

This is the peer reviewed version of the following article: Fortunel, C., Paine, C. E. T., Fine, P. V. A., Mesones, I., Goret, J.-Y., Burban, B., Cazal, J., Baraloto, C. (2016), There's no place like home: seedling mortality contributes to the habitat specialisation of tree species across Amazonia. *Ecology Letters*, 19: 1256–1266. doi: 10.1111/ele.12661, which has been published in final form at <http://onlinelibrary.wiley.com/doi/10.1111/ele.12661/full>. This article may be used for non-commercial purposes in accordance With Wiley Terms and Conditions for self-archiving.

ECOLOGY LETTERS

There's no place like home: seedling mortality contributes to the habitat specialization of tree species across Amazonia

| | |
|-------------------------------|---|
| Journal: | <i>Ecology Letters</i> |
| Manuscript ID | ELE-00487-2016.R1 |
| Manuscript Type: | Letters |
| Date Submitted by the Author: | n/a |
| Complete List of Authors: | Fortunel, Claire; University of California, Los Angeles, Department of Ecology and Evolutionary Biology Paine, C. E. Timothy; University of Stirling, Biological & Environmental Sciences Fine, Paul; University of California, Berkeley, Integrative Biology; Mesones, Italo; University of California, Berkeley, Integrative Biology Goret, Jean-Yves; INRA, UMR Ecologie des Forêts de Guyane Burban, Benoit; INRA, UMR Ecologie des Forêts de Guyane Cazal, Jocelyn; INRA, UMR Ecologie des Forêts de Guyane Baraloto, Christopher; Florida International University, International Center of Tropical Botany, Department of Biological Sciences |
| Key Words: | Amazon basin, forests habitats, habitat association, herbivory, light availability, plant lineages, seedling performance, soil fertility, tropical trees, rainfall temporal variation |
| | |

There’s no place like home: seedling mortality contributes to the habitat specialization of tree species across Amazonia

Claire Fortunel^{1,2*}, C. E. Timothy Paine³, Paul V. A. Fine⁴, Italo Mesones⁴, Jean-Yves Goret², Benoit Burban², Jocelyn Cazal², Christopher Baraloto^{2,5}

¹Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA

²INRA, UMR Ecologie des Forêts de Guyane, BP 709, 97387 Kourou Cedex, France

³Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, UK

⁴Department of Integrative Biology, University of California, Berkeley, CA 94720, USA

⁵International Center of Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL 33199, USA

Running title: Habitat specialization in tropical forests

Keywords: Amazon basin, forests habitats, habitat association, herbivory, light availability, plant lineages, rainfall temporal variation, seedling performance, soil fertility, tropical trees.

Type of article: Letters

Number of words in the abstract: 150

23 **Number of words in main text** (excluding abstract, acknowledgements, references, table and
24 figure legends): 4983

25 **Number of references:** 50

26 **Number of figures:** 3

27 **Number of tables:** 3

28

29 * To whom correspondence should be addressed: Department of Ecology and Evolutionary
30 Biology, University of California, Los Angeles, CA 90095; E-mail: cl.fortunel@gmail.com

31

32 **Statement of authorship:** CF, CB and PVAF designed the study. CF, CB, PVAF, IM, JYG, BB,
33 and JC set up the reciprocal transplant experiment and performed the seedling censuses. CF and
34 CETP analyzed the data. CF, CB and PVAF wrote the first draft of the manuscript. All authors
35 contributed to revisions.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Abstract

Understanding the mechanisms generating species distributions remains a challenge, especially in hyperdiverse tropical forests. We evaluated the role of rainfall variation, soil gradients and herbivory on seedling mortality, and how variation in seedling performance along these gradients contributes to habitat specialization. In a four-year experiment, replicated at the two extremes of the Amazon basin, we reciprocally transplanted 4638 tree seedlings of 41 habitat-specialist species from seven phylogenetic lineages among the three most important forest habitats of lowland Amazonia. Rainfall variation, flooding and soil gradients strongly influenced seedling mortality, whereas herbivory had negligible impact. Seedling mortality varied strongly among habitats, consistent with predictions for habitat specialists in most lineages. This suggests that seedling performance is a primary determinant of the habitat associations of adult trees across Amazonia. It further suggests that tree diversity, currently mostly harbored in terra firme forests, may be strongly impacted by the predicted climate changes in Amazonia.

Introduction

Spatial turnover in species composition is an important contributor to the overall regional species diversity of the Amazon basin (Gentry 1988; ter Steege *et al.* 2006, 2013), which represents about 40 % of the world's tropical forest (Hubbell *et al.* 2008) and harbors the highest diversity of tree species on the planet (Slik *et al.* 2015). This beta-diversity correlates strongly with climatic and edaphic gradients (ter Steege *et al.* 2006; Davidar *et al.* 2007), suggesting a tight species-specific coupling of environmental factors and optimal strategies for survival and growth (Engelbrecht *et al.* 2007; Toledo *et al.* 2012). In the face of rapid climate change in the tropics (Asner *et al.* 2010; Feeley *et al.* 2012), understanding the variation in performance of tree species along environmental gradients takes on special significance. In recent years, the western Amazon has witnessed both the longest drought (2009) and the highest flood levels (2012) in recorded history (Lewis *et al.* 2011; Satyamurty *et al.* 2013). These extreme events are likely not only to impact the performance of adult trees (Brienen *et al.* 2015) but also to stress tree seedlings, which may impact forest composition over the long term (Kursar *et al.* 2009; Lucas *et al.* 2013). Differential performance of seedlings of co-occurring species is a major contributor to the distribution of adult trees (Brenes-Arguedas *et al.* 2009; Comita *et al.* 2009; Metz 2012). Thus, disentangling the ecological mechanisms influencing seedling performance will lead to a better understanding of habitat specialization of tropical trees (Fine *et al.* 2004).

To assess the effects of abiotic and trophic factors on seedling performance, we reciprocally transplanted species among contrasting habitats while manipulating the presence of herbivores. The experiment was replicated in French Guiana and Peru, spanning broad soil fertility and rainfall seasonality gradients: French Guianan sites are characterized by infertile eroded clay soils adjacent to nutrient-poor sands and a pronounced dry season, whereas Peruvian sites are

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

situated on fertile clay soils adjacent to nutrient-poor sands and have no annual dry season but experience high water levels associated with flooding of large rivers (Baraloto *et al.* 2011). Such a broad experimental scope is key to determine the consistency of the influence of abiotic and trophic factors on seedling performance across Amazonia.

We focused on the three most-common habitats of lowland Amazonian forests: terra firme forests on clay-rich soils, seasonally-flooded forests and white-sand forests. These habitats span the ranges of resource availability, flooding, drought, forest structure, and floristic composition found in lowland Amazonia (Fine *et al.* 2010; Baraloto *et al.* 2011). Terra firme forests have relatively nutrient-rich soils with high clay content, and experience relatively minor abiotic stresses (Baraloto *et al.* 2011). Seasonally-flooded forests have relatively nutrient-rich soils but experience at least three months of annual flooding where the water table reaches the soil surface, which imposes a severe stress from low soil oxygen (Parolin *et al.* 2004; Lucas *et al.* 2013). The soils underlying white-sand forests are among the most nutrient-poor that have been recorded worldwide (Quesada *et al.* 2011). Moreover, water availability becomes extremely low in white-sand forests during droughts (Baraloto *et al.* 2006).

When abiotic stress is limited and sufficient light is available, terra firme specialists are predicted to outcompete seasonally-flooded and white-sand specialists because of lower investment in flood and drought tolerance and/or herbivore defense mechanisms. In addition, if natural enemies preferentially attack non-specialists, they can interact with abiotic factors to drive habitat specialization, in particular when sufficient light is available to allow fast seedling growth (Fine *et al.* 2004). However, tropical tree seedlings typically spend years in the shaded understory before a gap in the forest canopy provides sufficient light for them to reach a size at which they start competing with neighboring trees (Paine *et al.* 2008; Lasky *et al.* 2015). We

thus focus our study on seedling mortality in the shaded understory in order to understand the ecological mechanisms that operate at this critical life stage.

