

1 **Title:** The Maximum Entropy Formalism of statistical mechanics in a biological  
2 application: a quantitative analysis of tropical forest ecology.

3  
4 **Authors:** Edwin Pos\*,1,2 Luiz de Souza Coelho,3 Diogenes de Andrade Lima  
5 Filho,3 Rafael P. Salomão,4,5 Iêda Leão Amaral,3 Francisca Dionízia de Almeida  
6 Matos,3 Carolina V. Castilho,6 Oliver L. Phillips,7 Juan Ernesto Guevara,8,9 Marcelo  
7 de Jesus Veiga Carim,10 Dairon Cárdenas López,11 William E. Magnusson,12  
8 Florian Wittmann,13,14 Mariana Victória Irume,3 Maria Pires Martins,3 Daniel  
9 Sabatier,15 José Renan da Silva Guimarães,10 Jean-François Molino,15 Olaf S.  
10 Bánki,2 Maria Teresa Fernandez Piedade,16 Nigel C.A. Pitman,17 Abel Monteagudo  
11 Mendoza,18 José Ferreira Ramos,3 Joseph E. Hawes,19 Everton José Almeida,20  
12 Luciane Ferreira Barbosa,20 Larissa Cavalheiro,20 Márcia Cléia Vilela dos Santos,20  
13 Bruno Garcia Luize,21 Evlyn Márcia Moraes de Leão Novo,22 Percy Núñez  
14 Vargas,23 Thiago Sanna Freire Silva,24 Eduardo Martins Venticinque,25 Angelo  
15 Gilberto Manzatto,26 Neidiane Farias Costa Reis,27 John Terborgh,28,29 Katia  
16 Regina Casula,27 Euridice N. Honorio Coronado,30,7 Juan Carlos Montero,31,3  
17 Beatriz S. Marimon,32 Ben Hur Marimon-Junior,32 Ted R. Feldpausch,33,7 Alvaro  
18 Duque,34 Chris Baraloto,35 Nicolás Castaño Arboleda,11 Julien Engel,15,35 Pascal  
19 Petronelli,36 Charles Eugene Zartman,3 Timothy J. Killeen,37 Rodolfo Vasquez,18  
20 Bonifacio Mostacedo,38 Rafael L. Assis,39 Jochen Schöngart,16 Hernán  
21 Castellanos,40 Marcelo Brilhante de Medeiros,41 Marcelo Fragomeni Simon,41 Ana  
22 Andrade,42 José Luís Camargo,42 Layon O. Demarchi,16 William F. Laurance,29  
23 Susan G.W. Laurance,29 Emanuelle de Sousa Farias,43,44 Maria Aparecida Lopes,45  
24 José Leonardo Lima Magalhães,46,47 Henrique Eduardo Mendonça Nascimento,3  
25 Helder Lima de Queiroz,48 Gerardo A. Aymard C.,49 Roel Brienem,7 Juan David  
26 Cardenas Revilla,3 Flávia R.C. Costa,3 Adriano Quaresma,16 Ima Célia Guimarães  
27 Vieira,5 Bruno Barçante Ladvocat Cintra,50 Pablo R. Stevenson,51 Yuri Oliveira  
28 Feitosa,52 Joost F. Duivenvoorden,53 Hugo F. Mogollón,54 Leandro Valle Ferreira,5  
29 James A. Comiskey,55,56 Freddie Draper,57,35 José Julio de Toledo,58 Gabriel  
30 Damasco,59 Nállarett Dávila,60 Roosevelt García-Villacorta,61,62 Aline Lopes,16,63  
31 Alberto Vicentini,12 Janaína Costa Noronha,64 Flávia Rodrigues Barbosa,64  
32 Rainiellen de Sá Carpanedo,64 Thaise Emilio,65,12 Carolina Levis,66,67 Domingos  
33 de Jesus Rodrigues,64 Juliana Schietti,3 Priscila Souza,3 Alfonso Alonso,56  
34 Francisco Dallmeier,56 Vitor H.F. Gomes,68,69 Jon Lloyd,70 David Neill,71 Daniel  
35 Praia Portela de Aguiar,16 Alejandro Araujo-Murakami,72 Luzmila Arroyo,72  
36 Fernanda Antunes Carvalho,12,73 Fernanda Coelho de Souza,12,7 Dário Dantas do  
37 Amaral,5 Kenneth J. Feeley,74,75 Rogerio Gribel,3 Marcelo Petratti Pansonato,3,76  
38 Jos Barlow,77 Erika Berenguer,78,77 Joice Ferreira,47 Paul V.A. Fine,59 Marcelino  
39 Carneiro Guedes,79 Eliana M. Jimenez,80 Juan Carlos Licona,31 Maria Cristina  
40 Peñuela Mora,81 Carlos A. Peres,82 Boris Eduardo Villa Zegarra,83 Carlos Cerón,84  
41 Terry W. Henkel,85 Paul Maas,2 Marcos Silveira,86 Juliana Stropp,87 Raquel  
42 Thomas-Caesar,88 Tim R. Baker,7 Doug Daly,89 Kyle G. Dexter,90,91 John Ethan  
43 Householder,13 Isau Huamantupa-Chuquimaco,23 Toby Pennington,33,91 Marcos  
44 Ríos Paredes,92 Alfredo Fuentes,93,94 José Luis Marcelo Pena,95 Miles R.  
45 Silman,96 J. Sebastián Tello,94 Jerome Chave,97 Fernando Cornejo Valverde,98  
46 Anthony Di Fiore,99 Renato Richard Hilário,58 Juan Fernando Phillips,100 Gonzalo  
47 Rivas-Torres,101,102 Tinde R. van Andel,2,103 Patricio von Hildebrand,104  
48 Edelcilio Marques Barbosa,3 Luiz Carlos de Matos Bonates,3 Hilda Paulette Dávila

