

PLOS ONE

Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession --Manuscript Draft--

Manuscript Number:	PONE-D-14-30895R3
Article Type:	Research Article
Full Title:	Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession
Short Title:	Functional strategies and succession in dry and wet tropical forest
Corresponding Author:	Madelon Lohbeck Wageningen University Wageningen, NETHERLANDS
Keywords:	dry deciduous forest; Functional trait; functional trait trade-off; functional strategy; Mexico; secondary succession; PCA; wet evergreen forest
Abstract:	<p>Global plant trait studies have revealed fundamental trade-offs in plant resource economics. We evaluated such trait trade-offs during secondary succession in two species-rich tropical ecosystems that contrast in precipitation: dry deciduous and wet evergreen forests of Mexico. Species turnover with succession in dry forest largely relates to increasing water availability and in wet forest to decreasing light availability. We hypothesized that while functional trait trade-offs are similar in the two forest systems, the successful plant strategies in these communities will be different, as contrasting filters affect species turnover.</p> <p>Research was carried out in 15 dry secondary forest sites (5-63 years after abandonment) and in 17 wet secondary forest sites (<1-25 years after abandonment). We used 11 functional traits measured on 132 species to make species-trait PCA biplots for dry and wet forest and compare trait trade-offs. We evaluated whether multivariate plant strategies changed during succession, by calculating a 'Community-Weighted Mean' plant strategy, based on species scores on the first two PCA-axes. Trait spectra reflected two main trade-off axes that were similar for dry and wet forest species: acquisitive versus conservative species, and drought avoiding species versus evergreen species with large animal-dispersed seeds. These trait associations were consistent when accounting for evolutionary history. Successional changes in the most successful plant strategies reflected different functional trait spectra depending on the forest type. In dry forest the community changed from having drought avoiding strategies early in succession to increased abundance of evergreen strategies with larger seeds late in succession. In wet forest the community changed from species having mainly acquisitive strategies to those with more conservative strategies during succession. These strategy changes were explained by increasing water availability during dry forest succession and increasing light scarcity during wet forest succession. Although similar trait spectra were observed among dry and wet secondary forest species, the consequences for succession were different resulting from contrasting environmental filters.</p>
Order of Authors:	Madelon Lohbeck Edwin Lebrija-Trejos Miguel Martínez-Ramos Jorge A. Meave Lourens Poorter Frans Bongers
Opposed Reviewers:	
Response to Reviewers:	See uploaded letter to the editor
Additional Information:	
Question	Response

<p>Financial Disclosure</p> <p>Please describe all sources of funding that have supported your work. A complete funding statement should do the following:</p> <p>Include grant numbers and the URLs of any funder's website. Use the full name, not acronyms, of funding institutions, and use initials to identify authors who received the funding.</p> <p>Describe the role of any sponsors or funders in the study design, data collection and analysis, decision to publish, or preparation of the manuscript. If they had <u>no role</u> in any of the above, include this sentence at the end of your statement: "<i>The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.</i>"</p> <p>If the study was unfunded, provide a statement that clearly indicates this, for example: "<i>The author(s) received no specific funding for this work.</i>"</p> <p>* typeset</p>	<p>ML and FB were supported by a research grant from Wageningen University and Research Center. FB and MMR were supported by NSF-LTREB DEB-0639393 and #DEB 1147429. MMR was supported by grants SEMARNAT-CONACYT 2002-C01-0597, SEP-CONACYT CB-2005-01-51043, SEP-CONACYT 2009-129740. ELT acknowledges support by CONACYT (personal scholarship), CONACYT-SEMARNAT (grant 2002-C01-0267), PAPIIT (grant IN216007) and SNI, SENACYT, Panama. JAM was supported by SEP CONACYT-2009-01-128136. LP was partly supported by the Nucleo DiverSus project, which was supported by the Inter-American Institute for Global Change Research (IAI)CRN 2015 and SGP-CRA2015 (through National Science Foundation grants GEO-0452325 and GEO-1138881). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.</p>
<p>Competing Interests</p> <p>You are responsible for recognizing and disclosing on behalf of all authors any competing interest that could be perceived to bias their work, acknowledging all financial support and any other relevant financial or non-financial competing interests.</p> <p>Do any authors of this manuscript have competing interests (as described in the PLOS Policy on Declaration and Evaluation of Competing Interests)?</p> <p>If yes, please provide details about any and all competing interests in the box below. Your response should begin with this statement: <i>I have read the journal's policy and the authors of this manuscript have the following competing interests:</i></p> <p>If no authors have any competing</p>	<p>The authors have declared that no competing interests exist</p>

<p>interests to declare, please enter this statement in the box: <i>"The authors have declared that no competing interests exist."</i></p> <p>* typeset</p>	
<p>Ethics Statement</p> <p>You must provide an ethics statement if your study involved human participants, specimens or tissue samples, or vertebrate animals, embryos or tissues. All information entered here should also be included in the Methods section of your manuscript. Please write "N/A" if your study does not require an ethics statement.</p> <p>Human Subject Research (involved human participants and/or tissue)</p> <p>All research involving human participants must have been approved by the authors' Institutional Review Board (IRB) or an equivalent committee, and all clinical investigation must have been conducted according to the principles expressed in the Declaration of Helsinki. Informed consent, written or oral, should also have been obtained from the participants. If no consent was given, the reason must be explained (e.g. the data were analyzed anonymously) and reported. The form of consent (written/oral), or reason for lack of consent, should be indicated in the Methods section of your manuscript.</p> <p>Please enter the name of the IRB or Ethics Committee that approved this study in the space below. Include the approval number and/or a statement indicating approval of this research.</p> <p>Animal Research (involved vertebrate animals, embryos or tissues)</p> <p>All animal work must have been conducted according to relevant national and international guidelines. If your study involved non-human primates, you must provide details regarding animal welfare and steps taken to ameliorate suffering; this is in accordance with the recommendations of the Weatherall report, "The use of non-human primates in</p>	<p>Since all secondary forest plots are located on privately owned land, permission from landowners to enter the sites and collect plant material was provided before conducting this research.</p>

<p>research." The relevant guidelines followed and the committee that approved the study should be identified in the ethics statement.</p> <p>If anesthesia, euthanasia or any kind of animal sacrifice is part of the study, please include briefly in your statement which substances and/or methods were applied.</p> <p>Please enter the name of your Institutional Animal Care and Use Committee (IACUC) or other relevant ethics board, and indicate whether they approved this research or granted a formal waiver of ethical approval. Also include an approval number if one was obtained.</p> <p>Field Permit</p> <p>Please indicate the name of the institution or the relevant body that granted permission.</p>	
<p>Data Availability</p> <p>PLOS journals require authors to make all data underlying the findings described in their manuscript fully available, without restriction and from the time of publication, with only rare exceptions to address legal and ethical concerns (see the PLOS Data Policy and FAQ for further details). When submitting a manuscript, authors must provide a Data Availability Statement that describes where the data underlying their manuscript can be found.</p> <p>Your answers to the following constitute your statement about data availability and will be included with the article in the event of publication. Please note that simply stating 'data available on request from the author' is not acceptable. If, however, your data are only available upon request from the author(s), you must answer "No" to the first question below, and explain your exceptional situation in the text box provided.</p> <p>Do the authors confirm that all data underlying the findings described in their manuscript are fully available without restriction?</p>	<p>Yes - all data are fully available without restriction</p>
<p>Please describe where your data may be found, writing in full sentences. Your answers should be entered into the box</p>	<p>All relevant data are within the paper and its Supporting Information files</p>

below and will be published in the form you provide them, if your manuscript is accepted. If you are copying our sample text below, please ensure you replace any instances of **XXX** with the appropriate details.

If your data are all contained within the paper and/or Supporting Information files, please state this in your answer below. For example, "All relevant data are within the paper and its Supporting Information files."

If your data are held or will be held in a public repository, include URLs, accession numbers or DOIs. For example, "All **XXX** files are available from the **XXX** database (accession number(s) **XXX**, **XXX**)." If this information will only be available after acceptance, please indicate this by ticking the box below.

If neither of these applies but you are able to provide details of access elsewhere, with or without limitations, please do so in the box below. For example:

"Data are available from the **XXX** Institutional Data Access / Ethics Committee for researchers who meet the criteria for access to confidential data."

"Data are from the **XXX** study whose authors may be contacted at **XXX**."

* typeset

Additional data availability information:

Dear Paul Fine,

We hereby resubmit the manuscript entitled “**Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession**” (authors Lohbeck, Lebrija-Trejos, Martínez-Ramos, Meave, Poorter and Bongers) as a research article to PLOS ONE.

Thank you for the additional suggestions to improve this manuscript. Below we respond to the specific comments that you raised.

We are looking forward to hear from you.

With kind regards,

On behalf of all authors,
Madelon Lohbeck

Dear Dr. Lohbeck,

Thank you for submitting your manuscript for review to PLOS ONE. After careful consideration, we feel that your manuscript will likely be suitable for publication if it is revised to address the points below. Therefore, my decision is "Minor Revision."

We invite you to submit a revised version of the manuscript that addresses the following points:

Thank you for your resubmission and your attention to my previous comments. I am only requesting a few minor changes before accepting this manuscript.

1. Abstract, line 23. Replace "driven by" with "correlates with".

Changed into ‘relates to..’ it now reads: “Species turnover with succession in dry forest largely relates to increasing water availability and in wet forest to decreasing light availability.”

2. Abstract. Add in results of PIC tests somewhere in the abstract.

This was added in line 35-36 “These trait associations were consistent when accounting for evolutionary history.”

3. Introduction, line 74 and line 75 -- replace "driven by" with "correlates with". Natural enemies interact with light and water availability and can sometimes also "drive" succession. Just say "correlates with" and there will be no confusion.

Changed into ‘related to..’ it now reads: “In tropical wet forest, succession is related to a gradient of decreasing light availability over time [] whereas in dry forest it is related to a gradient of increasing water availability over time [].”

4. line 82, replace "coping" with "tolerance."

Changed accordingly

5. line 116 "high biodiversity" is very vague. Relative to what? either delete or add something quantitative here (number of species per plot, for example)

I removed 'high biodiversity'. Although data is available in the reference cited (746 plant species in the region), the same statement could be made for the wet forest region which is also highly diverse (not mentioned in the manuscript as it stands). Although I think it is valuable to mention that both regions are characterized by high biodiversity levels, it is hard to back this up with data that is comparable in the two regions (i.e. using a similar sampling design).

6. lines 159-161. Either delete this sentence or change "legitimized" to "we consider the use of species average trait values appropriate to test our hypotheses."

Changed accordingly

7. line 265. There is a problem with this sentence. maybe add an "and" after "biotic seed dispersal"? .. I am not sure what is coinciding with an increased seed size. Please rewrite for clarity.

Changed as follows: "The first principal component reflected variation from a deciduous strategy with abiotically (mainly wind-) dispersed species towards evergreen species that invested in biotic seed dispersal, in the dry forest biotic seed dispersal also coincided with an increased seed size (Fig. 1)."

We encourage you to submit your revision within forty-five days of the date of this decision.

When your files are ready, please submit your revision by logging on to <http://pone.edmgr.com/> and following the Submissions Needing Revision link. Do not submit a revised manuscript as a new submission. Before uploading, you should proofread your manuscript very closely for mistakes and grammatical errors. Should your manuscript be accepted for publication, you may not have another chance to make corrections as we do not offer pre-publication proofs.

If you would like to make changes to your financial disclosure, please include your updated statement in your cover letter.

In addition, when submitting your revision please include the following items:

- A rebuttal letter that responds to each point brought up by the academic editor and reviewer(s). This letter should be uploaded as a 'Response to Reviewers' file.
- A clean revised manuscript as your 'Manuscript' file.

- A marked-up copy of the changes made from the previous article file as a 'Revised Manuscript with Track Changes' file. This can be done using 'track changes' in programs such as MS Word and/or highlighting any changes in the new document.

For more information on how to upload your revised submission, see our video:

<http://blogs.plos.org/everyone/2011/05/10/how-to-submit-your-revised-manuscript/>

If you choose not to submit a revision, please notify us.

Yours sincerely,

Paul V. A. Fine
Academic Editor
PLOS ONE

Madelon Lohbeck et al.

1 **Functional trait strategies of trees in dry and wet tropical forests are similar but differ**
2 **in their consequences for succession**

3

4 Madelon Lohbeck ^{*} ^{1,3}, Edwin Lebrija-Trejos ^{1,2,4}, Miguel Martínez-Ramos ³, Jorge A. Meave
5 ⁴, Lourens Poorter ¹, Frans Bongers ¹

6

7 ¹ Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700
8 AA Wageningen, The Netherlands

9 ² Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama

10 ³ Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México,

11 Campus Morelia, Antigua Carretera a Pátzcuaro 8701, Ex-hacienda de San José de la Huerta,
12 58190 Morelia, Michoacán, Mexico

13 ⁴ Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad

14 Nacional Autónoma de México, 04510 México, Distrito Federal, Mexico

15

16 * Correspondence author: madelon.lohbeck@wur.nl

17

18

19 **Abstract**

20 Global plant trait studies have revealed fundamental trade-offs in plant resource economics.
21 We evaluated such trait trade-offs during secondary succession in two species-rich tropical
22 ecosystems that contrast in precipitation: dry deciduous and wet evergreen forests of Mexico.
23 Species turnover with succession in dry forest largely relates to increasing water availability
24 and in wet forest to decreasing light availability. We hypothesized that while functional trait
25 trade-offs are similar in the two forest systems, the successful plant strategies in these
26 communities will be different, as contrasting filters affect species turnover.
27 Research was carried out in 15 dry secondary forest sites (5-63 years after abandonment) and
28 in 17 wet secondary forest sites (<1-25 years after abandonment). We used 11 functional
29 traits measured on 132 species to make species-trait PCA biplots for dry and wet forest and
30 compare trait trade-offs. We evaluated whether multivariate plant strategies changed during
31 succession, by calculating a 'Community-Weighted Mean' plant strategy, based on species
32 scores on the first two PCA-axes.
33 Trait spectra reflected two main trade-off axes that were similar for dry and wet forest
34 species: acquisitive versus conservative species, and drought avoiding species versus
35 evergreen species with large animal-dispersed seeds. These trait associations were consistent
36 when accounting for evolutionary history. Successional changes in the most successful plant
37 strategies reflected different functional trait spectra depending on the forest type. In dry forest
38 the community changed from having drought avoiding strategies early in succession to
39 increased abundance of evergreen strategies with larger seeds late in succession. In wet forest
40 the community changed from species having mainly acquisitive strategies to those with more
41 conservative strategies during succession. These strategy changes were explained by
42 increasing water availability during dry forest succession and increasing light scarcity during
43 wet forest succession.

44 Although similar trait spectra were observed among dry and wet secondary forest species, the
45 consequences for succession were different resulting from contrasting environmental filters.

46 Keywords: dry deciduous forest, functional trait, functional trait trade-off, functional strategy,
47 Mexico, secondary succession, PCA, wet evergreen forest

48

49 **Introduction**

50 Trade-offs in plant traits and resource economics are consistent at the global scale [1,2,3].
51 These give insight into comprehensive dimensions of multivariate functional trait variation,
52 or what we call ‘functional trait spectra’. As functional traits are indicators of ecological
53 strategies, the study of trait spectra and trade-offs allows us to explore the complex interplay
54 of different strategies [4]. For example, the worldwide leaf economics spectrum runs from a
55 plant strategy with cheap-to-construct acquisitive leaves with high photosynthetic rates that
56 maximize resource capture to a strategy with expensive-to-construct conservative leaves that
57 tolerate stress and physical damage and better conserve the acquired resources [2]. Such an
58 economic spectrum has not only been found for leaves, but also for other plant organs like
59 roots and stems [3,5], and it has been found across different climatic regions [2,6]. This
60 economics spectrum at the tissue level underlies the trade-off between growth and survival at
61 the whole-plant level [7], as in resource rich environments acquisitive strategies thrive by fast
62 growth (and high mortality) whilst in resource-poor environments conservative strategies
63 thrive by persistence (and high survival). This fundamental trade-off describes variation
64 among plants in the established phase. In contrast, different trade-offs are found in the
65 regenerative phase, where plants have to arrive and establish successfully at a site. As a
66 result, traits related to the regenerative phase are largely decoupled from those related to the
67 established phase [8]. The trade-off between seed size and seed number plays an important
68 role in explaining the differential success of species in the regenerative phase [e.g. 9]. Small
69 seeds are produced in large numbers and are often wind-dispersed, which is advantageous
70 when colonizing new sites [10], but their small seed size comes at the expense of a lower per
71 capita establishment success [11]. Large seeds produce robust seedlings [12], which is
72 advantageous when colonizing shaded sites [13], and they are often animal-dispersed,
73 enhancing directed dispersal to safe sites [14].