Reciprocal transplant experiments are especially useful because they allow for equal sample sizes to disentangle the mechanisms shaping habitat specialization within and among lineages. Phylogenetic replication is important because the relative investment in growth and defense strategies varies among lineages (Fine *et al.* 2004, 2006; Baraloto *et al.* 2012). Moreover fast demographic rates have been shown to promote high diversification rates in Amazonian tree lineages (Baker *et al.* 2014). In this study, we focused on 41 species from seven monophyletic lineages that occur across Amazonia, differ in diversification rates and include species associated with each of the three habitats. By comparing habitat-mediated seedling performance within and among lineages, we can investigate whether different strategies at the seedling stage may contribute to habitat specialization and lineage diversification.

In particular, we addressed the following questions:

1. How do abiotic and trophic factors influence seedling mortality across Amazonia? We expect rainfall variation, soil and light factors to primarily influence seedling mortality, whereas herbivory would exacerbate abiotic effects on seedling mortality (Fine *et al.* 2004; Brenes-Arguedas *et al.* 2009). In particular, we expect greater seedling mortality with lower rainfall (Engelbrecht & Kursar 2003; Brenes-Arguedas *et al.* 2009), lower soil fertility (Baraloto *et al.* 2006; Santiago *et al.* 2012) and less available light (Andersen *et al.* 2014). Additionally, we expect those effects to increase with increasing differences between local conditions of transplantation and the home habitat of the specialist.

2. Does differential seedling performance across the steep habitat gradients reflect habitat specialization? We propose a novel framework that underlines two distinct processes that

1
2
3 118 contribute to habitat specialization: habitat specialists can become locally abundant either
4
5 119 because (i) they perform better in their home habitat than in other habitats, a classical definition
6
7
8 120 of habitat specialization from reciprocal transplants (Bennington *et al.* 2012); and/or (ii) they
9
10 121 perform better in their home habitat than other species from the regional pool that are not
11
12 122 strongly associated with that habitat. We refer to these as the best at home and home advantage
13
14 123 hypotheses respectively (Table 1). Differential performance of species among habitats may arise
15
16
17 124 through several mechanisms. We expect that flooding and drought are important drivers of
18
19 125 seedling performance, favoring seasonally-flooded and white-sand specialists, respectively, in
20
21 126 their home habitats (Baraloto *et al.* 2005, 2007); whereas trophic filters are key to explain the
22
23 127 dominance of terra firme specialists in their home habitat, so long as sufficient light is available
24
25
26 128 for growth (Fine *et al.* 2004).

27
28
29 129 3. Are the effects of biotic and trophic factors on seedling performance consistent across
30
31 130 countries and lineages? We predict contrasts in seedling performance among habitats to be
32
33 131 stronger in Peru than in French Guiana because of higher soil fertility and more extreme flooding
34
35 132 regimes (Baraloto *et al.* 2011). We predict that within-lineage contrasts among habitat specialists
36
37 133 will be relatively consistent among lineages (Fine *et al.* 2006); alternatively, lineages with rapid
38
39 134 diversification rates could exhibit more marked contrasts in seedling performance (Baker *et al.*
40
41
42 135 2014).

43
44
45 136 To test our hypotheses, we conducted a reciprocal transplant experiment at an unprecedented
46
47 137 scale, with 4638 seedlings belonging to 41 habitat-specialist species over more than four years
48
49 138 across three contrasting habitats and two countries. We provide a novel, comprehensive
50
51
52 139 framework to test how variation in seedling performance contributes to habitat specialization.
53
54
55
56
57
58
59
60

1
2
3 140 Our study is the first to quantify environmental variables describing the habitat of transplantation
4
5 141 to test the mechanisms generating habitat specialization in tropical trees at a continental scale.
6
7
8 142

10 143 **Methods**

12 144 *Study sites*

15 145 In both French Guiana and Peru, we selected 60 sites divided equally among the three
16
17 146 habitats (terra firme, seasonally-flooded and white-sand forests) that cover the ranges of soil
18
19
20 147 fertility and flooding in both countries (Baraloto *et al.* 2011). Sites were separated by at least 15
21
22 148 m and located adjacent to permanent plots in the Laussat Reserve in northwestern French
23
24 149 Guiana, and in the Allpahuayo-Mishana National Reserve in northeastern Peru (Baraloto *et al.*
25
26 150 2011). At each site, we established paired experimental 2 m by 2 m plots in areas of shaded
27
28 151 understory. We covered the exclosure plot with 1-mm nylon mesh to reduce herbivory, and, as
29
30 152 the netting reduced incident light by about 8 %, we placed netting above the control plot to
31
32 153 replicate any treatment shading (Fine *et al.* 2004). In each country, we thus established 120 plots
33
34 154 (60 controls and 60 exclosures) corresponding to 40 replicate plots in each habitat. Every month,
35
36 155 litter that accumulated on the roof of each plot was removed and spread evenly on the ground
37
38 156 beneath, thereby reducing the shading effect of litter and stains on the netting and equalizing it
39
40 157 across plots receiving different intensities of litterfall.
41
42
43
44
45

46 158 At the start of the experiment, we determined light availability and soil fertility and texture
47
48 159 in all 120 plots in each country (Table S1). Hemispherical photos were taken at the center of the
49
50 160 roof of each plot with a fish-eye lens at 1.5 m high (Coolpix 995, Nikon). Total light availability
51
52 161 (%) was estimated with the Gap Light Analyzer software (Frazer *et al.* 1999). In each plot, 0-15
53
54 162 cm depth soil cores were bulked, dried at 25°C to constant mass and sieved to 2 mm for
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

subsequent physical and chemical analyses at the University of California, Davis Analytical Laboratory (see details in Baraloto *et al.* 2011). From April 2010 to December 2013, soil water volume content ($\text{m}^3_{\text{water}} \cdot \text{m}^{-3}_{\text{soil}}$) was measured monthly in each plot in French Guiana using a soil moisture sensor (TRIME-PICO 64, Imko).

For each country, we retrieved the cumulative daily rainfall series ($\text{mm} \cdot \text{day}^{-1}$, Table S1) over the course of the experiment from the estimate 3B42-V7 of Tropical Rainfall Measuring Mission of NASA's Goddard Earth Science Data and Information Services Center (<http://disc.gsfc.nasa.gov/precipitation/tovas>). Our experiment ran from 2009 to 2013, during which mean annual rainfall was 2210 and 3085 mm in French Guiana and Peru respectively. In French Guiana, our experiment coincided with the region's longest recorded drought in 2009. In both countries, it also coincided with the highest recorded flood levels in 2012. Specifically, all seedlings were submerged in Peruvian seasonally-flooded plots between March 25th and June 13th 2012, a total of 49 days of complete inundation, whereas all seedlings experienced a saturated soil with a water table at the soil surface in French Guianan seasonally-flooded plots between April 11th and August 7th 2012, a total of 118 days during which soil water volume content remained above 80 %.

Species selection and transplantation

We focused on seven widespread monophyletic lineages that include species associated with each of the three habitats (Table 2). These lineages are phylogenetically dispersed within the eudicots, the dominant angiosperms in tropical rainforests, with representatives of euasterids (*Micropholis* [Sapotaceae] and *Licania* [Chrysobalanaceae]), fabids (*Inga* and *Swartzia* [Fabaceae] and *Eschweilera* [Lecythidaceae]), and malvids (Bombacoideae [Malvaceae] and *Protium* [Burseraceae]). The seven lineages span the range of estimated diversification rates

reported for more than 50 tropical tree lineages (Baker *et al.* 2014). We selected two to five species from each lineage that are common in the regional species pool and associated with terra firme, seasonally-flooded or white-sand forests, as determined by our tree inventories of a network of 74 plots across both countries (Baraloto *et al.* 2011). We included seven lineages and 25 species in French Guiana, and six lineages and 16 species in Peru. Our designations of habitat association for these 41 species are consistent with species accounts from many published sources (e.g. Fine *et al.* 2010; ter Steege *et al.* 2013).