49 Doza,92 Émile Fonty,105,15 Ricardo Zárate Gómez,106 Therany Gonzales,107  
50 George Pepe Gallardo Gonzales,92 Jean-Louis Guillaumet†,108 Bruce Hoffman,109  
51 André Braga Junqueira,110 Yadvinder Malhi,111 Ires Paula de Andrade Miranda,3  
52 Linder Felipe Mozombite Pinto,92 Adriana Prieto,112 Agustín Rudas,112 Ademir R.  
53 Ruschel,47 Natalino Silva,113 César I.A. Vela,114 Vincent Antoine Vos,115 Eglée L.  
54 Zent,116 Stanford Zent,116 Bianca Weiss Albuquerque,16 Angela Cano,51,117  
55 Diego F. Correa,51,118 Janaina Barbosa Pedrosa Costa,79 Bernardo Monteiro  
56 Flores,119 Milena Holmgren,120 Marcelo Trindade Nascimento,121 Alexandre A.  
57 Oliveira,76 Hirma Ramirez-Angulo,122 Maira Rocha,16 Veridiana Vizoni  
58 Scudeller,123 Rodrigo Sierra,124 Milton Tirado,124 Maria Natalia Umaña,125  
59 Geertje van der Heijden,126 Emilio Vilanova Torre,122,127 Corine Vriesendorp,17  
60 Ophelia Wang,128 Kenneth R. Young,129 Manuel Augusto Ahuite Reategui,130  
61 Cláudia Baider,131,76 Henrik Balslev,132 Sasha Cárdenas,51 Luisa Fernanda  
62 Casas,51 William Farfan-Rios,23,133,94 Cid Ferreira,3 Reynaldo Linares-  
63 Palomino,56 Casimiro Mendoza,134,135 Italo Mesones,59 Armando Torres-  
64 Lezama,122 Ligia Estela Urrego Giraldo,34 Daniel Villaruel,72 Roderick Zagt,136  
65 Miguel N. Alexiades,137 Karina Garcia-Cabrera,96 Lionel Hernandez,40 William  
66 Milliken,65 Walter Palacios Cuenca,138 Susamar Pansini,27 Daniela Pauletto,139  
67 Freddy Ramirez Arevalo,140 Adeilza Felipe Sampaio,27 Elvis H. Valderrama  
68 Sandoval,141,140 Luis Valenzuela Gamarra,18 Gerhard Boenisch,142 Jens  
69 Kattge,143 Nathan Kraft,144 Aurora Levesley,7 Karina Melgaço,7 Georgia  
70 Pickavance,7 Lourens Poorter,67 Hans ter Steege,2,145

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72 \* Corresponding author: e.t.pos@uu.nl

73 † Deceased 01-2018

74

## 75 Affiliations

76 1Ecology & Biodiversity Group, Utrecht University, Padualaan 8, Utrecht, 3584 CH,  
77 The Netherlands

78 2Naturalis Biodiversity Center, PO Box 9517, Leiden, 2300 RA, The Netherlands

79 3Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia -  
80 INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil

81 4Programa Professor Visitante Nacional Sênior na Amazônia - CAPES, Universidade  
82 Federal Rural da Amazônia, Av. Perimetral, s/n, Belém, PA, Brazil

83 5Coordenação de Botânica, Museu Paraense Emílio Goeldi, Av. Magalhães Barata  
84 376, C.P. 399, Belém, PA, 66040-170, Brazil

85 6EMBRAPA – Centro de Pesquisa Agroflorestal de Roraima, BR 174, km 8 –  
86 Distrito Industrial, Boa Vista, RR, 69301-970, Brazil

87 7School of Geography, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK

88 8Grupo de Investigación en Biodiversidad, Medio Ambiente y Salud-BIOMAS,  
89 Universidad de las Américas, Campus Queri, Quito, Ecuador

90 9Keller Science Action Center, The Field Museum, 1400 S. Lake Shore Drive,  
91 Chicago, IL, 60605-2496, USA

92 10Departamento de Botânica, Instituto de Pesquisas Científicas e Tecnológicas do  
93 Amapá - IEPA, Rodovia JK, Km 10, Campus do IEPA da Fazendinha, Amapá,  
94 68901-025, Brazil

95 11Herbario Amazónico Colombiano, Instituto SINCHI, Calle 20 No 5-44, Bogotá,  
96 DC, Colombia

- 97 12Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da  
98 Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375,  
99 Brazil
- 100 13Dep. of Wetland Ecology, Institute of Geography and Geoecology, Karlsruhe  
101 Institute of Technology - KIT, Josefstr.1, Rastatt, D-76437, Germany
- 102 14Biogeochemistry, Max Planck Institute for Chemistry, Hahn-Meitner Weg 1,  
103 Mainz, 55128, Germany
- 104 15AMAP, IRD, Cirad, CNRS, INRA, Université de Montpellier, Montpellier, F-  
105 34398, France
- 106 16Coordenação de Dinâmica Ambiental, Instituto Nacional de Pesquisas da  
107 Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375,  
108 Brazil
- 109 17Science and Education, The Field Museum, 1400 S. Lake Shore Drive, Chicago,  
110 IL, 60605-2496, USA
- 111 18Jardín Botánico de Missouri, Oxapampa, Pasco, Peru
- 112 19Applied Ecology Research Group, School of Life Sciences, Anglia Ruskin  
113 University, East Road, Cambridge, CB1 1PT, UK
- 114 20ICNHS, Universidade Federal de Mato Grosso, Av. Alexandre Ferronato, 1200,  
115 Sinop, MT, 78557-267, Brazil
- 116 21Departamento de Ecologia, Universidade Estadual Paulista - UNESP – Instituto de  
117 Biociências – IB, Av. 24 A, 1515, Bela Vista, Rio Claro, SP, 13506-900, Brazil
- 118 22Divisao de Sensoriamento Remoto – DSR, Instituto Nacional de Pesquisas  
119 Espaciais – INPE, Av. dos Astronautas, 1758, Jardim da Granja, São José dos  
120 Campos, SP, 12227-010, Brazil
- 121 23Herbario Vargas, Universidad Nacional de San Antonio Abad del Cusco, Avenida  
122 de la Cultura, Nro 733, Cusco, Cuzco, Peru
- 123 24Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA,  
124 UK
- 125 25Centro de Biociências, Departamento de Ecologia, Universidade Federal do Rio  
126 Grande do Norte, Av. Senador Salgado Filho, 3000 , Natal, RN, 59072-970, Brazil
- 127 26Departamento de Biologia, Universidade Federal de Rondônia, Rodovia BR 364 s/n  
128 Km 9,5 - Sentido Acre, Unir, Porto Velho, RO, 76.824-027, Brazil
- 129 27Programa de Pós- Graduação em Biodiversidade e Biotecnologia PPG- Bionorte,  
130 Universidade Federal de Rondônia, Campus Porto Velho Km 9,5 bairro Rural, Porto  
131 Velho, RO, 76.824-027, Brazil
- 132 28Department of Biology and Florida Museum of Natural History, University of  
133 Florida, Gainesville, FL, 32611, USA
- 134 29Centre for Tropical Environmental and Sustainability Science and College of  
135 Science and Engineering, James Cook University, Cairns, Queensland, 4870,  
136 Australia
- 137 30Instituto de Investigaciones de la Amazonía Peruana (IIAP), Av. A. Quiñones km  
138 2,5, Iquitos, Loreto, 784, Peru
- 139 31Instituto Boliviano de Investigacion Forestal, Av. 6 de agosto #28, Km. 14, Doble  
140 via La Guardia, Casilla 6204, Santa Cruz, Santa Cruz, Bolivia
- 141 32Programa de Pós-Graduação em Ecologia e Conservação, Universidade do Estado  
142 de Mato Grosso, Nova Xavantina, MT, Brazil
- 143 33Geography, College of Life and Environmental Sciences, University of Exeter,  
144 Rennes Drive, Exeter, EX4 4RJ, UK
- 145 34Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Calle 64  
146 x Cra 65, Medellín, Antioquia, 1027, Colombia

