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LETTER

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

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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 specialisation. In a 4-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 harboured in terra firme forests, may be strongly impacted by the predicted climate changes in Amazonia.

Keywords

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

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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 harbours 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 specialisation 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 characterised by infertile eroded clay soils adjacent to nutrient-poor sands and a pronounced dry season, whereas Peruvian sites are 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 the 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,

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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 3 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 defence mechanisms. In addition, if natural enemies preferentially attack non-specialists, they can interact with abiotic factors to drive habitat specialisation, 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 neighbouring 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 specialisation within and among lineages. Phylogenetic replication is important because the relative investment in growth and defence 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 specialisation 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 specialisation? We propose a novel framework that underlines two distinct processes that contribute to habitat specialisation: habitat specialists can become locally abundant either because (1) they perform better in their home habitat than in other habitats, a classical definition of habitat specialisation from reciprocal transplants (Bennington *et al.* 2012); and/or (2) they perform better in their home habitat than other species from the regional pool that are not strongly associated with that habitat. We refer to these as the best at home and home advantage hypotheses respectively (Table 1). Differential performance of species among habitats may arise through several mechanisms. We expect that flooding and drought are important drivers of seedling performance, favouring seasonally flooded and white-sand specialists, respectively, in their home habitats (Baraloto *et al.* 2005; Baraloto *et al.* 2007), whereas trophic filters are key to explain the dominance of terra firme specialists in their home habitat, so long as sufficient light is available for growth (Fine *et al.* 2004).

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

To test our hypotheses, we conducted a reciprocal transplant experiment at an unprecedented scale, with 4638 seedlings belonging to 41 habitat-specialist species over more than 4 years across three contrasting habitats and two countries. We provide a novel, comprehensive framework to test how variation in seedling performance contributes to habitat specialisation. Our study is the first to quantify environmental variables describing the habitat of transplantation to test the mechanisms generating habitat specialisation in tropical trees at a continental scale.

METHODS

Study sites

In both French Guiana and Peru, we selected 60 sites divided equally among the three habitats (terra firme, seasonally flooded and white-sand forests) that cover the ranges of soil fertility and flooding in both countries (Baraloto *et al.* 2011). Sites were separated by at least 15 m and located adjacent to permanent plots in the Laussat Reserve in northwestern French Guiana, and in the Allpahuayo-Mishana National Reserve in northeastern Peru (Baraloto *et al.* 2011). At each site, we established paired experimental 2 m by 2 m plots in areas of shaded understory. We covered the exclosure plot with 1-mm nylon mesh to reduce herbivory, and, as the netting reduced incident light by about 8%, we placed netting

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 of each of the three habitats

	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.

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. Abbreviations: Seasonally flooded (SF), terra firme (TF) and white-sand (WS) forests.

above the control plot to replicate any treatment shading (Fine *et al.* 2004). In each country, we thus established 120 plots (60 controls and 60 exclosures) corresponding to 40 replicate plots in each habitat. Every month, litter that accumulated on the roof of each plot was removed and spread evenly on the ground beneath, thereby reducing the shading effect of litter and stains on the netting and equalising it across plots receiving different intensities of litterfall.

At the start of the experiment, we determined light availability and soil fertility and texture in all 120 plots in each country (Table S1). Hemispherical photos were taken at the centre of the roof of each plot with a fish-eye lens at 1.5 m high (Coolpix 995, Nikon, Tokyo, Japan). Total light availability (%) was estimated with the Gap Light Analyzer software (Frazer *et al.* 1999). In each plot, 0–15 cm depth soil cores were bulked, dried at 25°C to constant mass and sieved to 2 mm for 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 ($m^3{}_{water}.m^{-3}{}_{soil}$) 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 (mm 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 asterids (*Micropholis* [Sapotaceae] and *Eschweilera* [Lecythidaceae]), fabids (*Inga* and *Swartzia* [Fabaceae] and *Licania* [Chrysobalanaceae]), and malvids (Bombacoideae [Malvaceae] and *Protium* [Burseraceae]). The seven lineages include low, medium and highly diversifying clades when compared with estimated diversification rates reported for more than 50 tropical tree lineages in a recent study (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

Table 2 The 41 habitat-specialist species included in the reciprocal transplant experiment, sorted by country, lineage and home habitat

