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

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24 32 **Statement of authorship:** CF, CB and PVAF designed the study. CF, CB, PVAF, IM, JYG, BB,
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26
27 33 and JC set up the reciprocal transplant experiment and performed the seedling censuses. CF and
28
29 34 CETP analyzed the data. CF, CB and PVAF wrote the first draft of the manuscript. All authors
30
31
32 35 contributed to revisions.

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3 36 **Abstract**
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5 37 Understanding the mechanisms generating species distributions remains a challenge, especially
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8 38 in hyperdiverse tropical forests. We evaluated the role of rainfall variation, soil gradients and
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10 39 herbivory on seedling mortality, and how variation in seedling performance along these gradients
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12 40 contributes to habitat specialization. In a four-year experiment, replicated at the two extremes of
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14 41 the Amazon basin, we reciprocally transplanted 4638 tree seedlings of 41 habitat-specialist
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16 42 species from seven phylogenetic lineages among the three most important forest habitats of
17
18 43 lowland Amazonia. Rainfall variation, flooding and soil gradients strongly influenced seedling
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20 44 mortality, whereas herbivory had negligible impact. Seedling mortality varied strongly among
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22 45 habitats, consistent with predictions for habitat specialists in most lineages. This suggests that
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24 46 seedling performance is a primary determinant of the habitat associations of adult trees across
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26 47 Amazonia. It further suggests that tree diversity, currently mostly harbored in terra firme forests,
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28 48 may be strongly impacted by the predicted climate changes in Amazonia.
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49 **Introduction**

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

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

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3 72 situated on fertile clay soils adjacent to nutrient-poor sands and have no annual dry season but
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5 73 experience high water levels associated with flooding of large rivers (Baraloto *et al.* 2011). Such
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8 74 a broad experimental scope is key to determine the consistency of the influence of abiotic and
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10 75 trophic factors on seedling performance across Amazonia.

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12 76 We focused on the three most-common habitats of lowland Amazonian forests: terra firme
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14 77 forests on clay-rich soils, seasonally-flooded forests and white-sand forests. These habitats span
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16 78 the ranges of resource availability, flooding, drought, forest structure, and floristic composition
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18 79 found in lowland Amazonia (Fine *et al.* 2010; Baraloto *et al.* 2011). Terra firme forests have
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20 80 relatively nutrient-rich soils with high clay content, and experience relatively minor abiotic
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22 81 stresses (Baraloto *et al.* 2011). Seasonally-flooded forests have relatively nutrient-rich soils but
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24 82 experience at least three months of annual flooding where the water table reaches the soil
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26 83 surface, which imposes a severe stress from low soil oxygen (Parolin *et al.* 2004; Lucas *et al.*
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28 84 2013). The soils underlying white-sand forests are among the most nutrient-poor that have been
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30 85 recorded worldwide (Quesada *et al.* 2011). Moreover, water availability becomes extremely low
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32 86 in white-sand forests during droughts (Baraloto *et al.* 2006).

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38 87 When abiotic stress is limited and sufficient light is available, terra firme specialists are
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40 88 predicted to outcompete seasonally-flooded and white-sand specialists because of lower
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42 89 investment in flood and drought tolerance and/or herbivore defense mechanisms. In addition, if
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44 90 natural enemies preferentially attack non-specialists, they can interact with abiotic factors to
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46 91 drive habitat specialization, in particular when sufficient light is available to allow fast seedling
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48 92 growth (Fine *et al.* 2004). However, tropical tree seedlings typically spend years in the shaded
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50 93 understory before a gap in the forest canopy provides sufficient light for them to reach a size at
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52 94 which they start competing with neighboring trees (Paine *et al.* 2008; Lasky *et al.* 2015). We
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3 95 thus focus our study on seedling mortality in the shaded understory in order to understand the
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6 96 ecological mechanisms that operate at this critical life stage.
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8 97 Reciprocal transplant experiments are especially useful because they allow for equal sample
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10 98 sizes to disentangle the mechanisms shaping habitat specialization within and among lineages.
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12 99 Phylogenetic replication is important because the relative investment in growth and defense
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14 100 strategies varies among lineages (Fine *et al.* 2004, 2006; Baraloto *et al.* 2012). Moreover fast
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16 101 demographic rates have been shown to promote high diversification rates in Amazonian tree
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18 102 lineages (Baker *et al.* 2014). In this study, we focused on 41 species from seven monophyletic
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20 103 lineages that occur across Amazonia, differ in diversification rates and include species associated
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22 104 with each of the three habitats. By comparing habitat-mediated seedling performance within and
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24 105 among lineages, we can investigate whether different strategies at the seedling stage may
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26 106 contribute to habitat specialization and lineage diversification.
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32 107 In particular, we addressed the following questions:
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34 108 1. How do abiotic and trophic factors influence seedling mortality across Amazonia? We
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36 109 expect rainfall variation, soil and light factors to primarily influence seedling mortality, whereas
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38 110 herbivory would exacerbate abiotic effects on seedling mortality (Fine *et al.* 2004; Brenes-
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40 111 Arguedas *et al.* 2009). In particular, we expect greater seedling mortality with lower rainfall
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42 112 (Engelbrecht & Kursar 2003; Brenes-Arguedas *et al.* 2009), lower soil fertility (Baraloto *et al.*
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44 113 2006; Santiago *et al.* 2012) and less available light (Andersen *et al.* 2014). Additionally, we
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46 114 expect those effects to increase with increasing differences between local conditions of
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48 115 transplantation and the home habitat of the specialist.
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53 116 2. Does differential seedling performance across the steep habitat gradients reflect habitat
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55 117 specialization? We propose a novel framework that underlines two distinct processes that
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3 118 contribute to habitat specialization: habitat specialists can become locally abundant either
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5 119 because (i) they perform better in their home habitat than in other habitats, a classical definition
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8 120 of habitat specialization from reciprocal transplants (Bennington *et al.* 2012); and/or (ii) they
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10 121 perform better in their home habitat than other species from the regional pool that are not
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12 122 strongly associated with that habitat. We refer to these as the best at home and home advantage
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14 123 hypotheses respectively (Table 1). Differential performance of species among habitats may arise
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16 124 through several mechanisms. We expect that flooding and drought are important drivers of
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18 125 seedling performance, favoring seasonally-flooded and white-sand specialists, respectively, in
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20 126 their home habitats (Baraloto *et al.* 2005, 2007); whereas trophic filters are key to explain the
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22 127 dominance of terra firme specialists in their home habitat, so long as sufficient light is available
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24 128 for growth (Fine *et al.* 2004).