- 147 35International Center for Tropical Botany (ICTB) Department of Biological  
148 Sciences, Florida International University, 11200 SW 8th Street, OE 243, Miami, FL,  
149 33199, USA  
150 36Cirad UMR Ecofog, AgrosParisTech,CNRS,INRA,Univ Guyane, Campus  
151 agronomique, Kourou Cedex, 97379, France  
152 37Agteca-Amazonica, Santa Cruz, Bolivia  
153 38Facultad de Ciencias Agrícolas, Universidad Autónoma Gabriel René Moreno,  
154 Santa Cruz, Santa Cruz, Bolivia  
155 39Natural History Museum, University of Oslo, Postboks 1172, Oslo, 0318, Norway  
156 40Centro de Investigaciones Ecológicas de Guayana, Universidad Nacional  
157 Experimental de Guayana, Calle Chile, urbaniz Chilemex, Puerto Ordaz, Bolivar,  
158 Venezuela  
159 41Prédio da Botânica e Ecologia, Embrapa Recursos Genéticos e Biotecnologia,  
160 Parque Estação Biológica, Av. W5 Norte, Brasilia, DF, 70770-917, Brazil  
161 42Projeto Dinâmica Biológica de Fragmentos Florestais, Instituto Nacional de  
162 Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM,  
163 69067-375, Brazil  
164 43Laboratório de Ecologia de Doenças Transmissíveis da Amazônia (EDTA),  
165 Instituto Leônidas e Maria Deane, Fiocruz, Rua Terezina, 476, Adrianópolis, Manaus,  
166 AM, 69060-001, Brazil  
167 44Programa de Pós-graduação em Biodiversidade e Saúde, Instituto Oswaldo Cruz -  
168 IOC/FIOCRUZ, Pav. Arthur Neiva – Térreo, Av. Brasil, 4365 – Manguinhos, Rio de  
169 Janeiro, RJ, 21040-360, Brazil  
170 45Instituto de Ciências Biológicas, Universidade Federal do Pará, Av. Augusto  
171 Corrêa 01, Belém, PA, 66075-110, Brazil  
172 46Programa de Pós-Graduação em Ecologia, Universidade Federal do Pará, Av.  
173 Augusto Corrêa 01, Belém, PA, 66075-110, Brazil  
174 47Embrapa Amazônia Oriental, Trav. Dr. Enéas Pinheiro s/nº, Belém, PA, 66095-  
175 100, Brazil  
176 48Diretoria Técnico-Científica, Instituto de Desenvolvimento Sustentável Mamirauá,  
177 Estrada do Bexiga, 2584, Tefé, AM, 69470-000, Brazil  
178 49Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT),  
179 UNELLEZ-Guanare, Guanare, Portuguesa, 3350, Venezuela  
180 50Instituto de Biociências - Dept. Botanica, Universidade de Sao Paulo - USP, Rua  
181 do Matão 277, Cidade Universitária, São Paulo, SP, 05508-090, Brazil  
182 51Laboratorio de Ecología de Bosques Tropicales y Primatología, Universidad de los  
183 Andes, Carrera 1 # 18a- 10, Bogotá, DC, 111711, Colombia  
184 52Programa de Pós-Graduação em Biologia (Botânica), Instituto Nacional de  
185 Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM,  
186 69067-375, Brazil  
187 53Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam,  
188 Sciencepark 904, Amsterdam, 1098 XH, The Netherlands  
189 54Endangered Species Coalition, 8530 Geren Rd., Silver Spring, MD, 20901, USA  
190 55Inventory and Monitoring Program, National Park Service, 120 Chatham Lane,  
191 Fredericksburg, VA, 22405, USA  
192 56Center for Conservation and Sustainability, Smithsonian Conservation Biology  
193 Institute, 1100 Jefferson Dr. SW, Suite 3123, Washington, DC, 20560-0705, USA  
194 57Department of Global Ecology, Carnegie Institution for Science, 260 Panama St.,  
195 Stanford, CA, 94305, USA

- 196 58Universidade Federal do Amapá, Ciências Ambientais, Rod. Juscelino Kubitschek  
197 km2, Macapá, AP, 68902-280, Brazil
- 198 59Department of Integrative Biology, University of California, Berkeley, CA, 94720-  
199 3140, USA
- 200 60Biologia Vegetal, Universidade Estadual de Campinas, Caixa Postal 6109,  
201 Campinas, SP, 13.083-970, Brazil
- 202 61Department of Ecology and Evolutionary Biology, Cornell University, Corson Hall,  
203 215 Tower Road, Ithaca, NY, 14850, USA
- 204 62Peruvian Center for Biodiversity and Conservation (PCBC), Iquitos, Peru
- 205 63Department of Ecology, University of Brasilia, Brasilia, DF, 70904-970, Brazil
- 206 64ICNHS, Federal University of Mato Grosso, Av. Alexandre Ferronato 1200, Setor  
207 Industrial, Sinop, MT, 78.557-267, Brazil
- 208 65Natural Capital and Plant Health, Royal Botanic Gardens, Kew, Richmond, Surrey,  
209 TW9 3AB, UK
- 210 66Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da  
211 Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375,  
212 Brazil
- 213 67Forest Ecology and Forest Management Group, Wageningen University &  
214 Research, Droevendaalsesteeg 3, Wageningen, P.O. Box 47, 6700 AA, The  
215 Netherlands
- 216 68Escola de Negócios Tecnologia e Inovação, Centro Universitário do Pará, Belém,  
217 PA, Brazil
- 218 69Universidade Federal do Pará, Rua Augusto Corrêa 01, Belém, PA, 66075-110,  
219 Brazil
- 220 70Faculty of Natural Sciences, Department of Life Sciences, Imperial College  
221 London, Silwood Park, South Kensington Campus, London, SW7 2AZ, UK
- 222 71Ecosistemas, Biodiversidad y Conservación de Especies, Universidad Estatal  
223 Amazónica, Km. 2 1/2 vía a Tena (Paso Lateral), Puyo, Pastaza, Ecuador
- 224 72Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel  
225 Rene Moreno, Avenida Irala 565 Casilla Postal 2489, Santa Cruz, Santa Cruz,  
226 Bolivia
- 227 73Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas,  
228 Departamento de Genética, Ecologia e Evolução, Av. Antônio Carlos, 6627  
229 Pampulha, Belo Horizonte, MG, 31270-901, Brazil
- 230 74Department of Biology, University of Miami, Coral Gables, FL, 33146, USA
- 231 75Fairchild Tropical Botanic Garden, Coral Gables, FL, 33156, USA
- 232 76Instituto de Biociências - Dept. Ecologia, Universidade de Sao Paulo - USP, Rua do  
233 Matão, Trav. 14, no. 321, Cidade Universitária, São Paulo, SP, 05508-090, Brazil
- 234 77Lancaster Environment Centre, Lancaster University, Lancaster, Lancashire, LA1  
235 4YQ, UK
- 236 78Environmental Change Institute, University of Oxford, Oxford, Oxfordshire, OX1  
237 3QY, UK
- 238 79Empresa Brasileira de Pesquisa Agropecuária, Embrapa Amapá, Rod. Juscelino  
239 Kubitschek km 5, Macapá, Amapá, 68903-419, Brazil
- 240 80Grupo de Ecología y Conservación de Fauna y Flora Silvestre, Instituto Amazónico  
241 de Investigaciones Imani, Universidad Nacional de Colombia sede Amazonia, Leticia,  
242 Amazonas, Colombia
- 243 81Universidad Regional Amazónica IKIAM, Km 7 via Muyuna, Tena, Napo, Ecuador
- 244 82School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ,  
245 UK

