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Steidinger, BS, Crowther, TW, Liang, J et al. (97 more authors) (2019) Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature*, 569 (7756). pp. 404-408. ISSN 0028-0836

<https://doi.org/10.1038/s41586-019-1128-0>

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1 **Title:** Climatic controls of decomposition drive the global biogeography of forest tree
2 symbioses

3
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69

70 **The identity of the dominant microbial symbionts in a forest determines the ability**
71 **of trees to access limiting nutrients from atmospheric or soil pools^{1,2}, sequester**
72 **carbon^{3,4} and withstand the impacts of climate change¹⁻⁷. Characterizing the global**
73 **distribution of symbioses, and identifying the factors that control it, are thus integral to**
74 **understanding present and future forest ecosystem functioning. Here we generate the first**
75 **spatially explicit map of forest symbiotic status using a global database of 1.2 million forest**
76 **inventory plots with over 28,000 tree species. Our analyses indicate that climatic variables,**
77 **and in particular climatically-controlled variation in decomposition rate, are the primary**
78 **drivers of the global distribution of major symbioses. We estimate that ectomycorrhizal**
79 **(EM) trees, which represent only 2% of all plant species⁸, constitute approximately 60% of**
80 **tree stems on Earth. EM symbiosis dominates forests where seasonally cold and dry**

81 climates inhibit decomposition, and are the predominant symbiosis at high latitudes and
82 elevation. In contrast, arbuscular mycorrhizal (AM) trees dominate aseasonally warm
83 tropical forests and occur with EM trees in temperate biomes where seasonally warm-and-
84 wet climates enhance decomposition. Continental transitions between AM and EM
85 dominated forests occur relatively abruptly along climate driven decomposition gradients,
86 which is likely caused by positive plant-microbe feedbacks. Symbiotic N-fixers, which are
87 insensitive to climatic controls on decomposition compared with mycorrhizal fungi, are
88 most abundant in arid biomes with alkaline soils and high maximum temperatures. The
89 climatically driven global symbiosis gradient we document represents the first spatially-
90 explicit, quantitative understanding of microbial symbioses at the global scale and
91 demonstrates the critical role of microbial mutualisms in shaping the distribution of plant
92 species.

93 Microbial symbionts strongly influence the functioning of forest ecosystems. They
94 exploit inorganic, organic² and/or atmospheric forms of nutrients that enable plant growth¹,
95 determine how trees respond to elevated CO₂⁶, regulate the respiratory activity of soil
96 microbes^{3,9}, and affect plant species diversity by altering the strength of conspecific negative
97 density dependence¹⁰. Despite growing recognition of the importance of root symbioses for
98 forest functioning^{1,6,11} and the potential to integrate symbiotic status into Earth system models
99 that predict functional changes to the terrestrial biosphere^{11,12}, we lack spatially-explicit,
100 quantitative maps of the different root symbioses at the global scale. Generating these
101 quantitative maps of tree symbiotic states would link the biogeography of functional traits of
102 belowground microbial symbionts with their 1.5 trillion host trees¹³, spread across Earth's
103 forests, woodlands, and savannas.

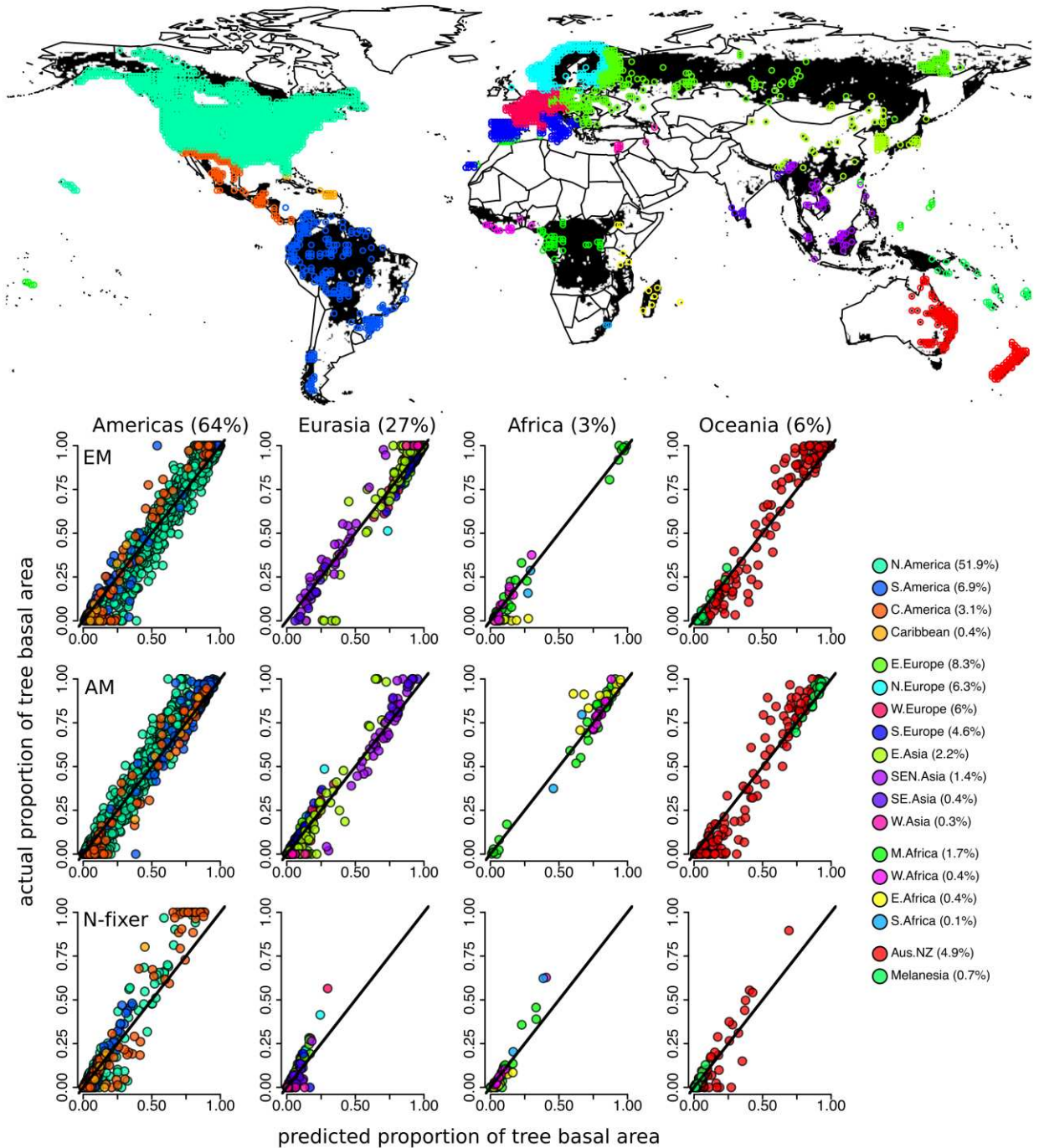
104 The dominant guilds of tree root symbionts, arbuscular mycorrhizal (AM) fungi,
105 ectomycorrhizal (EM) fungi, ericoid mycorrhizal (ErM) fungi, and nitrogen (N)-fixing bacteria
106 (N-fixer) are all based on the exchange of plant photosynthate for limiting macronutrients. The
107 AM symbiosis is the oldest of the four, having evolved nearly 500 million years ago, with EM,
108 ErM and N-fixer plant taxa having evolved multiple times from an AM basal state. Plants that
109 form the AM symbiosis are markedly more diverse than the other symbiotic groups, comprising
110 nearly 80% of all terrestrial plant species, and principally rely on AM fungi for enhancing
111 mineral phosphorus (P) uptake¹⁴. EM fungi evolved more recently from saprotrophic ancestors,
112 and as a result may be better than AM fungi at competing with free living soil microbes for
113 resources³. As such, some EM fungal lineages are more capable of mobilizing organic sources of
114 soil nutrients (particularly nitrogen) compared with AM fungi^{15,16}. Association with EM fungi,
115 but not AM fungi, has been shown to allow trees to accelerate photosynthesis in response to
116 increased atmospheric CO₂ when soil nitrogen (N) is limiting⁶ and to inhibit soil respiration by
117 decomposer microbes^{3,9} (but see ¹⁷). Because increased plant photosynthesis and decreased soil
118 respiration both reduce atmospheric CO₂ concentrations, the EM symbiosis is associated with
119 buffering the Earth's climate against anthropogenic changes.