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

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45 136 To test our hypotheses, we conducted a reciprocal transplant experiment at an unprecedented
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47 137 scale, with 4638 seedlings belonging to 41 habitat-specialist species over more than four years
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49 138 across three contrasting habitats and two countries. We provide a novel, comprehensive
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51 139 framework to test how variation in seedling performance contributes to habitat specialization.
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3 140 Our study is the first to quantify environmental variables describing the habitat of transplantation
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6 141 to test the mechanisms generating habitat specialization in tropical trees at a continental scale.
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10 143 **Methods**

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13 144 *Study sites*

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15 145 In both French Guiana and Peru, we selected 60 sites divided equally among the three
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17 146 habitats (terra firme, seasonally-flooded and white-sand forests) that cover the ranges of soil
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20 147 fertility and flooding in both countries (Baraloto *et al.* 2011). Sites were separated by at least 15
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22 148 m and located adjacent to permanent plots in the Laussat Reserve in northwestern French
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24 149 Guiana, and in the Allpahuayo-Mishana National Reserve in northeastern Peru (Baraloto *et al.*
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26 150 2011). At each site, we established paired experimental 2 m by 2 m plots in areas of shaded
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28 151 understory. We covered the enclosure plot with 1-mm nylon mesh to reduce herbivory, and, as
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30 152 the netting reduced incident light by about 8 %, we placed netting above the control plot to
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32 153 replicate any treatment shading (Fine *et al.* 2004). In each country, we thus established 120 plots
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34 154 (60 controls and 60 enclosures) corresponding to 40 replicate plots in each habitat. Every month,
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36 155 litter that accumulated on the roof of each plot was removed and spread evenly on the ground
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38 156 beneath, thereby reducing the shading effect of litter and stains on the netting and equalizing it
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40 157 across plots receiving different intensities of litterfall.
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46 158 At the start of the experiment, we determined light availability and soil fertility and texture
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48 159 in all 120 plots in each country (Table S1). Hemispherical photos were taken at the center of the
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50 160 roof of each plot with a fish-eye lens at 1.5 m high (Coolpix 995, Nikon). Total light availability
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52 161 (%) was estimated with the Gap Light Analyzer software (Frazer *et al.* 1999). In each plot, 0-15
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54 162 cm depth soil cores were bulked, dried at 25°C to constant mass and sieved to 2 mm for
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3 163 subsequent physical and chemical analyses at the University of California, Davis Analytical
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6 164 Laboratory (see details in Baraloto *et al.* 2011). From April 2010 to December 2013, soil water
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8 165 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
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10 166 moisture sensor (TRIME-PICO 64, Imko).

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13 167 For each country, we retrieved the cumulative daily rainfall series ($\text{mm} \cdot \text{day}^{-1}$, Table S1) over
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15 168 the course of the experiment from the estimate 3B42-V7 of Tropical Rainfall Measuring Mission
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17 169 of NASA's Goddard Earth Science Data and Information Services Center
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20 170 (<http://disc.gsfc.nasa.gov/precipitation/tovas>). Our experiment ran from 2009 to 2013, during
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22 171 which mean annual rainfall was 2210 and 3085 mm in French Guiana and Peru respectively. In
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24 172 French Guiana, our experiment coincided with the region's longest recorded drought in 2009. In
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26 173 both countries, it also coincided with the highest recorded flood levels in 2012. Specifically, all
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28 174 seedlings were submerged in Peruvian seasonally-flooded plots between March 25th and June
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30 175 13th 2012, a total of 49 days of complete inundation, whereas all seedlings experienced a
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32 176 saturated soil with a water table at the soil surface in French Guianan seasonally-flooded plots
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34 177 between April 11th and August 7th 2012, a total of 118 days during which soil water volume
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36 178 content remained above 80 %.