- 246 83Dirección de Evaluación Forestal y de Fauna Silvestre, Av. Javier Praod Oeste 693,  
247 Magdalena del Mar, Peru  
248 84Escuela de Biología Herbario Alfredo Paredes, Universidad Central, Ap. Postal  
249 17.01.2177, Quito, Pichincha, Ecuador  
250 85Department of Biological Sciences, Humboldt State University, 1 Harpst Street,  
251 Arcata, CA, 95521, USA  
252 86Museu Universitário / Centro de Ciências Biológicas e da Natureza / Laboratório de  
253 Botânica e Ecologia Vegetal, Universidade Federal do Acre, Rio Branco, AC, 69915-  
254 559, Brazil  
255 87Institute of Biological and Health Sciences, Federal University of Alagoas, Av.  
256 Lourival Melo Mota, s/n, Tabuleiro do Martins, Maceio, AL, 57072-970, Brazil  
257 88Iwokrama International Centre for Rain Forest Conservation and Development,  
258 Georgetown, Guyana  
259 89New York Botanical Garden, 2900 Southern Blvd, Bronx, New York, NY, 10458-  
260 5126, USA  
261 90School of Geosciences, University of Edinburgh, 201 Crew Building, King's  
262 Buildings, Edinburgh, EH9 3JN, UK  
263 91Tropical Diversity Section, Royal Botanic Garden Edinburgh, 20a Inverleith Row,  
264 Edinburgh, Scotland, EH3 5LR, UK  
265 92Servicios de Biodiversidad EIRL, Jr. Independencia 405, Iquitos, Loreto, 784, Peru  
266 93Herbario Nacional de Bolivia, Universitario UMSA, Casilla 10077 Correo Central,  
267 La Paz, La Paz, Bolivia  
268 94Center for Conservation and Sustainable Development, Missouri Botanical Garden,  
269 P.O. Box 299, St. Louis, MO, 63166-0299, USA  
270 95Universidad Nacional de Jaén, Carretera Jaén San Ignacio Km 23, Jaén, Cajamarca,  
271 06801, Peru  
272 96Biology Department and Center for Energy, Environment and Sustainability, Wake  
273 Forest University, 1834 Wake Forest Rd, Winston Salem, NC, 27106, USA  
274 97Laboratoire Evolution et Diversité Biologique, CNRS and Université Paul Sabatier,  
275 UMR 5174 EDB, Toulouse, 31000, France  
276 98Andes to Amazon Biodiversity Program, Madre de Dios, Madre de Dios, Peru  
277 99Department of Anthropology, University of Texas at Austin, SAC 5.150, 2201  
278 Speedway Stop C3200, Austin, TX, 78712, USA  
279 100Fundación Puerto Rastrojo, Cra 10 No. 24-76 Oficina 1201, Bogotá, DC,  
280 Colombia  
281 101Colegio de Ciencias Biológicas y Ambientales-COCIBA & Galapagos Institute  
282 for the Arts and Sciences-GAIAS, Universidad San Francisco de Quito-USFQ, Quito,  
283 Pichincha, Ecuador  
284 102Department of Wildlife Ecology and Conservation, University of Florida, 110  
285 Newins-Ziegler Hall, Gainesville, FL, 32611, USA  
286 103Biosystematics group, Wageningen University, Droevendaalsesteeg 1,  
287 Wageningen, 6708 PB, The Netherlands  
288 104Fundación Estación de Biología, Cra 10 No. 24-76 Oficina 1201, Bogotá, DC,  
289 Colombia  
290 105Direction régionale de la Guyane, ONF, Cayenne, F-97300, French Guiana  
291 106PROTERRA, Instituto de Investigaciones de la Amazonía Peruana (IIAP), Av. A.  
292 Quiñones km 2,5, Iquitos, Loreto, 784, Peru  
293 107ACEER Foundation, Jirón Cusco N° 370, Puerto Maldonado, Madre de Dios,  
294 Peru

- 295 108Département EV, Muséum national d'histoire naturelle de Paris, 16 rue Buffon,  
296 Paris, 75005, France
- 297 109Amazon Conservation Team, Doekhieweg Oost #24, Paramaribo, Suriname
- 298 110Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona,  
299 08193 Bellaterra, Barcelona, Spain
- 300 111Environmental Change Institute, Oxford University Centre for the Environment,  
301 Dyson Perrins Building, South Parks Road, Oxford, England, OX1 3QY, UK
- 302 112Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado  
303 7945, Bogotá, DC, Colombia
- 304 113Instituto de Ciência Agrárias, Universidade Federal Rural da Amazônia, Av.  
305 Presidente Tancredo Neves 2501, Belém, PA, 66.077-830, Brazil
- 306 114Escuela Profesional de Ingeniería Forestal, Universidad Nacional de San Antonio  
307 Abad del Cusco, Jirón San Martín 451, Puerto Maldonado, Madre de Dios, Peru
- 308 115Universidad Autónoma del Beni José Ballivián, Campus Universitario Final, Av.  
309 Ejército, Riberalta, Beni, Bolivia
- 310 116Laboratory of Human Ecology, Instituto Venezolano de Investigaciones  
311 Científicas - IVIC, Ado 20632, Caracas, DC, 1020A, Venezuela
- 312 117Cambridge University Botanic Garden, 1 Brookside., Cambridge, CB2 1JE, UK
- 313 118School of Agriculture and Food Sciences - ARC Centre of Excellence for  
314 Environmental Decisions CEED, The University of Queensland, St. Lucia, QLD  
315 4072, Australia
- 316 119University of Campinas, Plant Biology Department, Rua Monteiro Lobato, 255,  
317 Cidade Universitária Zeferino Vaz, Barão Geraldo, Campinas, São Paulo, CEP  
318 13083-862, Brazil
- 319 120Resource Ecology Group, Wageningen University & Research,  
320 Droevendaalsesteeg 3a, Lumen, building number 100, Wageningen, Gelderland, 6708  
321 PB, The Netherlands
- 322 121Laboratório de Ciências Ambientais, Universidade Estadual do Norte Fluminense,  
323 Av. Alberto Lamego 2000, Campos dos Goyatacazes, RJ, 28013-620, Brazil
- 324 122Instituto de Investigaciones para el Desarrollo Forestal (INDEFOR), Universidad  
325 de los Andes, Conjunto Forestal, 5101, Mérida, Mérida, Venezuela
- 326 123Departamento de Biología, Universidade Federal do Amazonas - UFAM –  
327 Instituto de Ciências Biológicas – ICB1, Av General Rodrigo Octavio 6200, Manaus,  
328 AM, 69080-900, Brazil
- 329 124GeoIS, El Día 369 y El Telégrafo, 3° Piso, Quito, Pichincha, Ecuador
- 330 125Department of Ecology and Evolutionary Biology, University of Michigan, Ann  
331 Arbor, MI, 48109, USA
- 332 126University of Nottingham, University Park, Nottingham, NG7 2RD, UK
- 333 127School of Environmental and Forest Sciences, University of Washington, Seattle,  
334 WA, 98195-2100, USA
- 335 128Environmental Science and Policy, Northern Arizona University, Flagstaff, AZ,  
336 86011, USA
- 337 129Geography and the Environment, University of Texas at Austin, 305 E. 23rd  
338 Street, CLA building, Austin, TX, 78712, USA
- 339 130Medio Ambiente, PLUSPRETOL, Iquitos, Loreto, Peru
- 340 131The Mauritius Herbarium, Agricultural Services, Ministry of Agro-Industry and  
341 Food Security, Reduit, 80835, Mauritius
- 342 132Department of Bioscience, Aarhus University, Building 1540 Ny Munkegade,  
343 Aarhus C, Aarhus, DK-8000, Denmark

