appendix VI). Despite having no quantitative range shift prediction information, *Iriartea deltoidea* and *Dictyocaryum lamarckianum* were included in order to observe potential differences between monocot and dicot species, as both are monocots. Both *I. deltoidea* and *D. lamarckianum* are large-seeded palm species, as such, they are expected to be migrating upslope, similar to other large-seeded palms (?). Seedlings of *Myrcia spp.* are difficult to reliably identify to species in the field and were thus sampled as a composite of three potential species: *Myrcia splendens*, *M. fallax*, and *M. rostrata*, referred to as *Myrcia spp.*.

Sampling and Measurement

Species were sampled in three plots representing the upper, middle and lower elevational extents of their ranges (Figure ??). Within each plot, a maximum of 10 seedlings were sampled. Seedling mortality creates a narrow bottleneck for tree survival in closed canopy tropical forests, seedlings are particularly sensitive to environment stress. Previous studies having demonstrated seedling vulnerable to climate change (?). something about dispersal not catching up at the same rate. To minimise the chance of pseudo-replication of sampled seedlings, seedlings closer than 5 m to another seedling were excluded from the analysis, as it cannot be guaranteed that the stems are not connected by a stolon or rhizome, it also ensures that competition radius measurements are truly independent. Within a cluster of seedlings, each seedling was assigned a number and a random number table was used to choose a single seedling for measurement.

Proxies for photosynthetic efficiency or is it capacity??? were measured on the highest fully-expanded leaf of each seedling. Leaf photosynthetic efficiency can be used as an indicator of physiological stress levels. Plants with a lower photosynthetic efficiency are more stressed than those with a higher efficiency. Chlorophyll-a fluorescence was measured using a Walz mini-PAM II (Walz Effeltrich, Germany), on a randomly selected area of adaxial leaf surface, avoiding prominent leaf veins according to (). Chlorophyll-a measurements were used to calculate F_v/F_m according to ?:

$$F_v/F_m = (F_m - F_o)/F_m \quad (1)$$

Where F_m is the maximal fluorescence in the dark and F_o is the minimal fluorescence in the dark (?). Fluorescence measurements were taken after exposing the seedling to 30 minutes of total darkness, to ensure complete dark adaptation (?). Dark-adapted F_v/F_m measures the photosynthetic efficiency of the leaf by relaxing the reaction centres prior to the fluorescence measurement. F_v/F_m is preferable to other chlorophyll fluorescence measures as it removes the noise created by environmental conditions at the time of measurement, instead providing a measure of the underlying photosynthetic efficiency. A reduction in F_v/F_m is indicative of plant stress. Here, individuals with F_v/F_m values <0.7 are said to be experiencing stress (?).

In addition to F_v/F_m leaf relative chlorophyll content was measured using a multi-spectral SPAD-meter (Minolta SPAD-502Plus, Spectrum Technologies, Plainfield, Illinois, USA). To account for variation in chlorophyll content across the leaf REF, SPAD measurements were taken at three random points on the leaf and the geometric mean was used in analyses.

Leaf and whole-plant morphological measurements

To assess adult-seedling competition interactions an adapted version of the Iterative Hegyi Index was implemented (???). Our adapted 'Iterative Seedling Index' (ISI) uses adult tree trunk diameter at ~1.3 m from ground level (Diameter at Breast Height, DBH) and the distance of trees from the seedling to calculate an index for each seedling, higher values indicate greater competition pressure from surrounding adult trees:

$$ISI_i = \log\left(\sum_{j=1}^n \left(\frac{1}{DIST_{ij}} D_j\right)\right) \quad (2)$$

where D_j is the DBH of a competitor tree and $DIST_{ij}$ is the euclidean distance between seedling i and competitor tree j . ISI was log transformed for analysis, as results spanned multiple orders of magnitude. The 'iterative' aspect refers to the selection of competitor trees. The radius around the seedling is divided into 12 30° sectors, only the nearest tree >10 cm DBH within each sector is measured (Figure ??). The size of the competition radius (C_R) is defined as:

$$C_R = 2 \times \sqrt{\frac{10,000}{N}} \quad (3)$$

where N is the number of trees >10 cm DBH per ha (stand density). Stand density data was taken from ABERG census data within each plot (ABERG unpublished data) and used to estimate C_R for VC, for which no stand density data exists (Supplementary material). C_R was rounded to the nearest metre for ease of measurement (Table ??). An iterative selection method for competitive trees assumes that if the path between two trees is blocked, the intensity of competition between them will be greatly reduced (?).

Statistical Analysis

A matrix of linear mixed effects models were compared to test for the presence and strength of the relationship between each competition variable and each plant trait. All model variables were standardised to allow easy comparison of effect sizes, according to (???). Model quality was compared using Akaike Information Criteria (AIC) (?), Akaike weights (W_i), and fixed effect pseudo- R^2 values (R_M^2).

Add linear mixed model set up as an equation or schematic diagram or something

Simple linear regressions investigated the relationship between competition intensity and elevation. All statistical analyses were conducted using R, version 3.2.4 (?).

Results

$$Chl = 0.53e^{0.0364 \times SPAD}$$

Discussion

Conclusion

Forest structure based competition affects physiological stress independently of elevation