74 These traits and trait trade-offs are used to explain species' success along successional
75 gradients. In tropical wet forest, succession is related to a gradient of decreasing light
76 availability over time [e.g. 15] whereas in dry forest it is related to a gradient of increasing
77 water availability over time [16,17]. Dry forest species experience, therefore, stressful
78 conditions during the dry and hot early stages of succession, while wet forest species do so
79 during the shaded late stages of succession. We showed previously that, at the *community-*
80 *level*, the community-weighted mean (CWM) of *individual* functional traits changed with
81 tropical forest succession in Mexico [17]. The type of traits that changed differed largely
82 between dry and wet forests [18]. In dry forest early-successional communities had trait
83 values related to drought tolerance and optimal light acquisition, whereas late-successional
84 communities had trait values related to large seeds and biotic dispersal. In wet forest early-
85 successional communities also had trait values related to optimal light acquisition, whereas
86 late-successional communities had trait values related to increased leaf toughness. Here we
87 expand on the previous analysis, and explore differences in *species-level* trait trade-offs
88 between dry and wet forest species, and to what extent this can be translated into different
89 *multivariate plant strategies* between dry and wet forest species. Since environmental
90 gradients filter species based on multiple traits, identifying changes in multivariate plant
91 strategies is needed to further advance our understanding of ecological restoration [cf. 19].

92 The present study focuses on trait trade-offs *at the species level*, and how *multivariate plant*
93 *strategies* change during succession. To this end we described plant strategies using 11
94 functional traits measured on 132 species found in 32 secondary forest sites belonging to dry
95 and wet tropical forest in Mexico. We hypothesized the existence of two major trait- or
96 strategy spectra, namely the spectrum of species with acquisitive versus those with
97 conservative trait values, which is important in the established phase of plants, and the
98 spectrum of small seeded wind-dispersed species versus large seeded animal-dispersed

99 species, which is important in the regeneration phase. We expected that in dry forest water is
100 the main limiting factor, and that tree communities show a change from predominantly
101 conservative to acquisitive strategies over time, whereas in wet forest light is the main
102 limiting factor, and the communities show a change from predominantly acquisitive to
103 conservative strategies over time. We also expected that the seed size spectrum would play an
104 important role in both forest types, reflecting an increase in the proportion of large seeded
105 animal-dispersed species along succession.

106 **Methods**

107 *Ethics statement*

108 Since all secondary forest plots are located on privately owned land, permission from
109 landowners to enter the sites and collect plant material was provided before conducting this
110 research.

111 *Research locations*

112 *Tropical dry forest.* Research plots in tropical dry forest surround the village of Nizanda on
113 the Pacific watershed of the Isthmus of Tehuantepec in Oaxaca, southern Mexico (16°39'N,
114 95°00'W). Mean annual temperature is 26 °C and mean annual precipitation is 900 mm, of
115 which > 90 % concentrates between late May and mid-October [20]. The vegetation is
116 predominantly tropical dry deciduous forest, characterized by a low canopy stature (ca. 7 m
117 tall) [21,22]. The 15 secondary forest plots (900 m²) with different fallow ages (6-64 years)
118 were established on abandoned maize fields. Within each plot four parallel 5 × 20 m transects
119 were set up, and further divided into four 5 × 5 m quadrats. In one quadrat all individuals
120 with DBH ≥ 1cm were identified and measured, in a second all individuals with DBH ≥ 2.5
121 cm and in the remaining two all individuals with DBH ≥ 5 cm, with these sampling criteria
122 being randomly assigned to each quadrat. Variables measured on each individual were scaled

123 up to the plot level according to sampling effort per size-class (i.e., all stems $1 \text{ cm} \leq \text{DBH} \leq$
124 2.5 cm were multiplied by four, and $2.5 \text{ cm} \leq \text{DBH} \leq 5 \text{ cm}$ by two, to make sampling effort
125 comparable across size-classes, after which all stems are added up). For further details see
126 Lebrija-Trejos et al. [20].

127 *Tropical wet forest.* Research plots in the tropical wet forest surround the village of Loma
128 Bonita in the Marqués de Comillas region in Chiapas, southeastern Mexico ($16^{\circ}01' \text{N}$,
129 $90^{\circ}55' \text{W}$). Mean annual temperature is $24 \text{ }^{\circ}\text{C}$ and mean annual precipitation is 3000 mm ,
130 with a dry period ($< 100 \text{ mm month}^{-1}$) from February through April [23]. The research area is
131 characterized by small hills and valleys with sandy and clay soils of low pH (< 5.5). The 17
132 secondary forest plots (1000 m^2) with different fallow ages ($< 1\text{-}25 \text{ years}$) were established
133 on abandoned maize fields. Each plot was divided into two $10 \times 50 \text{ m}$ subplots. In one
134 subplot all individuals with $\text{DBH} \geq 1 \text{ cm}$ were identified and measured, in the second all
135 individuals $\text{DBH} \geq 5 \text{ cm}$. Again, measured variables were scaled to the plot level up
136 according to sampling effort per size-class (i.e., stems $1 \text{ cm} \leq \text{DBH} \leq 5 \text{ cm}$ were multiplied
137 by two to make sampling effort comparable to $\text{DBH} \geq 5 \text{ cm}$, after which all stems are added
138 up).

139 *Functional traits*

140 Those species that made up at least 80 % of the basal area in the plots were selected for
141 functional trait measurements (excluding cacti in dry forest, as their functional traits are
142 difficult to compare with trees), because they accurately describe the community-weighted
143 mean [24,25]. This resulted in a total of 132 species: 51 dry forest species and 81 wet forest
144 species (see Table S1 in supplementary materials for the list of species per forest type). We
145 measured seven leaf traits: leaf area (m^2), specific leaf area- SLA (m^2/kg), leaf dry matter
146 content- LDMC (g/g), leaf density (g/cm^3), leaf thickness (mm), leaf compoundness

147 (0=simple, 1=compound), petiole length (cm); one whole plant trait: deciduousness
148 (0=evergreen, 1=deciduous); one stem trait: wood density- WD (g/cm^3); and two regenerative
149 traits: seed size (mm^3) and dispersal syndrome (0=abiotic, 1=biotic). Traits were measured
150 following standardized protocols [26,27]. In the wet forest sites, leaf traits were measured for
151 two sun-lit leaves for 10 adult trees per species (5 individuals for specific force to punch) of
152 ca. 5 m high, and in dry forest for 5 sun-lit leaves for 5 adult trees per species with a DBH of
153 10-30 cm. Functional trait measurements took place within the study areas, but not inside the
154 plots. For wood density measurements in the wet forest 15 of the 81 species were taken from
155 comparable Mexican ecosystems. The binary traits leaf compoundness, deciduousness, and
156 dispersal syndrome were scored based on field observations, local informants, herbaria, and
157 literature; for detailed methods on functional trait measurements see supplementary material
158 in [18]. We used species' average trait values although we recognize that intraspecific trait
159 variation may play an important role in species adaptation along environmental gradients.
160 However, given the extensive species-level trait data set (132 species) together with the high
161 species turnover during succession, for the purpose of this study we consider the use of
162 species average trait values appropriate to test our hypotheses.

163 *Statistical analysis*

164 We used principal component analysis to quantify spectra of trait-based multivariate plant
165 strategies for each forest type separately. The PCA biplots show the main trade-offs across
166 (standardized) functional traits based on principal axes of variation, where binary variables
167 are treated as dummy variables. Trait spectra for dry and wet forest species were compared
168 by correlating the correlation coefficients of all pairwise trait combinations; in each site 11
169 traits were measured, resulting in 55 pairwise trait correlations per site. Subsequently the
170 pairwise trait correlation coefficients derived from dry forest species were correlated with the
171 pairwise trait correlation coefficients derived from wet forest species. Spearman correlation

172 coefficients were used, since not all traits are normally distributed, except for relating the
173 binary variables [deciduousness (De), leaf compoundness (LC) and biotic dispersal (Di)]
174 when we used the Phi coefficient, a measure of association between binary variables whose
175 interpretation is similar to correlation coefficients.

176 We also examined whether the trait associations found were influenced by evolutionary
177 histories. To this end, we recovered phylogenetic trees for the dry forest species and the wet
178 forest species using Phylomatic [28], scaling branch lengths to one. For all traits and each
179 forest type we explored phylogenetic signal (Blomberg's K [29]) and compared this to
180 random trait distributions over the phylogenetic tree, using the package "Picante" [30].

181 Phylogenetically independent contrasts were computed as the difference in the mean trait
182 values for pairs of sister species and nodes, using the package "Ape" [31] and we compared
183 whether trait associations were similar with and without considering phylogeny [32].

184 Species scores on the first two principal components of the PCA were scaled up to
185 community level using the Community Weighted Mean (CWM) [24,33], which is calculated
186 as follows:

$$\text{CWM} = \sum_{i=1}^S w_i \times x_i$$

187 where S is the total number of species, w_i is the relative basal area of the i^{th} species and x_i is
188 the score on the PCA axis of the i^{th} species. Relative basal area is a measure of species'
189 relative contributions to the total basal area represented by functional trait measurements in
190 each plot (which is in turn at least 80 % of total basal area in a plot). The relative basal area
191 was used for weighting, rather than the abundance, because it reflects the species' biomass,
192 an indicator of plant performance and adaptation to local conditions. These community
193 weighted mean scores on the PCA axes reflect the average multivariate plant strategy in the
194 community, and were regressed against stand basal area (m^2/ha) (including cacti in the case

195 of dry forest). Stand basal area is a structural variable of succession and logarithmically
196 relates to forest age in both forest types [see supplementary material in 18]. Stand basal area
197 was used, and not age, because it better reflects aboveground biomass, understory light
198 interception and environmental conditions [16] as well as competitive interactions [34]. All
199 statistical analyses were carried out using R v. 2.13.1 [35]; for multivariate analysis we used
200 the package ‘Vegan’ [36].

201 **Results**

202 The first two component axes of the PCAs for dry and wet forest species captured more than
203 half of the variation in species trait values (Fig. 1, Table 1). The ordination biplots indicated
204 that the spectra of functional trait-based strategies of the dry forest species were similar to
205 those of the wet forest species. This was confirmed when the pairwise correlation coefficients
206 of the dry forest were plotted against those of the wet forest (Fig. 2, Table 2); the highly
207 significant positive correlation indicated that the same trait associations were found for the
208 species of the two forest types. The first PCA axes were largely related to phenology and
209 reproductive strategies, with deciduous, small-seeded wind-dispersed species on the left side,
210 and species with large seeds, biotic seed dispersal, and thick leaves on the right side (Fig. 1).
211 We will therefore refer to this axis as the deciduousness/ reproductive effort strategy axis.
212 The second PCA axes were related to the plant economics spectrum, with species having
213 acquisitive trait values (e.g., high SLA) at the lower side, and those having conservative trait
214 values (e.g., high leaf density, LDMC and WD) at the upper side (Fig. 1). We refer to this
215 axis as the acquisitive/conservative strategy axis.

216 There were also some differences between forest types. For example, plants with large
217 leaf laminae and petioles (high LA and PL) had an acquisitive strategy in dry forest (as they
218 were associated with high SLA), whereas such plants rather coincided with a drought
219 avoiding strategy in wet forest (as they were associated with deciduousness, Fig. 1).

220 Moreover, in dry forest a conservative strategy tended to be associated with a drought
221 avoiding strategy, as the suite of conservative traits (LD, LDMC, WD) tended towards the
222 left side of the biplot where species that are deciduous are positioned. Instead, in wet forest a
223 conservative strategy tended to be associated with species that also have large seeds and that
224 are biotically dispersed, as the conservative traits tended towards the right side of the biplot
225 where evergreen species that invest in large biotically dispersed seeds are positioned.

226 Phylogenetic analyses showed that most traits were distributed non-randomly over the
227 phylogenetic tree (Table S2). Correlating the coefficients of the pairwise trait associations
228 (Table 2) with the associations based on their phylogenetic independent contrast (Table S3)
229 resulted in very tight relationships (Pearson coefficients of 0.97, $P < 0.001$, for both dry and
230 wet forest), indicating that the phylogenetic signal did not confound the multivariate trait
231 strategies found in this study.

232 Directional changes in community-weighted PCA scores indicated successional
233 turnover in multivariate plant strategies for both forest types (Fig. 3). Interestingly, the main
234 axis that mattered was different for dry and wet forest. Successional changes in dry forest
235 were associated with increasing species scores along the first PCA axis (from high
236 importance of deciduousness early in succession to increased reproductive effort later in
237 succession; Fig. 3a), whereas successional changes in wet forest were associated with
238 increasing species scores along the second PCA axis (from acquisitive trait values early in
239 succession to conservative trait values later in succession; Fig. 3b). Results were similar
240 when using age instead of basal area, though dry forest change in multivariate plant strategies
241 proved somewhat stronger whereas wet forest change was weaker and no longer significant
242 (see Figure S1 in Supporting Information).

243 Discussion

244 We found that tree species from communities growing under very contrasting conditions (dry
245 and wet) face similar functional trait trade-offs, thus confirming the existence of universal
246 trait spectra. The functional turnover with succession in the two forest types, however,
247 reflected different trait spectra, and hence, the changing dominance of different plant
248 strategies. During dry forest succession, species strategies shifted from high importance of
249 deciduousness early in succession towards increased reproductive effort late in succession,
250 whereas during wet forest succession species strategies changed from acquisitive towards
251 conservative strategies. This indicated that dry and wet forest species face different filters
252 during forest succession.

253 Associations between traits may be influenced by evolutionary history, where the
254 presence of particular clades with contrasting characteristics could confound their ecological
255 interpretation [32]. Phylogenetic analyses showed that although most traits showed
256 significant phylogenetic signal, this did not influence the trait associations found, similar to
257 previous studies [e.g. 6]. Therefore, below we discuss the multivariate trait spectra found in
258 this manuscript in terms of ecological strategies and their relevance for succession in dry and
259 wet tropical forest.

260 *Dry and wet secondary forest species showed similar trait trade-offs*

261 We hypothesized the existence of two major trade-off axes underlying trait variation in dry
262 and wet forest species, namely the acquisitive-conservative spectrum, and the seed size
263 spectrum, with the spectra reflecting multivariate strategy axes. Our results largely confirmed
264 this hypothesis. The first principal component reflected variation from a deciduous strategy
265 with abiotically (mainly wind-) dispersed species towards evergreen species that invested in
266 biotic seed dispersal, in the dry forest biotic seed dispersal also coincided with an increased
267 seed size (Fig. 1). Deciduous species shed their leaves to avoid desiccation and this is an

268 important adaptation to survive severe droughts [17,37,38], which are common in dry forest
269 sites. In both dry and wet forests, deciduous species often also had compound leaves.
270 Compound-leaved species often have photonastic leaves, which can avoid high insolation and
271 therefore high temperature and excessive evaporation by folding their leaflets at noon or
272 during the dry season (e.g., some Fabaceae species). Compoundness also increases leaf
273 cooling and control of water loss [39] and is an efficient way of increasing leaf area for light
274 capture [40]. In both dry and wet forest deciduousness was independent of the acquisitive-
275 conservative continuum, suggesting that deciduous and evergreen species can possess similar
276 resource economics. This is contrary to previous research in temperate forests [41] and across
277 forest types [42]. In line with our results, evidence from another Mexican dry forest shows
278 that the deciduous-evergreen dichotomy does not adequately reflect the variation in leaf and
279 stem functional traits [43]; instead, the *duration* of leaf retention during the dry season
280 reflects this variation better and correlates with resource economics, where conservative
281 species retain their leaves longer during the dry season.