37 179 ***Species selection and transplantation***

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41 180 We focused on seven widespread monophyletic lineages that include species associated with
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43 181 each of the three habitats (Table 2). These lineages are phylogenetically dispersed within the
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45 182 eudicots, the dominant angiosperms in tropical rainforests, with representatives of euasterids
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47 183 (*Micropholis* [Sapotaceae] and *Licania* [Chrysobalanaceae]), fabids (*Inga* and *Swartzia*
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49 184 [Fabaceae] and *Eschweilera* [Lecythidaceae]), and malvids (Bombacoideae [Malvaceae] and
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51 185 *Protium* [Bursaceae]). The seven lineages span the range of estimated diversification rates
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3 186 reported for more than 50 tropical tree lineages (Baker *et al.* 2014). We selected two to five
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5 187 species from each lineage that are common in the regional species pool and associated with terra
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7 188 firme, seasonally-flooded or white-sand forests, as determined by our tree inventories of a
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10 189 network of 74 plots across both countries (Baraloto *et al.* 2011). We included seven lineages and
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12 190 25 species in French Guiana, and six lineages and 16 species in Peru. Our designations of habitat
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14 191 association for these 41 species are consistent with species accounts from many published
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16 192 sources (e.g. Fine *et al.* 2010; ter Steege *et al.* 2013).

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20 193 We collected seeds and/or recently germinated seedlings from at least three parent trees
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22 194 within the home habitat of each species and distributed them evenly across plots. Seeds were
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24 195 germinated in a shade house before transplantation in the field. One seedling per species was
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26 196 randomly planted in each plot, with a 30-cm grid spacing that corresponds to a density (9
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28 197 individuals.m⁻²) at which competition among seedlings is minimal (Paine *et al.* 2008).
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30 198 Transplantation was completed between March and May 2009 in French Guiana and between
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32 199 March and April 2010 in Peru. Monthly assessments of seedling mortality were conducted until
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34 200 November 2013 in French Guiana and until July 2012 in Peru, giving a total experimental
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36 201 duration of 53 months in French Guiana and 29 months in Peru, resulting in 130,589 and 86,144
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38 202 observations in French Guiana and Peru, respectively. Seedling height was measured at the
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40 203 beginning and end of the experiment. We calculated seedling relative growth rate for height over
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42 204 the duration of the experiment in each country.
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48 ***Statistical analyses***

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50 206 We used generalized linear mixed models (GLMMs) in each country to test how
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52 207 environmental gradients influence temporal variation in seedling mortality (Q_1). We predicted
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54 208 monthly seedling mortality ($mortality_t$) as a binary response variable using the abiotic variables,
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3 209 herbivore-exclusion treatment and plant lineage. Species identity was included as a random
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5 210 effect to account for different species responses to abiotic variables and herbivory ($R \text{ species}_i$).
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8 211 Plot identity was included as a random effect to account for autocorrelation in seedling mortality
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10 212 among plots ($R \text{ plot}_j$). Initial analyses indicated that temporal variation in rainfall in each country
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12 213 affected seedling mortality and, consistently with studies on climate effect on tree performance
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14 214 (e.g. Uriarte *et al.* 2016), the best rainfall indicator was the mean daily precipitation that had
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16 215 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
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18 216 continuous covariate. To describe abiotic gradients, we selected the variables best describing the
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20 217 major axes of a principal component analysis of all abiotic variables in the 120 plots in each
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22 218 country (Fig. S1), which were soil nitrogen content (soil_N), soil sand content ($\text{soil}_{\text{Sand}}$) and total
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24 219 light availability (light). All continuous predictor variables were scaled to mean 0 and standard
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26 220 deviation 1 to allow their relative effect sizes to be evaluated.

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31 221 We compared two alternate GLMMs to evaluate if abiotic effects on seedling mortality
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33 222 increase with increasing differences between local conditions of habitat of transplantation and
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35 223 home habitat of the specialist (Q_1). The first GLMM included terms for environmental
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37 224 differences (Δ) between habitat of transplantation and home habitat of the specialist:
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39 225 $mortality_t = lineage * (\Delta\text{soil}_N + \Delta\text{soil}_{\text{sand}} + \Delta\text{light} + \text{rain}_{30\text{days}} + \text{treatment}) +$
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41 226 $R \text{ species}_i + R \text{ plot}_j$, where ‘*’ denotes interaction between terms. The second GLMM had
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43 227 terms for local conditions of habitat of transplantation: $mortality_t = lineage * (\text{soil}_N +$
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45 228 $\text{soil}_{\text{sand}} + \text{light} + \text{rain}_{30\text{days}} + \text{treatment}) + R \text{ species}_i + R \text{ plot}_j$. We selected the best
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47 229 model between these two alternate GLMMs in each country using the Bayesian Information
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49 230 Criterion (BIC; Burnham & Anderson 2004). We determined the significance of each term of the
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3 231 best model in each country using likelihood ratio test statistics with 1000 parametric bootstrap
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6 232 replicates (Halekoh & Højsgaard 2014).

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8 233 To address the predictions of the best at home and home advantage hypotheses (Q₂ and Q₃),
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10 234 we used generalized linear models (GLMs) in each country to test the effects of habitat of
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12 235 transplantation on seedling performance at the end of the experiment (mortality_f and growth_f) for
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14 236 (i) each group of habitat specialists (e.g. all white-sand specialists) using $performance_f =$
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17 237 $habitat_{home} * habitat_{transplantation}$ (Q₂), and (ii) each group of habitat specialists by lineage
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20 238 using $performance_f = lineage * habitat_{home} * habitat_{transplantation}$ (Q₃). We used
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23 239 Tukey's HSD tests to examine the best at home and the home advantage hypotheses (Q₂ and Q₃),
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25 240 which make different predictions for specialists from different habitats (Table 1).