- 344 133Living Earth Collaborative, Washington University in Saint Louis, St. Louis, MO,  
345 63130, USA
- 346 134Escuela de Ciencias Forestales (ESFOR), Universidad Mayor de San Simon  
347 (UMSS), Sacta, Cochabamba, Bolivia
- 348 135FOMABO, Manejo Forestal en las Tierras Tropicales de Bolivia, Sacta,  
349 Cochabamba, Bolivia
- 350 136Tropenbos International, Lawickse Allee 11 PO Box 232, Wageningen, 6700 AE,  
351 The Netherlands
- 352 137School of Anthropology and Conservation, University of Kent, Marlowe Building,  
353 Canterbury, Kent, CT2 7NR, UK
- 354 138Herbario Nacional del Ecuador, Universidad Técnica del Norte, Quito, Pichincha,  
355 Ecuador
- 356 139Instituto de Biodiversidade e Floresta, Universidade Federal do Oeste do Pará,  
357 Rua Vera Paz, Campus Tapajós, Santarém, PA, 68015-110, Brazil
- 358 140Facultad de Biología, Universidad Nacional de la Amazonia Peruana, Pevas 5ta  
359 cdra, Iquitos, Loreto, Peru
- 360 141Department of Biology, University of Missouri, St. Louis, MO, 63121, USA
- 361 142Department of Biogeochemical Integration, Max-Planck-Institute for  
362 Biogeochemistry, P.O. Box 10 01 64, Jena, 07701, Germany
- 363 143Functional Biogeography, Max-Planck-Institute for Biogeochemistry, P.O. Box  
364 10 01 64, Jena, 07701, Germany
- 365 144Department of Ecology and Evolutionary Biology, UCLA, 621 Charles E. Young  
366 Drive South, Box 951606, Los Angeles, CA, 90095, USA
- 367 145Systems Ecology, Vrije Universiteit Amsterdam, De Boelelaan 1087, Amsterdam,  
368 1081 HV, The Netherlands
- 369
- 370
- 371



372 **Abstract** In a time of rapid global change, the question of what determines patterns in  
373 species abundance distribution remains a priority for understanding the complex  
374 dynamics of ecosystems. The constrained maximization of information entropy  
375 provides a framework for the understanding of such complex systems dynamics by a  
376 quantitative analysis of important constraints via predictions using least biased  
377 probability distributions. We apply it to over two thousand hectares of Amazonian  
378 tree inventories across seven forest types and thirteen functional traits, representing  
379 major global axes of plant strategies. Results show that constraints formed by regional  
380 relative abundances of genera explain almost ten times more of local relative  
381 abundances than constraints based on either directional or stabilizing selection for  
382 specific functional traits, although the latter does show clear signals of environmental  
383 dependency. These results provide a quantitative insight by inference from large-scale  
384 data using cross-disciplinary methods, furthering our understanding of ecological  
385 dynamics.

386

387 **Key words:** maximum entropy, information theory, biodiversity, Amazon rainforest.

388

## 389 **Introduction**

390 Drivers of species distributions and their predictions have been a long-standing search  
391 in ecology, with approaches varying from deterministic [1–6] to neutral [7–11] and  
392 almost everything in between (e.g. near-neutral, continuum or emergent-  
393 neutral: [12,13]). Most models are based on prior assumptions of processes that drive  
394 community dynamics. The Maximum Entropy Formalism (hereafter called MEF),  
395 however, makes no such a-priori assumptions in generating predictions of  
396 distributions, including those of species abundances [14,15,24,16–23]. It is a useful  
397 construct to infer processes driving community dynamics given the constraints  
398 imposed by prior knowledge (e.g. functional traits or summed regional abundances),  
399 as it does not include any bias introduced by potentially unjustified assumptions (29).  
400 Quantifying the relative importance of these distinct constraints can thus provide  
401 additional answers to understand the complexity of community dynamics (see  
402 Supporting Materials SM: boxes S1-S3). This is especially so because, although many  
403 different tests are available that link variation in taxon abundances to 1) trait variation,  
404 2) taxon turnover between habitats or environments and 3) the distance decay of  
405 similarities between samples, none quantify the importance of these relative to each  
406 other. The MEF as applied here, however, is capable of and designed to do exactly  
407 this by decomposing variation to separate information explained by each of these  
408 aspects in a four-step model (Box S2) (25). Its application to an unprecedented large  
409 tree inventory database on genus level taxonomy consisting of > 2,000 1-ha plots  
410 distributed over Amazonia [25] and a genus trait database of 13 key functional traits  
411 representing global axes of plant strategies [26] allows us to advance the study of  
412 Amazonian tree community dynamics from a new cross-disciplinary perspective.

413

414

## 415 **Results**

416 Principles from information theory [14,15,27] can be used in an ecological setting to  
417 predict the most likely abundance state for each taxon while simultaneously  
418 maximizing entropy based on constraints. Maximization of entropy allows  
419 quantifying the information yield for each constraint and therefor identifies which  
420 constraints reduce entropy the most. Here we specifically use Shipley's mathematical  
421 model to quantify probabilities, similar to earlier studies [28,29].