We collected seeds and/or recently germinated seedlings from at least three parent trees within the home habitat of each species and distributed them evenly across plots. Seeds were germinated in a shade house before transplantation in the field. One seedling per species was randomly planted in each plot, with a 30-cm grid spacing that corresponds to a density (9 individuals.m⁻²) at which competition among seedlings is minimal (Paine *et al.* 2008). Transplantation was completed between March and May 2009 in French Guiana and between March and April 2010 in Peru. Monthly assessments of seedling mortality were conducted until November 2013 in French Guiana and until July 2012 in Peru, giving a total experimental duration of 53 months in French Guiana and 29 months in Peru, resulting in 130,589 and 86,144 observations in French Guiana and Peru, respectively. Seedling height was measured at the beginning and end of the experiment. We calculated seedling relative growth rate for height over the duration of the experiment in each country.

Statistical analyses

We used generalized linear mixed models (GLMMs) in each country to test how environmental gradients influence temporal variation in seedling mortality (Q_1). We predicted monthly seedling mortality (mortality_t) as a binary response variable using the abiotic variables,

herbivore-exclusion treatment and plant lineage. Species identity was included as a random effect to account for different species responses to abiotic variables and herbivory ($R \text{ species}_i$). Plot identity was included as a random effect to account for autocorrelation in seedling mortality among plots ($R \text{ plot}_j$). Initial analyses indicated that temporal variation in rainfall in each country affected seedling mortality and, consistently with studies on climate effect on tree performance (e.g. Uriarte *et al.* 2016), the best rainfall indicator was the mean daily precipitation that had fallen in the 30-days census interval ($\text{rain}_{30\text{days}}$). To account for this, we included $\text{rain}_{30\text{days}}$ as a continuous covariate. To describe abiotic gradients, we selected the variables best describing the major axes of a principal component analysis of all abiotic variables in the 120 plots in each country (Fig. S1), which were soil nitrogen content (soil_N), soil sand content ($\text{soil}_{\text{Sand}}$) and total light availability (light). All continuous predictor variables were scaled to mean 0 and standard deviation 1 to allow their relative effect sizes to be evaluated.

We compared two alternate GLMMs to evaluate if abiotic effects on seedling mortality increase with increasing differences between local conditions of habitat of transplantation and home habitat of the specialist (Q_1). The first GLMM included terms for environmental differences (Δ) between habitat of transplantation and home habitat of the specialist:

$$\text{mortality}_t = \text{lineage} * (\Delta \text{soil}_N + \Delta \text{soil}_{\text{Sand}} + \Delta \text{light} + \text{rain}_{30\text{days}} + \text{treatment}) + R \text{ species}_i + R \text{ plot}_j$$

where ‘*’ denotes interaction between terms. The second GLMM had terms for local conditions of habitat of transplantation: $\text{mortality}_t = \text{lineage} * (\text{soil}_N + \text{soil}_{\text{Sand}} + \text{light} + \text{rain}_{30\text{days}} + \text{treatment}) + R \text{ species}_i + R \text{ plot}_j$. We selected the best model between these two alternate GLMMs in each country using the Bayesian Information Criterion (BIC; Burnham & Anderson 2004). We determined the significance of each term of the

best model in each country using likelihood ratio test statistics with 1000 parametric bootstrap replicates (Halekoh & Højsgaard 2014).

To address the predictions of the best at home and home advantage hypotheses (Q_2 and Q_3), we used generalized linear models (GLMs) in each country to test the effects of habitat of transplantation on seedling performance at the end of the experiment ($mortality_f$ and $growth_f$) for (i) each group of habitat specialists (e.g. all white-sand specialists) using $performance_f = habitat_{home} * habitat_{transplantation}$ (Q_2), and (ii) each group of habitat specialists by lineage using $performance_f = lineage * habitat_{home} * habitat_{transplantation}$ (Q_3). We used Tukey's HSD tests to examine the best at home and the home advantage hypotheses (Q_2 and Q_3), which make different predictions for specialists from different habitats (Table 1).

All analyses were conducted in the R 3.2.5 statistical platform (R Development Core Team 2016) using package *ade4* (Dray & Dufour 2007), *lme4* (Bates 2005) and *pbkrtest* (Halekoh & Højsgaard 2014).

Results

Effects of rainfall, soil and light on seedling mortality rates

Increasing rainfall strongly reduced seedling mortality in French Guiana and Peru (Table 3, see details in Table S2). This rainfall effect was consistent across habitat specialists (Fig. 1a,c) and lineages (Fig. S2) in both countries. Overall, seedling mortality decreased with increasing soil sand content and light availability in both countries (Table S2). Seedling mortality decreased with increasing soil nitrogen content in French Guiana but not in Peru (Table S2). Specialists from contrasting habitats, on the other hand, showed variable responses to soil and light factors. Seasonally-flooded specialists showed higher seedling mortality with increasing soil sand

1
2
3 254 content in French Guiana but not in Peru (Fig. 1b,d). Terra firme specialists exhibited higher
4
5 255 seedling mortality with increasing soil sand content in both countries. White-sand specialists
6
7
8 256 exhibited lower seedling mortality with increasing soil sand content in French Guiana, but
9
10 257 showed the opposite pattern in Peru. In addition, the effects of soil and light factors on seedling
11
12 258 mortality varied strongly among lineages (Fig. S2), species (Fig. S3) and countries (Table S2). In
13
14 259 both countries, seedling mortality was much better explained by soil and light conditions in the
15
16 260 plot of transplantation (Table S2) than by increasing differences between local conditions of
17
18 261 transplantation and the home habitat (Table S3) ($\Delta\text{BIC}=41.84$ in French Guiana and 56.72 in
19
20 262 Peru).

21
22 263 ***Differences in seedling mortality among habitats and countries***

23
24
25 264 The best at home and home advantage hypotheses make context dependent predictions
26
27 265 (Table 1). Synthesizing the patterns of mortality across lineages and countries, our specific
28
29 266 predictions were broadly supported by the evidence, with 4 out of 6, and 6 out of 6 of the
30
31 267 predictions met in French Guiana and Peru respectively (Fig. 2). As predicted, seasonally-
32
33 268 flooded specialists did not experience significant differences in mortality when planted into other
34
35 269 habitats in either country (Fig. 2, best at home). Moreover, they showed lower mortality than
36
37 270 terra firme and white-sand specialists in seasonally-flooded forests in both countries (Fig. 2,
38
39 271 home advantage). This difference was especially pronounced in Peru, where species not
40
41 272 associated with flooded forests experienced more than twice the mortality rate of seasonally-
42
43 273 flooded specialists (Fig. 2b). In both countries, terra firme specialists exhibited lower mortality at
44
45 274 home than in other habitats (Fig. 2, best at home). We predicted no home advantage of terra
46
47 275 firme specialists, yet results were equivocal with a slight home advantage of terra firme
48
49 276 specialists in French Guiana but not in Peru (Fig. 2, home advantage). Also as predicted, white-
50
51
52
53
54
55
56
57
58
59
60

277 sand specialists had lower mortality at home than in other habitats in both countries (Fig. 2, best
 278 at home) and had lower mortality than seasonally-flooded and terra firme specialists in white-
 279 sands in Peru but not in French Guiana (Fig. 2, home advantage). In addition, seedling mortality
 280 at the end of the experiment was lower in French Guiana than in Peru (31.8 and 49.2 %
 281 respectively, F -value=146.60, $P<0.001$).

282 ***Differences in seedling mortality within and among lineages***

283 Considering seedling mortality within lineages in each country, we found further
 284 evidence for the specific predictions of the best at home and the home advantage hypotheses
 285 (Fig. 3 and S4). As expected, seasonally-flooded forest specialists generally showed similar
 286 mortality between home and other habitats (Fig. 3, best at home), with seasonally-flooded forest
 287 specialists from only one lineage (*Inga*) surviving better at home in Peru. Seasonally-flooded
 288 forest specialists enjoyed consistent, strong home advantages over non-specialist congeners in
 289 Peru (Fig. 3), whereas only two seasonally-flooded forest specialists (*P. opacum* and *L.*
 290 *macrophylla*) showed home advantage in French Guiana (Fig. S4). Terra firme specialists
 291 typically had low mortality at home in both countries (Fig. 3, best at home), but this low
 292 mortality in terra firme was frequently equaled by congeners specialized to other habitats (Fig.
 293 S4), consistent with our prediction that terra firme specialists would not exhibit home
 294 advantages. White-sand specialists from one lineage (Bombacoideae) in French Guiana and from
 295 all lineages in Peru exhibited the lowest mortality rates in their home habitat (Fig. 3, best at
 296 home), but they were nearly extirpated from seasonally-flooded forests in Peru (Fig. S4). In Peru,
 297 white-sand specialists from two lineages (*Protium* and *Swartzia*) had much lower mortality in
 298 white-sands than did congeners with contrasting habitat preferences (Fig. 3, home advantage).