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27 241 All analyses were conducted in the R 3.2.5 statistical platform (R Development Core Team
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29 242 2016) using package *ade4* (Dray & Dufour 2007), *lme4* (Bates 2005) and *pbkrtest* (Halekoh &
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31 243 Højsgaard 2014).

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35 36 37 245 **Results**

38 39 246 ***Effects of rainfall, soil and light on seedling mortality rates***

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41 247 Increasing rainfall strongly reduced seedling mortality in French Guiana and Peru (Table 3,
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43 248 see details in Table S2). This rainfall effect was consistent across habitat specialists (Fig. 1a,c)
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46 249 and lineages (Fig. S2) in both countries. Overall, seedling mortality decreased with increasing
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49 250 soil sand content and light availability in both countries (Table S2). Seedling mortality decreased
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51 251 with increasing soil nitrogen content in French Guiana but not in Peru (Table S2). Specialists
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53 252 from contrasting habitats, on the other hand, showed variable responses to soil and light factors.
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56 253 Seasonally-flooded specialists showed higher seedling mortality with increasing soil sand
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3 254 content in French Guiana but not in Peru (Fig. 1b,d). Terra firme specialists exhibited higher
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5 255 seedling mortality with increasing soil sand content in both countries. White-sand specialists
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8 256 exhibited lower seedling mortality with increasing soil sand content in French Guiana, but
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10 257 showed the opposite pattern in Peru. In addition, the effects of soil and light factors on seedling
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12 258 mortality varied strongly among lineages (Fig. S2), species (Fig. S3) and countries (Table S2). In
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14 259 both countries, seedling mortality was much better explained by soil and light conditions in the
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16 260 plot of transplantation (Table S2) than by increasing differences between local conditions of
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18 261 transplantation and the home habitat (Table S3) ($\Delta\text{BIC}=41.84$ in French Guiana and 56.72 in
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20 262 Peru).

24 263 *Differences in seedling mortality among habitats and countries*

26 264 The best at home and home advantage hypotheses make context dependent predictions
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28 265 (Table 1). Synthesizing the patterns of mortality across lineages and countries, our specific
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30 266 predictions were broadly supported by the evidence, with 4 out of 6, and 6 out of 6 of the
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32 267 predictions met in French Guiana and Peru respectively (Fig. 2). As predicted, seasonally-
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34 268 flooded specialists did not experience significant differences in mortality when planted into other
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36 269 habitats in either country (Fig. 2, best at home). Moreover, they showed lower mortality than
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38 270 terra firme and white-sand specialists in seasonally-flooded forests in both countries (Fig. 2,
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40 271 home advantage). This difference was especially pronounced in Peru, where species not
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42 272 associated with flooded forests experienced more than twice the mortality rate of seasonally-
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44 273 flooded specialists (Fig. 2b). In both countries, terra firme specialists exhibited lower mortality at
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46 274 home than in other habitats (Fig. 2, best at home). We predicted no home advantage of terra
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48 275 firme specialists, yet results were equivocal with a slight home advantage of terra firme
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50 276 specialists in French Guiana but not in Peru (Fig. 2, home advantage). Also as predicted, white-
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3 277 sand specialists had lower mortality at home than in other habitats in both countries (Fig. 2, best
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5 278 at home) and had lower mortality than seasonally-flooded and terra firme specialists in white-
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7 279 sands in Peru but not in French Guiana (Fig. 2, home advantage). In addition, seedling mortality
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9 280 at the end of the experiment was lower in French Guiana than in Peru (31.8 and 49.2 %
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11 281 respectively, F-value=146.60, P<0.001).
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13 282 ***Differences in seedling mortality within and among lineages***

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17 283 Considering seedling mortality within lineages in each country, we found further
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19 284 evidence for the specific predictions of the best at home and the home advantage hypotheses
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21 285 (Fig. 3 and S4). As expected, seasonally-flooded forest specialists generally showed similar
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23 286 mortality between home and other habitats (Fig. 3, best at home), with seasonally-flooded forest
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25 287 specialists from only one lineage (*Inga*) surviving better at home in Peru. Seasonally-flooded
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27 288 forest specialists enjoyed consistent, strong home advantages over non-specialist congeners in
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29 289 Peru (Fig. 3), whereas only two seasonally-flooded forest specialists (*P. opacum* and *L.*
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31 290 *macrophylla*) showed home advantage in French Guiana (Fig. S4). Terra firme specialists
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33 291 typically had low mortality at home in both countries (Fig. 3, best at home), but this low
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35 292 mortality in terra firme was frequently equaled by congeners specialized to other habitats (Fig.
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37 293 S4), consistent with our prediction that terra firme specialists would not exhibit home
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39 294 advantages. White-sand specialists from one lineage (Bombacoideae) in French Guiana and from
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41 295 all lineages in Peru exhibited the lowest mortality rates in their home habitat (Fig. 3, best at
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43 296 home), but they were nearly extirpated from seasonally-flooded forests in Peru (Fig. S4). In Peru,
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45 297 white-sand specialists from two lineages (*Protium* and *Swartzia*) had much lower mortality in
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47 298 white-sands than did congeners with contrasting habitat preferences (Fig. 3, home advantage).
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3 299 Although we observed different degrees of contrasting species performance among lineages, we
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6 300 found no pattern consistent with lineage age or diversification rate (Table 2).
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8 301 ***Growth and herbivory***