120 In contrast to mycorrhizal fungi, which extract nutrients from the soil, symbiotic N-fixers
121 (Rhizobia and Actinobacteria) convert atmospheric N₂ to plant-usable forms. Symbiotic N-fixers
122 are responsible for a large fraction of biological soil-N inputs, which can increase N-availability
123 in forests where they are locally abundant¹⁸. Both N-fixing bacteria and EM fungi often demand
124 more plant photosynthate than does the AM symbiosis^{14,19,20}. Because tree growth and
125 reproduction are limited by access to inorganic, organic and atmospheric sources of N, the
126 distribution of these root symbioses is likely to reflect both environmental conditions that

127 maximize the cost-benefit ratio of symbiotic exchange as well as physiological constraints on
128 different symbionts.

129 In one of the earliest efforts to understand the functional biogeography of plant root
130 symbioses, Sir David Read²¹ categorically classified biomes by their perceived dominant
131 mycorrhizal type and hypothesized that seasonal climates favor hosts associating with EM fungi
132 due to their ability to compete directly for organic N. By contrast, it has been proposed that
133 sensitivity to low temperatures has prevented N-fixers from dominating outside the tropics,
134 despite the potential for N-fixation to alleviate N-limitation in boreal forests^{20,22}. However,
135 global scale tests of these proposed biogeographic patterns and their proposed climate drivers are
136 lacking or inconclusive²³⁻²⁵ and we have no understanding of the regional variations in this
137 proposed latitudinal trend. To address this research gap, we compiled the first global ground-
138 sourced survey database to reveal numerical abundances of each symbiosis across the global
139 forested biomes, rather than incidence (presence or absence, e.g.,²³⁻²⁵), which is essential for
140 identifying the shapes and potential mechanisms underlying transitions in forest symbiotic state
141 along climatic gradients^{26,27}.

142 We determined the abundance of tree symbioses using GFBi, an extension from the plot-
143 based Global Forest Biodiversity (GFB²⁸) database, which contains over 1.2 million forest
144 inventory plots of individual-based measurement records from which we derive abundance
145 information for entire tree communities (Figure 1).



146

147 **Figure 1.** A map of 1 by 1 degree grid cells where we analyzed the proportion of tree stems
 148 and basal area for different symbiotic guilds (above). Circles show the location of training
 149 data, colored by geographic origin, while black squares show the extent of model
 150 projections. Panels below the map show actual vs. predicted proportion of basal area for
 151 ectomycorrhizal (EM), arbuscular mycorrhizal (AM), and N-fixer trees by continent and
 152 subregion, and demonstrate globally consistent model performance.

153 Using published literature on the evolutionary histories of mycorrhizal and N-fixer
154 symbioses^{8,25,29-33}, we assigned plant species from the GFBi to one of 5 symbiotic guilds: AM,
155 EM, ErM, N-fixer, and non- or weakly-mycorrhizal (NM). Most plants with symbioses derived
156 from the AM state retain the genetic potential to associate with AM fungi¹⁴. Thus, consistent
157 with other studies in this field²⁹, we assigned tree species to the AM-exclusive guild if they were
158 not EM, ericoid mycorrhizal, non-mycorrhizal, or N-fixers. While there is some uncertainty in
159 such assignments, direct investigation of mycorrhizal status when done supports this
160 assumption³⁴. Because individual measurements of mycorrhizal colonization are not possible at
161 this scale, our models represent potential symbiotic associations.