282 Biotically dispersed, evergreen species, having large seeds (in dry forest) and thick
283 leaves marked the other end of the deciduousness/reproductive effort strategy axis. The
284 positive correlation between seed size and biotic dispersal in dry forest has been widely found
285 [44]. The lack of association in wet forest could be due to the fact that most species are
286 biotically dispersed, here differences in seed volume may instead be related to different
287 animal disperser-groups rather than the abiotic-biotic dichotomy. Biotic dispersal enhances
288 the chance to be dispersed to safe sites, whereas larger seed size increases establishment
289 success [12], which is important in shaded environments [13]. Across plant communities
290 thicker leaves are associated with evergreen plants, confirming leaf thickness as a predictor of
291 leaf lifespan [45]. Within a Bolivian tropical moist forest, however, leaf thickness is largely
292 unrelated to leaf lifespan [46]. The association between abiotic dispersal and deciduousness

293 was expected: wind dispersal is common in tropical dry forest and such wind-dispersed seeds
294 are predominantly dispersed in the dry season, when most deciduous species have shed their
295 leaves and the forest canopy is more open, leading to more efficient wind dispersal [47,48].
296 The second trade-off axis reflected the strategy axis of resource acquisition versus
297 conservation, in line with the leaf-, stem- and plant economics spectrum, and the growth-
298 survival trade-off [1,2,3,5,7,49]. Species with cost-efficient leaf area display (high SLA)
299 marked the acquisitive side of this strategy axis; in dry forest this was also associated with
300 large laminas and petioles. High SLA enhances light capture, leaf cooling and gas exchange
301 and enables high photosynthetic capacity and growth rates [e.g. 50]. Species with high leaf
302 density, LDMC and WD marked the conservative side of this strategy axis. Leaf dry matter
303 content and leaf density are indicators of leaf lifespan, resistance against damage [51] and
304 tolerance to drought; dense leaves have smaller cells with thicker and firmer cell walls
305 restricting the modulus of elasticity, thereby avoiding loss of turgor at low leaf water
306 potential [52,53]. High WD is associated with thin and short xylem vessels, thick cell walls,
307 small pit-pores and decreased lumen area, and thus species with dense wood are more
308 resistant against xylem cavitation [54, but see also 55]. High WD also reduces the risk of
309 damage in storms and of stem rot by pathogens [56,57], and indicates drought resistance in
310 drier habitats, where xylem cavitation is the most important cause of tree death [58]. Notably,
311 in our study wood density was associated with the leaf economics spectrum, in line with
312 previous work linking stem and leaf economics [5,43,59], but contrasting with studies
313 suggesting that leaf economics spectrum and wood economics spectrum are largely
314 decoupled [49,60].

315 *Dry and wet forest succession are characterized by different multivariate strategy axes*

316 We used the community-weighted means of species scores on the two PCA axes to quantify
317 the position of secondary forest communities along these spectra (or multivariate strategy

318 axes) of trait variation. Doing so, we found that in both dry and wet forest, directional
319 changes in the dominance of plant strategies took place with secondary succession (Fig. 3).
320 However, the main axis of change was different for dry and wet forest. We found that the
321 first PCA axis, reflecting seed size and deciduousness, was the main axis for successional
322 change in dry forest while the second PCA axis, reflecting the acquisitive -conservative
323 strategy axis, was the main axis for successional change in wet forest (Fig. 3). This indicated
324 that successional changes in multivariate plant strategies in dry and wet tropical forest were
325 characterized by independent axes of plant strategy variation. If indeed dry forest succession
326 is mainly driven by the water gradient and wet forest succession by the light gradient, this
327 would indicate that drought and shade tolerance are largely decoupled, and that these abilities
328 depend on different trait combinations, as has been found in other studies [61,62,63].

329 In dry forest the main axis of variation was not the acquisitive conservative trade-off,
330 as we anticipated, but the axis that described seed size and drought avoidance strategies. Dry
331 forest changes in functional composition were characterized by the gradient of compound-
332 leaved, deciduous species early in succession towards larger-seeded species that were more
333 often animal dispersed and had thicker leaves later in succession. This finding confirms
334 previous studies showing that deciduousness and leaf compoundness are particularly
335 important during the extra dry environments in early-successional stages [cf. 17,37,64]. The
336 proportion of species that depend on animals for seed dispersal increased during tropical dry
337 forest succession (though it remained low compared to wet forest sites: Fig. 3a), as did the
338 seed size. This confirms that early-successional species invest in many small seeds that can
339 travel large distances (e.g., by wind), whereas late-successional species are more likely to
340 invest in fruits that attract biotic dispersers to enhance directional dispersal. Given that the
341 second principal component (acquisitive/conservative strategy axis) was relatively
342 unimportant, it is likely that in our dry forest sequence drought avoidance (characterized by

343 deciduousness) was more important than drought resistance (characterized by conservative
344 traits).

345 In wet forest, the main axis of variation was described by changes in functional composition
346 from acquisitive to conservative trait values (Fig. 3b), a result that complies with expectations
347 based on decreasing light availability during succession [18,24,65,66,67]. Regenerative traits
348 did not play a role in species assembly along the gradient of wet forest succession as we
349 found no increase in biotically-dispersed trees, nor an increase in seed size. Instead, biotic
350 dispersal was common throughout the successional gradient, in line with previous studies
351 [68]. Increasing seed size, an important trait for establishment success under shaded
352 conditions [13] was not found; possibly it could start playing a role at later successional
353 stages or in forest positioned in a more intact landscape forest-matrix.

354 We investigated a dry (900 mm/yr) and a wet forest (3000 mm/yr) chronosequence and
355 showed that tree species are constrained by similar trade-offs, though this had different
356 consequences for the success of plant strategies during succession. This confirms that dry and
357 wet forest species face different filters during succession. A challenging issue is how the
358 relative strength of these different filters (light and water) changes along the large
359 precipitation gradient found across tropical regions and the consequences thereof for
360 functional composition of successional communities. This is relevant because throughout the
361 tropics the importance of secondary and degraded forests is increasing [69] and there is great
362 need to understand its effects on biodiversity and ecosystem functioning [70]. Moreover,
363 restoration plantings with local species that mimic natural regeneration may be needed to
364 speed up forest recovery and improve biodiversity conservation and ecosystem services
365 delivery [71]. A switch from water being replaced by light as the main filter somewhere
366 along the precipitation gradient has direct consequences for forest restoration activities and
367 the selection of to-be-planted species with characteristics that fit with the main filters [cf. 72].

368 This study showed that similar trait spectra were observed among dry and wet secondary
369 forest species, but with different consequences for succession. In dry forest succession the
370 dominant plant strategies changed from drought avoiding species towards species that invest
371 in large biotically dispersed seeds, which can be explained by water limitations in early
372 succession. In wet forest succession the dominant plant strategies changed from species
373 having acquisitive towards species with conservative strategies, which can be explained by
374 decreasing light availability as the main driver of wet forest succession.

375

376 **Acknowledgements.** We are indebted to the people of Nizanda, Oaxaca, and Loma Bonita,
377 Chiapas, for their hospitality and assistance during field work. We appreciate landowners'
378 cooperation and permission to enter their fields and collect plant material for conducting this
379 research. This work received invaluable input from many people: Gilberto Jamangapé, Jorge
380 Rodríguez-Velázquez, Marco Romero, Eduardo A. Pérez-García, Eva van den Elzen, Erik
381 Peters, Paul van Esch, Michiel van Breugel, Alejandra Tauro, Eunice Romero-Pérez and
382 Horacio Paz. Special thanks to Renske Onstein for her advice regarding the phylogenetic
383 analyses.

384 **References**

- 385 1. Díaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, et al. (2004) The plant
386 traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*
387 15: 295-304.
- 388 2. Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, et al. (2004) The worldwide leaf
389 economics spectrum. *Nature* 428: 821-827.
- 390 3. Reich PB (2014) The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto.
391 *Journal of Ecology* 102: 275-301.
- 392 4. Wright IJ, Ackerly DD, Bongers F, Harms KE, Ibarra-Manríquez G, et al. (2007)
393 Relationships among ecologically important dimensions of plant trait variation in seven
394 Neotropical forests. *Annals of Botany* 99: 1003-1015.
- 395 5. Freschet GT, Cornelissen JHC, Van Logtestijn RSP, Aerts R (2010) Evidence of the ‘plant
396 economics spectrum’ in a subarctic flora. *Journal of Ecology* 98: 362-373.
- 397 6. Fortunel C, Fine PVA, Baraloto C, Dalling J (2012) Leaf, stem and root tissue strategies
398 across 758 Neotropical tree species. *Functional Ecology* 26: 1153-1161.
- 399 7. Sterck FJ, Poorter L, Schieving F (2006) Leaf traits determine the growth-survival trade-
400 off across rain forest tree species. *The American Naturalist* 167: 758-765.
- 401 8. Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, et al. (1997) Integrated
402 screening validates primary axes of specialisation in plants. *Oikos* 79: 259-281.
- 403 9. Foster S, Janson CH (1985) The relationship between seed size and establishment
404 conditions in tropical woody plants. *Ecology* 66: 773-780.
- 405 10. Hammond DS, Brown VK (1995) Seed size of woody plants in relation to disturbance,
406 dispersal, soil type in wet Neotropical forests. *Ecology* 76: 2544-2561.
- 407 11. Dalling JW, Hubbell SP (2002) Seed size, growth rate and gap microsite conditions as
408 determinants of recruitment success for pioneer species. *Journal of Ecology* 90: 557-568.

- 409 12. Westoby M, Leishman M, Lord J, Poorter H, Schoen DJ (1996) Comparative ecology of
410 seed size and dispersal [and discussion]. *Philosophical Transactions of the Royal Society*
411 *B: Biological Sciences* 351: 1309-1318.
- 412 13. Leishman M, Wright IJ, Moles AT, Westoby M (2000) The evolutionary ecology of seed
413 size. In: Fenner M, editor. *Seeds: The Ecology of Regeneration in Plant Communities*. 2nd
414 ed. Wallingford, UK: CAB International.
- 415 14. Jansen PA, Bongers F, Van Der Meer PJ (2008) Is farther seed dispersal better? Spatial
416 patterns of offspring mortality in three rainforest tree species with different dispersal
417 abilities. *Ecography* 31: 43-52.
- 418 15. Nicotra AB, Chazdon RL, Iriarte SVB (1999) Spatial heterogeneity of light and woody
419 seedling regeneration in tropical wet forests. *Ecology* 80: 1908-1926.
- 420 16. Lebrija-Trejos E, Pérez-García EA, Meave JA, Poorter L, Bongers F (2011)
421 Environmental changes during secondary succession in a tropical dry forest in Mexico.
422 *Journal of Tropical Ecology* 27: 477-489.
- 423 17. Pineda-García F, Paz H, Meinzer FC (2013) Drought resistance in early and late
424 secondary successional species from a tropical dry forest: the interplay between xylem
425 resistance to embolism, sapwood water storage and leaf shedding. *Plant, Cell &*
426 *Environment* 36: 405-418.
- 427 18. Lohbeck M, Poorter L, Lebrija-Trejos E, Martínez-Ramos M, Meave JA, et al. (2013)
428 Successional changes in functional composition contrast for dry and wet tropical forest.
429 *Ecology* 94: 1211-1216.
- 430 19. Jager MM, Richardson SJ, Bellingham PJ, Clearwater MJ, Laughlin DC (2015) Soil
431 fertility induces coordinated responses of multiple independent functional traits. *Journal of*
432 *Ecology* 103: 374-385.

- 433 20. Lebrija-Trejos E, Bongers F, Pérez-García EA, Meave JA (2008) Successional change
434 and resilience of a very dry tropical deciduous forest following shifting agriculture.
435 *Biotropica* 40: 422-431.
- 436 21. Pérez-García EA, Meave JA, Gallardo C (2001) Vegetación y flora de la región de
437 Nizanda, Istmo de Tehuantepec, Oaxaca, México. *Acta Botanica Mexicana* 56: 19-88.
- 438 22. Pérez-García EA, Meave JA, Villaseñor J, Gallardo-Cruz J, Lebrija-Trejos E (2010)
439 Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous
440 landscape of Nizanda, Oaxaca, Mexico. *Folia Geobotanica* 45: 143-161.
- 441 23. van Breugel M, Martínez-Ramos M, Bongers F (2006) Community dynamics during
442 early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology*
443 22: 663-674.
- 444 24. Garnier E, Cortez J, Billes G, Navas M-L, Roumet C, et al. (2004) Plant functional
445 markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630-
446 2637.
- 447 25. Pakeman RJ, Quested HM (2007) Sampling plant functional traits: What proportion of
448 the species need to be measured? *Applied Vegetation Science* 10: 91-96.
- 449 26. Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, et al. (2003) A handbook
450 of protocols for standardised and easy measurement of plant functional traits worldwide.
451 *Australian Journal of Botany* 51: 335-380.
- 452 27. Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, et al. (2013) New
453 handbook for standardised measurement of plant functional traits worldwide. *Australian*
454 *Journal of Botany* 61: 167-234.
- 455 28. Webb CO, Donoghue MJ (2005) *PhyloMatic*: tree assembly for applied phylogenetics.
456 *Molecular Ecology Notes* 5: 181-183.

- 457 29. Blomberg S, Garland Jr. T, Ives AR (2003) Testing for phylogenetic signal in
458 comparative data: behavioral traits are more reliable. *Evolution* 57: 717-745.
- 459 30. Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, et al. (2010) Picante: R
460 tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463-1464.
- 461 31. Paradis E, Claude J, Strimmer K (2004) APE: Analyses of Phylogenetics and Evolution
462 in R language. *Bioinformatics* 20: 289-290.
- 463 32. Ackerly DD, Reich PB (1999) Convergence and correlations among leaf size and
464 function in seed plants: a comparative test using independent contrasts. *American Journal*
465 *of Botany* 86: 1272-1281.
- 466 33. Lavorel S, Grigulis K, McIntyre S, Williams NSG, Garden D, et al. (2007) Assessing
467 functional diversity in the field – methodology matters! *Functional Ecology* 22: 134-147.
- 468 34. Paquette A, Messier C (2011) The effect of biodiversity on tree productivity: from
469 temperate to boreal forests. *Global Ecology and Biogeography* 20: 170-180.
- 470 35. R Development Core Team (2011) R: A Language and Environment for Statistical
471 Computing. 2.13.1 ed. Vienna: R Foundation for Statistical Computing.
- 472 36. Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, et al. (2011) R-package
473 *Vegan: Community Ecology Package*. R package version 2.0-2 ed.
- 474 37. Poorter L, Markesteijn L (2008) Seedling traits determine drought tolerance of tropical
475 tree species. *Biotropica* 40: 321-331.
- 476 38. Méndez-Alonzo R, Pineda-García F, Paz H, Rosell JA, Olson ME (2013) Leaf phenology
477 is associated with soil water availability and xylem traits in a tropical dry forest. *Trees* 27:
478 745-754.
- 479 39. Yates MJ, Anthony Verboom G, Rebelo AG, Cramer MD (2010) Ecophysiological
480 significance of leaf size variation in Proteaceae from the Cape Floristic Region. *Functional*
481 *Ecology* 24: 485-492.