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10 302 Seedling growth patterns across lineages and countries supported many predictions of the
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12 303 best at home and home advantage hypotheses, with 4 out of 6, and 5 out of 6 of our predictions
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14 304 met in French Guiana and Peru respectively (Table 1, Fig. S5). Seasonally-flooded specialists
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16 305 grew more rapidly at home than in other habitats in both countries; in Peruvian seasonally-
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18 306 flooded forests, they grew faster than terra firme and white-sand specialists. Terra firme
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20 307 specialists grew more rapidly at home than elsewhere in Peru, but in terra firme forests in both
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22 308 countries, they grew no faster than specialists from other habitats. White-sand specialists had
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24 309 higher growth rates at home than in other habitats in French Guiana, and grew faster than
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26 310 specialists from other habitats in both countries. Over the course of the experiment, seedlings
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28 311 grew faster in French Guiana than in Peru (0.013 vs. 0.010 mm.mm⁻¹.month⁻¹ respectively, F-
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30 312 value=53.23, P<0.001).
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36 313 Seedling growth rates were consistent with those reported by Baraloto *et al.* (2005) for
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38 314 seedlings transplanted to shaded understory sites in French Guiana. Seedlings grew about five
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40 315 times slower than seedlings in a similar experiment installed a few kilometers from our Peruvian
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42 316 site (Fine *et al.* 2004), which incorporated three of the same lineages and some of the same
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44 317 species, but which was installed in areas with much higher light availability. Nevertheless,
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46 318 slower growth in our experiment may have limited leaf production and thus herbivore attack on
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48 319 new leaves. In fact, although rates of herbivory were significantly greater in the controls than in
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50 320 the exclosures (4.70 and 1.65 % respectively), they were about three times lower than rates
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52 321 reported by Fine *et al.* (2004). We found that herbivore protection reduced seedling mortality in
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3 322 French Guiana but not in Peru (Table S2), and thus for the seedlings in our study it played no
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5 323 consistent role in generating habitat associations across Amazonia.
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10 325 **Discussion**

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12 326 Using a reciprocal transplant experiment replicated at two ends of the Amazon basin, we
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14 327 investigated the effects of temporal variation in rainfall and soil gradients, controlling for
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16 328 herbivores, on seedling mortality of habitat specialists. We highlight differential patterns of
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18 329 seedling performance that reflect habitat specialization within and among tree lineages and that
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20 330 likely contribute to the distribution of trees across Amazonia.
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24 331 ***Variation in seedling mortality along abiotic gradients***

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26 332 Integrating quantitative rainfall fluctuations over the course of the experiment in each
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28 333 country, we showed compelling evidence for the role of rainfall variation on seedling mortality.
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30 334 Seedling mortality was lower during periods of elevated rainfall for all habitat specialists in both
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32 335 countries (Fig. 1), consistent with previous studies showing a strong sensitivity of tropical tree
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34 336 seedlings to water addition (Engelbrecht & Kursar 2003; Brenes-Arguedas *et al.* 2009) and
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36 337 between dry and wet seasons (Lin *et al.* 2012; Brenes-Arguedas *et al.* 2013). Moreover, extreme
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38 338 flooding in 2012 in Peru led to the elevated mortality of non-specialists in seasonally-flooded
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40 339 forests (Fig. 2). Our study thus emphasizes the importance of seasonal and inter-annual
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42 340 variations in climate, in addition to climatic averages, to better understand how seedling
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44 341 dynamics, and subsequent tree species distributions, will respond to the increasing frequency or
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46 342 severity of droughts and floods that are predicted to occur in the Amazon (Asner *et al.* 2010;
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48 343 IPCC 2014).
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3 344 In both countries, seedling mortality decreased with increasing soil sand content, which
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5 345 contrasts with previous work showing greater mortality in the nutrient-poor soils of white-sand
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8 346 forests than in the fertile soils of terra firme and seasonally-flooded forests (Baraloto *et al.* 2006;
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10 347 Santiago *et al.* 2012). Habitat specialists sometimes exhibited contrasting sensitivity to local
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12 348 abiotic factors between countries. For instance, white-sand specialists had lower mortality with
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15 349 increasing soil sand content in French Guiana, whereas they showed the opposite pattern in Peru
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17 350 (Fig. 1). This divergence may arise because of differences in abiotic gradients between countries:
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19 351 soil fertility and sand content vary independently in French Guiana but co-vary in Peru (Fig. S1).
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21 352 A challenge for future studies will be to disentangle the links between climate variation and soil
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23 353 components (water, nutrients and mycorrhizae), and their relative effects on plant performance to
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25 354 better understand the underlying mechanisms shaping species distributions.
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29 355 ***How seedling mortality contributes to habitat specialization***

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31 356 Overall, we found strong support for our predictions regarding habitat specialization (Table
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33 357 1), suggesting that abiotic filtering at the seedling stage plays a vital role in determining the beta-
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35 358 diversity of tropical tree communities along environmental gradients. In particular, seasonally-
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37 359 flooded specialists had a strong home advantage, which may stem from their ability to tolerate
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39 360 the anoxia associated with flooding (Parolin *et al.* 2004; Lucas *et al.* 2013). Seasonally-flooded
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41 361 specialists did not perform best at home, which suggests that they may be dispersal-limited
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43 362 across habitats (Baraloto *et al.* 2007). White-sand specialists outperformed others at home, likely
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45 363 because they can tolerate drought stress and low soil fertility (Baraloto *et al.* 2006). White-sand
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47 364 specialists performed best at home, which may be due to stress from low soil oxygen during
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49 365 heavy rains or pathogen attack in seasonally-flooded and terra firme forests. Finally, terra firme
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51 366 specialists showed no strong home advantage but survived best at home, suggesting that they
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3 367 may be particularly vulnerable to drought and flooding in white-sand and flooded forests,
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5 368 respectively.