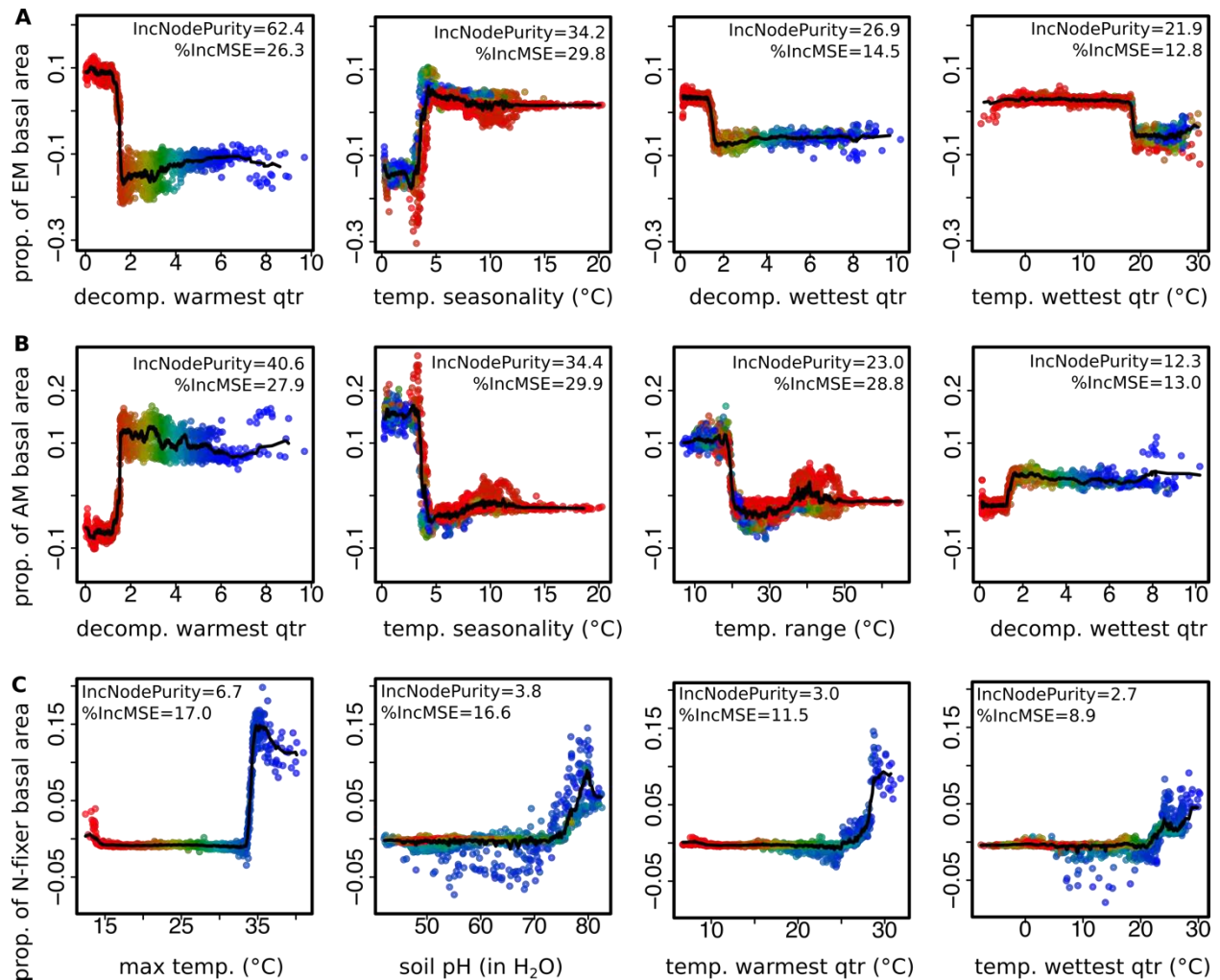
162 To identify the key factors structuring symbiotic distributions we assembled 70 global
163 predictor layers: 19 climatic (annual, monthly, and quarterly temperature and precipitation
164 variables), 14 soil chemical (total soil N density, microbial N, C:N ratios and soil P fractions,
165 pH, cation exchange capacity), 5 soil physical (soil texture and bulk density), 26 vegetative
166 indices (leaf area index, total stem density, enhanced vegetation index means and variances), and
167 5 topographic variables (elevation, hillshade) (Table S7). Because decomposition is the dominant
168 process by which soil nutrients become available to plants, we generated 5 additional layers that
169 estimate the climatic control of decomposition. We parameterized decomposition coefficients
170 according to the Yasso07 model^{35,36} using the following equation:

$$171 \quad k = \text{Exp}(0.095T_i - 0.00014 T_i^2) (1 - \text{Exp}[-1.21 P_i]), \quad (1)$$

172 where P_i and T_i are precipitation and mean temperature, either quarterly or annually, and the
173 constants $0.0095 (= \beta_1)$, $0.00014 (= \beta_2)$, and $-1.21 (= \gamma)$ are parameters fit using a previous global
174 study of leaf litter mass-loss³⁶. Although local decomposition rates can vary significantly based
175 on litter quality or microbial community composition³⁷, climate is the primary control at the

176 global scale³⁶. Decomposition coefficients describe how fast different chemical pools of leaf
177 litter lose mass over time relative to a parameter, α , that accounts for leaf-chemistry.
178 Decomposition coefficients (k) with values of 0.5 and 2 indicate a halving and doubling of
179 decomposition rates relative to α , respectively (Supplemental Materials).

180 Given the large set of possible environmental predictors, we used the random forest
181 machine-learning algorithm to identify the best predictors of global symbiosis distributions. The
182 random forest algorithm averages multiple regression trees, each of which uses a random subset
183 of all the model variables to predict a response. These regression trees identify optimal values
184 along a predictor-gradient to “split” the model response into different nodes (e.g., predictions
185 could be “split” into nodes of 50 or 75% of EM basal area depending on whether mean annual
186 temperature is $>$ or $<$ 20°C). We ranked the importance of each variable according to inc node
187 purity, which measures the decrease in model error that occurs whenever the response is split on
188 that variable (Figure 2ABC). We first determined the influence and relationship of all 75
189 predictor layers on forest symbiotic state and then optimized our models using a stepwise
190 reduction in variables, from least- to most-important. Soil chemical, vegetative, and topographic
191 variables were the first to be eliminated from our models in this way. In a subsequent model that
192 included only layers of climate, decomposition, and certain soil physical and chemical
193 information, we found that the 4 most important variables accounted for $>$ 85% of the explained
194 variability. We plot the partial-fits of these four variables for each symbiotic guild (Figure
195 2ABC).



196 **Figure 2. Partial plots of residual variation explained by the four most important**
 197 **predictors of the proportion of tree basal area belonging to the (A) ectomycorrhizal (EM),**
 198 **(B) arbuscular mycorrhizal (AM), and (C) N-fixer symbiotic guilds. Variables are listed in**
 199 **declining importance from left to right, as determined by inc node purity, with points**
 200 **colored with a red-green-blue gradient according to their position on the x-axis of the most**
 201 **important variable (left-most panels for each guild), allowing cross visualization between**
 202 **predictors. Each panel lists two measures of variable importance, inc node purity (used for**
 203 **sorting) and %IncMSE (see Supplemental Information for description). Decomposition**
 204 **rates in (A) and (B) are in units of leaf litter mass loss per quarter. The abundance of each**
 205 **symbiont type transitions sharply along climatic gradients, suggesting that sites near the**
 206 **threshold are particularly vulnerable to switching their dominant symbiont guild with**
 207 **climate changes.**

208

209 The three most numerically abundant tree symbiotic guilds each have reliable
 210 environmental signatures, with the four most important predictors accounting for 81, 79, and
 211 52% of the total variability in EM, AM, and N-fixer relative basal area, respectively. Models for