Country	Family	Lineage	Species	Home habitat	Mean percent mortality (%)	Mean RGR in height (mm mm^{-1} month^{-1})
French Guiana	Malvaceae	Bombacoideae	*Pachira aquatica*	🟦	35.8	0.007
			Eriotheca globosa	🟥	11.7	0.013
			Eriotheca longitubulosa	🟥	25.8	0.010
			Pachira flaviflora	🟧	54.2	0.018
	Lecythidaceae	*Eschweilera*	*Eschweilera coriacea*	🟦	29.2	0.007
			Eschweilera sagotiana	🟥	15.8	0.005
	Fabaceae	*Inga*	*Inga thibaudiana*	🟦	11.7	0.023
			Inga cayennensis	🟥	24.4	0.022
			Inga pezizifera	🟥	16.7	0.014
			Inga stipularis	🟧	6.7	0.015
	Chrysobalanaceae	*Licania*	*Licania macrophylla*	🟦	40.0	0.004
			Licania heteromorpha	🟥	68.3	0.001
	Sapotaceae	*Micropholis*	*Micropholis guyanensis*	🟦	25.0	0.007
			Micropholis egensis	🟥	15.8	0.015
			Micropholis venulosa	🟧	32.4	0.020
	Burseraceae	*Protium*	*Protium opacum*	🟦	10.0	0.013
			Protium decandrum	🟥	29.2	0.013
			Protium gallicum	🟥	50.0	0.018
			Protium subserratum	🟥	49.2	0.011
			Protium aracouchini	🟧	30.8	0.016
			Protium heptaphyllum	🟧	67.5	0.018
	Fabaceae	*Swartzia*	*Swartzia polyphylla*	🟦	35.0	0.011
			Swartzia grandifolia	🟥	30.0	0.012
			Swartzia panacoco	🟥	43.0	0.011
			Swartzia bannia	🟧	80.0	0.007
Peru	Malvaceae	Bombacoideae	*Eriotheca sp.1*	🟦	20.0	0.011
			Pachira cf insignis	🟥	27.5	0.010
			Pachira brevipes	🟧	49.2	0.010
	Lecythidaceae	*Eschweilera*	*Eschweilera aff chartaceifolia*	🟦	42.9	0.009
			Eschweilera grandiflora	🟥	46.7	0.009
	Fabaceae	*Inga*	*Inga coruscans*	🟦	52.5	0.010
			Inga auristellae	🟥	40.8	0.005
			Inga lopadadenia	🟧	46.7	0.007
	Sapotaceae	*Micropholis*	*Micropholis guyanensis*	🟥	49.2	0.010
			Micropholis venulosa	🟧	41.7	0.015
	Burseraceae	*Protium*	*Protium meridionale*	🟦	58.3	0.015
			Protium unifoliolatum	🟦	74.2	0.016
			Protium sagotianum	🟥	65.0	0.005
			Protium heptaphyllum	🟧	63.3	0.012
	Fabaceae	*Swartzia*	*Swartzia cf laevicarpa*	🟥	67.5	0.004
			Swartzia benthamiana	🟧	41.7	0.009

Colours indicate home habitat for each habitat-specialist species: blue: seasonally flooded forest, red: terra firme forest, yellow: white-sand forest. Mean percent mortality 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 fast in *Inga* and *Licania* (Baker *et al.* 2014).

16 species in Peru. Our designations of habitat association for these 41 species are consistent with species accounts from many published sources (e.g. ter Steege *et al.* 2013; Fine *et al.* 2010).

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 generalised 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 species_i). Plot identity was included as a random effect to account for autocorrelation in seedling mortality among plots (R 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 (soil_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:

$$\begin{aligned}\text{mortality}_t = \text{lineage} * \big(&\Delta\text{soil}_\text{N} + \Delta\text{soil}_\text{Sand} + \Delta\text{light} + \text{rain}_{30\text{days}}\\ &+ \text{treatment}\big) + \text{R species}_i + \text{R plot}_j,\end{aligned}$$

where '$*$' denotes interaction between terms. The second GLMM had terms for local conditions of habitat of transplantation:

$$\begin{aligned}\text{mortality}_t = \text{lineage} * \big(&\text{soil}_\text{N} + \text{soil}_\text{Sand} + \text{light} + \text{rain}_{30\text{days}}\\ &+ \text{treatment}\big) + \text{R species}_i + \text{R plot}_j.\end{aligned}$$

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 generalised 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 $\text{performance}_f = \text{habitat}_\text{home} * \text{habitat}_\text{transplantation}$ (Q_2), and (ii) each group of habitat specialists by lineage using $\text{performance}_f = \text{lineage} * \text{habitat}_\text{home} * \text{habitat}_\text{transplantation}$ (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