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8 369 Mechanisms operating at life stages other than the seedling stage can also influence habitat
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10 370 association in trees, including seed dispersal, seed predation and competition among established
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12 371 adult trees (Wright 2002). However the seedling stage has been increasingly recognized as a
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14 372 critical determinant of forest dynamics (Comita *et al.* 2009; Metz 2012; Green *et al.* 2014).
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16 373 Evaluating forest dynamics in a fifty-year study in an Australian tropical forest, Green *et al.*
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18 374 (2014) found that non-random mortality with respect to species identity occurred mostly at the
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20 375 seedling stage. The strong habitat-mediated differences in seedling mortality found in our study
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22 376 may thus largely shape patterns of habitat association found in adult trees at the scale of the
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24 377 Amazon region.

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29 378 Predicted climate changes in Amazonia may strongly impact tree species composition via
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31 379 this strong habitat-related variation in seedling mortality. In particular, as terra firme forests
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33 380 cover more than 80 % of lowland Amazonia (ter Steege *et al.* 2000) and harbor at least 80 % of
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35 381 its tree diversity (ter Steege *et al.* 2013), the vulnerability of terra firme specialists to extreme
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37 382 climatic events may have disproportionate consequences for Amazonian diversity. Recent global
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39 383 models of climate change over the next fifty years predict that the Amazon basin is likely to
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41 384 experience more extreme floods and droughts (IPCC 2014), which could promote habitat
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43 385 expansion for seasonally-flooded and white-sand specialists respectively at the expense of terra
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45 386 firme specialists. Indeed, a recent modeling study predicted that late-successional trees from clay
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47 387 soil habitats are much more vulnerable to climate change than those in sandy soil habitats
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49 388 (Levine *et al.* 2016). The magnitude of these climatic effects may be higher in the western
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3 389 Amazon where seasonally-flooded specialists are uniquely tolerant to flooding and only white-
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5 390 sand specialists are well adapted to short-term dry spells.

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8 391 ***Contrasting habitat-mediated seedling mortality among countries and congeners***

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10 392 Patterns of habitat specialization were stronger in Peru than in French Guiana, a difference
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12 393 that could have at least two causes. First, French Guianan forests generally have poorer soils and
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14 394 experience less rainfall but greater seasonality than Peruvian forests (Baraloto *et al.* 2011). This
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16 395 may filter the entire regional species pool for survival-oriented strategies, allowing greater
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18 396 tolerance of low resource availability and drier conditions (Baraloto *et al.* 2007). Indeed,
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20 397 seedling mortality was lower in French Guiana than in Peru, and congeneric species in some
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22 398 lineages in French Guiana exhibited similar seedling mortality in all habitats (e.g. *Eschweilera*,
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24 399 *Inga* and *Micropholis* species with mortality rates lower than 30 % after four years), making the
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26 400 potential advantages of habitat specialists harder to detect. Second, seasonally-flooded specialists
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28 401 in Peru were especially resistant to the extreme flood that occurred in 2012, resulting in the
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30 402 almost complete mortality of white-sand and terra firme specialists planted in the seasonally-
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32 403 flooded plots. High water levels associated with flooding of large rivers means that inundation is
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34 404 a frequent occurrence in Peru but comparatively rare in French Guiana, suggesting that periodic
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36 405 flooding may be a much stronger filter in the western Amazon (Parolin *et al.* 2004).

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38 406 Habitat-specialist congeners exhibited contrasting habitat-related seedling performance for
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40 407 three out of seven lineages in French Guiana and for all six lineages in Peru. We selected these
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42 408 focal lineages in part because they included species associated with contrasting habitats, and we
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44 409 demonstrated that seedling mortality patterns were consistent with the habitat association
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46 410 patterns of adult trees. This result is consistent with the hypothesis that different strategies at the
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48 411 seedling stage could be involved in the evolution of habitat specialization. Contrasts in seedling
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3 412 performance among congeners were not consistent with difference in lineage diversification
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5 413 rates, suggesting that seedling strategies vary among lineages (Fine *et al.* 2006). Adaptations to
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7 414 survive abiotic and trophic stresses at the seedling stage are likely to involve life history
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9 415 tradeoffs that confer advantages in one habitat while being disadvantageous in another habitat.
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11 416 For example, seedlings of white-sand specialists grew slower but invested more in defense than
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13 417 those of terra firme specialists, suggesting a growth-defense tradeoff in five lineages (Fine *et al.*
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15 418 2006). Similar tradeoffs could exist for drought and flood tolerance because allocation to
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17 419 structures such as increased root depth or pneumatophores presumably diverts photosynthate,
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19 420 which could otherwise be used for height growth (Parolin *et al.* 2004). The stronger patterns of
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21 421 habitat specialization in Peru than in French Guiana suggest that habitat-mediated speciation may
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23 422 be more likely to occur in the western Amazon, where environmental gradients are steeper and
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25 423 forest dynamics are faster (Quesada *et al.* 2011; Baker *et al.* 2014). For example, Fine *et al.*
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27 424 (2014) conducted biogeographic reconstructions of the fossil-calibrated phylogeny of the
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29 425 Protieae (Burseraceae) and found that Guianan species most likely dispersed from Amazonian
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31 426 ancestors. Thus habitat specialists currently found in French Guiana may have inherited their
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33 427 habitat-associated traits from Amazonian ancestors and subsequently expanded their range
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35 428 eastward.
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429 **Conclusion**

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

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3 435 strong patterns of habitat specialization observed among tropical trees, and thereby contributes to
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6 436 the spatial turnover in species composition across Amazonia.
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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 laeivicarpa</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.