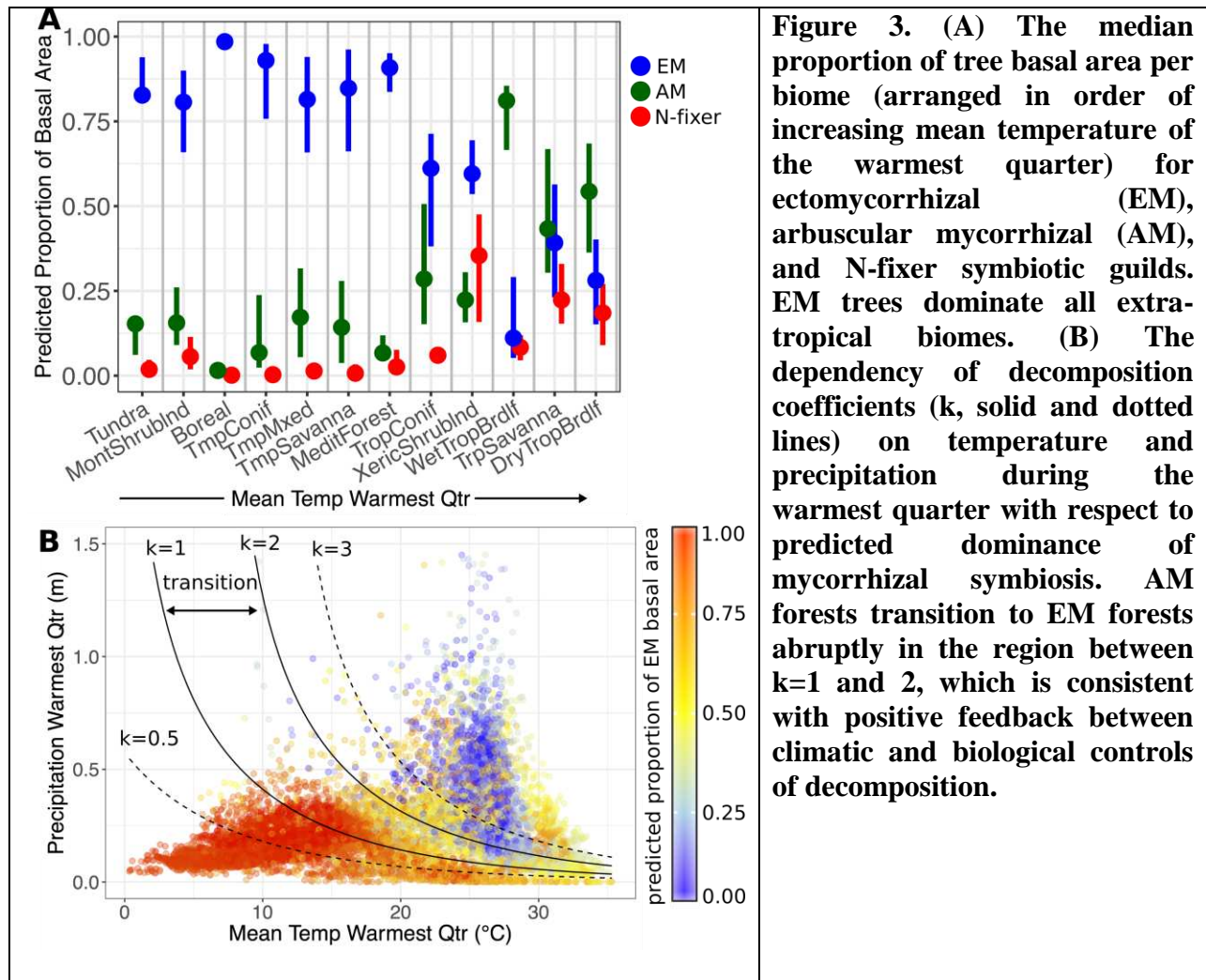
212 ErM and NM lack strong predictive power given the relative rarity of these symbiotic states
213 amongst trees, although the raw data do identify some local abundance hotspots for ErM (Figure
214 S1). As a result, we focus the remainder of results and discussion on the three major tree
215 symbiotic states (EM, AM, N-fixer). Despite the fact that data from N. and S. America constitute
216 65% of the training data (at the 1 by 1 degree grid scale), our models accurately predict the
217 proportional abundances of the three major symbioses across all major geographic regions
218 (Figure 1). The high performance of our models, which is robust to both K-fold cross-validation
219 and rarefying samples so that all continents are represented with equal depth (Figures S10-12),
220 suggest that regional variations in climate (including indirect effects on decomposition) and soil
221 pH (for N-fixers) are the primary factors influencing the relative dominance of each guild at the
222 global scale (geographic origin only explained ~2-5% of the variability in residual relative
223 abundance) (Figure 1BCD, Table S8).

224 Random forest models should not be projected across predictor gradients that fall outside
225 the ranges of their training data (e.g., grid cells with higher mean annual temperatures than the
226 maximum used to fit the models). To prevent the over-projecting of our models over pixels
227 where we lacked training data, we subset a global grid of predictor layers depending on whether
228 (1) the grid cell fell within the top 60% of land surface with respect to tree stem density¹³ and
229 either (2) fell within the univariate distribution of all the predictor layers from our training data
230 and/or (3) fell within an 8-dimensional hypervolume defined by the unique set of the 4-best
231 predictors of the relative abundance of each guild (Figure 2, Supplemental Materials). We then
232 projected our models across only those grid cells that met these criteria, which constitutes 46%
233 of the global land surface and 88% of global tree stems (Figure 1; Figure S16). While model
234 validation indicates that our projections are robust, additional ground truthing of predictions to

235 identify any discrepancies would be incredibly valuable. If such discrepancies exist they can
236 help fine tune climate-symbiosis models, or identify areas where climate might favor invasion
237 by symbioses that have not yet evolved or dispersed to a particular biogeographic region.

238 In contrast to a recent global analysis of root traits, which concluded that plant evolution
239 has favored reduced dependence on mycorrhizal fungi³⁸, we find that trees associating with the
240 relatively more C-demanding and recently-derived EM fungi^{14,19} represent the dominant tree-
241 symbiosis. By taking the average proportion of EM trees, weighted by spatially-explicit global
242 predictions for tree stem density¹³, we estimate that approximately 60% of trees on earth are EM,
243 despite the fact that only 2% of plant species associate with EM fungi (vs. 80% associating with
244 AM fungi)^{8,29}. Outside of the tropics, the estimate for EM relative abundance increases to
245 approximately 80% of trees.