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 and 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 content in French Guiana but not in Peru (Fig. 1b and d). Terra firme specialists exhibited higher seedling mortality with increasing soil sand content in both countries. White-sand specialists exhibited lower seedling mortality with increasing soil sand content in French Guiana, but showed the opposite pattern in Peru. In addition, the effects of soil and light factors on seedling mortality varied strongly among lineages (Fig. S2), species (Fig. S3) and countries (Table S2). In both countries, seedling mortality was much better explained by soil and light conditions in the plot of transplantation (Table S2) than by increasing differences between local conditions of transplantation and the home habitat (Table S3) (ΔBIC = 41.84 in French Guiana and 56.72 in Peru).

Differences in seedling mortality among habitats and countries

The best at home and home advantage hypotheses make context dependent predictions (Table 1). Synthesising the

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

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

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).

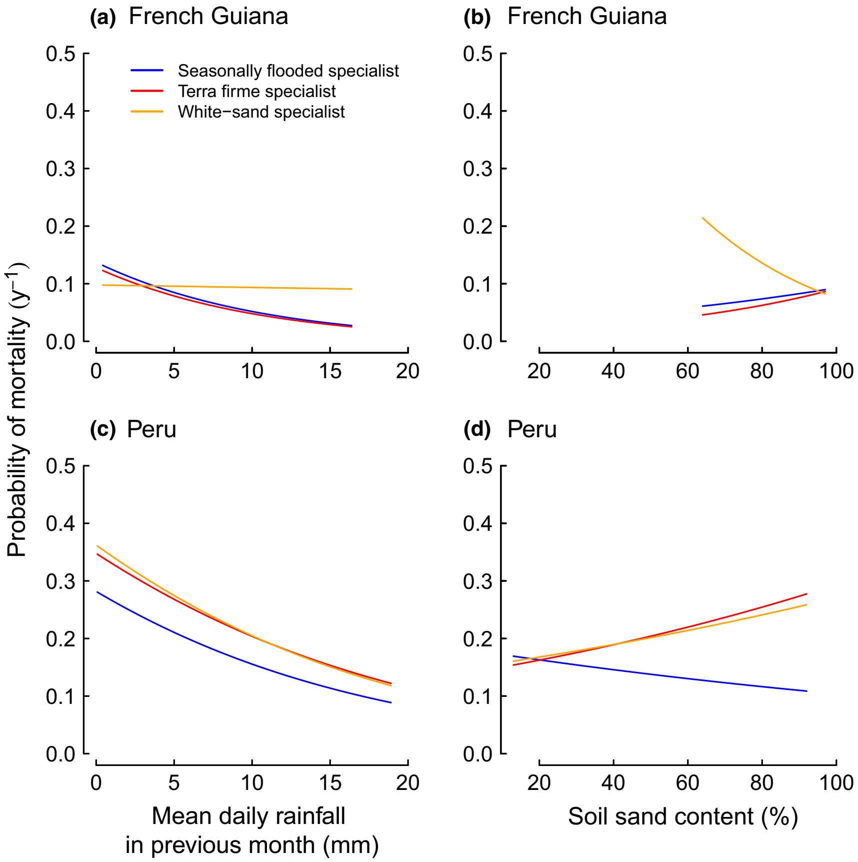

Figure 1 Effects of local values of rainfall and soil sand content on the probability of mortality of seedlings of habitat-specialist species from three forest habitats in (a and b) French Guiana and (c and d) in Peru. Effects were predicted from the best generalised mixed models for mortality in each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

patterns of mortality across lineages and countries, these specific predictions were broadly supported by the evidence, with 4 out of 6, and 6 out of 6 of the predictions met in French Guiana and Peru respectively (Fig. 2). As predicted, seasonally flooded specialists did not experience significant differences in mortality when planted into other habitats in either country (Fig. 2, best at home). Moreover, they showed lower mortality than terra firme and white-sand specialists in seasonally flooded forests in both countries (Fig. 2, home advantage). This difference was especially pronounced in Peru, where species not associated with flooded forests experienced more than twice the mortality of seasonally flooded specialists (Fig. 2b). In both countries, terra firme specialists exhibited lower mortality at home than in other habitats (Fig. 2, best at home). We predicted no home advantage of terra firme specialists, yet results were equivocal with a slight home advantage of terra firme specialists in French Guiana but not in Peru (Fig. 2, home advantage). Also as predicted, white-sand specialists had lower mortality at home than in other habitats in both countries (Fig. 2, best at home) and had lower mortality than seasonally flooded and terra firme specialists in white-sands in Peru but not in French Guiana (Fig. 2, home advantage). In addition, seedling mortality at the end of the experiment was lower in French Guiana than in Peru (31.8 and 49.2%, respectively, F-value = 146.60, $P < 0.001$).