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3 **Figure S3:** Effects of local values of soil nitrogen content, soil sand content and light availability
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5 on the probability of mortality of seedlings of each habitat-specialist species in French Guiana
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12 **Figure S4:** Mortality rates at the end of the experiment of seedlings of 25 habitat-specialist
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14 species from seven phylogenetic lineages in French Guiana and 16 habitat-specialist species
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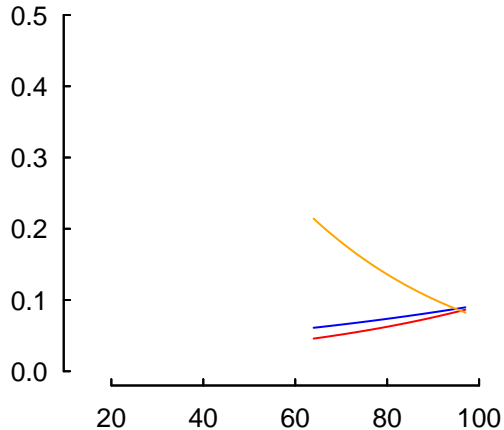
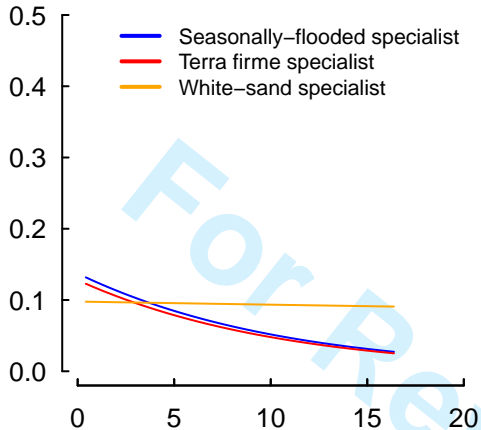
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(a) French Guiana

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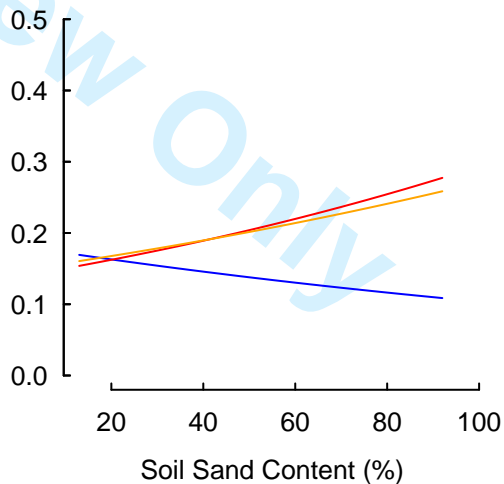
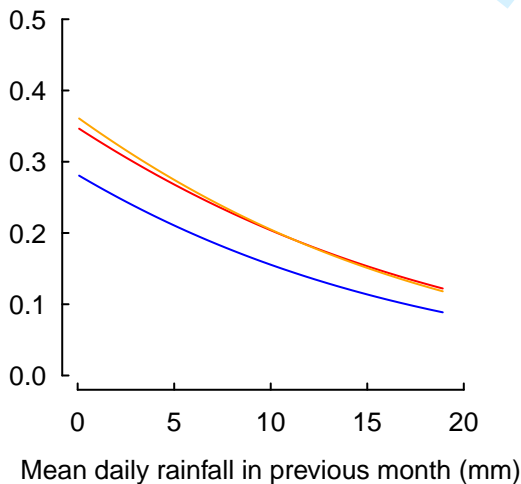
(b) French Guiana

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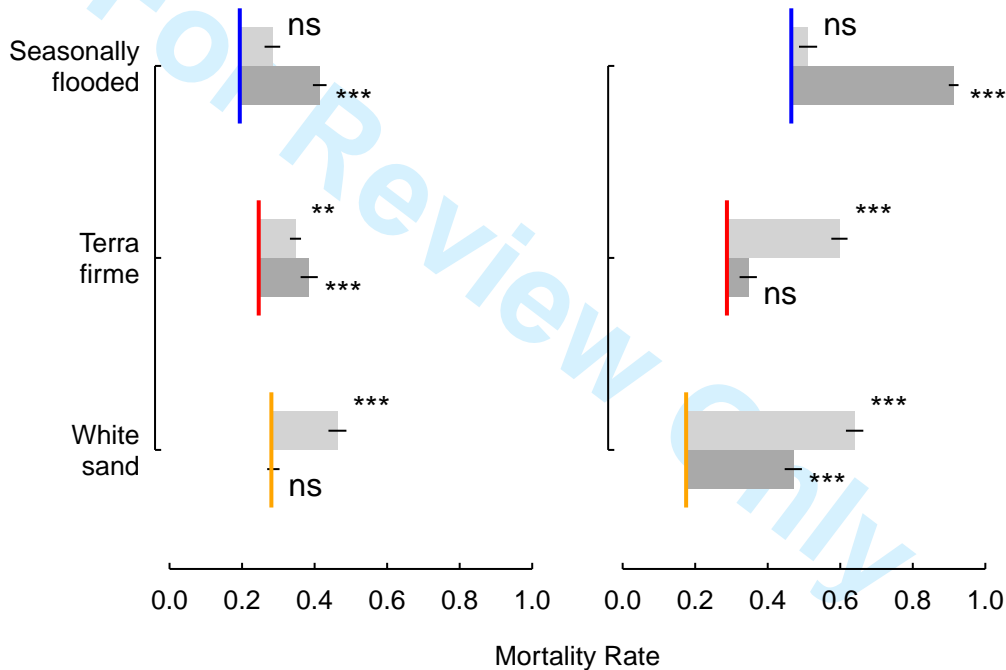
(c) Peru