- 482 40. Niinemets Ü (1998) Are compound-leaved woody species inherently shade-intolerant?
483 An analysis of species ecological requirements and foliar support costs. *Plant Ecology*
484 134: 1-11.
- 485 41. Givnish TJ (2002) Adaptive significance of evergreen vs deciduous leaves: Solving the
486 triple paradox. *Silva Fennica* 36: 703-734.
- 487 42. Villar R, Merino J (2001) Comparison of leaf construction costs in woody species with
488 differing leaf life-spans in contrasting ecosystems. *New Phytologist* 151: 213-226.
- 489 43. Méndez-Alonzo R, Paz H, Zuluaga RC, Rosell JA, Olson M (2012) Coordinated
490 evolution of leaf and stem economics in tropical dry forest trees. *Ecology* 93: 2397–2406.
- 491 44. Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, et al. (2005) Factors that
492 shape seed mass evolution. *PNAS* 102: 10540-10544.
- 493 45. Reich PB, Uhl C, Walters MB, Ellsworth DS (1991) Leaf lifespan as a determinant of leaf
494 structure and function among 23 amazonian tree species. *Oecologia* 86: 16-24.
- 495 46. Kitajima K, Poorter L (2010) Tissue-level leaf toughness, but not lamina thickness,
496 predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytologist*
497 186: 708-721.
- 498 47. Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annual Review of Ecology*
499 *and Systematics* 13: 201-228.
- 500 48. Bullock SH (1995) Plant reproduction in neotropical dry forest. In: Bullock SH, Mooney
501 HA, editors. *Seasonally Dry Tropical Forests*. Cambridge: Cambridge University Press.
- 502 49. Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, et al. (2009) Towards a
503 worldwide wood economics spectrum. *Ecology Letters* 12: 351-366.
- 504 50. Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R (2009) Causes and consequences
505 of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565-588.

- 506 51. Kitajima K, Llorens A-M, Stefanescu C, Timchenko MV, Lucas PW, et al. (2012) How
507 cellulose-based leaf toughness and lamina density contribute to long leaf lifespans of
508 shade-tolerant species. *New Phytologist* 195: 640-652.
- 509 52. Baltzer JL, Davies SJ, Bunyavejchewin S, Noor NSM (2008) The role of desiccation
510 tolerance in determining tree species distributions along the Malay–Thai Peninsula.
511 *Functional Ecology* 22: 221-231.
- 512 53. Kursar TA, Engelbrecht BMJ, Burke A, Tyree MT, Ei Omari B, et al. (2009) Tolerance to
513 low leaf water status of tropical tree seedlings is related to drought performance and
514 distribution. *Functional Ecology* 23: 93-102.
- 515 54. Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood
516 density and structure are linked to prevention of xylem implosion by negative pressure.
517 *Oecologia* 126: 457-461.
- 518 55. Zieminska K, Butler DW, Gleason SM, Wright IJ, Westoby M (2013) Fibre wall and
519 lumen fractions drive wood density variation across 24 Australian angiosperms. *AoB*
520 *PLANTS* 5: plt046.
- 521 56. Augspurger CK, Kelly CK (1984) Pathogen mortality of tropical tree seedlings:
522 Experimental studies of the effects of dispersal distance, seedling density, and light
523 conditions. *Oecologia* 61: 211-217.
- 524 57. Romero C, Bolker BM (2008) Effects of stem anatomical and structural traits on
525 responses to stem damage: an experimental study in the Bolivian Amazon. *Canadian*
526 *Journal of Forest Research* 38: 611-618.
- 527 58. Cavender-Bares J, Kitajima K, Bazzaz FA (2004) Multiple trait associations in relation to
528 habitat differentiation among 17 Floridian oak species. *Ecological Monographs* 74: 635-
529 662.

- 530 59. Ishida A, Nakano T, Yazaki K, Matsuki S, Koike N, et al. (2008) Coordination between
531 leaf and stem traits related to leaf carbon gain and hydraulics across 32 drought-tolerant
532 angiosperms. *Oecologia* 156: 193-202.
- 533 60. Baraloto C, Paine CET, Poorter L, Beauchene J, Bonal D, et al. (2010) Decoupled leaf
534 and stem economics in rain forest trees. *Ecology Letters* 13: 1338-1347.
- 535 61. Holmgren M (2000) Combined effects of shade and drought on tulip poplar seedlings:
536 trade-off in tolerance or facilitation? *Oikos* 90: 67-78.
- 537 62. Sack L (2004) Responses of temperate woody seedlings to shade and drought: do trade-
538 offs limit potential niche differentiation? *Oikos* 107: 110-127.
- 539 63. Markesteijn L, Poorter L (2009) Seedling root morphology and biomass allocation of 62
540 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology* 97:
541 311-325.
- 542 64. Ross MS, Carrington M, Flynn LJ, Ruiz PL (2001) Forest succession in tropical
543 hardwood hammocks of the Florida Keys: Effects of direct mortality from hurricane
544 Andrew. *Biotropica* 33: 23-33.
- 545 65. Dahlgren JP, Eriksson O, Bolmgren K, Strindell M, Ehrlén J (2006) Specific leaf area as
546 a superior predictor of changes in field layer abundance during forest succession. *Journal*
547 *of Vegetation Science* 17: 577-582.
- 548 66. Kahmen S, Poschod P (2004) Plant functional trait responses to grassland succession
549 over 25 years. *Journal of Vegetation Science* 15: 21-32.
- 550 67. Poorter L, van Gils S, Toledo M, Carreño-Rocabado G, Peña-Claros M (*in press*) Fast
551 recovery of community functional properties during secondary forest succession. *Ecology*.
- 552 68. Young KR, Ewel JJ, Brown BJ (1987) Seed dynamics during forest succession in Costa
553 Rica. *Plant Ecology* 71: 157-173.

- 554 69. FAO (2010) Global forest resources assessment 2010. Chapter 2: Extent of forest
555 resources. Rome, Italy. 9-48 p.
- 556 70. MA (2005) Millennium Ecosystems Assessment. Washington DC, USA: World
557 Resources Institute.
- 558 71. Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on
559 degraded lands. *Science* 320: 1458-1460.
- 560 72. Martínez-Garza C, Bongers F, Poorter L (2013) Are functional traits good predictors of
561 species performance in restoration plantings in tropical abandoned pastures? *Forest*
562 *Ecology and Management* 303: 35-45.
- 563
- 564

565 Data. This file contains data belonging to the article " Functional trait strategies of trees in
566 dry and wet tropical forests are similar but differ in their consequences for succession" by M.
567 Lohbeck, E. Lebrija-Trejos, M. Martínez-Ramos, J.A. Meave, L. Poorter and F. Bongers.
568 Data are presented per forest type, the first two sheets containing the data from the Principal
569 Components Analyses (Figure 1). Presented are the traits, their eigenvector scores and the
570 species scores on the first four axes. The last two sheets present the secondary forest plot
571 data, their fallow ages, stand basal area and their Community-Weighted Mean scores on the
572 first two PCA axes (see methods, Figure 3 and Figure S1).

573

574 **Figure Legends**

575 Figure 1. Results of the Principal Component Analyses applied to functional traits of tree
576 species from Mexican tropical dry and wet forests. (a) PCA of dry forest species (n = 51), (b)
577 PCA of wet forest species (n = 81). Species (grey symbols) were separated based on their
578 functional traits shown as arrows; LA= leaf area, SLA = specific leaf area, LD= leaf density,
579 LT= leaf thickness, LDMC= leaf dry matter content, PL= petiole length, WD= wood density,
580 LC= leaf compoundness (0=simple, 1=compound), Di= dispersal syndrome (0=abiotic,
581 1=biotic), De= deciduousness (0=evergreen, 1=deciduous). LA and PL were ln-transformed.

582

583 Figure 2. Correlation coefficients (CC) of all pairwise trait combinations (11 traits, resulting
584 in 55 pairwise trait combinations per forest type, see Table 2) of dry forest species plotted
585 against those of wet forest species. Correlation coefficients represent Spearman coefficients
586 except when relating binary variables, then the Phi coefficient was used. The pairwise
587 correlation coefficients of dry forest proved to be significantly correlated with those of the
588 wet forest (Pearson product moment correlation [R], $P < 0.001$), indicating that trait spectra
589 are consistent across the two different forest types.

590

591 Figure 3. Changes in the dominant plant strategies with succession. Stand basal area was used
 592 to indicate succession; it increased asymptotically with successional age and reflects
 593 successional change in vegetation structure. Functional composition was calculated using the
 594 community-weighted mean of species scores on the principal component axes. (a) Dry forest
 595 succession (open symbols, broken regression line) was characterized by changes along the
 596 first PCA axis (Fig. 1a) and reflected changes from deciduous species to evergreen species
 597 that invest in a secure reproductive strategy. (b) Wet forest succession (filled symbols,
 598 continuous regression line) was characterized by changes along the second PCA axis (Fig.
 599 1b) and reflected changes from an acquisitive strategy to a conservative strategy. Given is the
 600 r^2 , * $P < 0.05$; ** $P < 0.01$. See Figure S1 in supplementary materials for the trends with
 601 fallow age as an indicator of succession.

602

603

604 **Tables**

605 Table 1. Eigenvector scores of functional traits on the two main principal components for dry
 606 forest and for wet forest. Values in parentheses indicate variance accounted for by each axis.

607 [§]Variable was ln-transformed.

Traits	Dry forest		Wet forest	
	PC1 (34%)	PC2 (26%)	PC1 (27%)	PC2 (25%)
LA [§]	-0.141	-0.378	0.446	0.026
SLA	-0.072	-0.327	0.163	-0.352
LDMC	-0.327	0.343	-0.158	0.528
LD	-0.328	0.290	0.032	0.574
LT	0.383	-0.014	-0.205	-0.231

Madelon Lohbeck et al.

PL [§]	-0.094	-0.482	0.513	0.031
LC	-0.401	0.012	0.411	0.225
WD	-0.205	0.458	-0.275	0.364
De	-0.424	-0.230	0.340	0.150
Di	0.424	0.230	-0.279	-0.038
SV	0.206	-0.025	-0.079	0.079

608

609

610 Table 2. Spearman coefficients of the pairwise relations between variables and the principal
 611 components (Fig. 1). Relations between the binary variables (LC, De and Di) are Phi
 612 coefficients. [§]Variable was ln-transformed. Lower-left half of the matrix corresponds to dry
 613 forest species (n = 51), Upper-right half corresponds to wet forest species (n = 81).
 614 * P < 0.05, ** P < 0.01, *** P < 0.001.

	PCA1	PCA2	LA [§]	SLA	LDM C	LD	LT	PL [§]	LC	WD	De	Di	SV
PCA1		-0.08	0.75 ***	0.33 **	-0.33 **	-0.04	-0.36 ***	0.89 ***	0.68 ***	-0.48 ***	0.48 ***	-0.45 ***	-0.23 *
PCA2	-0.01		0.08	-0.59 ***	0.86 ***	0.94 ***	-0.25 *	0.04	0.38 ***	0.58 ***	0.22 *	0.06	0.23 *
LA [§]	-0.18	-0.71 ***		-0.07	-0.17	0.09	-0.12	0.79 ***	0.56 ***	-0.26 *	0.26 *	-0.10	-0.07
SLA	-0.16	-0.51 ***	0.18		-0.50 ***	-0.57 ***	-0.50 ***	0.11	-0.03	-0.29 **	0.05	-0.26 *	-0.10
LDM C	-0.70 ***	0.42 **	-0.09	-0.24		0.80 ***	-0.21	-0.19	0.05	0.49 ***	-0.01	0.15	0.18
LD	-0.72 ***	0.49 ***	-0.16	-0.29 *	0.64 ***		-0.27 *	0.07	0.34 **	0.45 ***	0.17	0.08	0.16
LT	0.78 ***	-0.05	-0.01	-0.47 ***	-0.44 **	-0.65 ***		-0.24 *	-0.31 **	-0.08	-0.15	0.23 *	-0.09
PL [§]	-0.04	-0.77 ***	0.63 ***	0.09	-0.18	-0.27	0.15		0.57 ***	-0.35 **	0.36 ***	-0.31 **	-0.17
LC	-0.77 ***	-0.10	0.28 *	0.09	0.63 ***	0.40 **	-0.41 **	0.15		-0.07	0.47 ***	-0.18	0.09
WD	-0.41 **	0.59 ***	-0.29 *	-0.26	0.54 ***	0.51 ***	-0.29 *	-0.39 **	0.28 *		-0.11	0.11	0.29 **
De	-0.76 ***	-0.43 **	0.28	0.28	0.28 *	0.30 *	-0.49 ***	0.36 **	0.55 ***	0.13		-0.48 ***	-0.05
Di	0.76 ***	0.43 **	-0.28	-0.28	-0.28 *	-0.30 *	0.49 ***	-0.36 **	-0.55 ***	-0.13	-1.00 ***		0.21
SV	0.50 ***	-0.02	0.25	-0.31 *	-0.30 *	-0.30 *	0.52 ***	0.18	-0.34 *	-0.27	-0.50 ***	0.50 ***	

615
616

617 Supplementary materials
618

619 Figure S1. Changes in the dominant plant strategies with succession, using two different
620 indicators of succession: stand basal area (a, b) and fallow age (c, d). Functional composition
621 was calculated using the community-weighted mean of species scores on the principal
622 component axes (Fig 1). Dry forest succession (open symbols, [d], broken regression line)
623 was characterized by changes along the first PCA axis and reflected changes from deciduous
624 species to evergreen species that invest in a secure reproductive strategy. This was significant
625 when using stand basal area as a successional indicator (a), and when using fallow age (c).
626 Wet forest succession (solid symbols, [w], continuous regression line) was characterized by
627 changes along the second PCA axis and reflected changes from an acquisitive strategy to a
628 conservative strategy. This was significant when using stand basal area as successional
629 indicator (b), but not when using fallow age (d). Given is the r^2 , * $P < 0.05$; ** $P < 0.01$.

630

631 Table S1. List of species included in this study, in alphabetical order and grouped per forest
632 type. These species represent at least 80% of the basal area of each secondary forest plot. All
633 species except *Aragebortia* sp. (wet forest) were used in the phylogenetic analysis, as for this
634 species the family was unknown.

635

636 Table S2. Phylogenetic signal for each of the functional traits for the two forest types (a: dry
637 forest, b: wet forest). Given are Blomberg's K [29], the variance based on the observed trait
638 distribution on the phylogeny, the randomized mean and the statistical significance of the
639 difference between the observed phylogenetic signal and the random scenario (based on 999
640 randomizations).