422

### 423 *Predictive power of the four-step model*

424 Using a uniform prior and both CWM and CWV as constraints accounted for 23% on  
425 average of total deviance between observed and predicted relative abundances  
426 (measured by  $R^2_{KL}$  values, see Box S2 equation 5). Filtered by forest type this was  
427 36% for podzol forests, *várzea* 25%, *igapó* 23%, swamp forests 34%, 24% and 21%  
428 for Guyana Shield and Pebas *terra firme* respectively and 20% for Brazilian Shield  
429 *terra firme* forests (see Table S1 for detailed decomposition). Using observed  
430 metacommunity relative abundances as prior regardless of CWM or CWV values  
431 accounted on average 58% for the combined dataset with all forest types between 50  
432 and 60%, except for the Guyana Shield *terra firme* with 63%. Including both trait  
433 constraints and the metacommunity prior performed slightly better for the combined  
434 dataset (average 62%), with a minimum of 56% for *igapó* forests and a maximum of  
435 66% for the Guyana Shield *terra firme* forests. To compensate for spurious  
436 relationships between regional abundances and local trait constraints, regardless of  
437 selection, explanatory power was regarded relative to model bias yielding the pure  
438 trait and metacommunity effects (Box S3, Fig. 2 and Table S1). This lowered the  
439 proportion of information accounted for and yielded average pure metacommunity

440 effects of 43% for the overall dataset ranging between 30 and 48% for each forest  
441 type separately with pure trait effects explaining only 5% of information for the  
442 combined dataset on average with for each forest type between 3 and 8%. Although  
443 the latter was lowered substantially, the explanatory power did appear to be strongly  
444 dependent on forest type. Supplementary material provides additional results relating  
445 to the predictive power of each model as well as the spatial gradient between the pure  
446 trait and metacommunity effect ratios (Figs. S2-3).

447

#### 448 *Direction and strength of selection of trait-based constraints*

449 Each trait showed significant differences in lambda when compared between forest  
450 types (Fig. S1). Scatterplots of CWM trait values versus lambda show that, in general,  
451 higher lambda values correspond with higher CWM trait values (Figure S7), although  
452 the relationships are complex. Greater trait dissimilarity also correlated positively  
453 with proportion of deviance attributable to pure trait effects (Pearson R of .23; Fig.  
454 S9), supporting a trait-based selection. All traits except leaf nitrogen content also  
455 showed reduction of variance accompanied a strong difference in community  
456 weighted mean values associated with lambdas (either positive or negative), in line  
457 with expectations of trait-based selection (Fig. S10).

458

#### 459 *Effect of regional metacommunity prior*

460 There was a remarkable similar mean 21% decrease of the information explained  
461 purely by the metacommunity prior for each forest type (Fig. 3). It should be noted  
462 there is an obvious risk that when sampling size is increased, this also includes more  
463 environmental heterogeneity as samples are coming from a variety of localities  
464 potentially leading to changing composition. If this were the case, however, the

465 regional prior ( $q_i$  from Fig. S1 and Box S2) would also change, as taxa might be  
466 abundant in some places but rare or absent in others. As the metacommunity effect is  
467 the explained information that remains relative to any trait effects (i.e. information  
468 unique to the neutral prior) and the pure trait effects are the explained information  
469 remaining after correcting for pure metacommunity effects (Box S3) this effect should  
470 then be accompanied by an increase in pure trait effect for each sample. This was not  
471 observed, not even within the different forest types. Instead, the trait effect gradually  
472 went up and then remained constant (Fig. S4).

473

#### 474 **Discussion**

475 The MEF emerges from a well-founded theoretical and empirical body of ecology and  
476 evolutionary biology, regarding natural selection, migration and population  
477 dynamics [16,22,29,42,43]. From an ecological point of view it can be used to  
478 quantify the relative association between directional or stabilizing selection for  
479 functional traits versus the importance of relative regional abundance regardless of  
480 these traits by imposing these as constraints. Our results show that pure trait effects,  
481 on average, explained only 5% of the information when all forest types were taken  
482 together whereas the pure metacommunity effect, however, explained almost ten  
483 times more with an average value of 43%. Greater trait dissimilarity was positively  
484 associated with higher pure trait effects, indicating trait-based selection, although the  
485 assumed influence of dispersal regardless of these traits appeared to confer more  
486 information explaining tree genus composition of the Amazon rainforest. The strength  
487 and direction of selection indicated clear selective pressure for life history strategies  
488 of either growth or protection, depending on forest type (see appendix S-A for a  
489 detailed exploration of ecological interpretation).

490 Despite showing clear patterns in environmental selection and dispersal effects, there  
491 was a large proportion of information left unexplained (44% on average). Potentially,  
492 local demographic stochasticity could weaken any link between functional traits  
493 measured and regional abundances of genera. This would, however, mean that almost  
494 half of the information contained in relative abundances are the result of random  
495 population dynamics and are not structurally governed. Alternatively, this could be  
496 due to functional traits reflective of processes not taken into account in this study,  
497 such as traits reflective of interactions between trophic levels. Another and at least  
498 equally likely hypothesis for (local) unexplained information is that when scaling up,  
499 the ratio of genus richness to total abundance decreases rather rapidly at first but  
500 levels out as at some point relatively non-overlapping habitats are included in the  
501 regional abundance distributions and more genera are included again due to the  
502 different habitats. This would result in a change of the regional abundance distribution  
503 (the prior) to which each local community is compared, resulting in higher local  
504 unexplained information. Further study into these aspects could provide additional  
505 insight, although as of yet the data necessary for these scales is lacking.

506 Although the initial explanatory power of the metacommunity prior differed between  
507 forest types, the decay pattern was very similar. As the effects of either traits or the  
508 metacommunity are measured in the goodness-of-fit predictions on local relative  
509 abundances, this implies that at small spatial scales the surrounding regional  
510 abundances provide better estimators than functional traits, while at larger spatial  
511 scales this shifts to the traits. The ecological translation would be that on small spatial  
512 scales, local communities share similar environmental conditions leaving dispersal  
513 and drift acting in changing community composition, at least for genus level  
514 taxonomy. As the potential regional pool is increased, more and more environmental

515 heterogeneity and non-overlapping regions are likely to be introduced. The more  
516 gradual decline of *terra firme* forests can then arguably be attributed to these forests  
517 having the largest relative surface area of Amazonia (even for the separate  
518 subregions), potentially giving these forests an almost continuous metacommunity  
519 without gaps, resulting in a more gradual transition from metacommunity to trait  
520 relative importance. The fact the metacommunity effects do not change anymore after  
521 certain distances would indicate the effect of dispersal potentially occurs over very  
522 large distances. It should be noted that as these calculations are done at community  
523 and genus level, they do not measure single dispersal events but rather the effect of  
524 dispersal on community composition much deeper in time. In other words, this effect  
525 suggests more than a dispersal event every now and then. Instead, it argues for  
526 prolonged mixing of forests on large geographical and temporal scales, supported by  
527 recent findings demonstrating a lack of geographical phylogenetic structure of  
528 lineages for Amazonian tree genera [44].