(d) Peru



(a) French Guiana

(b) Peru

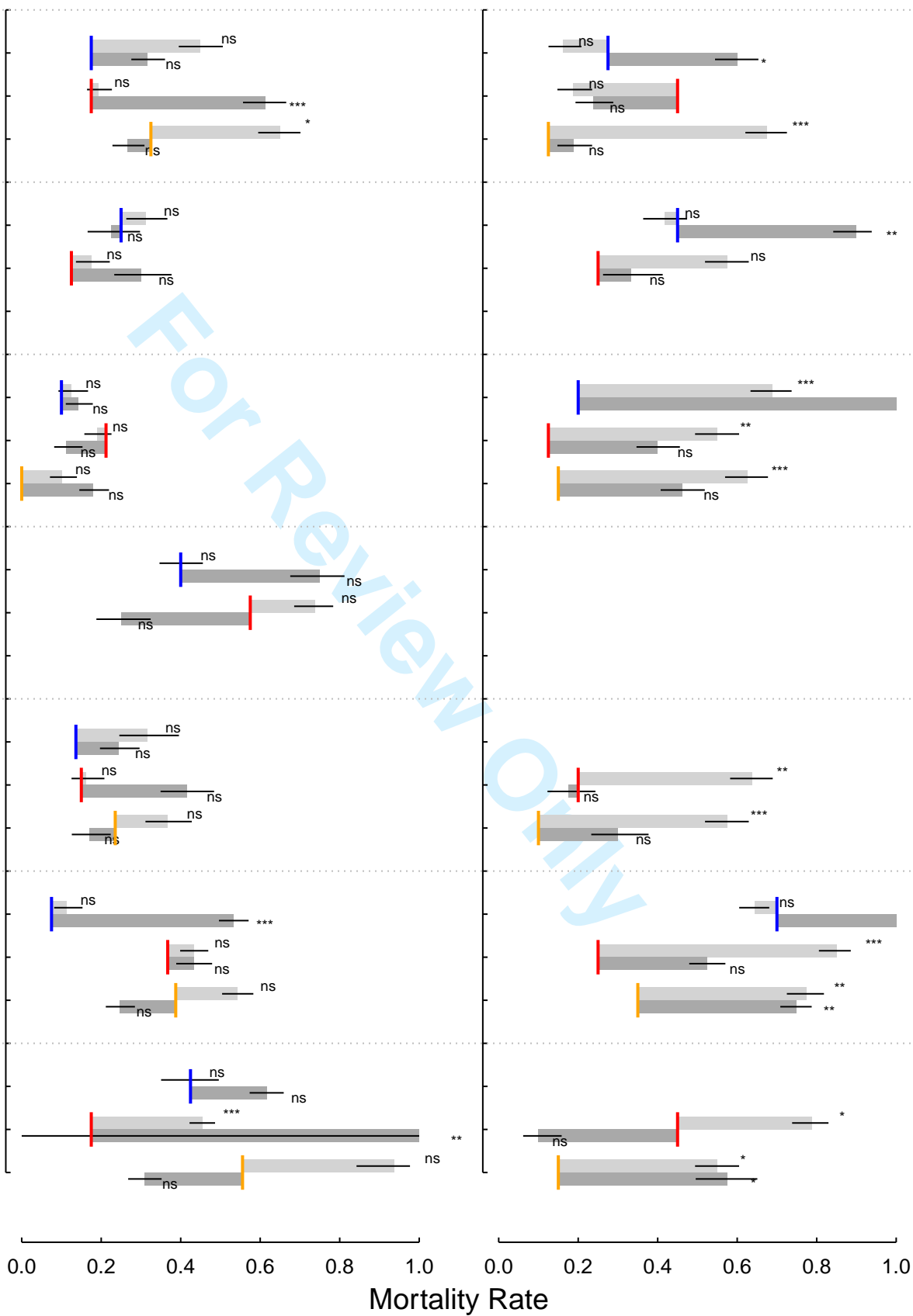


| Seasonally-flooded specialist in home habitat
 | Terra firme specialist in home habitat
 | White-sand specialist in home habitat
 | Specialist away from home habitat (best at home)
 | Non-specialist in focal habitat (home advantage)

(a) French Guiana

(b) Peru

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| Seasonally-flooded specialist in home habitat Specialist away from home habitat (best at home)
| Terra firme specialist in home habitat Non-specialist in focal habitat (home advantage)
| White-sand specialist in home habitat