641

642 Table S3. Spearman coefficients of the pairwise relations between Phylogenetic Independent
643 Contrasts. Relations between the binary variables (LC, De and Di) are Phi coefficients.
644 [§]Traits were ln-transformed prior to PIC calculation. Lower-left half of the matrix
645 corresponds to dry forest species (n = 51), Upper-right half corresponds to wet forest species
646 (n = 80). * P < 0.05, ** P < 0.01, *** P < 0.001. These values are very similar to the original
647 pairwise trait-correlations (Table 2), as resulting from the strong correlation between the
648 correlation coefficient in this table and those of Table 2 (Pearson 0.97, P < 0.001)
649

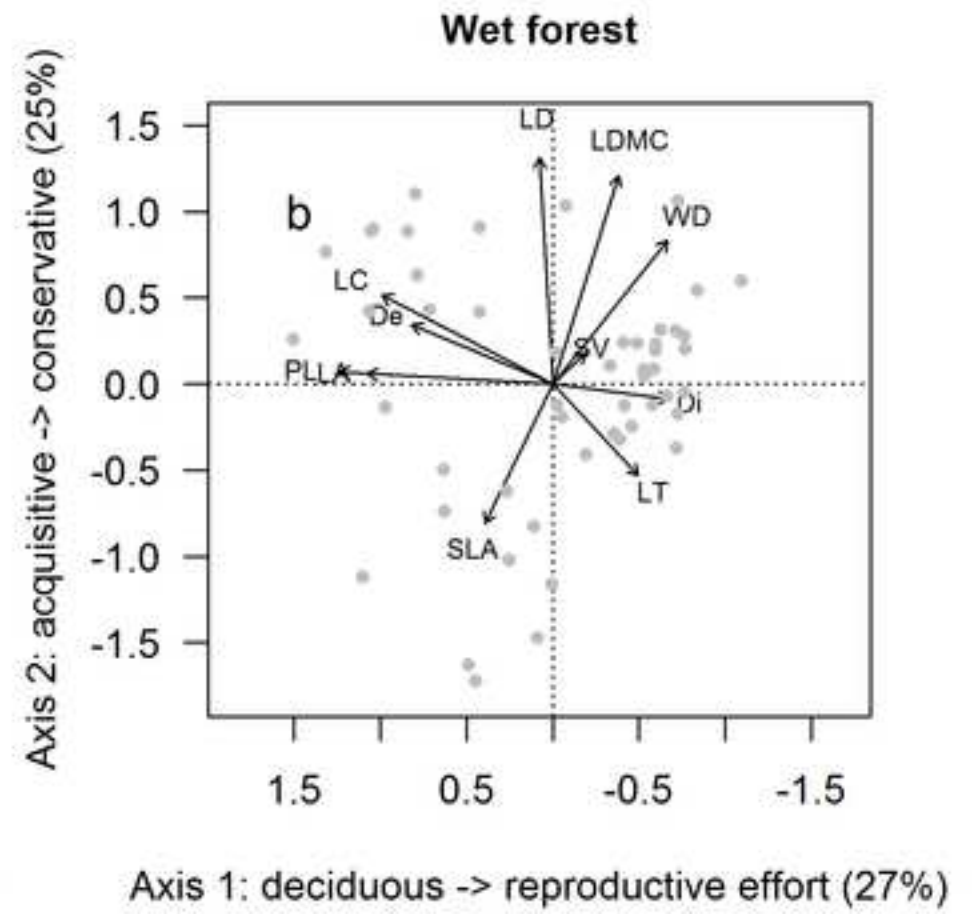
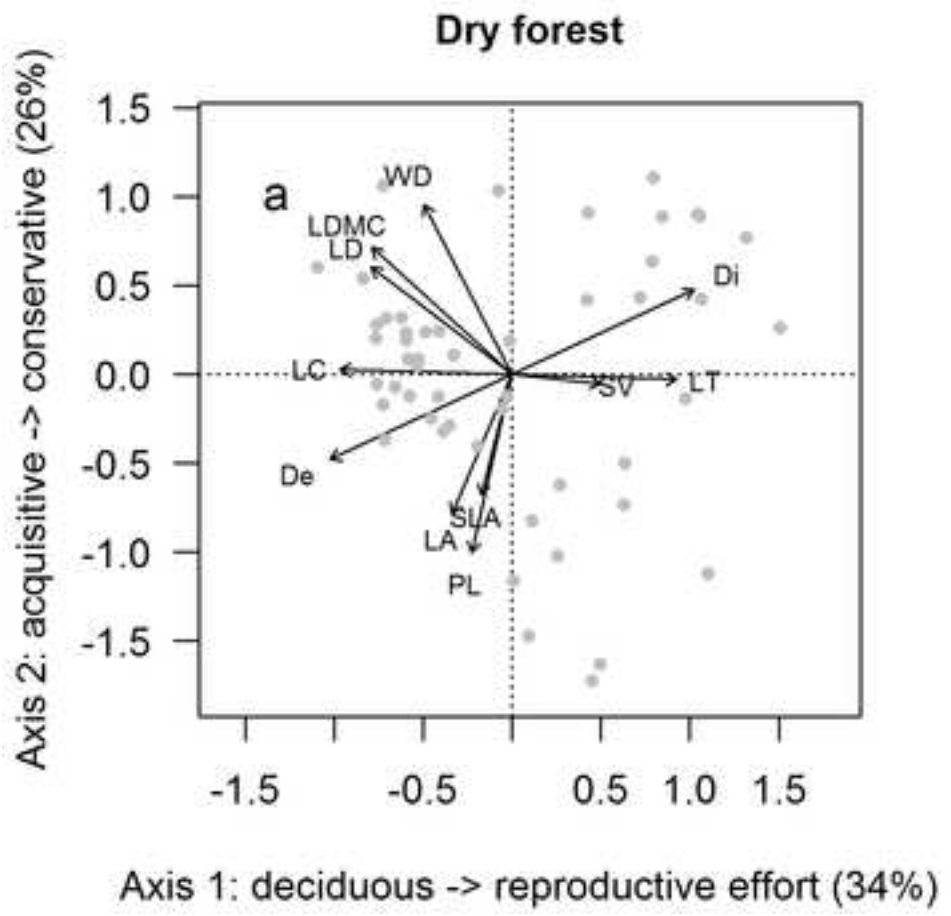
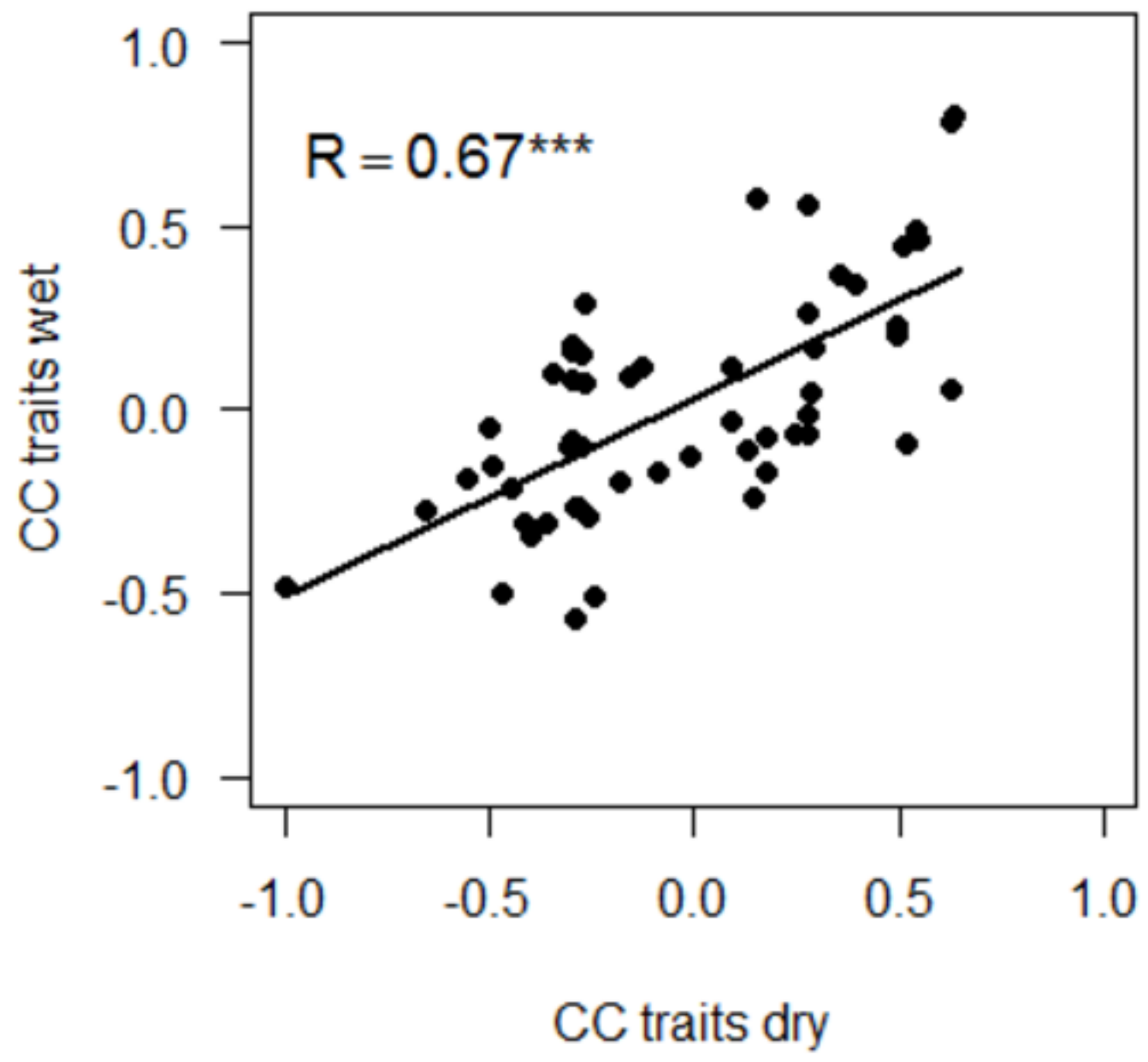
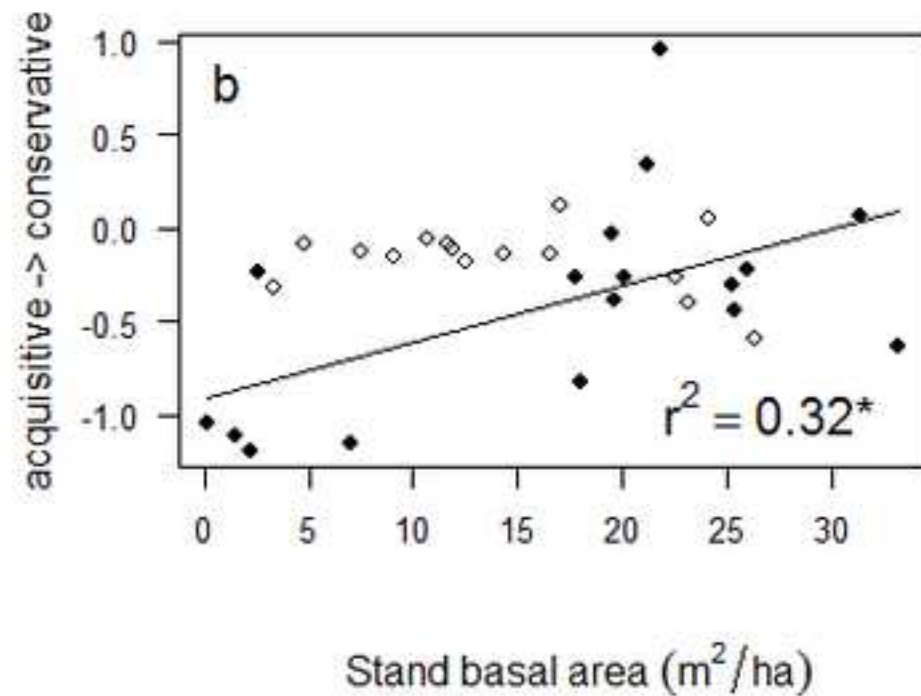
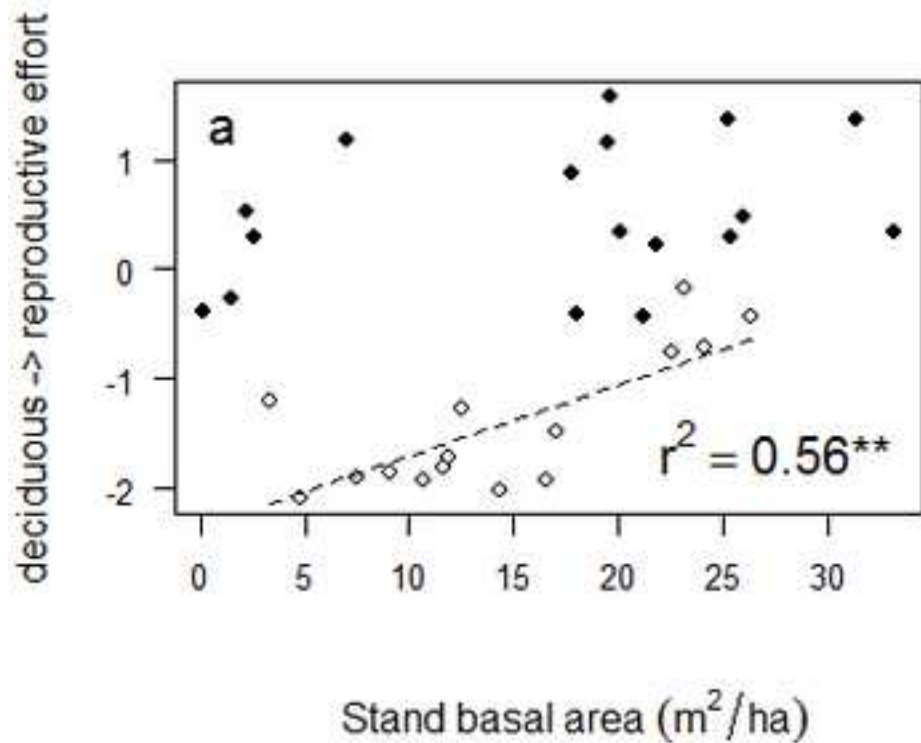


Figure2

[Click here to download high resolution image](#)





- ◊ dry forest plots
- dry forest trend
- wet forest plots
- wet forest trend

Figure S1.

[Click here to download Supporting Information: Figure_SupMat.tiff](#)

Table S1

[Click here to download Supporting Information: TableS1.docx](#)

Table S2

[Click here to download Supporting Information: TableS2.docx](#)

Table S3

[Click here to download Supporting Information: TableS3.docx](#)

Data

[Click here to download Supporting Information: PlosONE_data1.xlsx](#)

funding statement

[Click here to download Other: Funding statement_new2.docx](#)

Madelon Lohbeck et al.

1 **Functional trait strategies of trees in dry and wet tropical forests are similar but differ**
2 **in their consequences for succession**

3

4 Madelon Lohbeck ^{*} ^{1,3}, Edwin Lebrija-Trejos ^{1,2,4}, Miguel Martínez-Ramos ³, Jorge A. Meave
5 ⁴, Lourens Poorter ¹, Frans Bongers ¹

6

7 ¹ Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700
8 AA Wageningen, The Netherlands

9 ² Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama

10 ³ Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México,

11 Campus Morelia, Antigua Carretera a Pátzcuaro 8701, Ex-hacienda de San José de la Huerta,
12 58190 Morelia, Michoacán, Mexico

13 ⁴ Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad

14 Nacional Autónoma de México, 04510 México, Distrito Federal, Mexico

15

16 ^{*} Correspondence author: madelon.lohbeck@wur.nl

17

18

19 **Abstract**

20 Global plant trait studies have revealed fundamental trade-offs in plant resource economics.

21 We evaluated such trait trade-offs during secondary succession in two species-rich tropical
22 ecosystems that contrast in precipitation: dry deciduous and wet evergreen forests of Mexico.

23 Species turnover with succession in dry forest ~~is~~ largely ~~driven by~~ relates to increasing water
24 availability and in wet forest ~~by~~ to decreasing light availability. We hypothesized that while
25 functional trait trade-offs are similar in the two forest systems, the successful plant strategies
26 in these communities will be different, as contrasting filters affect species turnover.

27 Research was carried out in 15 dry secondary forest sites (5-63 years after abandonment) and
28 in 17 wet secondary forest sites (<1-25 years after abandonment). We used 11 functional
29 traits measured on 132 species to make species-trait PCA biplots for dry and wet forest and
30 compare trait trade-offs. We evaluated whether multivariate plant strategies changed during
31 succession, by calculating a 'Community-Weighted Mean' plant strategy, based on species
32 scores on the first two PCA-axes.

33 Trait spectra reflected two main trade-off axes that were similar for dry and wet forest
34 species: acquisitive versus conservative species, and drought avoiding species versus
35 evergreen species with large animal-dispersed seeds. These trait associations were consistent
36 when accounting for evolutionary history. Successional changes in the most successful plant
37 strategies reflected different functional trait spectra depending on the forest type. In dry forest
38 the community changed from having drought avoiding strategies early in succession to
39 increased abundance of evergreen strategies with larger seeds late in succession. In wet forest
40 the community changed from species having mainly acquisitive strategies to those with more
41 conservative strategies during succession. These strategy changes were explained by
42 increasing water availability during dry forest succession and increasing light scarcity during
43 wet forest succession.

44 Although similar trait spectra were observed among dry and wet secondary forest species, the
45 consequences for succession were different resulting from contrasting environmental filters.