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

299 Although we observed different degrees of contrasting species performance among lineages, we
300 found no pattern consistent with lineage age or diversification rate (Table 2).

301 ***Growth and herbivory***

302 Seedling growth patterns across lineages and countries supported many predictions of the
303 best at home and home advantage hypotheses, with 4 out of 6, and 5 out of 6 of our predictions
304 met in French Guiana and Peru respectively (Table 1, Fig. S5). Seasonally-flooded specialists
305 grew more rapidly at home than in other habitats in both countries; in Peruvian seasonally-
306 flooded forests, they grew faster than terra firme and white-sand specialists. Terra firme
307 specialists grew more rapidly at home than elsewhere in Peru, but in terra firme forests in both
308 countries, they grew no faster than specialists from other habitats. White-sand specialists had
309 higher growth rates at home than in other habitats in French Guiana, and grew faster than
310 specialists from other habitats in both countries. Over the course of the experiment, seedlings
311 grew faster in French Guiana than in Peru (0.013 vs. 0.010 mm.mm⁻¹.month⁻¹ respectively, F-
312 value=53.23, P<0.001).

313 Seedling growth rates were consistent with those reported by Baraloto *et al.* (2005) for
314 seedlings transplanted to shaded understory sites in French Guiana. Seedlings grew about five
315 times slower than seedlings in a similar experiment installed a few kilometers from our Peruvian
316 site (Fine *et al.* 2004), which incorporated three of the same lineages and some of the same
317 species, but which was installed in areas with much higher light availability. Nevertheless,
318 slower growth in our experiment may have limited leaf production and thus herbivore attack on
319 new leaves. In fact, although rates of herbivory were significantly greater in the controls than in
320 the exclosures (4.70 and 1.65 % respectively), they were about three times lower than rates
321 reported by Fine *et al.* (2004). We found that herbivore protection reduced seedling mortality in

French Guiana but not in Peru (Table S2), and thus for the seedlings in our study it played no consistent role in generating habitat associations across Amazonia.

Discussion

Using a reciprocal transplant experiment replicated at two ends of the Amazon basin, we investigated the effects of temporal variation in rainfall and soil gradients, controlling for herbivores, on seedling mortality of habitat specialists. We highlight differential patterns of seedling performance that reflect habitat specialization within and among tree lineages and that likely contribute to the distribution of trees across Amazonia.

Variation in seedling mortality along abiotic gradients

Integrating quantitative rainfall fluctuations over the course of the experiment in each country, we showed compelling evidence for the role of rainfall variation on seedling mortality. Seedling mortality was lower during periods of elevated rainfall for all habitat specialists in both countries (Fig. 1), consistent with previous studies showing a strong sensitivity of tropical tree seedlings to water addition (Engelbrecht & Kursar 2003; Brenes-Arguedas *et al.* 2009) and between dry and wet seasons (Lin *et al.* 2012; Brenes-Arguedas *et al.* 2013). Moreover, extreme flooding in 2012 in Peru led to the elevated mortality of non-specialists in seasonally-flooded forests (Fig. 2). Our study thus emphasizes the importance of seasonal and inter-annual variations in climate, in addition to climatic averages, to better understand how seedling dynamics, and subsequent tree species distributions, will respond to the increasing frequency or severity of droughts and floods that are predicted to occur in the Amazon (Asner *et al.* 2010; IPCC 2014).

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

In both countries, seedling mortality decreased with increasing soil sand content, which contrasts with previous work showing greater mortality in the nutrient-poor soils of white-sand forests than in the fertile soils of terra firme and seasonally-flooded forests (Baraloto *et al.* 2006; Santiago *et al.* 2012). Habitat specialists sometimes exhibited contrasting sensitivity to local abiotic factors between countries. For instance, white-sand specialists had lower mortality with increasing soil sand content in French Guiana, whereas they showed the opposite pattern in Peru (Fig. 1). This divergence may arise because of differences in abiotic gradients between countries: soil fertility and sand content vary independently in French Guiana but co-vary in Peru (Fig. S1). A challenge for future studies will be to disentangle the links between climate variation and soil components (water, nutrients and mycorrhizae), and their relative effects on plant performance to better understand the underlying mechanisms shaping species distributions.

How seedling mortality contributes to habitat specialization

Overall, we found strong support for our predictions regarding habitat specialization (Table 1), suggesting that abiotic filtering at the seedling stage plays a vital role in determining the beta-diversity of tropical tree communities along environmental gradients. In particular, seasonally-flooded specialists had a strong home advantage, which may stem from their ability to tolerate the anoxia associated with flooding (Parolin *et al.* 2004; Lucas *et al.* 2013). Seasonally-flooded specialists did not perform best at home, which suggests that they may be dispersal-limited across habitats (Baraloto *et al.* 2007). White-sand specialists outperformed others at home, likely because they can tolerate drought stress and low soil fertility (Baraloto *et al.* 2006). White-sand specialists performed best at home, which may be due to stress from low soil oxygen during heavy rains or pathogen attack in seasonally-flooded and terra firme forests. Finally, terra firme specialists showed no strong home advantage but survived best at home, suggesting that they

may be particularly vulnerable to drought and flooding in white-sand and flooded forests, respectively.

Mechanisms operating at life stages other than the seedling stage can also influence habitat association in trees, including seed dispersal, seed predation and competition among established adult trees (Wright 2002). However the seedling stage has been increasingly recognized as a critical determinant of forest dynamics (Comita *et al.* 2009; Metz 2012; Green *et al.* 2014). Evaluating forest dynamics in a fifty-year study in an Australian tropical forest, Green *et al.* (2014) found that non-random mortality with respect to species identity occurred mostly at the seedling stage. The strong habitat-mediated differences in seedling mortality found in our study may thus largely shape patterns of habitat association found in adult trees at the scale of the Amazon region.

Predicted climate changes in Amazonia may strongly impact tree species composition via this strong habitat-related variation in seedling mortality. In particular, as terra firme forests cover more than 80 % of lowland Amazonia (ter Steege *et al.* 2000) and harbor at least 80 % of its tree diversity (ter Steege *et al.* 2013), the vulnerability of terra firme specialists to extreme climatic events may have disproportionate consequences for Amazonian diversity. Recent global models of climate change over the next fifty years predict that the Amazon basin is likely to experience more extreme floods and droughts (IPCC 2014), which could promote habitat expansion for seasonally-flooded and white-sand specialists respectively at the expense of terra firme specialists. Indeed, a recent modeling study predicted that late-successional trees from clay soil habitats are much more vulnerable to climate change than those in sandy soil habitats (Levine *et al.* 2016). The magnitude of these climatic effects may be higher in the western

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Amazon where seasonally-flooded specialists are uniquely tolerant to flooding and only white-sand specialists are well adapted to short-term dry spells.

Contrasting habitat-mediated seedling mortality among countries and congeners

Patterns of habitat specialization were stronger in Peru than in French Guiana, a difference that could have at least two causes. First, French Guianan forests generally have poorer soils and experience less rainfall but greater seasonality than Peruvian forests (Baraloto *et al.* 2011). This may filter the entire regional species pool for survival-oriented strategies, allowing greater tolerance of low resource availability and drier conditions (Baraloto *et al.* 2007). Indeed, seedling mortality was lower in French Guiana than in Peru, and congeneric species in some lineages in French Guiana exhibited similar seedling mortality in all habitats (e.g. *Eschweilera*, *Inga* and *Micropholis* species with mortality rates lower than 30 % after four years), making the potential advantages of habitat specialists harder to detect. Second, seasonally-flooded specialists in Peru were especially resistant to the extreme flood that occurred in 2012, resulting in the almost complete mortality of white-sand and terra firme specialists planted in the seasonally-flooded plots. High water levels associated with flooding of large rivers means that inundation is a frequent occurrence in Peru but comparatively rare in French Guiana, suggesting that periodic flooding may be a much stronger filter in the western Amazon (Parolin *et al.* 2004).