246 Turnover among the major symbiotic guilds results in a tri-modal latitudinal abundance
247 gradient, with the proportion of EM trees increasing (and AM trees decreasing) with distance
248 from the equator, while N-fixing trees reach peak abundance in the arid zone around 30 degrees
249 (Figure 3A, Figure 4). These trends are driven by abrupt transitional regions along continental
250 climatic gradients (Figure 2), which skew the distribution of symbioses among biomes (Figure
251 3A) and drive strong patterns across geographic and topographic features that influence climate.
252 For example, moving north or south from the equator, the first transitional zone separates warm
253 (aseasonal), AM-dominated, tropical broadleaf forests (>75% median basal area, vs. 8% for EM
254 trees) from the rest of the EM-dominated world forest system (Figure 2AB; Figure 3A). It
255 stretches longitudinally across 25 degrees N and S, just beyond the dry tropical broadleaf forests
256 (with 25% EM tree basal area; Figure 3A), where average monthly temperature variation reaches
257 3-5°C (Figure 2AB).



258 Moving further N or S, the second transitional climate zone separates regions where
 259 decomposition coefficients during the warmest quarter of the year are less than 2 (see Figure 3B
 260 for the associated temperature and precipitation ranges). In N. America and China, this transition
 261 zone spans longitudinally around 50 degrees N, separating the mixed AM / EM temperate forests
 262 from their neighboring EM dominated boreal forests (75 vs 100% EM tree basal area,
 263 respectively; Figure 3A). This transitional decomposition zone bypasses W. Europe, which has
 264 temperature seasonality $> 5^{\circ}\text{C}$, but lacks sufficiently wet summers to accelerate decomposition
 265 coefficients beyond values associated with mixed AM/EM forests. The latitudinal transitions in
 266 symbiotic state observed among biomes are mirrored by within-biome transitions along elevation

267 gradients. For example, in tropical Mexico, warm and wet quarter decomposition coefficients <
268 2 occur along the slopes of the Sierra Madre, where mixed AM-exclusive and N-fixer woodlands
269 in arid climates transition to EM dominated tropical coniferous forests (75% basal area, Figure
270 3A, Figure 4ABC, Figure S17-19). The southern hemisphere, which lacks the landmass to
271 support extensive boreal forests, experiences a similar latitudinal transition in decomposition
272 rates along the ecotone separating its tropical and temperate biomes, around 28 degrees S.

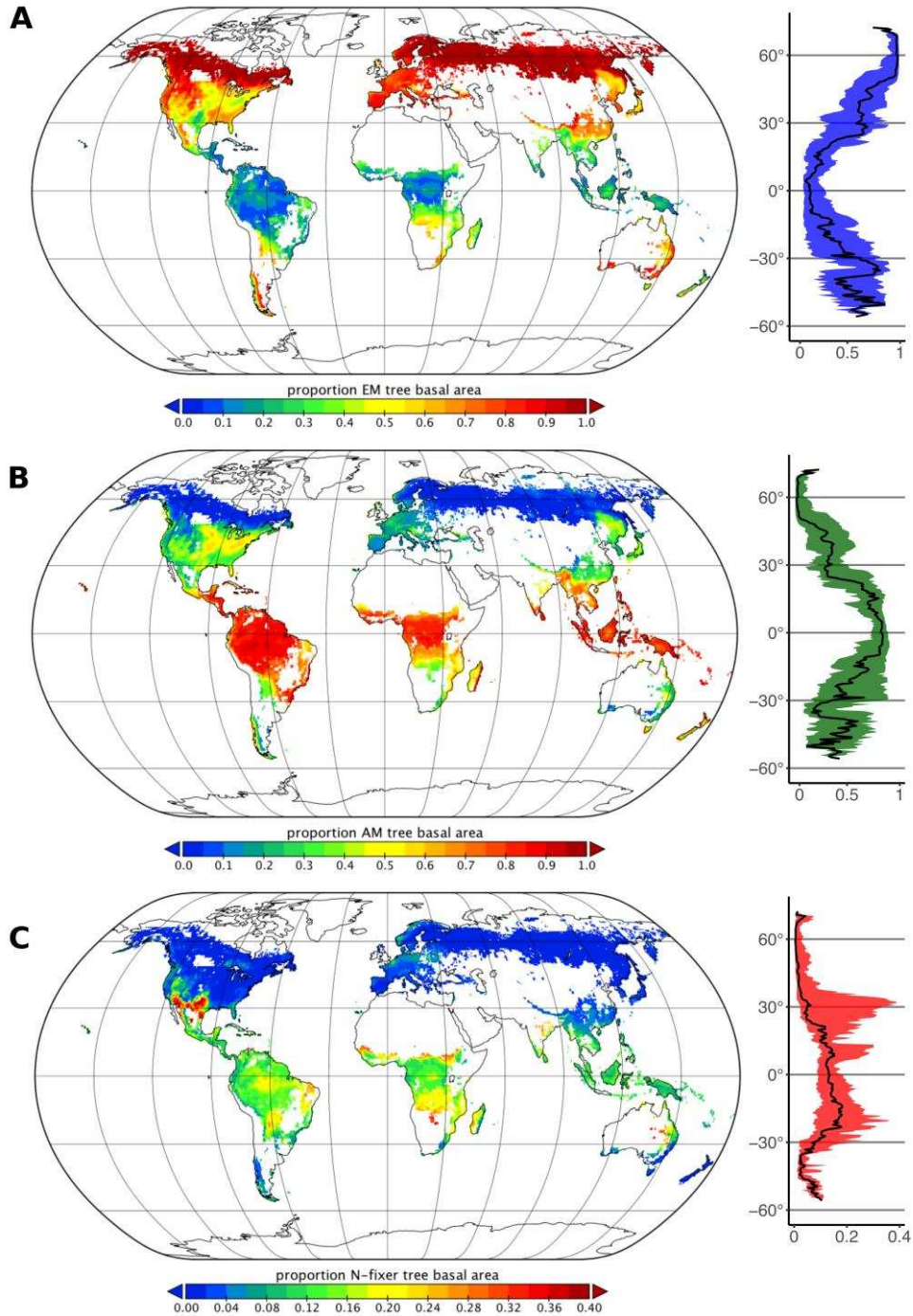
273 The abrupt transitions that we detected between forest symbiotic states along
274 environmental gradients suggest that positive feedbacks may exist between climatic and
275 biological controls of decomposition^{11,36}. In contrast to AM fungi, some EM fungi can use
276 oxidative enzymes to mineralize organic nutrients from leaf litter, converting nutrients to plant-
277 usable forms before transferring them to their host trees^{2,5}. Relative to AM trees, the leaf litter of
278 EM trees is also chemically more resistant to decomposition, with higher C:N ratios and higher
279 concentrations of decomposition-inhibiting secondary compounds¹¹. Thus, EM leaf litter can
280 exacerbate climatic barriers to decomposition, promoting conditions where EM fungi have
281 superior nutrient-acquiring abilities to AM-fungi^{5,11}. Such positive-feedbacks are known to cause
282 abrupt ecosystem transitions along smooth environmental gradients between woodlands and
283 grasses: trees suppress fires, which promotes seedling recruitment, while grass fuels fires, which
284 kill tree seedlings³⁹. Our study provides the first evidence that rapid transitions in tree
285 community structure along climate gradients could also be governed by positive-feedbacks
286 between symbiotic guilds and nutrient cycling; although other types of interactions, such as
287 environmentally sensitive competition hierarchies among symbiotic guilds, could also lead to
288 abrupt transitions without specifically invoking feedback effects. In either case, the existence of
289 abrupt transitions suggests that trees and associated microbial symbionts in transitional regions

290 along decomposition gradients should be susceptible to drastic turnover in symbiotic state with
291 future environmental changes⁴⁰.