46 Keywords: dry deciduous forest, functional trait, functional trait trade-off, functional strategy,
47 Mexico, secondary succession, PCA, wet evergreen forest

48

49 **Introduction**

50 Trade-offs in plant traits and resource economics are consistent at the global scale [1,2,3].
51 These give insight into comprehensive dimensions of multivariate functional trait variation,
52 or what we call ‘functional trait spectra’. As functional traits are indicators of ecological
53 strategies, the study of trait spectra and trade-offs allows us to explore the complex interplay
54 of different strategies [4]. For example, the worldwide leaf economics spectrum runs from a
55 plant strategy with cheap-to-construct acquisitive leaves with high photosynthetic rates that
56 maximize resource capture to a strategy with expensive-to-construct conservative leaves that
57 tolerate stress and physical damage and better conserve the acquired resources [2]. Such an
58 economic spectrum has not only been found for leaves, but also for other plant organs like
59 roots and stems [3,5], and it has been found across different climatic regions [2,6]. This
60 economics spectrum at the tissue level underlies the trade-off between growth and survival at
61 the whole-plant level [7], as in resource rich environments acquisitive strategies thrive by fast
62 growth (and high mortality) whilst in resource-poor environments conservative strategies
63 thrive by persistence (and high survival). This fundamental trade-off describes variation
64 among plants in the established phase. In contrast, different trade-offs are found in the
65 regenerative phase, where plants have to arrive and establish successfully at a site. As a
66 result, traits related to the regenerative phase are largely decoupled from those related to the
67 established phase [8]. The trade-off between seed size and seed number plays an important
68 role in explaining the differential success of species in the regenerative phase [e.g. 9]. Small
69 seeds are produced in large numbers and are often wind-dispersed, which is advantageous
70 when colonizing new sites [10], but their small seed size comes at the expense of a lower per
71 capita establishment success [11]. Large seeds produce robust seedlings [12], which is
72 advantageous when colonizing shaded sites [13], and they are often animal-dispersed,
73 enhancing directed dispersal to safe sites [14].

74 These traits and trait trade-offs are used to explain species' success along successional
75 gradients. In tropical wet forest, succession is ~~driven by~~related to a gradient of decreasing
76 light availability over time [e.g. 15] whereas in dry forest it is ~~driven by~~related to a gradient
77 of increasing water availability over time [16,17]. Dry forest species experience, therefore,
78 stressful conditions during the dry and hot early stages of succession, while wet forest species
79 do so during the shaded late stages of succession. We showed previously that, at the
80 *community-level*, the community-weighted mean (CWM) of *individual* functional traits
81 changed with tropical forest succession in Mexico [17]. The type of traits that changed
82 differed largely between dry and wet forests [18]. In dry forest early-successional
83 communities had trait values related to drought ~~coping~~ tolerance and optimal light
84 acquisition, whereas late-successional communities had trait values related to large seeds and
85 biotic dispersal. In wet forest early-successional communities also had trait values related to
86 optimal light acquisition, whereas late-successional communities had trait values related to
87 increased leaf toughness. Here we expand on the previous analysis, and explore differences in
88 *species-level* trait trade-offs between dry and wet forest species, and to what extent this can
89 be translated into different *multivariate plant strategies* between dry and wet forest species.
90 Since environmental gradients filter species based on multiple traits, identifying changes in
91 multivariate plant strategies is needed to further advance our understanding of ecological
92 restoration [cf. 19].

93 The present study focuses on trait trade-offs *at the species level*, and how *multivariate plant*
94 *strategies* change during succession. To this end we described plant strategies using 11
95 functional traits measured on 132 species found in 32 secondary forest sites belonging to dry
96 and wet tropical forest in Mexico. We hypothesized the existence of two major trait- or
97 strategy spectra, namely the spectrum of species with acquisitive versus those with
98 conservative trait values, which is important in the established phase of plants, and the

99 spectrum of small seeded wind-dispersed species versus large seeded animal-dispersed
100 species, which is important in the regeneration phase. We expected that in dry forest water is
101 the main limiting factor, and that tree communities show a change from predominantly
102 conservative to acquisitive strategies over time, whereas in wet forest light is the main
103 limiting factor, and the communities show a change from predominantly acquisitive to
104 conservative strategies over time. We also expected that the seed size spectrum would play an
105 important role in both forest types, reflecting an increase in the proportion of large seeded
106 animal-dispersed species along succession.

107 **Methods**

108 *Ethics statement*

109 Since all secondary forest plots are located on privately owned land, permission from
110 landowners to enter the sites and collect plant material was provided before conducting this
111 research.

112 *Research locations*

113 *Tropical dry forest.* Research plots in tropical dry forest surround the village of Nizanda on
114 the Pacific watershed of the Isthmus of Tehuantepec in Oaxaca, southern Mexico (16°39'N,
115 95°00'W). Mean annual temperature is 26 °C and mean annual precipitation is 900 mm, of
116 which > 90 % concentrates between late May and mid-October [20]. The vegetation is
117 predominantly tropical dry deciduous forest, characterized by a low canopy stature (ca. 7 m
118 tall) ~~with a high biodiversity~~ [21,22]. The 15 secondary forest plots (900 m²) with different
119 fallow ages (6-64 years) were established on abandoned maize fields. Within each plot four
120 parallel 5 × 20 m transects were set up, and further divided into four 5 × 5 m quadrats. In one
121 quadrat all individuals with DBH ≥ 1cm were identified and measured, in a second all
122 individuals with DBH ≥ 2.5 cm and in the remaining two all individuals with DBH ≥ 5 cm,

123 with these sampling criteria being randomly assigned to each quadrat. Variables measured on
124 each individual were scaled up to the plot level according to sampling effort per size-class
125 (i.e., all stems $1 \text{ cm} \leq \text{DBH} \leq 2.5 \text{ cm}$ were multiplied by four, and $2.5 \text{ cm} \leq \text{DBH} \leq 5 \text{ cm}$ by
126 two, to make sampling effort comparable across size-classes, after which all stems are added
127 up). For further details see Lebrija-Trejos et al. [20].

128 *Tropical wet forest.* Research plots in the tropical wet forest surround the village of Loma
129 Bonita in the Marqués de Comillas region in Chiapas, southeastern Mexico ($16^{\circ}01' \text{N}$,
130 $90^{\circ}55' \text{W}$). Mean annual temperature is $24 \text{ }^{\circ}\text{C}$ and mean annual precipitation is 3000 mm ,
131 with a dry period ($< 100 \text{ mm month}^{-1}$) from February through April [23]. The research area is
132 characterized by small hills and valleys with sandy and clay soils of low pH (< 5.5). The 17
133 secondary forest plots (1000 m^2) with different fallow ages ($< 1\text{-}25 \text{ years}$) were established
134 on abandoned maize fields. Each plot was divided into two $10 \times 50 \text{ m}$ subplots. In one
135 subplot all individuals with $\text{DBH} \geq 1 \text{ cm}$ were identified and measured, in the second all
136 individuals $\text{DBH} \geq 5 \text{ cm}$. Again, measured variables were scaled to the plot level up
137 according to sampling effort per size-class (i.e., stems $1 \text{ cm} \leq \text{DBH} \leq 5 \text{ cm}$ were multiplied
138 by two to make sampling effort comparable to $\text{DBH} \geq 5 \text{ cm}$, after which all stems are added
139 up).

140 *Functional traits*

141 Those species that made up at least 80 % of the basal area in the plots were selected for
142 functional trait measurements (excluding cacti in dry forest, as their functional traits are
143 difficult to compare with trees), because they accurately describe the community-weighted
144 mean [24,25]. This resulted in a total of 132 species: 51 dry forest species and 81 wet forest
145 species (see Table S1 in supplementary materials for the list of species per forest type). We
146 measured seven leaf traits: leaf area (m^2), specific leaf area- SLA (m^2/kg), leaf dry matter

147 content- LDMC (g/g), leaf density (g/cm³), leaf thickness (mm), leaf compoundness
148 (0=simple, 1=compound), petiole length (cm); one whole plant trait: deciduousness
149 (0=evergreen, 1=deciduous); one stem trait: wood density- WD (g/cm³); and two regenerative
150 traits: seed size (mm³) and dispersal syndrome (0=abiotic, 1=biotic). Traits were measured
151 following standardized protocols [26,27]. In the wet forest sites, leaf traits were measured for
152 two sun-lit leaves for 10 adult trees per species (5 individuals for specific force to punch) of
153 ca. 5 m high, and in dry forest for 5 sun-lit leaves for 5 adult trees per species with a DBH of
154 10-30 cm. Functional trait measurements took place within the study areas, but not inside the
155 plots. For wood density measurements in the wet forest 15 of the 81 species were taken from
156 comparable Mexican ecosystems. The binary traits leaf compoundness, deciduousness, and
157 dispersal syndrome were scored based on field observations, local informants, herbaria, and
158 literature; for detailed methods on functional trait measurements see supplementary material
159 in [18]. We used species' average trait values although we recognize that intraspecific trait
160 variation may play an important role in species adaptation along environmental gradients.
161 However, given the extensive species-level trait data set (132 species) together with the high
162 species turnover during succession, for the purpose of this study we consider the use of
163 species average trait values appropriate to test our hypotheses~~we consider the use of species~~
164 ~~average trait values legitimized.~~

165 *Statistical analysis*

166 We used principal component analysis to quantify spectra of trait-based multivariate plant
167 strategies for each forest type separately. The PCA biplots show the main trade-offs across
168 (standardized) functional traits based on principal axes of variation, where binary variables
169 are treated as dummy variables. Trait spectra for dry and wet forest species were compared
170 by correlating the correlation coefficients of all pairwise trait combinations; in each site 11
171 traits were measured, resulting in 55 pairwise trait correlations per site. Subsequently the

172 pairwise trait correlation coefficients derived from dry forest species were correlated with the
173 pairwise trait correlation coefficients derived from wet forest species. Spearman correlation
174 coefficients were used, since not all traits are normally distributed, except for relating the
175 binary variables [deciduousness (De), leaf compoundness (LC) and biotic dispersal (Di)]
176 when we used the Phi coefficient, a measure of association between binary variables whose
177 interpretation is similar to correlation coefficients.

178 We also examined whether the trait associations found were influenced by evolutionary
179 histories. To this end, we recovered phylogenetic trees for the dry forest species and the wet
180 forest species using Phylomatic [28], scaling branch lengths to one. For all traits and each
181 forest type we explored phylogenetic signal (Blomberg's K [29]) and compared this to
182 random trait distributions over the phylogenetic tree, using the package "Picante" [30].

183 Phylogenetically independent contrasts were computed as the difference in the mean trait
184 values for pairs of sister species and nodes, using the package "Ape" [31] and we compared
185 whether trait associations were similar with and without considering phylogeny [32].

186 Species scores on the first two principal components of the PCA were scaled up to
187 community level using the Community Weighted Mean (CWM) [24,33], which is calculated
188 as follows:

$$\text{CWM} = \sum_{i=1}^S w_i \times x_i$$

189 where S is the total number of species, w_i is the relative basal area of the i^{th} species and x_i is
190 the score on the PCA axis of the i^{th} species. Relative basal area is a measure of species'
191 relative contributions to the total basal area represented by functional trait measurements in
192 each plot (which is in turn at least 80 % of total basal area in a plot). The relative basal area
193 was used for weighting, rather than the abundance, because it reflects the species' biomass,
194 an indicator of plant performance and adaptation to local conditions. These community

195 weighted mean scores on the PCA axes reflect the average multivariate plant strategy in the
196 community, and were regressed against stand basal area (m^2/ha) (including cacti in the case
197 of dry forest). Stand basal area is a structural variable of succession and logarithmically
198 relates to forest age in both forest types [see supplementary material in 18]. Stand basal area
199 was used, and not age, because it better reflects aboveground biomass, understory light
200 interception and environmental conditions [16] as well as competitive interactions [34]. All
201 statistical analyses were carried out using R v. 2.13.1 [35]; for multivariate analysis we used
202 the package ‘Vegan’ [36].

203 **Results**

204 The first two component axes of the PCAs for dry and wet forest species captured more than
205 half of the variation in species trait values (Fig. 1, Table 1). The ordination biplots indicated
206 that the spectra of functional trait-based strategies of the dry forest species were similar to
207 those of the wet forest species. This was confirmed when the pairwise correlation coefficients
208 of the dry forest were plotted against those of the wet forest (Fig. 2, Table 2); the highly
209 significant positive correlation indicated that the same trait associations were found for the
210 species of the two forest types. The first PCA axes were largely related to phenology and
211 reproductive strategies, with deciduous, small-seeded wind-dispersed species on the left side,
212 and species with large seeds, biotic seed dispersal, and thick leaves on the right side (Fig. 1).
213 We will therefore refer to this axis as the deciduousness/ reproductive effort strategy axis.
214 The second PCA axes were related to the plant economics spectrum, with species having
215 acquisitive trait values (e.g., high SLA) at the lower side, and those having conservative trait
216 values (e.g., high leaf density, LDMC and WD) at the upper side (Fig. 1). We refer to this
217 axis as the acquisitive/conservative strategy axis.

218 There were also some differences between forest types. For example, plants with large
219 leaf laminas and petioles (high LA and PL) had an acquisitive strategy in dry forest (as they

220 were associated with high SLA), whereas such plants rather coincided with a drought
221 avoiding strategy in wet forest (as they were associated with deciduousness, Fig. 1).
222 Moreover, in dry forest a conservative strategy tended to be associated with a drought
223 avoiding strategy, as the suite of conservative traits (LD, LDMC, WD) tended towards the
224 left side of the biplot where species that are deciduous are positioned. Instead, in wet forest a
225 conservative strategy tended to be associated with species that also have large seeds and that
226 are biotically dispersed, as the conservative traits tended towards the right side of the biplot
227 where evergreen species that invest in large biotically dispersed seeds are positioned.

228 Phylogenetic analyses showed that most traits were distributed non-randomly over the
229 phylogenetic tree (Table S2). Correlating the coefficients of the pairwise trait associations
230 (Table 2) with the associations based on their phylogenetic independent contrast (Table S3)
231 resulted in very tight relationships (Pearson coefficients of 0.97, $P < 0.001$, for both dry and
232 wet forest), indicating that the phylogenetic signal did not confound the multivariate trait
233 strategies found in this study.

234 Directional changes in community-weighted PCA scores indicated successional
235 turnover in multivariate plant strategies for both forest types (Fig. 3). Interestingly, the main
236 axis that mattered was different for dry and wet forest. Successional changes in dry forest
237 were associated with increasing species scores along the first PCA axis (from high
238 importance of deciduousness early in succession to increased reproductive effort later in
239 succession; Fig. 3a), whereas successional changes in wet forest were associated with
240 increasing species scores along the second PCA axis (from acquisitive trait values early in
241 succession to conservative trait values later in succession; Fig. 3b). Results were similar
242 when using age instead of basal area, though dry forest change in multivariate plant strategies
243 proved somewhat stronger whereas wet forest change was weaker and no longer significant
244 (see Figure S1 in Supporting Information).

245 **Discussion**

246 We found that tree species from communities growing under very contrasting conditions (dry
247 and wet) face similar functional trait trade-offs, thus confirming the existence of universal
248 trait spectra. The functional turnover with succession in the two forest types, however,
249 reflected different trait spectra, and hence, the changing dominance of different plant
250 strategies. During dry forest succession, species strategies shifted from high importance of
251 deciduousness early in succession towards increased reproductive effort late in succession,
252 whereas during wet forest succession species strategies changed from acquisitive towards
253 conservative strategies. This indicated that dry and wet forest species face different filters
254 during forest succession.

255 Associations between traits may be influenced by evolutionary history, where the
256 presence of particular clades with contrasting characteristics could confound their ecological
257 interpretation [32]. Phylogenetic analyses showed that although most traits showed
258 significant phylogenetic signal, this did not influence the trait associations found, similar to
259 previous studies [e.g. 6]. Therefore, below we discuss the multivariate trait spectra found in
260 this manuscript in terms of ecological strategies and their relevance for succession in dry and
261 wet tropical forest.