Habitat-specialist congeners exhibited contrasting habitat-related seedling performance for three out of seven lineages in French Guiana and for all six lineages in Peru. We selected these focal lineages in part because they included species associated with contrasting habitats, and we demonstrated that seedling mortality patterns were consistent with the habitat association patterns of adult trees. This result is consistent with the hypothesis that different strategies at the seedling stage could be involved in the evolution of habitat specialization. Contrasts in seedling

performance among congeners were not consistent with difference in lineage diversification rates, suggesting that seedling strategies vary among lineages (Fine *et al.* 2006). Adaptations to survive abiotic and trophic stresses at the seedling stage are likely to involve life history tradeoffs that confer advantages in one habitat while being disadvantageous in another habitat. For example, seedlings of white-sand specialists grew slower but invested more in defense than those of terra firme specialists, suggesting a growth-defense tradeoff in five lineages (Fine *et al.* 2006). Similar tradeoffs could exist for drought and flood tolerance because allocation to structures such as increased root depth or pneumatophores presumably diverts photosynthate, which could otherwise be used for height growth (Parolin *et al.* 2004). The stronger patterns of habitat specialization in Peru than in French Guiana suggest that habitat-mediated speciation may be more likely to occur in the western Amazon, where environmental gradients are steeper and forest dynamics are faster (Quesada *et al.* 2011; Baker *et al.* 2014). For example, Fine *et al.* (2014) conducted biogeographic reconstructions of the fossil-calibrated phylogeny of the Protieae (Burseraceae) and found that Guianan species most likely dispersed from Amazonian ancestors. Thus habitat specialists currently found in French Guiana may have inherited their habitat-associated traits from Amazonian ancestors and subsequently expanded their range eastward.

Conclusion

Quantifying abiotic variables describing contrasting forest habitats, we shed light on the mechanisms driving tropical tree habitat specialization at the scale of the Amazon basin. Rainfall variation, flooding and soil factors were the main drivers of seedling mortality across the Amazon region, whereas herbivory had a limited impact. Variation in the responses of habitat specialists to gradients of rainfall seasonality, flooding and soil fertility likely generates the

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

strong patterns of habitat specialization observed among tropical trees, and thereby contributes to the spatial turnover in species composition across Amazonia.

Acknowledgements

We thank the many colleagues who participated in field work in French Guiana, especially Alec Baxt, Damien Bonal, Saint Omer Cazal, Kyle Dexter, Julian Donald, Aurélie Dourdain, Julien Engel, Zachari Jolin, Seth Kauppinen, Martinus Koese, Frits Kwasie, Benjamin Leudet, Greg Lamarre, Audin Patient, Marcos Ríos, Richard Sante, Clément Stahl and Elvis Valderrama; and in Peru, especially Fabio Casado, Julio Grandez Ríos and Julio Sanchez. Research was supported by a collaborative NSF DEB-0743103/0743800 to CB and PVAf; and by an INRA Package grant to CB. This work has benefited from an ‘Investissement d’Avenir’ grant managed by Agence Nationale de la Recherche (CEBA, ref. ANR-10-LABX-0025). This manuscript was improved by suggestions from Liza Comita and three anonymous reviewers.

References

1. Andersen, K.M., Turner, B.L. & Dalling, J.W. (2014). Seedling performance trade-offs influencing habitat filtering along a soil nutrient gradient in a tropical forest. *Ecology*, 95, 3399–3413.

2. Asner, G.P., Loarie, S.R. & Heyder, U. (2010). Combined effects of climate and land-use change on the future of humid tropical forests. *Conserv. Lett.*, 3, 395–403.

3. Baker, T.R., Pennington, R.T., Magallon, S., Gloor, E., Laurance, W.F., Alexiades, M., *et al.* (2014). Fast demographic traits promote high diversification rates of Amazonian trees. *Ecol. Lett.*, 17, 527–536.
4. Baraloto, C., Bonal, D. & Goldberg, D.E. (2006). Differential seedling growth response to soil resource availability among nine neotropical tree species. *J. Trop. Ecol.*, 22, 487–497.
5. Baraloto, C., Goldberg, D.E. & Bonal, D. (2005). Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology*, 86, 2461–2472.
6. Baraloto, C., Hardy, O.J., Paine, C.E.T., Dexter, K.G., Cruaud, C., Dunning, L.T., *et al.* (2012). Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *J. Ecol.*, 100, 690–701.
7. Baraloto, C., Morneau, F., Bonal, D., Blanc, L. & Ferry, B. (2007). Seasonal water stress tolerance and habitat associations within four neotropical tree genera. *Ecology*, 88, 478–489.
8. Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Hérault, B., *et al.* (2011). Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Glob. Chang. Biol.*, 17, 2677–2688.
9. Bates, D. (2005). Fitting linear mixed models in R. *R News*, 5, 27–30.

1
2
3 481 10.Bennington, C.C., Fetcher, N., Vavrek, M.C., Shaver, G.R., Cummings, K.J. & McGraw, J.B.
4
5 482 (2012). Home site advantage in two long-lived arctic plant species: results from two 30-year
6
7 483 reciprocal transplant studies. *J. Ecol.*, 100, 841–851.
8
9 484
10
11
12 485 11.Brenes-Arguedas, T., Coley, P.D. & Kursar, T.A. (2009). Pests vs. drought as determinants of
13
14 486 plant distribution along a tropical rainfall gradient. *Ecology*, 90, 1751–1761.
15
16 487
17
18
19 488 12.Brenes-Arguedas, T., Roddy, A.B. & Kursar, T.A. (2013). Plant traits in relation to the
20
21 489 performance and distribution of woody species in wet and dry tropical forest types in Panama.
22
23 490 *Funct. Ecol.*, 27, 392–402.
24
25 491
26
27
28 492 13.Brienen, R.J.W., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J., *et al.*
29
30 493 (2015). Long-term decline of the Amazon carbon sink. *Nature*, 519, 344–8.
31
32 494
33
34
35 495 14.Burnham, K.P. & Anderson, D.R. (2004). Multimodel inference - understanding AIC and BIC
36
37 496 in model selection. *Sociol. Methods Res.*, 33, 261–304.
38
39 497
40
41
42 498 15.Comita, L.S., Uriarte, M., Thompson, J., Jonckheere, I., Canham, C.D. & Zimmerman, J.K.
43
44 499 (2009). Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *J.*
45
46 500 *Ecol.*, 97, 1346–1359.
47
48 501
49
50
51 502 16.Davidar, P., Rajagopal, B., Mohandass, D., Puyravaud, J.P., Condit, R.S., Wright, S.J., *et al.*
52
53 503 (2007). The effect of climatic gradients, topographic variation and species traits on the beta
54
55
56
57
58
59
60

- diversity of rain forest trees. *Glob. Ecol. Biogeogr.*, 16, 510–518.
- 505
- 17.Dray, S. & Dufour, A.B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *J. Stat. Softw.*, 22, 1–20.
- 508
- 18.Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L., *et al.* (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, 447, 80–82.
- 512
- 19.Engelbrecht, B.M.J. & Kursar, T.A. (2003). Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia*, 136, 383–393.
- 515
- 20.Feeley, K.J., Malhi, Y., Zelazowski, P. & Silman, M.R. (2012). The relative importance of deforestation, precipitation change, and temperature sensitivity in determining the future distributions and diversity of Amazonian plant species. *Glob. Chang. Biol.*, 18, 2636–2647.
- 519
- 21.Fine, P.V.A., García-Villacorta, R., Pitman, N.C.A., Mesones, I., Kembel, S.W., Garcia-Villacorta, R., *et al.* (2010). A floristic study of the white-sand forests of Peru. *Ann. Missouri Bot. Gard.*, 97, 283–305.
- 523
- 22.Fine, P.V.A., Mesones, I. & Coley, P.D. (2004). Herbivores promote habitat specialization by trees in Amazonian forests. *Science (80-.)*, 305, 663–665.