292 To illustrate the sensitivity of global patterns of tree symbiosis to climate change, we use
293 the climate relationships we developed for current climate to project potential changes due to
294 climate change. Relative to our global predictions using the most recent climate data, model
295 predictions using the projected climates for 2070 suggest the abundance of EM trees will decline
296 by as much as 10% (using a relative concentration pathway of 8.5 W/m²; Figure S25). Due to
297 their position along decomposition gradients relative to the abrupt shift from EM to AM forests
298 (Figure 2AB), our models predict the largest declines in EM abundance will occur along the
299 boreal-temperate ecotone, although declines in species abundances can lag decades, or even
300 centuries or millennia, behind associated climatic changes⁴¹. The predicted decline in EM trees
301 corroborates the results of common garden transfer and simulated warming experiments, which
302 demonstrate that some important EM hosts will decline at the boreal-temperate ecotone in altered
303 climates⁴²⁻⁴⁴. Because of the low tree diversity in boreal forests, tree species loss around
304 transition zones may have major consequences for forest related economic activity⁴⁵.

305

306



307

308 **Figure 4. Predicted global maps (left) and latitudinal gradients (right, with solid line**
 309 **indicating the median and colored ribbon spanning the range from the 5% and 95%**
 310 **quantiles) of the proportion of tree basal area for (A) ectomycorrhizal (EM), (B)**
 311 **arbuscular mycorrhizal (AM), and (C) N-fixer symbiotic guilds.**
 312

313 The change in dominant nutrient exchange symbioses along climate gradients highlights
314 the interconnection between atmospheric and soil compartments of the biosphere. The transition
315 from AM to EM dominance corresponds with a shift from P to N limitation of plant growth with
316 increasing latitude⁴⁶⁻⁴⁸. Including published global projections of total soil N or P, microbial N,
317 or soil P fractions (labile, occluded, organic, and apatite) did not increase the amount of variation
318 explained by the model or alter the variables identified as most important, and thus were dropped
319 from our analysis. However, this does not necessarily mean that soil nutrient availability is
320 unimportant at the global scale, as the best-available global data likely do not adequately
321 represent local nutrient availability^{49,50}. Rather, our finding that climatic controls of
322 decomposition best predict the dominant mycorrhizal associations mechanistically links
323 symbiont physiology with climatic controls of soil nutrient release from leaf litter. These
324 findings are consistent with Read's hypothesis²¹ that slow decomposition at high latitudes favors
325 EM fungi due to their increased capacity to liberate organic nutrients². Thus, while more
326 experiments are necessary to understand the specific mechanism by which nutrient competition
327 favors dominance of AM or EM symbioses²⁶, we propose that the latitudinal and elevational
328 transitions from AM to EM dominated forests be called Read's Rule.

329 While our analyses focus on prediction at large spatial scales appropriate to the available
330 data, our findings with respect to Read's Rule also provide insight into how soil factors structure
331 the fine-scale distributions of tree symbioses within our grid cells. For example, while at a coarse
332 scale we find that EM trees are relatively rare in many wet tropical forests, individual tropical
333 sites in our raw data span the full range from 0 – 100 % EM basal area. In much of the wet
334 tropics, these EM dominated sites exist as outliers within a matrix of predominantly AM trees. In
335 an apparent exception that proves Read's Rule, in aseasonal warm neotropical climates, which

336 accelerate leaf-decomposition and promote regional AM dominance (Figure 3), EM dominated
337 tree stands can develop in sites where poor soils and recalcitrant litter slow decomposition and N
338 mineralization^{26,51}. Landscape-scale variation in the relative abundance of symbiotic states also
339 changes along climate gradients, with variability highest in xeric and temperate biomes (Figure
340 S2), suggesting that the potential of local nutrient variability to favor particular symbioses is
341 contingent on climate.

342 Whereas EM trees are associated with ecosystems where plant growth is thought to be
343 primarily N-limited, N-fixer trees are not. Our results highlight the global extent of the “N-
344 cycling paradox,” wherein some metrics suggest that N-limitation is greater in the temperate
345 zone⁴⁶⁻⁴⁸, yet N-fixing trees are relatively more common in the tropics^{20,52,53} (Figure 3A). We
346 find that N-fixers, which we estimate represent 7% of all trees, dominate forests with annual max
347 temperatures >35°C and alkaline soils (particularly in North America and Africa, Figure 2C).
348 They have the highest relative abundance in xeric shrublands (24%), tropical savannas (21%),
349 and dry broadleaf forest biomes (20%), but are nearly absent from boreal forests (<1%) (Figure
350 3A, Figure 4). The decline in N-fixer tree abundance we observed with increasing latitude is also
351 associated with a previously documented latitudinal shift in the identity of N-fixing microbes,
352 from facultative N-fixing rhizobial bacteria in tropical forests to obligate N-fixing actinorhizal
353 bacteria in temperate forests⁵². Our data are not capable of fully disentangling the several
354 hypotheses that have been proposed to reconcile the N-cycling paradox^{20,54}. However, our results
355 are consistent with the model prediction²² and regional empirical evidence^{27,55,56} that N-fixing
356 trees are particularly important in arid biomes. Based primarily on the observed positive,
357 nonlinear association of N-fixer relative abundance with the mean temperature of the hottest

358 month (Figure 2C), our models predict a two-fold increase in N-fixer relative abundance when
359 transitioning from humid to dry tropical forest biomes (Figure 3A).