262 *Dry and wet secondary forest species showed similar trait trade-offs*

263 We hypothesized the existence of two major trade-off axes underlying trait variation in dry
264 and wet forest species, namely the acquisitive-conservative spectrum, and the seed size
265 spectrum, with the spectra reflecting multivariate strategy axes. Our results largely confirmed
266 this hypothesis. The first principal component reflected variation from a deciduous strategy
267 with abiotically (mainly wind-) dispersed species towards evergreen species that invested in
268 biotic seed dispersal, in the dry forest biotic seed dispersal also coinciding with an

269 increased seed size (Fig. 1). Deciduous species shed their leaves to avoid desiccation and this
270 is an important adaptation to survive severe droughts [17,37,38], which are common in dry
271 forest sites. In both dry and wet forests, deciduous species often also had compound leaves.
272 Compound-leaved species often have photonastic leaves, which can avoid high insolation and
273 therefore high temperature and excessive evaporation by folding their leaflets at noon or
274 during the dry season (e.g., some Fabaceae species). Compoundness also increases leaf
275 cooling and control of water loss [39] and is an efficient way of increasing leaf area for light
276 capture [40]. In both dry and wet forest deciduousness was independent of the acquisitive-
277 conservative continuum, suggesting that deciduous and evergreen species can possess similar
278 resource economics. This is contrary to previous research in temperate forests [41] and across
279 forest types [42]. In line with our results, evidence from another Mexican dry forest shows
280 that the deciduous-evergreen dichotomy does not adequately reflect the variation in leaf and
281 stem functional traits [43]; instead, the *duration* of leaf retention during the dry season
282 reflects this variation better and correlates with resource economics, where conservative
283 species retain their leaves longer during the dry season.

284 Biotically dispersed, evergreen species, having large seeds (in dry forest) and thick
285 leaves marked the other end of the deciduousness/reproductive effort strategy axis. The
286 positive correlation between seed size and biotic dispersal in dry forest has been widely found
287 [44]. The lack of association in wet forest could be due to the fact that most species are
288 biotically dispersed, here differences in seed volume may instead be related to different
289 animal disperser-groups rather than the abiotic-biotic dichotomy. Biotic dispersal enhances
290 the chance to be dispersed to safe sites, whereas larger seed size increases establishment
291 success [12], which is important in shaded environments [13]. Across plant communities
292 thicker leaves are associated with evergreen plants, confirming leaf thickness as a predictor of
293 leaf lifespan [45]. Within a Bolivian tropical moist forest, however, leaf thickness is largely

294 unrelated to leaf lifespan [46]. The association between abiotic dispersal and deciduousness
295 was expected: wind dispersal is common in tropical dry forest and such wind-dispersed seeds
296 are predominantly dispersed in the dry season, when most deciduous species have shed their
297 leaves and the forest canopy is more open, leading to more efficient wind dispersal [47,48].
298 The second trade-off axis reflected the strategy axis of resource acquisition versus
299 conservation, in line with the leaf-, stem- and plant economics spectrum, and the growth-
300 survival trade-off [1,2,3,5,7,49]. Species with cost-efficient leaf area display (high SLA)
301 marked the acquisitive side of this strategy axis; in dry forest this was also associated with
302 large laminas and petioles. High SLA enhances light capture, leaf cooling and gas exchange
303 and enables high photosynthetic capacity and growth rates [e.g. 50]. Species with high leaf
304 density, LDMC and WD marked the conservative side of this strategy axis. Leaf dry matter
305 content and leaf density are indicators of leaf lifespan, resistance against damage [51] and
306 tolerance to drought; dense leaves have smaller cells with thicker and firmer cell walls
307 restricting the modulus of elasticity, thereby avoiding loss of turgor at low leaf water
308 potential [52,53]. High WD is associated with thin and short xylem vessels, thick cell walls,
309 small pit-pores and decreased lumen area, and thus species with dense wood are more
310 resistant against xylem cavitation [54, but see also 55]. High WD also reduces the risk of
311 damage in storms and of stem rot by pathogens [56,57], and indicates drought resistance in
312 drier habitats, where xylem cavitation is the most important cause of tree death [58]. Notably,
313 in our study wood density was associated with the leaf economics spectrum, in line with
314 previous work linking stem and leaf economics [5,43,59], but contrasting with studies
315 suggesting that leaf economics spectrum and wood economics spectrum are largely
316 decoupled [49,60].

317 *Dry and wet forest succession are characterized by different multivariate strategy axes*

318 We used the community-weighted means of species scores on the two PCA axes to quantify
319 the position of secondary forest communities along these spectra (or multivariate strategy
320 axes) of trait variation. Doing so, we found that in both dry and wet forest, directional
321 changes in the dominance of plant strategies took place with secondary succession (Fig. 3).
322 However, the main axis of change was different for dry and wet forest. We found that the
323 first PCA axis, reflecting seed size and deciduousness, was the main axis for successional
324 change in dry forest while the second PCA axis, reflecting the acquisitive -conservative
325 strategy axis, was the main axis for successional change in wet forest (Fig. 3). This indicated
326 that successional changes in multivariate plant strategies in dry and wet tropical forest were
327 characterized by independent axes of plant strategy variation. If indeed dry forest succession
328 is mainly driven by the water gradient and wet forest succession by the light gradient, this
329 would indicate that drought and shade tolerance are largely decoupled, and that these abilities
330 depend on different trait combinations, as has been found in other studies [61,62,63].

331 In dry forest the main axis of variation was not the acquisitive conservative trade-off,
332 as we anticipated, but the axis that described seed size and drought avoidance strategies. Dry
333 forest changes in functional composition were characterized by the gradient of compound-
334 leaved, deciduous species early in succession towards larger-seeded species that were more
335 often animal dispersed and had thicker leaves later in succession. This finding confirms
336 previous studies showing that deciduousness and leaf compoundness are particularly
337 important during the extra dry environments in early-successional stages [cf. 17,37,64]. The
338 proportion of species that depend on animals for seed dispersal increased during tropical dry
339 forest succession (though it remained low compared to wet forest sites: Fig. 3a), as did the
340 seed size. This confirms that early-successional species invest in many small seeds that can
341 travel large distances (e.g., by wind), whereas late-successional species are more likely to
342 invest in fruits that attract biotic dispersers to enhance directional dispersal. Given that the

343 second principal component (acquisitive/conservative strategy axis) was relatively
344 unimportant, it is likely that in our dry forest sequence drought avoidance (characterized by
345 deciduousness) was more important than drought resistance (characterized by conservative
346 traits).

347 In wet forest, the main axis of variation was described by changes in functional composition
348 from acquisitive to conservative trait values (Fig. 3b), a result that complies with expectations
349 based on decreasing light availability during succession [18,24,65,66,67]. Regenerative traits
350 did not play a role in species assembly along the gradient of wet forest succession as we
351 found no increase in biotically-dispersed trees, nor an increase in seed size. Instead, biotic
352 dispersal was common throughout the successional gradient, in line with previous studies
353 [68]. Increasing seed size, an important trait for establishment success under shaded
354 conditions [13] was not found; possibly it could start playing a role at later successional
355 stages or in forest positioned in a more intact landscape forest-matrix.

356 We investigated a dry (900 mm/yr) and a wet forest (3000 mm/yr) chronosequence and
357 showed that tree species are constrained by similar trade-offs, though this had different
358 consequences for the success of plant strategies during succession. This confirms that dry and
359 wet forest species face different filters during succession. A challenging issue is how the
360 relative strength of these different filters (light and water) changes along the large
361 precipitation gradient found across tropical regions and the consequences thereof for
362 functional composition of successional communities. This is relevant because throughout the
363 tropics the importance of secondary and degraded forests is increasing [69] and there is great
364 need to understand its effects on biodiversity and ecosystem functioning [70]. Moreover,
365 restoration plantings with local species that mimic natural regeneration may be needed to
366 speed up forest recovery and improve biodiversity conservation and ecosystem services
367 delivery [71]. A switch from water being replaced by light as the main filter somewhere

368 along the precipitation gradient has direct consequences for forest restoration activities and
369 the selection of to-be-planted species with characteristics that fit with the main filters [cf. 72].

370 This study showed that similar trait spectra were observed among dry and wet secondary
371 forest species, but with different consequences for succession. In dry forest succession the
372 dominant plant strategies changed from drought avoiding species towards species that invest
373 in large biotically dispersed seeds, which can be explained by water limitations in early
374 succession. In wet forest succession the dominant plant strategies changed from species
375 having acquisitive towards species with conservative strategies, which can be explained by
376 decreasing light availability as the main driver of wet forest succession.

377

378 **Acknowledgements.** We are indebted to the people of Nizanda, Oaxaca, and Loma Bonita,
379 Chiapas, for their hospitality and assistance during field work. We appreciate landowners'
380 cooperation and permission to enter their fields and collect plant material for conducting this
381 research. This work received invaluable input from many people: Gilberto Jamangapé, Jorge
382 Rodríguez-Velázquez, Marco Romero, Eduardo A. Pérez-García, Eva van den Elzen, Erik
383 Peters, Paul van Esch, Michiel van Breugel, Alejandra Tauro, Eunice Romero-Pérez and
384 Horacio Paz. Special thanks to Renske Onstein for her advice regarding the phylogenetic
385 analyses.

386 **References**

- 387 1. Díaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, et al. (2004) The plant
388 traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*
389 15: 295-304.
- 390 2. Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, et al. (2004) The worldwide leaf
391 economics spectrum. *Nature* 428: 821-827.
- 392 3. Reich PB (2014) The world-wide 'fast-slow' plant economics spectrum: a traits manifesto.
393 *Journal of Ecology* 102: 275-301.
- 394 4. Wright IJ, Ackerly DD, Bongers F, Harms KE, Ibarra-Manríquez G, et al. (2007)
395 Relationships among ecologically important dimensions of plant trait variation in seven
396 Neotropical forests. *Annals of Botany* 99: 1003-1015.
- 397 5. Freschet GT, Cornelissen JHC, Van Logtestijn RSP, Aerts R (2010) Evidence of the 'plant
398 economics spectrum' in a subarctic flora. *Journal of Ecology* 98: 362-373.
- 399 6. Fortunel C, Fine PVA, Baraloto C, Dalling J (2012) Leaf, stem and root tissue strategies
400 across 758 Neotropical tree species. *Functional Ecology* 26: 1153-1161.
- 401 7. Sterck FJ, Poorter L, Schieving F (2006) Leaf traits determine the growth-survival trade-
402 off across rain forest tree species. *The American Naturalist* 167: 758-765.
- 403 8. Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, et al. (1997) Integrated
404 screening validates primary axes of specialisation in plants. *Oikos* 79: 259-281.
- 405 9. Foster S, Janson CH (1985) The relationship between seed size and establishment
406 conditions in tropical woody plants. *Ecology* 66: 773-780.
- 407 10. Hammond DS, Brown VK (1995) Seed size of woody plants in relation to disturbance,
408 dispersal, soil type in wet Neotropical forests. *Ecology* 76: 2544-2561.
- 409 11. Dalling JW, Hubbell SP (2002) Seed size, growth rate and gap microsite conditions as
410 determinants of recruitment success for pioneer species. *Journal of Ecology* 90: 557-568.

- 411 12. Westoby M, Leishman M, Lord J, Poorter H, Schoen DJ (1996) Comparative ecology of
412 seed size and dispersal [and discussion]. *Philosophical Transactions of the Royal Society*
413 *B: Biological Sciences* 351: 1309-1318.
- 414 13. Leishman M, Wright IJ, Moles AT, Westoby M (2000) The evolutionary ecology of seed
415 size. In: Fenner M, editor. *Seeds: The Ecology of Regeneration in Plant Communities*. 2nd
416 ed. Wallingford, UK: CAB International.
- 417 14. Jansen PA, Bongers F, Van Der Meer PJ (2008) Is farther seed dispersal better? Spatial
418 patterns of offspring mortality in three rainforest tree species with different dispersal
419 abilities. *Ecography* 31: 43-52.
- 420 15. Nicotra AB, Chazdon RL, Iriarte SVB (1999) Spatial heterogeneity of light and woody
421 seedling regeneration in tropical wet forests. *Ecology* 80: 1908-1926.
- 422 16. Lebrija-Trejos E, Pérez-García EA, Meave JA, Poorter L, Bongers F (2011)
423 Environmental changes during secondary succession in a tropical dry forest in Mexico.
424 *Journal of Tropical Ecology* 27: 477-489.
- 425 17. Pineda-García F, Paz H, Meinzer FC (2013) Drought resistance in early and late
426 secondary successional species from a tropical dry forest: the interplay between xylem
427 resistance to embolism, sapwood water storage and leaf shedding. *Plant, Cell &*
428 *Environment* 36: 405-418.
- 429 18. Lohbeck M, Poorter L, Lebrija-Trejos E, Martínez-Ramos M, Meave JA, et al. (2013)
430 Successional changes in functional composition contrast for dry and wet tropical forest.
431 *Ecology* 94: 1211-1216.
- 432 19. Jager MM, Richardson SJ, Bellingham PJ, Clearwater MJ, Laughlin DC (2015) Soil
433 fertility induces coordinated responses of multiple independent functional traits. *Journal of*
434 *Ecology* 103: 374-385.

- 435 20. Lebrija-Trejos E, Bongers F, Pérez-García EA, Meave JA (2008) Successional change
436 and resilience of a very dry tropical deciduous forest following shifting agriculture.
437 *Biotropica* 40: 422-431.
- 438 21. Pérez-García EA, Meave JA, Gallardo C (2001) Vegetación y flora de la región de
439 Nizanda, Istmo de Tehuantepec, Oaxaca, México. *Acta Botanica Mexicana* 56: 19-88.
- 440 22. Pérez-García EA, Meave JA, Villaseñor J, Gallardo-Cruz J, Lebrija-Trejos E (2010)
441 Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous
442 landscape of Nizanda, Oaxaca, Mexico. *Folia Geobotanica* 45: 143-161.
- 443 23. van Breugel M, Martínez-Ramos M, Bongers F (2006) Community dynamics during
444 early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology*
445 22: 663-674.
- 446 24. Garnier E, Cortez J, Billes G, Navas M-L, Roumet C, et al. (2004) Plant functional
447 markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630-
448 2637.
- 449 25. Pakeman RJ, Quested HM (2007) Sampling plant functional traits: What proportion of
450 the species need to be measured? *Applied Vegetation Science* 10: 91-96.
- 451 26. Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, et al. (2003) A handbook
452 of protocols for standardised and easy measurement of plant functional traits worldwide.
453 *Australian Journal of Botany* 51: 335-380.
- 454 27. Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, et al. (2013) New
455 handbook for standardised measurement of plant functional traits worldwide. *Australian*
456 *Journal of Botany* 61: 167-234.
- 457 28. Webb CO, Donoghue MJ (2005) *PhyloMatic*: tree assembly for applied phylogenetics.
458 *Molecular Ecology Notes* 5: 181-183.

- 459 29. Blomberg S, Garland Jr. T, Ives AR (2003) Testing for phylogenetic signal in
460 comparative data: behavioral traits are more reliable. *Evolution* 57: 717-745.
- 461 30. Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, et al. (2010) Picante: R
462 tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463-1464.
- 463 31. Paradis E, Claude J, Strimmer K (2004) APE: Analyses of Phylogenetics and Evolution
464 in R language. *Bioinformatics* 20: 289-290.
- 465 32. Ackerly DD, Reich PB (1999) Convergence and correlations among leaf size and
466 function in seed plants: a comparative test using independent contrasts. *American Journal*
467 *of Botany* 86: 1272-1281.
- 468 33. Lavorel S, Grigulis K, McIntyre S, Williams NSG, Garden D, et al. (2007) Assessing
469 functional diversity in the field – methodology matters! *Functional Ecology* 22: 134-147.
- 470 34. Paquette A, Messier C (2011) The effect of biodiversity on tree productivity: from
471 temperate to boreal forests. *Global Ecology and Biogeography* 20: 170-180.
- 472 35. R Development Core Team (2011) R: A Language and Environment for Statistical
473 Computing. 2.13.1 ed. Vienna: R Foundation for Statistical Computing.
- 474 36. Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, et al. (2011) R-package
475 *Vegan: Community Ecology Package*. R package version 2.0-2 ed.
- 476 37. Poorter L, Markesteijn L (2008) Seedling traits determine drought tolerance of tropical
477 tree species. *Biotropica* 40: 321-331.
- 478 38. Méndez-Alonzo R, Pineda-García F, Paz H, Rosell JA, Olson ME (2013) Leaf phenology
479 is associated with soil water availability and xylem traits in a tropical dry forest. *Trees* 27:
480 745-754.
- 481 39. Yates MJ, Anthony Verboom G, Rebelo AG, Cramer MD (2010) Ecophysiological
482 significance of leaf size variation in Proteaceae from the Cape Floristic Region. *Functional*
483 *Ecology* 24: 485-492.