1
2
3 527 23.Fine, P.V.A., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., *et al.*
4
5 528 (2006). The growth-defense trade-off and habitat specialization by plants in Amazonian forests.
6
7 529 *Ecology*, 87, S150–S162.
8
9 530
10
11
12 531 24.Fine, P.V.A., Zapata, F. & Daly, D.C. (2014). Investigating processes of neotropical rain
13
14 532 forest tree diversification by examining the evolution and historical biogeography of the Protieae
15
16 533 (Burseraceae). *Evolution (N. Y.)*, 68, 1988–2004.
17
18 534
19
20
21 535 25.Frazer, G.W., Canham, C.D. & Lertzman, K.P. (1999). Gap Light Analyzer (GLA), Version
22
23 536 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-
24
25 537 colour fisheye photographs, users manual and program documentation. .
26
27 538
28
29
30 539 26.Gentry, A.H. (1988). Changes in plant community diversity and floristic composition on
31
32 540 environmental and geographical gradients. *Ann. Missouri Bot. Gard.*, 75, 1–34.
33
34 541
35
36
37 542 27.Green, P.T., Harms, K.E. & Connell, J.H. (2014). Nonrandom, diversifying processes are
38
39 543 disproportionately strong in the smallest size classes of a tropical forest. *Proc. Natl. Acad. Sci.*,
40
41 544 111, 18649–18654.
42
43 545
44
45
46 546 28.Halekoh, U. & Højsgaard, S. (2014). A Kenward-Roger approximation and parametric
47
48 547 bootstrap methods for tests in linear mixed models - the R package pbkrtest. *J. Stat. Softw.*, 59,
49
50 548 1–32.
51
52 549
53
54
55
56
57
58
59
60

- 1
2
3 550 29. Hubbell, S.P., He, F.L., Condit, R., Borda-de-Agua, L., Kellner, J. & ter Steege, H. (2008).
4
5 551 How many tree species and how many of them are there in the Amazon will go extinct? *Proc.*
6
7 552 *Natl. Acad. Sci. U. S. A.*, 105, 11498–11504.
8
9 553
10
11
12 554 30. IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II*
13
14 555 *and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC*
15
16 556 *[Core Writ. Team; R.K. Pachauri L.A. Meyer (eds.)]*. Geneva; Switzerland.
17
18 557
19
20
21 558 31. Kursar, T.A., Engelbrecht, B.M.J., Burke, A., Tyree, M.T., El Omari, B. & Giraldo, J.P.
22
23 559 (2009). Tolerance to low leaf water status of tropical tree seedlings is related to drought
24
25 560 performance and distribution. *Funct. Ecol.*, 23, 93–102.
26
27 561
28
29 562 32. Lasky, J.R., Bachelot, B., Muscarella, R., Schwartz, N., Forero-Montaña, J., Nytch, C.J., *et al.*
30
31 563 (2015). Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. *Ecology*,
32
33 564 96, 2157–2169.
34
35 565
36
37 566 33. Levine, N.M., Zhang, K., Longo, M., Baccini, A., Phillips, O.L., Lewis, S.L., *et al.* (2016).
38
39 567 Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change.
40
41 568 *Proc. Natl. Acad. Sci.*, 113, 793–797.
42
43 569
44
45 570 34. Lewis, S.L., Brando, P.M., Phillips, O.L., van der Heijden, G.M.F. & Nepstad, D. (2011). The
46
47 571 2010 Amazon Drought. *Science* (80-.), 331, 554–554.
48
49 572
50
51
52
53
54
55
56
57
58
59
60

1
2
3 573 35.Lin, L., Comita, L.S., Zheng, Z. & Cao, M. (2012). Seasonal differentiation in density-
4
5 574 dependent seedling survival in a tropical rain forest. *J. Ecol.*, 100, 905–914.
6
7 575
8
9
10 576 36.Lucas, C.M., Bruna, E.M. & Nascimento, C.M.N. (2013). Seedling co-tolerance of multiple
11
12 577 stressors in a disturbed tropical floodplain forest. *Ecosphere*, 4, art3.
13
14 578
15
16
17 579 37.Metz, M.R. (2012). Does habitat specialization by seedlings contribute to the high diversity of
18
19 580 a lowland rain forest? *J. Ecol.*, 100, 969–979.
20
21 581
22
23
24 582 38.Paine, C.E.T., Harms, K.E., Schnitzer, S.A. & Carson, W.P. (2008). Weak competition
25
26 583 among tropical tree seedlings: Implications for species coexistence. *Biotropica*, 40, 432–440.
27
28 584
29
30
31 585 39.Parolin, P., De Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., *et al.* (2004).
32
33 586 Central Amazonian floodplain forests: Tree adaptations in a pulsing system. *Bot. Rev.*, 70, 357–
34
35 587 380.
36
37 588
38
39
40
41 589 40.Quesada, C.A., Lloyd, J., Anderson, L.O., Fyllas, N.M., Schwarz, M. & Czimczik, C.I.
42
43 590 (2011). Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences*, 8,
44
45 591 1415–1440.
46
47
48 592
49
50
51 593 41.R Development Core Team. (2016). R: A language and environment for statistical computing
52
53 594 [WWW Document]. URL <http://www.r-project.org>.
54
55 595
56
57
58
59
60

- 596 42.Santiago, L.S., Wright, S.J., Harms, K.E., Yavitt, J.B., Korine, C., Garcia, M.N., *et al.* (2012).
597 Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition. *J. Ecol.*,
598 100, 309–316.
599
- 600 43.Satyamurty, P., da Costa, C.P.W., Manzi, A.O. & Candido, L.A. (2013). A quick look at the
601 2012 record flood in the Amazon Basin. *Geophys. Res. Lett.*, 40, 1396–1401.
602
- 603 44.Slik, J.W.F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L.F., Ashton, P.,
604 *et al.* (2015). An estimate of the number of tropical tree species. *Proc. Natl. Acad. Sci.*, 112,
605 7422–7477.
606
- 607 45.ter Steege, H., Pitman, N.C. a, Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., *et al.*
608 (2013). Hyperdominance in the Amazonian tree flora. *Science*, 342, 1243092.
609
- 610 46.ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., *et al.*
611 (2006). Continental-scale patterns of canopy tree composition and function across Amazonia.
612 *Nature*, 443, 444–447.
613
- 614 47.ter Steege, H., Sabatier, D., Castellanos, H., Van Andel, T., Duivenvoorden, J., Adalardo De
615 Oliveira, A., *et al.* (2000). An analysis of the floristic composition and diversity of Amazonian
616 forests including those of the Guiana Shield. *J. Trop. Ecol.*, 16, 801–828.
617
- 618 48.Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balcázar, J., Chuvina, J., *et al.* (2012).

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

619 Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *J.*
620 *Ecol.*, 100, 253–263.

621

622 49.Uriarte, M., Lasky, J.R., Boukili, V.K. & Chazdon, R.L. (2016). A trait-mediated,
623 neighbourhood approach to quantify climate impacts on successional dynamics of tropical
624 rainforests. *Funct. Ecol.*, 30, 157–167.

625

626 50.Wright, S.J. (2002). Plant diversity in tropical forests: a review of mechanisms of species
627 coexistence. *Oecologia*, 130, 1–14.