360 Although soil microbes are a dominant component of forests, both in terms of diversity
361 and ecosystem functioning^{5,6,11}, identifying global-scale microbial biogeographic patterns
362 remains an ongoing research priority. Our analyses confirm that Read's Rule, which is one of the
363 first proposed biogeographic rules specific to microbial symbioses, successfully describes global
364 transitions between mycorrhizal guilds. More generally, climate driven turnover among the
365 major plant-microbe symbioses represents a fundamental biological pattern in the Earth system,
366 as forests transition from low-latitude arbuscular mycorrhizal, to N-fixer, to high-latitude
367 ectomycorrhizal ecosystems. The predictions of our model (which we make available as a global
368 raster layer) can now be used to represent these critical ecosystem variations in global
369 biogeochemical models used to predict climate-biogeochemical feedbacks within and between
370 trees, soils, and the atmosphere. Additionally, the layer containing the proportion abundance of
371 N-fixing trees can be used to map potential symbiotic N-fixation, which links together
372 atmospheric pools of C and N. Future work can extend our findings to incorporate multiple plant
373 growth forms and non-forested biomes, where similar patterns likely exist, to generate a
374 complete global perspective. Our predictive maps leverage the most comprehensive global forest
375 dataset to generate the first quantitative global map of forest tree symbioses, demonstrating how
376 nutritional mutualisms are coupled with the global distribution of plant communities.

377 **Acknowledgments**

378 This work is supported in part by the Key Project of National Key Research and Development
379 Plan, China (2017YFC0504005); the new faculty start-up grant, Department of Forestry and
380 Natural Resources, Purdue University; Dept. of Energy (DOE) Biological and Environmental

381 Research Program Early Career Research Grant DE-SC0016097; DOB Ecology, Plant-for-the-
382 Planet and the German Ministry for Economic Development and Cooperation; São Paulo
383 Research Foundation, #2014/14503-7; São Paulo Research Foundation (FAPESP), #2003/12595-
384 7; Proyecto FONACIT No. 1998003436 and UNELLEZ No. 23198105; EU, Sumforest –
385 REFORM, Risk Resilient Forest Management, FKZ: 2816ERA02S; U.S. National Science
386 Foundation Long-Term Ecological Research grant DEB-1234162, German Science Foundation
387 (DFG), KROOF Tree and stand-level growth reactions on drought in mixed versus pure forests
388 of Norway spruce and European beech, PR 292/12-1; Bavarian State Ministry for Food,
389 Agriculture and Forestry, W07 longterm yield experiments, 7831-26625-2017 and Project No
390 E33; The Deutsche Forschungsgemeinschaft (DFG) Priority Program 1374 Biodiversity
391 Exploratories; The International Tropical Timber Organization, ITTO-Project PD 53/00 Rev.3
392 (F); The State Forest Management Centre, Estonia, and the Environmental Investment Centre,
393 Estonia; Natural Sciences and Engineering Research Council of Canada Discover Grant Project
394 (RGPIN-2014-04181 and STPGP428641); European Structural Funds by FEDER 2014-2020
395 GY0006894; European Investment Funds by FEDER/COMPETE/POCI-Operational
396 Competitiveness and Internationalization Programme, under Project POCI-01-0145-FEDER-
397 006958 and National Funds by FCT - Portuguese Foundation for Science and Technology, under
398 the project UID/AGR/04033/2013; Vietnam National Foundation for Science and Technology
399 Development (NAFOSTED-106-NN.06-2016.10); German Research Foundation (DFG, FOR
400 1246); The project LIFE+ ForBioSensing PL Comprehensive monitoring of stand dynamics in
401 Bialowieza Forest co-funded by Life Plus (contract number LIFE13 ENV/PL/000048) and the
402 National Fund for Environmental Protection and Water Management in Poland (contract number
403 485/2014/WN10/OP-NM-LF/D); National Natural Scientific Foundation of China (31660055

404 and 31660074); The Polish State Forests National Forest Holding (2016); The Dutch Ministry of
405 Economic Affairs for funding the Dutch National Forest Inventory; The Grant 11-TE11-0100
406 from the U.S. National Space and Aeronautics Administration; the Tropical Ecology,
407 Assessment, and Monitoring (TEAM) / Conservation International project for funding the data
408 collection, and the National Institut Research Amazon (INPA); The Ministère des Forêts, de la
409 Faune et des Parcs du Québec (Canada); The Exploratory plots of FunDivEUROPE received
410 funding from the European Union Seventh Framework Programme (FP7/2007-2013) under grant
411 agreement 265171; DBT, Govt. of India through the project ‘Mapping and quantitative
412 assessment of geographic distribution and population status of plant resources of Eastern
413 Himalayan region’ (sanction order No. BT/PR7928/NDB/52/9/2006 dated 29th September 2006);
414 The financial support from Natural Sciences and Engineering Research Council of Canada to S.
415 Dayanandan; Czech Science Foundation Standard Grant (16-09427S) and European Research
416 Council advanced grant (669609); RFBR #16-05-00496; The project implementation
417 Demonstration object on the transformation of declining spruce forests into ecologically more
418 stable multifunctional ecosystems, ITMS 26220220026, supported by the Research &
419 Development Operational Program funded by the ERDF; The Swedish NFI, Department of
420 Forest Resource Management, Swedish University of Agricultural Sciences SLU; The National
421 Research Foundation (NRF) of South Africa (89967 and 109244) and the South African
422 Research Chair Initiative; University Research Committee of the University of the South Pacific,
423 and New Colombo Plan Funding through the Department of Foreign Affairs and Trade of the
424 Australian government; The TEAM project in Uganda supported by the Moore foundation and
425 Buffett Foundation through Conservation International (CI) and Wildlife Conservation Society
426 (WCS); COBIMFO project funded by the Belgian Science Policy Office (Belspo), contract no.

427 SD/AR/01A; The German Federal Ministry of Education and Research (BMBF) under Grant
428 FKZ 01LL0908AD for the project “Land Use and Climate Change Interactions in the Vu Gia
429 Thu Bon River Basin, Central Vietnam” (LUCCI); Programme Tropenbos Côte d'Ivoire : projet
430 04/97-1111a du “Complément d’Inventaire de la Flore dans le Parc National de Tai”; The Danish
431 Council for Independent Research | Natural Sciences (TREECHANGE, grant 6108-00078B to
432 JCS) and VILLUM FONDEN (grant 16549); ERC Advanced Grant 291585 (“T-FORCES”) and
433 a Royal Society-Wolfson Research Merit Award; RAINFOR plots supported by the Gordon and
434 Betty Moore Foundation and the U.K. Natural Environment Research Council (NERC), notably
435 NERC Consortium Grants ‘AMAZONICA’ (NE/F005806/1), ‘TROBIT’ (NE/D005590/1), and
436 ‘BIO-RED’ (NE/N012542/1); Fundação de Amparo à Pesquisa e Inovação de Santa Catarina,
437 FAPESC (2016TR2524), Conselho Nacional de Desenvolvimento Científico e Tecnológico,
438 CNPq [312075/2013-8]; “Investissement d’Avenir” grant managed by Agence Nationale de la
439 Recherche (CEBA, ref. ANR- 10-LABX-25-01); CIFOR's Global Comparative Study on
440 REDD+ funded by the Norwegian Agency for Development Cooperation (Norad), the Australian
441 Department of Foreign Affairs and Trade (DFAT), the European Union (EU), the International
442 Climate Initiative (IKI) of the German Federal Ministry for the Environment, Nature
443 Conservation, Building and Nuclear Safety (BMUB), and the CGIAR Research Program on
444 Forests, Trees and Agroforestry (CRP-FTA), and donors to the CGIAR Fund; The Nature and
445 Biodiversity Conservation Union (NABU) under the project entitled “Biodiversity under Climate
446 Change: Community Based Conservation, Management and Development Concepts for the Wild
447 Coffee Forests”, funded by the German Federal Ministry for the Environment, Nature
448 Conservation and Nuclear Safety (BMU) through the International Climate Initiative (IKI); The
449 Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq); The institutional