Differences in seedling mortality within and among lineages

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

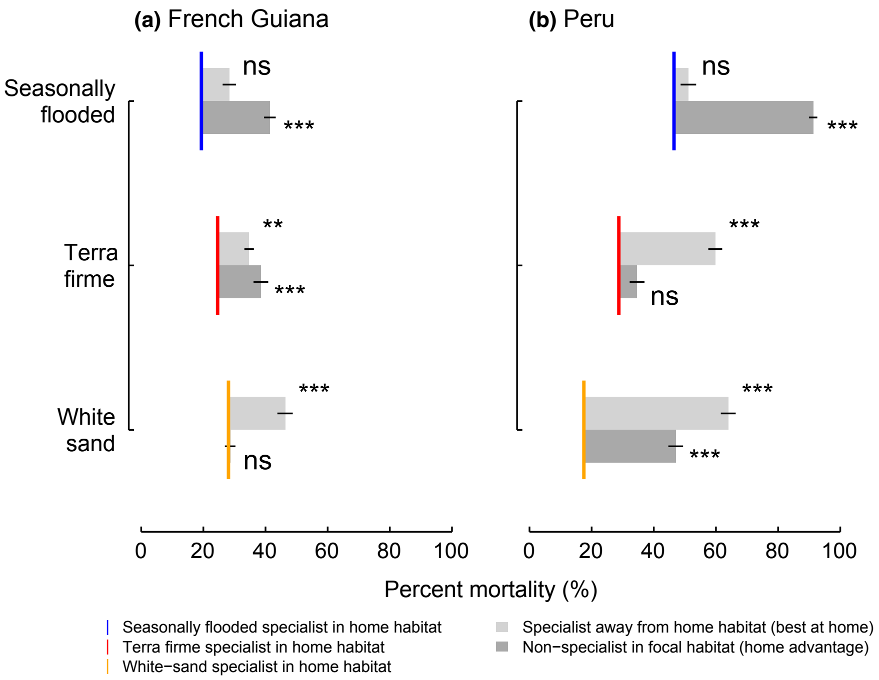

Figure 2 Percent mortality at the end of the experiment of seedlings of habitat-specialist species from three habitats in (a) French Guiana and (b) Peru. The mean percent mortality of habitat specialists in their home habitat is shown as vertical lines. Their percent mortality when planted in other habitats is shown with light grey bars, testing the best at home hypothesis (see first column in Table 1). The percent mortality of non-specialists planted into each focal habitat is shown as dark grey 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).

preferences (Fig. 3, home advantage). Although we observed different degrees of contrasting species performance among lineages, we found no pattern consistent with lineage age or diversification rate (Table 2).