628

Table 1: Predictions of the best at home and home advantage hypotheses. The first row and column lay out the predictions of each hypothesis for specialists on each of the three habitats. The best at home hypothesis predicts that habitat specialists perform better in their home habitats (comparisons made among rows), whereas the home advantage hypothesis predicts that habitat specialists outperform species associated with other habitat types (comparisons made among columns). Subsequent rows and columns detail the mechanisms expected to generating the predicted outcomes for each habitat specialist. Shaded cells indicate when habitat specialists are transplanted in their home habitat. Abbreviations: Seasonally-flooded (SF), terra firme (TF) and white-sand (WS) forests.

| | Best at home hypothesis | Planted into SF | Planted into TF | Planted into WS |
|---------------------------|---|--|---|--|
| Home advantage hypothesis | | SF specialists survive better than TF and WS specialists in SF | TF specialists have similar survival rates to SF and WS specialists in TF. | WS specialists survive better than SF and TF specialists in WS. |
| Originated from SF | SF specialists survive better in SF and TF. | No strong filter on survival because they can tolerate flooding. | A weak filter on survival because they are poorly adapted to grow in extreme shade. | Intermediate survival because adaptations to flooding may promote drought tolerance. Herbivory may exacerbate abiotic stress, if sufficient light is available for growth. |
| Originated from TF | TF specialists survive better in TF. | Low survival because flooding imposes stress from low soil oxygen (and possible fungal attack). | No strong filter on survival. | Low survival because of drought and/or low soil fertility. Herbivory may exacerbate abiotic stress, if sufficient light is available for growth. |
| Originated from WS | WS specialists survive better in WS. | Intermediate survival because flooding imposes possible stress from low soil oxygen (and possible fungal attack), but are adapted for higher water use efficiency. | A weak filter on survival because they are poorly adapted to grow in extreme shade. | No strong filter on survival because they can tolerate drought and low soil fertility. |

Table 2: The 41 habitat-specialist species included in the reciprocal transplant experiment, sorted by country, lineage and home habitat. Colors indicate home habitat for each habitat-specialist species: blue: seasonally-flooded forest, red: terra firme forest, yellow: white-sand forest. Mean mortality rates and relative growth rates (RGR) at the end of the experiment are indicated. Focal lineages span a broad range of diversification rates, from slow in *Micropholis* and Bombacoideae to high in *Inga* and *Licania* (Baker *et al.* 2014).

| Country | Family | Lineage | Species | Home habitat | Mean mortality rate | Mean RGR in height (mm.mm ⁻¹ . month ⁻¹) |
|---------------|------------------|--------------------|---------------------------------------|--------------|---------------------|---|
| French Guiana | Malvaceae | Bombacoideae | <i>Pachira aquatica</i> | ■ | 0.36 | 0.007 |
| | | | <i>Eriotheca globosa</i> | ■ | 0.12 | 0.013 |
| | | | <i>Eriotheca longitubulosa</i> | ■ | 0.26 | 0.010 |
| | | | <i>Pachira flaviflora</i> | ■ | 0.54 | 0.018 |
| | Lecythidaceae | <i>Eschweilera</i> | <i>Eschweilera coriacea</i> | ■ | 0.29 | 0.007 |
| | | | <i>Eschweilera sagotiana</i> | ■ | 0.16 | 0.005 |
| | Fabaceae | <i>Inga</i> | <i>Inga thibaudiana</i> | ■ | 0.12 | 0.023 |
| | | | <i>Inga cayennensis</i> | ■ | 0.24 | 0.022 |
| | | | <i>Inga pezizifera</i> | ■ | 0.17 | 0.014 |
| | | | <i>Inga stipularis</i> | ■ | 0.07 | 0.015 |
| | Chrysobalanaceae | <i>Licania</i> | <i>Licania macrophylla</i> | ■ | 0.40 | 0.004 |
| | | | <i>Licania heteromorpha</i> | ■ | 0.68 | 0.001 |
| | Sapotaceae | <i>Micropholis</i> | <i>Micropholis guyanensis</i> | ■ | 0.25 | 0.007 |
| | | | <i>Micropholis egensis</i> | ■ | 0.16 | 0.015 |
| | | | <i>Micropholis venulosa</i> | ■ | 0.32 | 0.020 |
| | Burseraceae | <i>Protium</i> | <i>Protium opacum</i> | ■ | 0.10 | 0.013 |
| | | | <i>Protium decandrum</i> | ■ | 0.29 | 0.013 |
| | | | <i>Protium gallicum</i> | ■ | 0.50 | 0.018 |
| | | | <i>Protium subserratum</i> | ■ | 0.49 | 0.011 |
| | | | <i>Protium aracouchini</i> | ■ | 0.31 | 0.016 |
| | | | <i>Protium heptaphyllum</i> | ■ | 0.68 | 0.018 |
| | Fabaceae | <i>Swartzia</i> | <i>Swartzia polyphylla</i> | ■ | 0.35 | 0.011 |
| | | | <i>Swartzia grandifolia</i> | ■ | 0.30 | 0.012 |
| | | | <i>Swartzia panacoco</i> | ■ | 0.43 | 0.011 |
| | | | <i>Swartzia bannia</i> | ■ | 0.80 | 0.007 |
| Peru | Malvaceae | Bombacoideae | <i>Eriotheca sp.1</i> | ■ | 0.20 | 0.011 |
| | | | <i>Pachira insignis-aquatica</i> | ■ | 0.28 | 0.010 |
| | | | <i>Pachira brevipes</i> | ■ | 0.49 | 0.010 |
| | Lecythidaceae | <i>Eschweilera</i> | <i>Eschweilera aff chartaceifolia</i> | ■ | 0.43 | 0.009 |
| | | | <i>Eschweilera grandiflora</i> | ■ | 0.47 | 0.009 |
| | Fabaceae | <i>Inga</i> | <i>Inga coruscans</i> | ■ | 0.53 | 0.010 |
| | | | <i>Inga auristellae</i> | ■ | 0.41 | 0.005 |
| | | | <i>Inga lopadadenia</i> | ■ | 0.47 | 0.007 |
| | Sapotaceae | <i>Micropholis</i> | <i>Micropholis guyanensis</i> | ■ | 0.49 | 0.010 |
| | | | <i>Micropholis venulosa</i> | ■ | 0.42 | 0.015 |
| | Burseraceae | <i>Protium</i> | <i>Protium meridionale</i> | ■ | 0.58 | 0.015 |
| | | | <i>Protium unifoliolatum</i> | ■ | 0.74 | 0.016 |
| | | | <i>Protium sagotianum</i> | ■ | 0.65 | 0.005 |
| | | | <i>Protium heptaphyllum</i> | ■ | 0.63 | 0.012 |
| | Fabaceae | <i>Swartzia</i> | <i>Swartzia cf laevicarpa</i> | ■ | 0.68 | 0.004 |
| | | | <i>Swartzia benthamiana</i> | ■ | 0.42 | 0.009 |

Table 3: Abiotic and trophic effects in the best generalized mixed models predicting seedling mortality in French Guiana and Peru, respectively (see Table S2 for model coefficients).

| | French Guiana | | | | Peru | | | |
|-----------------------------|---------------|--------|---------|-----|------|--------|---------|-----|
| | Df | LRT | P value | | Df | LRT | P value | |
| Genus | 6 | 3.374 | 0.8452 | ns | 5 | 17.489 | 0.0280 | * |
| Light availability | 1 | 2.560 | 0.1219 | ns | 1 | 0.633 | 0.4166 | ns |
| Soil N content | 1 | 0.339 | 0.5485 | ns | 1 | 2.869 | 0.1039 | ns |
| Soil sand content | 1 | 3.256 | 0.0759 | § | 1 | 0.131 | 0.7153 | ns |
| Rainfall | 1 | 65.947 | 0.0010 | *** | 1 | 70.198 | 0.0010 | *** |
| Exclosure treatment | 1 | 3.679 | 0.0609 | § | 1 | 2.671 | 0.0949 | § |
| Genus x Light availability | 6 | 5.836 | 0.4645 | ns | 5 | 11.609 | 0.0549 | § |
| Genus x Soil N content | 6 | 12.410 | 0.0559 | § | 5 | 4.494 | 0.4805 | ns |
| Genus x Soil sand content | 6 | 24.446 | 0.0020 | ** | 5 | 7.442 | 0.1988 | ns |
| Genus x Rainfall | 6 | 49.411 | 0.0010 | *** | 5 | 11.454 | 0.0410 | * |
| Genus x Exclosure treatment | 6 | 9.113 | 0.1618 | ns | 5 | 3.186 | 0.6893 | ns |

† Likelihood ratio test (LRT) statistics and P values were determined using 1000 parametric bootstrap replicates (*** P < 0.001; ** P < 0.01; * P < 0.05; § 0.05 < P < 0.10; ns: non-significant).

Figure legends

Figure 1: Effects of local values of rainfall and soil sand content on the probability of mortality of seedlings of habitat-specialist species from three forest habitats in (a,b) French Guiana and (c,d) in Peru. Effects were predicted from the best generalized mixed models for mortality in each country, holding other predictor variables constant at their median values (see Table S2).