- 484 40. Niinemets Ü (1998) Are compound-leaved woody species inherently shade-intolerant?
485 An analysis of species ecological requirements and foliar support costs. *Plant Ecology*
486 134: 1-11.
- 487 41. Givnish TJ (2002) Adaptive significance of evergreen vs deciduous leaves: Solving the
488 triple paradox. *Silva Fennica* 36: 703-734.
- 489 42. Villar R, Merino J (2001) Comparison of leaf construction costs in woody species with
490 differing leaf life-spans in contrasting ecosystems. *New Phytologist* 151: 213-226.
- 491 43. Méndez-Alonzo R, Paz H, Zuluaga RC, Rosell JA, Olson M (2012) Coordinated
492 evolution of leaf and stem economics in tropical dry forest trees. *Ecology* 93: 2397–2406.
- 493 44. Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, et al. (2005) Factors that
494 shape seed mass evolution. *PNAS* 102: 10540-10544.
- 495 45. Reich PB, Uhl C, Walters MB, Ellsworth DS (1991) Leaf lifespan as a determinant of leaf
496 structure and function among 23 amazonian tree species. *Oecologia* 86: 16-24.
- 497 46. Kitajima K, Poorter L (2010) Tissue-level leaf toughness, but not lamina thickness,
498 predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytologist*
499 186: 708-721.
- 500 47. Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annual Review of Ecology*
501 and Systematics 13: 201-228.
- 502 48. Bullock SH (1995) Plant reproduction in neotropical dry forest. In: Bullock SH, Mooney
503 HA, editors. *Seasonally Dry Tropical Forests*. Cambridge: Cambridge University Press.
- 504 49. Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, et al. (2009) Towards a
505 worldwide wood economics spectrum. *Ecology Letters* 12: 351-366.
- 506 50. Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R (2009) Causes and consequences
507 of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565-588.

- 508 51. Kitajima K, Llorens A-M, Stefanescu C, Timchenko MV, Lucas PW, et al. (2012) How
509 cellulose-based leaf toughness and lamina density contribute to long leaf lifespans of
510 shade-tolerant species. *New Phytologist* 195: 640-652.
- 511 52. Baltzer JL, Davies SJ, Bunyavejchewin S, Noor NSM (2008) The role of desiccation
512 tolerance in determining tree species distributions along the Malay–Thai Peninsula.
513 *Functional Ecology* 22: 221-231.
- 514 53. Kursar TA, Engelbrecht BMJ, Burke A, Tyree MT, Ei Omari B, et al. (2009) Tolerance to
515 low leaf water status of tropical tree seedlings is related to drought performance and
516 distribution. *Functional Ecology* 23: 93-102.
- 517 54. Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood
518 density and structure are linked to prevention of xylem implosion by negative pressure.
519 *Oecologia* 126: 457-461.
- 520 55. Zieminska K, Butler DW, Gleason SM, Wright IJ, Westoby M (2013) Fibre wall and
521 lumen fractions drive wood density variation across 24 Australian angiosperms. *AoB*
522 *PLANTS* 5: plt046.
- 523 56. Augspurger CK, Kelly CK (1984) Pathogen mortality of tropical tree seedlings:
524 Experimental studies of the effects of dispersal distance, seedling density, and light
525 conditions. *Oecologia* 61: 211-217.
- 526 57. Romero C, Bolker BM (2008) Effects of stem anatomical and structural traits on
527 responses to stem damage: an experimental study in the Bolivian Amazon. *Canadian*
528 *Journal of Forest Research* 38: 611-618.
- 529 58. Cavender-Bares J, Kitajima K, Bazzaz FA (2004) Multiple trait associations in relation to
530 habitat differentiation among 17 Floridian oak species. *Ecological Monographs* 74: 635-
531 662.

- 532 59. Ishida A, Nakano T, Yazaki K, Matsuki S, Koike N, et al. (2008) Coordination between
533 leaf and stem traits related to leaf carbon gain and hydraulics across 32 drought-tolerant
534 angiosperms. *Oecologia* 156: 193-202.
- 535 60. Baraloto C, Paine CET, Poorter L, Beauchene J, Bonal D, et al. (2010) Decoupled leaf
536 and stem economics in rain forest trees. *Ecology Letters* 13: 1338-1347.
- 537 61. Holmgren M (2000) Combined effects of shade and drought on tulip poplar seedlings:
538 trade-off in tolerance or facilitation? *Oikos* 90: 67-78.
- 539 62. Sack L (2004) Responses of temperate woody seedlings to shade and drought: do trade-
540 offs limit potential niche differentiation? *Oikos* 107: 110-127.
- 541 63. Markesteijn L, Poorter L (2009) Seedling root morphology and biomass allocation of 62
542 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology* 97:
543 311-325.
- 544 64. Ross MS, Carrington M, Flynn LJ, Ruiz PL (2001) Forest succession in tropical
545 hardwood hammocks of the Florida Keys: Effects of direct mortality from hurricane
546 Andrew. *Biotropica* 33: 23-33.
- 547 65. Dahlgren JP, Eriksson O, Bolmgren K, Strindell M, Ehrlén J (2006) Specific leaf area as
548 a superior predictor of changes in field layer abundance during forest succession. *Journal*
549 *of Vegetation Science* 17: 577-582.
- 550 66. Kahmen S, Poschlod P (2004) Plant functional trait responses to grassland succession
551 over 25 years. *Journal of Vegetation Science* 15: 21-32.
- 552 67. Poorter L, van Gils S, Toledo M, Carreño-Rocabado G, Peña-Claros M (*in press*) Fast
553 recovery of community functional properties during secondary forest succession. *Ecology*.
- 554 68. Young KR, Ewel JJ, Brown BJ (1987) Seed dynamics during forest succession in Costa
555 Rica. *Plant Ecology* 71: 157-173.

- 556 69. FAO (2010) Global forest resources assessment 2010. Chapter 2: Extent of forest
557 resources. Rome, Italy. 9-48 p.
- 558 70. MA (2005) Millennium Ecosystems Assessment. Washington DC, USA: World
559 Resources Institute.
- 560 71. Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on
561 degraded lands. *Science* 320: 1458-1460.
- 562 72. Martínez-Garza C, Bongers F, Poorter L (2013) Are functional traits good predictors of
563 species performance in restoration plantings in tropical abandoned pastures? *Forest
564 Ecology and Management* 303: 35-45.
- 565
- 566

567 Data. This file contains data belonging to the article " Functional trait strategies of trees in
568 dry and wet tropical forests are similar but differ in their consequences for succession" by M.
569 Lohbeck, E. Lebrija-Trejos, M. Martínez-Ramos, J.A. Meave, L. Poorter and F. Bongers.
570 Data are presented per forest type, the first two sheets containing the data from the Principal
571 Components Analyses (Figure 1). Presented are the traits, their eigenvector scores and the
572 species scores on the first four axes. The last two sheets present the secondary forest plot
573 data, their fallow ages, stand basal area and their Community-Weighted Mean scores on the
574 first two PCA axes (see methods, Figure 3 and Figure S1).

575

576 **Figure Legends**

577 Figure 1. Results of the Principal Component Analyses applied to functional traits of tree
578 species from Mexican tropical dry and wet forests. (a) PCA of dry forest species (n = 51), (b)
579 PCA of wet forest species (n = 81). Species (grey symbols) were separated based on their
580 functional traits shown as arrows; LA= leaf area, SLA = specific leaf area, LD= leaf density,
581 LT= leaf thickness, LDMC= leaf dry matter content, PL= petiole length, WD= wood density,
582 LC= leaf compoundness (0=simple, 1=compound), Di= dispersal syndrome (0=abiotic,
583 1=biotic), De= deciduousness (0=evergreen, 1=deciduous). LA and PL were ln-transformed.

584

585 Figure 2. Correlation coefficients (CC) of all pairwise trait combinations (11 traits, resulting
586 in 55 pairwise trait combinations per forest type, see Table 2) of dry forest species plotted
587 against those of wet forest species. Correlation coefficients represent Spearman coefficients
588 except when relating binary variables, then the Phi coefficient was used. The pairwise
589 correlation coefficients of dry forest proved to be significantly correlated with those of the
590 wet forest (Pearson product moment correlation [R], $P < 0.001$), indicating that trait spectra
591 are consistent across the two different forest types.

592

593 Figure 3. Changes in the dominant plant strategies with succession. Stand basal area was used
 594 to indicate succession; it increased asymptotically with successional age and reflects
 595 successional change in vegetation structure. Functional composition was calculated using the
 596 community-weighted mean of species scores on the principal component axes. (a) Dry forest
 597 succession (open symbols, broken regression line) was characterized by changes along the
 598 first PCA axis (Fig. 1a) and reflected changes from deciduous species to evergreen species
 599 that invest in a secure reproductive strategy. (b) Wet forest succession (filled symbols,
 600 continuous regression line) was characterized by changes along the second PCA axis (Fig.
 601 1b) and reflected changes from an acquisitive strategy to a conservative strategy. Given is the
 602 r^2 , * $P < 0.05$; ** $P < 0.01$. See Figure S1 in supplementary materials for the trends with
 603 fallow age as an indicator of succession.

604

605

606 **Tables**

607 Table 1. Eigenvector scores of functional traits on the two main principal components for dry
 608 forest and for wet forest. Values in parentheses indicate variance accounted for by each axis.

609 [§]Variable was ln-transformed.

Traits	Dry forest		Wet forest	
	PC1 (34%)	PC2 (26%)	PC1 (27%)	PC2 (25%)
LA [§]	-0.141	-0.378	0.446	0.026
SLA	-0.072	-0.327	0.163	-0.352
LDMC	-0.327	0.343	-0.158	0.528
LD	-0.328	0.290	0.032	0.574
LT	0.383	-0.014	-0.205	-0.231

Madelon Lohbeck et al.

PL [§]	-0.094	-0.482	0.513	0.031
LC	-0.401	0.012	0.411	0.225
WD	-0.205	0.458	-0.275	0.364
De	-0.424	-0.230	0.340	0.150
Di	0.424	0.230	-0.279	-0.038
SV	0.206	-0.025	-0.079	0.079

610

611

612 Table 2. Spearman coefficients of the pairwise relations between variables and the principal
 613 components (Fig. 1). Relations between the binary variables (LC, De and Di) are Phi
 614 coefficients. [§]Variable was ln-transformed. Lower-left half of the matrix corresponds to dry
 615 forest species (n = 51), Upper-right half corresponds to wet forest species (n = 81).
 616 * P < 0.05, ** P < 0.01, *** P < 0.001.

	PCA1	PCA2	LA [§]	SLA	LDM C	LD	LT	PL [§]	LC	WD	De	Di	SV
PCA1		-0.08	0.75 ***	0.33 **	-0.33 **	-0.04	-0.36 ***	0.89 ***	0.68 ***	-0.48 ***	0.48 ***	-0.45 ***	-0.23 *
PCA2	-0.01		0.08	-0.59 ***	0.86 ***	0.94 ***	-0.25 *	0.04	0.38 ***	0.58 ***	0.22 *	0.06	0.23 *
LA [§]	-0.18	-0.71 ***		-0.07	-0.17	0.09	-0.12	0.79 ***	0.56 ***	-0.26 *	0.26 *	-0.10	-0.07
SLA	-0.16	-0.51 ***	0.18		-0.50 ***	-0.57 ***	-0.50 ***	0.11	-0.03	-0.29 **	0.05	-0.26 *	-0.10
LDM C	-0.70 ***	0.42 **	-0.09	-0.24		0.80 ***	-0.21	-0.19	0.05	0.49 ***	-0.01	0.15	0.18
LD	-0.72 ***	0.49 ***	-0.16	-0.29 *	0.64 ***		-0.27 *	0.07	0.34 **	0.45 ***	0.17	0.08	0.16
LT	0.78 ***	-0.05	-0.01	-0.47 ***	-0.44 **	-0.65 ***		-0.24 *	-0.31 **	-0.08	-0.15	0.23 *	-0.09
PL [§]	-0.04	-0.77 ***	0.63 ***	0.09	-0.18	-0.27	0.15		0.57 ***	-0.35 **	0.36 ***	-0.31 **	-0.17
LC	-0.77 ***	-0.10	0.28 *	0.09	0.63 ***	0.40 **	-0.41 **	0.15		-0.07	0.47 ***	-0.18	0.09
WD	-0.41 **	0.59 ***	-0.29 *	-0.26	0.54 ***	0.51 ***	-0.29 *	-0.39 **	0.28 *		-0.11	0.11	0.29 **
De	-0.76 ***	-0.43 **	0.28	0.28	0.28 *	0.30 *	-0.49 ***	0.36 **	0.55 ***	0.13		-0.48 ***	-0.05
Di	0.76 ***	0.43 **	-0.28	-0.28	-0.28 *	-0.30 *	0.49 ***	-0.36 **	-0.55 ***	-0.13	-1.00 ***		0.21
SV	0.50 ***	-0.02	0.25	-0.31 *	-0.30 *	-0.30 *	0.52 ***	0.18	-0.34 *	-0.27	-0.50 ***	0.50 ***	

617
 618

619 Supplementary materials

620

621 Figure S1. Changes in the dominant plant strategies with succession, using two different
622 indicators of succession: stand basal area (a, b) and fallow age (c, d). Functional composition
623 was calculated using the community-weighted mean of species scores on the principal
624 component axes (Fig 1). Dry forest succession (open symbols, [d], broken regression line)
625 was characterized by changes along the first PCA axis and reflected changes from deciduous
626 species to evergreen species that invest in a secure reproductive strategy. This was significant
627 when using stand basal area as a successional indicator (a), and when using fallow age (c).
628 Wet forest succession (solid symbols, [w], continuous regression line) was characterized by
629 changes along the second PCA axis and reflected changes from an acquisitive strategy to a
630 conservative strategy. This was significant when using stand basal area as successional
631 indicator (b), but not when using fallow age (d). Given is the r^2 , * $P < 0.05$; ** $P < 0.01$.

632

633 Table S1. List of species included in this study, in alphabetical order and grouped per forest
634 type. These species represent at least 80% of the basal area of each secondary forest plot. All
635 species except *Aragebortia* sp. (wet forest) were used in the phylogenetic analysis, as for this
636 species the family was unknown.

637

638 Table S2. Phylogenetic signal for each of the functional traits for the two forest types (a: dry
639 forest, b: wet forest). Given are Blomberg's K [29], the variance based on the observed trait
640 distribution on the phylogeny, the randomized mean and the statistical significance of the
641 difference between the observed phylogenetic signal and the random scenario (based on 999
642 randomizations).

643

644 Table S3. Spearman coefficients of the pairwise relations between Phylogenetic Independent
645 Contrasts. Relations between the binary variables (LC, De and Di) are Phi coefficients.
646 [§]Traits were ln-transformed prior to PIC calculation. Lower-left half of the matrix
647 corresponds to dry forest species (n = 51), Upper-right half corresponds to wet forest species
648 (n = 80). * P < 0.05, ** P < 0.01, *** P < 0.001. These values are very similar to the original
649 pairwise trait-correlations (Table 2), as resulting from the strong correlation between the
650 correlation coefficient in this table and those of Table 2 (Pearson 0.97, P < 0.001)
651