529 Using an unprecedented scale of data and applying the Maximum Entropy Formalism  
530 from information theory we show that constraints formed by regional relative  
531 abundances of genera explain almost ten times more of local relative abundances than  
532 constraints based on either directional or stabilizing selection for specific functional  
533 traits, although the latter does show clear signals of environmental dependency. There  
534 is, however, still much to be explored due to the large unexplained effects and  
535 analyses on finer taxonomic (i.e. species level) and environmental (e.g. microhabitat)  
536 scales could resolve these issues. The relatively large effects of the regional pool of  
537 genera over great distances does suggest an important role for long term dispersal and  
538 mixing of Amazonian trees, especially for the Amazonian interior.

539

540 **Methods**

541 *Empirical data*

542 The ATDN (ter Steege et al.) consists of over 2000 tree inventory plots distributed  
543 over the Amazon basin and the Guiana Shield, collectively referred to as Amazonia.  
544 Only those plots with trees  $\geq 10$  cm diameter at breast height were used, leaving 2011  
545 plots with a mean of 558 individuals per plot identified to at least genus level. Most  
546 plots used are 1 ha in size (1414) with 492 being smaller (minimum size of .1 ha) and  
547 105 larger (maximum size of 80 ha). Genera have been standardized to the W3  
548 Tropicos database (“Tropicos Missouri Botanical Garden”) using the Taxonomic  
549 Name Resolution Service (TNRS [32]). After filtering based on above criteria and  
550 solving nomenclature issues, 1,121,935 individuals belonging to over 828 genera  
551 remained. Plots were distributed over seven abiotically different forest types: Podzol  
552 forests (PZ), *Igapó* (IG, black water flood forests), *Várzea* (VA white water flood  
553 forests), Swamp (SW) and *Terra firme* forests (TF) with subregions BS (Brazilian  
554 Shield), GS (Guyana Shield) and PB (Pebas).

555

556 *Functional traits and trait imputation*

557 Constraints were formed by community weighted means (CWM) and variance of  
558 functional traits (CWV), related to key ecological life history aspects on which natural  
559 selection potentially operates (Table 1). According to principles of natural selection,  
560 CWM values will be biased towards favourable trait values for that particular  
561 environment in the case of directional selection, as taxa with these traits will be more  
562 abundant due to environmental selection while stabilizing selection would decrease  
563 CWV values [33]. For many traits it has been shown earlier that the interspecific  
564 variability was larger than the intraspecific variability, allowing the use of data from



565 different sources to at least calculate a mean species trait value [34]. Genus trait  
566 values were computed as genus-level means of species values if known within the  
567 genus and considered constant for each genus. Genus level of taxonomy was used as  
568 the available trait database had the most information on this taxonomic level.  
569 Unknown values for traits were estimated by Multiple Imputation with Chained  
570 Equations (MICE) by delta adjustment, subtracting a fixed amount (delta), with  
571 sensitivity of this adjustment to the imputations of the observed versus imputed data  
572 analysed using density plots (Fig. S8) and a linear regression model [35]. Procedure  
573 was done using the *mice* package available on the R repository [36] under predictive  
574 mean matching (*pmm* setting, 50 iterations). Results showed imputations were stable  
575 and showed near identical patterns with each imputation scenario (see Figs S5-6 and  
576 Table S2). After imputation, all trait values were transformed to Community  
577 Weighted Means (CWM) of each trait ( $J$ ) for each plot ( $K$ ) ( $\bar{T}_{JK}$ ) as  $\bar{T}_{JK} =$   
578  $\sum_{i=1}^S t_{ij} r a_{ik}$  with  $ra$  the relative abundance of the  $i^{th}$  genus in the  $k^{th}$  plot, following  
579 earlier uses [37].

580

581 *MEF procedure predictions and ecological inference*

582 Figure 1 provides a schematic procedure overview, box S1 provides an overview of  
583 important terms and Boxes S2-3 mathematical details. Initially, a maximally  
584 uninformative prior is specified, where  $q_i$  (Box S1 equation 1) equals  $1/S$  and trait  
585 constraints are randomly permuted multiple times among genera to test whether  
586 inclusion of specified constraints significantly changes derived probability  
587 distributions (see also Roxburgh & Mokany, 2010). Subsequently, the same prior is  
588 used but now observed trait CWM or CWV belonging to specific genera are used as  
589 constraints. Third, observed regional abundances are used as prior with permuted  
590 trait constraints and finally both observed regional abundances and observed trait  
591 CWM/CWV are used as prior and constraints. *Maxent2* [28,29], an updated version  
592 of the *maxent* function currently in the FD library of R [39] provided the  
593 computational platform. Proportions of uncertainty explained by each model are given  
594 by the Kullback-Leibler divergence  $R^2_{KL}$ , a generalization of the classic  $R^2$  goodness  
595 of fit [29]. Pure trait, pure metacommunity, joint metacommunity-trait and  
596 unexplained effects are calculated as proportions of total biologically relevant  
597 information (Box S1 and Box S2). Data was rarefied to smallest sample size (swamp  
598 forests; 28) and calculations bootstrapped 25 times. Results indicated no significant  
599 change compared to using all data, hence the total dataset was used for all analyses.

600

601 *Strength and direction of selection*

602 Predictions of genus relative abundances are computed as a function of traits reflected  
603 in the CWM or CWV values and a series of constants ( $\lambda_{jk}$ : the Lagrange Multipliers).  
604 Each multiplier quantifies the association between a unit of change for a particular  
605 trait  $j$  and a proportional change in predicted relative abundance  $p_{ik}$  (the  $i^{\text{th}}$  genus in

606 the  $k^{\text{th}}$  community) considering all other traits are constant, formally described as:

607 
$$\frac{\partial p_{ik}}{\partial t_{ij}} = \lambda_{jk} p_{ik} (1 - p_{ik})$$
 (see appendix 1 from Sonnier, Navas, Fayolle, &

608 Shipley, 2012). Positive values indicate larger trait values associated with higher

609 abundances (positive selection), negative values indicate the opposite (negative

610 selection) with changes proportional to lambda. Values approximating zero indicate

611 no association between specific traits and relative abundances of species.

612 Decomposing  $\lambda_{jk}$  and comparing by means of a One-Way Analysis of Variance for

613 each trait separately between forest types allows studying both the strength and

614 direction of selection in different habitats. Note that this is done for the same

615 constraint between forest types, as lambda values for each constraint do not scale

616 linearly between different constraints.