450 project “EXTEMIT - K”, no. CZ.02.1.01/0.0/0.0/15_003/0000433 financed by OP RDE; EC DG
451 VIII grant BZ-5041 (ECOSYN), NWO-WOTRO (W84-204), and GTZ; AfriTRON network
452 plots funded by the local communities and NERC, ERC, European Union, Royal Society and
453 Leverhume Trust; BOLFOR (Proyecto de Manejo Forestal Sostenible- Bolivia); The Global
454 Environment Research Fund F-071 and D-1006, and JSPS KAKENHI Grant Numbers
455 JP17K15289; The National Institute of Biology(Now Research Center for Biology), LIPI
456 (Indonesian Institute of Sciences), Indonesia IFBN project (contract 4000114425/15/NL/FF/gp)
457 funded by ESA; NSF grant DBI-1565046; Swiss National Science Foundation (SNSF No.
458 130720, 147092); Projects D/9170/07, D/018222/08, D/023225/09 and D/032548/10 funded by
459 the Spanish Agency for International Development Cooperation [Agencia Española de
460 Cooperación Internacional para el Desarrollo (AECID)] and Fundación Biodiversidad, in
461 cooperation with the Universidad Mayor de San Simón (UMSS), the FOMABO (Manejo
462 Forestal en las Tierras Tropicales de Bolivia) project and CIMAL (Compañía Industrial
463 Maderera Ltda.); The Agency for Economic and Environmental Development (DDEE) of the
464 north province of New Caledonia (the projects Ecofor & Cogefor, 2011-2016); Russian Science
465 Foundation (16-17-10284 “The accumulation of carbon in forest soils and forest succession
466 status”); Norwegian Ministry of Food and Agriculture; A grant from the Royal Society and the
467 Natural Environment Research Council (UK) to S.L.L.; The Spanish Agency for International
468 Development Cooperation [Agencia Española de Cooperación Internacional para el Desarrollo
469 (AECID)] and Fundación Biodiversidad, in cooperation with the governments of Syria and
470 Lebanon; COBIMFO Project, Federal Science Policy, Belgium; Consejo Nacional de Ciencia y
471 Tecnología, Mexico; Comisión Nacional Forestla, Mexico; BEF-China project (FOR 891)
472 funded by the German Research Foundation (DFG); WWF Russell Train Fellowship to P.M.U.

473 (Grant ST54); Wildlife Conservation Society DRC Program under CARPE Funding; Seoul
474 National University Big Data Institute through the Data Science Research Project 2016, R&D
475 Program for Forest Science Technology (Project No. 2013069C10-1719-AA03 &
476 S111215L020110) funded by Korea Forest Service (Korea Forestry Promotion Institute); The
477 European Union’s Horizon 2020 research and innovation program within the framework of the
478 MultiFUNGtionality Marie Skłodowska-Curie Individual Fellowship (IF-EF) under grant
479 agreement 655815; Tropenbos International-Suriname; The Institute for World Forestry,
480 University of Hamburg; REMBIOFOR Project “Remote sensing based assessment of woody
481 biomass and carbon storage in forests” funded by The National Centre for Research and
482 Development, Warsaw, Poland, under the BIOSTRATEG program (agreement no.
483 BIOSTRATEG1/267755/4/NCBR/2015); The National Science Centre, Poland (Grant:
484 2011/02/A/NZ9/00108); Project “Environmental and genetic factors affecting productivity of
485 forest ecosystems on forest and post-industrial habitats” (2011-2015; no. OR/2717/3/11); Project
486 “Carbon balance of the major forest-forming tree species in Poland” (2007-2011; no. 1/07)
487 funded by the General Directorate of State Forests, Warsaw, Poland; and the research
488 professorship for "Ecosystem-based sustainable development" funded by Eberswalde University
489 for Sustainable Development. GK was supported by an Alexander von Humboldt fellowship.
490 GDAW was supported from a Newton International Fellowship from the Royal Society.

491

492 We thank the following agencies, initiatives, teams, and individuals for data collection and other
493 technical support: the Global Forest Biodiversity Initiative (GFBI) for establishing the data
494 standards and collaborative framework; United States Department of Agriculture, Forest Service,
495 Forest Inventory and Analysis (FIA) Program; University of Alaska Fairbanks; The SODEFOR,

496 Ivory Coast; the Queensland Herbarium and past Queensland Government Forestry and Natural
497 Resource Management Departments and staff for data collection for over seven decades. Ziaur
498 Rahman Laskar, Salam Dilip, Bijit, Bironjoy and Samar; Badru Mugerwa and Emmanuel
499 Akampurira, together with a team of field assistants (Valentine and Lawrence); all persons who
500 made the Third Spanish Forest Inventory possible, especially the main coordinator, J. A.
501 Villanueva (IFN3); Italian and Friuli Venezia Giulia Forest Services (Italy); Rafael Ávila and
502 Sharon van Tuylen, Insituto Nacional de Bosques (INAB), Guatemala for facilitating
503 Guatemalan data; The National Focal Center for Forest condition monitoring of Serbia (NFC),
504 Institute of Forestry, Belgrade, Serbia; The Thünen Institute of Forest Ecosystems (Germany) for
505 providing National Forest Inventory data; All TEAM data provided by the Tropical Ecology
506 Assessment and Monitoring (TEAM) Network, a collaboration between Conservation
507 International, the Missouri Botanical Garden, the Smithsonian Institution, and the Wildlife
508 Conservation Society, and partially funded by these institutions, the Gordon and Betty Moore
509 Foundation, and other donors, with thanks to all current and previous TEAM site manager and
510 other collaborators that helped collecting data; The people of the Redi Doti, Pierrekondre and
511 Cassipora village who were instrumental in assisting with the collection of data and sharing local
512 knowledge of their forest; and the dedicated members of the field crew of Kabo 2012 census.
513 Yadvinder Malhi's contribution was supported by an ERC Advanced Investigator Award GEM-
514 TRAITS (321131).

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