Growth and herbivory

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

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

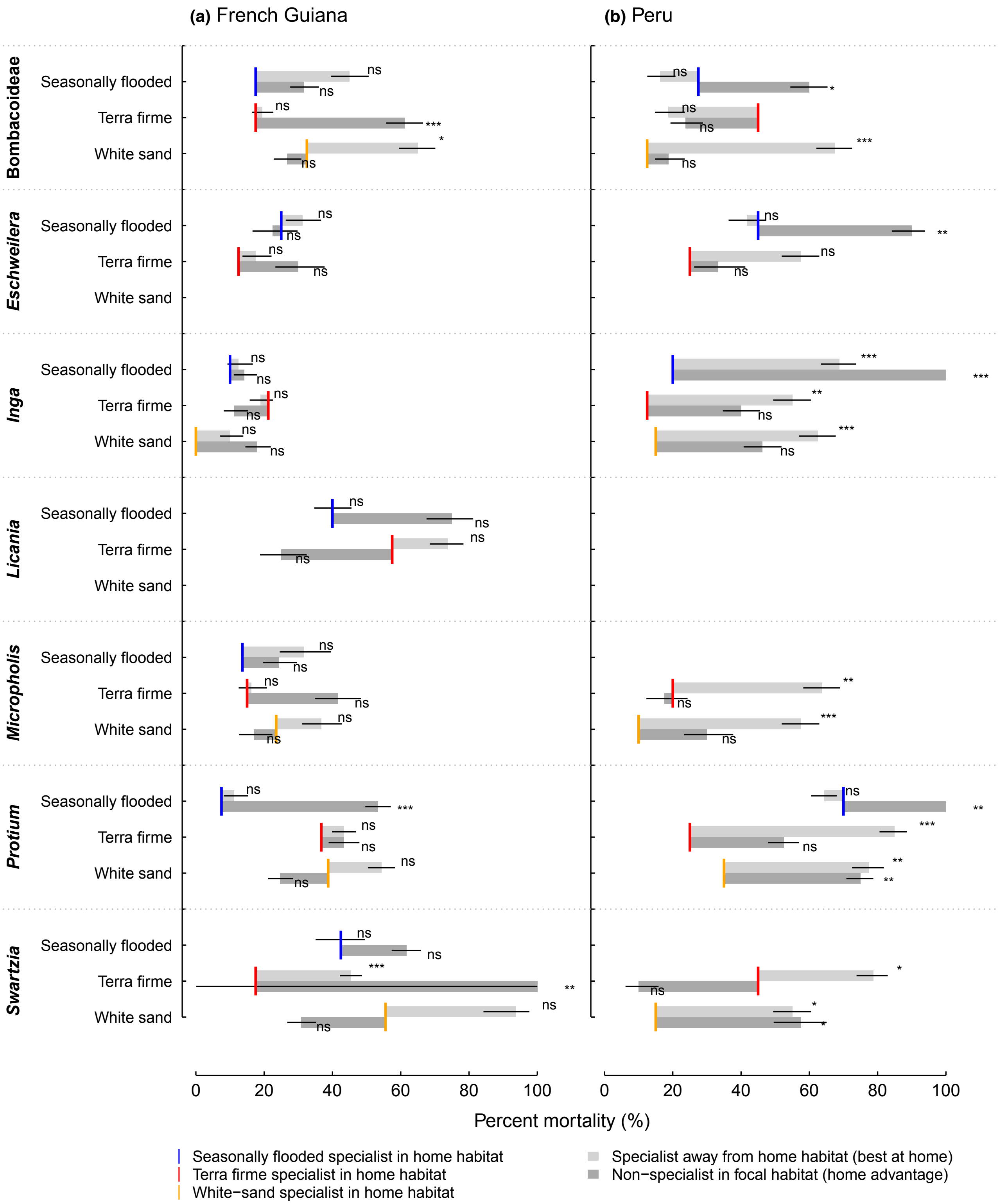

Figure 3 Percent mortality at the end of the experiment of seedlings of habitat-specialist species in (a) seven phylogenetic lineages in French Guiana and (b) six phylogenetic lineages in Peru. The mean percent mortality of habitat specialists in their home habitat is shown as vertical lines. Their percent mortality when planted in other habitats is shown with light-gray bars, testing the best at home hypothesis (see first column in Table 1). The percent 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 (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns: non-significant).

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 emphasises the importance of seasonal and interannual 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).

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 specialisation

Overall, we found strong support for our predictions regarding habitat specialisation (Table 1), suggesting that abiotic filtering at the seedling stage contributes to 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 recognised as a critical determinant of forest dynamics (Comita *et al.* 2009; Metz 2012; Green *et al.* 2014). Evaluating forest dynamics in a 50-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 harbour 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 50 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 modelling 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 Amazon where seasonally flooded specialists are uniquely tolerant to flooding and white-sand specialists are especially well adapted to short-term dry spells.

Contrasting habitat-mediated seedling mortality among countries and congeners

Patterns of habitat specialisation 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 percent mortality lower than 30% after 4 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 supports the hypothesis that different strategies at the seedling stage could be involved in the evolution of habitat specialisation. 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 defence than those of terra firme specialists, suggesting a growth-defence 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 specialisation 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 specialisation 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 strong patterns of habitat specialisation observed among tropical trees, and thereby contributes to the spatial turnover in species composition across Amazonia.

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AUTHORSHIP

CF, CB and PVAF designed the study. CF, CB, PVAF, IM, JYG, BB, and JC set up the reciprocal transplant experiment and performed the seedling censuses. CF and CETP analysed the data. CF, CB and PVAF wrote the first draft of the manuscript. All authors contributed to revisions.

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