Figure 2: Mortality rates at the end of the experiment of seedlings of habitat-specialist species from three habitats in (a) French Guiana and (b) Peru. The mean mortality rates of habitat specialists in their home habitat are shown as vertical lines. Their mortality rates when planted in other habitats are shown with light-gray bars, testing the best at home hypothesis (see first column in Table 1). The mortality of non-specialists planted into each focal habitat is shown as dark-gray bars, testing the home advantage hypothesis (see first row in Table 1). Error bars indicate one standard error of the mean. Significance of Tukey’s HSD test is indicated (*** $P < 0.001$; ** $P < 0.01$; ns: non-significant).

Figure 3: Mortality rates at the end of the experiment of seedlings of habitat-specialist species in (a) seven phylogenetic lineages in French Guiana and (b) six phylogenetic lineages in Peru. Formatting follows Figure 2.

Supporting information

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

Table S1: Climate, light and soil factors in French Guiana and Peru.

Table S2: Mean estimated parameters and the 95 % confidence intervals of the best generalized mixed models predicting seedling mortality in French Guiana and Peru as a function of abiotic gradients (here the local conditions of the habitat of transplantation), herbivory exclusion treatment and plant lineage.

Table S3: Mean estimated parameters and the 95 % confidence intervals of the generalized mixed models predicting seedling mortality in French Guiana and Peru as a function of abiotic gradients (here the differences (Δ) between home habitat and habitat of transplantation), herbivory exclusion treatment and plant lineage.

Figure S1: Correlation circles of the principal components analysis defined by soil fertility and texture, and light availability in French Guiana and Peru.

Figure S2: Effects of local values of rainfall and soil sand content on the probability of mortality of seedlings of habitat-specialist species from three forest habitats in seven phylogenetic lineages in French Guiana and six phylogenetic lineages in Peru.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Figure S3: Effects of local values of soil nitrogen content, soil sand content and light availability on the probability of mortality of seedlings of each habitat-specialist species in French Guiana and Peru.

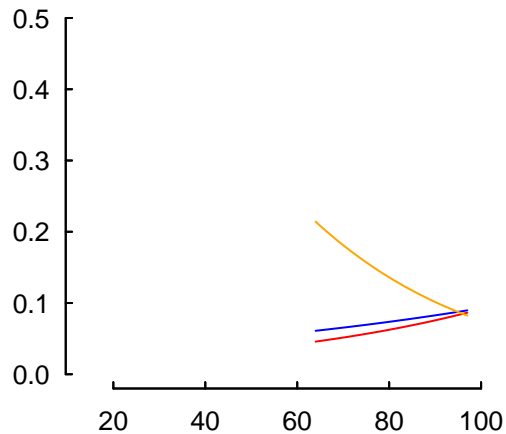
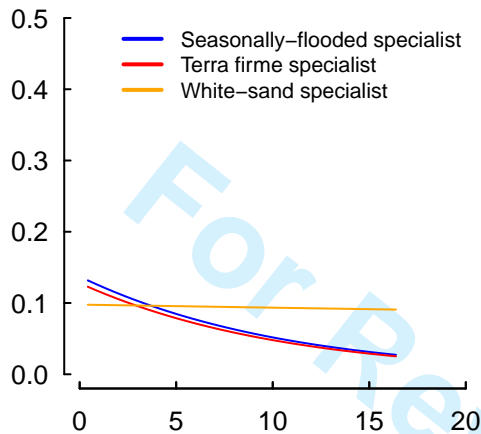
Figure S4: Mortality rates at the end of the experiment of seedlings of 25 habitat-specialist species from seven phylogenetic lineages in French Guiana and 16 habitat-specialist species from six phylogenetic lineages in Peru.

Figure S5: Growth rates at the end of the experiment of seedlings of habitat-specialist species from three habitats in French Guiana and Peru.

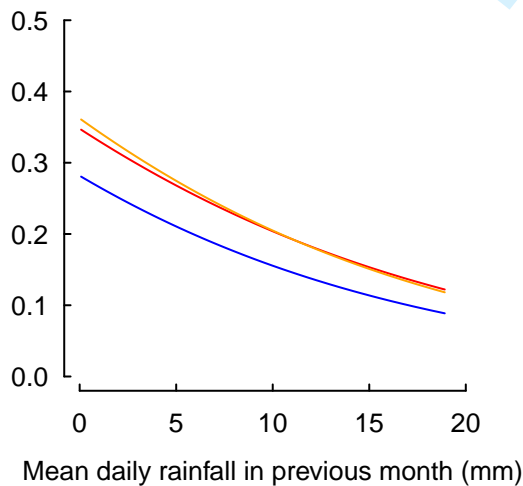
(a) French Guiana

Ecology Letters

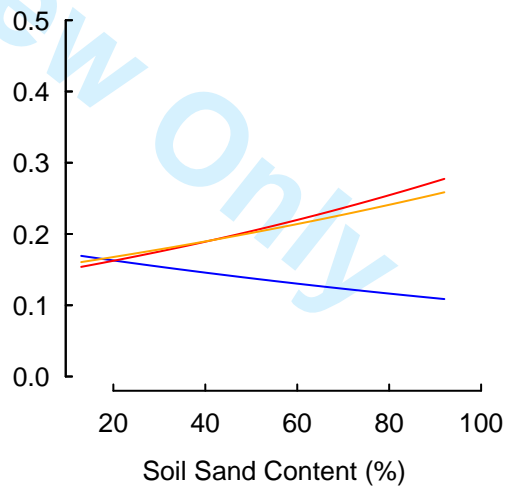
(b) French Guiana



(c) Peru

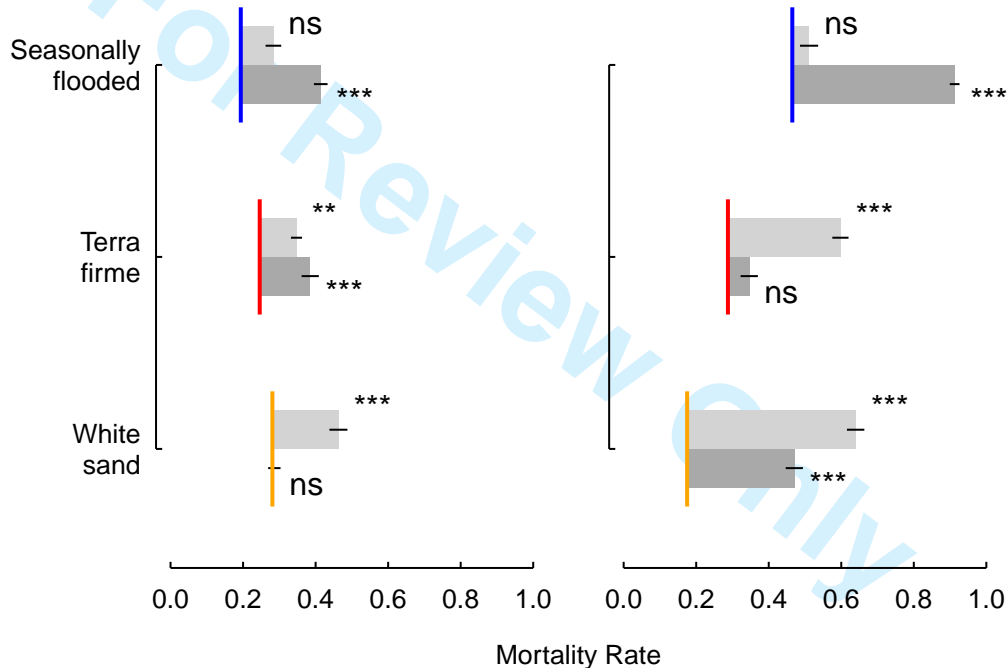


(d) Peru



(a) French Guiana

(b) Peru



| Seasonally-flooded specialist in home habitat
 | Terra firme specialist in home habitat
 | White-sand specialist in home habitat

| Specialist away from home habitat (best at home)
 | Non-specialist in focal habitat (home advantage)

(a) French Guiana

(b) Peru