617

618 *Estimation of metacommunity size*

619 Iteratively increasing the regional species pool taken into account as prior in

620 concentric circles of a fixed radius of 50 km allows estimating the spatial effect of

621 metacommunity size. The relationship between pure metacommunity effect and radius

622 of metacommunity size was fitted using a smoothing loess regression (function *loess*

623 and *predict*; R-package *stats* [41] with span set at 0.1). Fits subsequently were used

624 to predict values of metacommunity effect based on geographical distance to visualize

625 general patterns for each forest type. Exponential decay of pure metacommunity

626 effect was described using a self-start asymptotic regression function (*SSasymp*) of

627 the form  $y(t) \sim y_f + (y_0 - y_f)e^{-\exp(\log(a))t}$  (*nls* from *stats*, R Core Team, 2016).

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916

917 **Author Contributions:**

918 E.T. Pos and H. ter Steege designed the experiment. E.T.Pos wrote R-scripts,  
919 analysed the results and took the lead in writing the manuscript, H. ter Steege  
920 supervised the writing and provided regular feedback both for the manuscript and the  
921 interpretation of the results. All other authors provided feedback on the manuscript  
922 and provided their data from the Amazon Tree Diversity Network or trait data.  
923 Authors E.T. Pos to L.V. Gamarra provided tree inventory data, authors G. Boenisch,  
924 J. Kattge, N. Kraft, A. Levesley, K. Melgaço, G. Pickavance, L. Poorter provided data  
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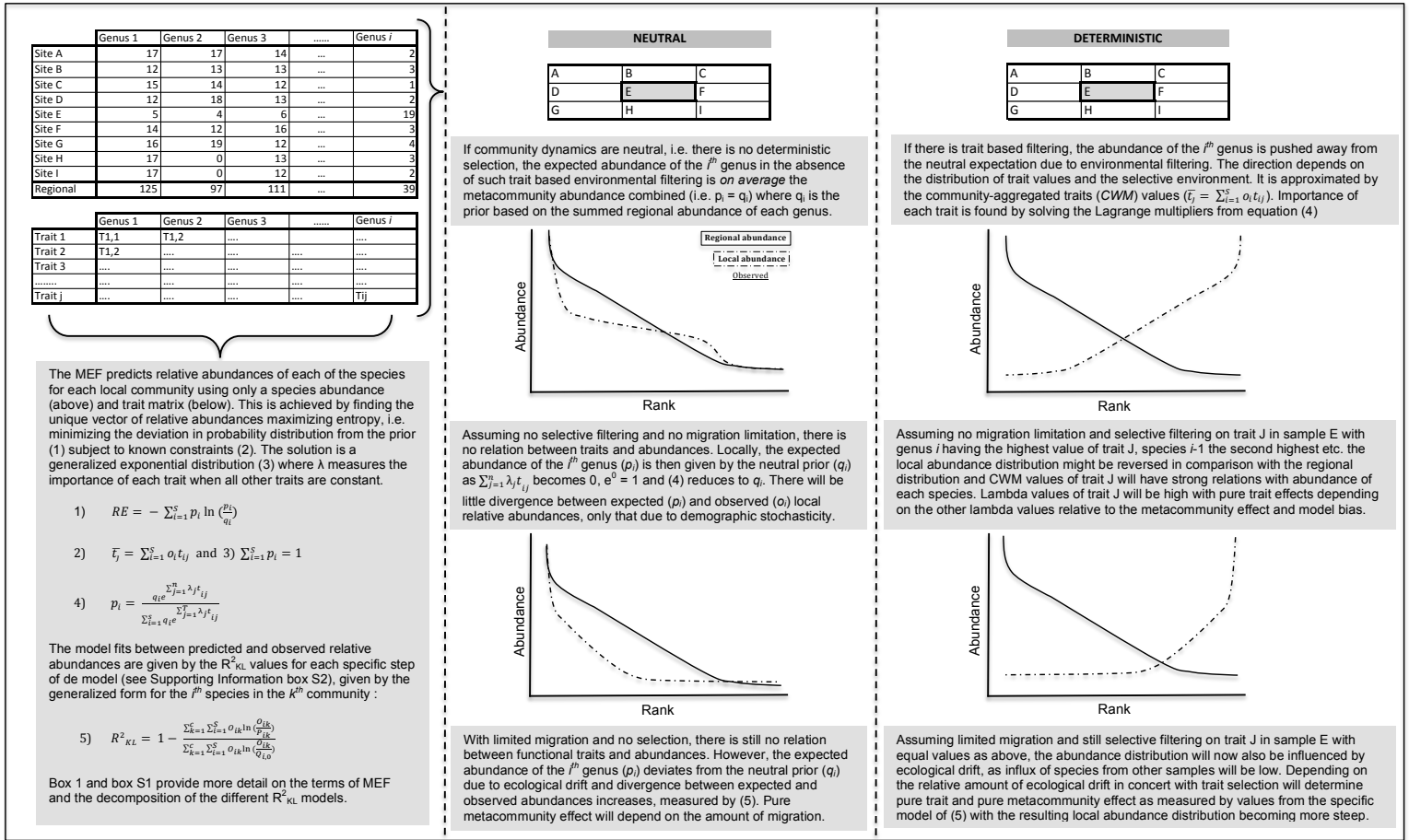
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TABLE 1

Functional trait	Units	Mean	SD	Est %	Associated challenge
Wood density ( <i>WD</i> )	g/cm <sup>3</sup>	0.63	0.17	30	Longevity [45]
Seed Mass Class ( <i>SMC</i> )	categorical (1-8)	4.3	1.4	31	Dispersal, Fecundity, Establishment [45]
Specific Leaf Area ( <i>SLA</i> )	mm <sup>2</sup> /mg	15	5.9	41	Establishment, Plasticity, Disturbance [45]
Leaf nitrogen content ( <i>N</i> )	mg/g	22.3	7.30	41	Photosynthetic capacity [45]
Leaf phosphorus content ( <i>P</i> )	mg/g	1	0.77	50	Limited available P for metabolism [46]
Leaf carbon content ( <i>C</i> )	mg/g	468	38.1	54	Herbivore resistance (C:N) [47]
Latex	1=no, 2=yes	1.2	0.43	46	Herbivore resistance [48]
Resin	1=no, 2=yes	1.1	0.35	58	Herbivore resistance [48]
Root Nodules ( <i>Nodules</i> )	1=no, 2=yes	1.1	0.28	0	Nitrogen fixation [49]
Ectomycorrhiza ( <i>EctoMyco</i> )	1=no, 2=yes	1.01	0.11	0	Organic N fixation [50], heavy metal pollution [51]
Aluminum accumulation ( <i>AlAcc</i> )	1=no, 2=yes	1.1	0.21	3	Heavy metal pollution [52]
Fleshy Fruits ( <i>Fleshy</i> )	1=no, 2=yes	1.6	0.50	7	Dispersal ( <i>specificity</i> ) [53]
Winged seeds ( <i>Wings</i> )	1=no, 2=yes	1.2	0.42	39	Dispersal ( <i>limitation</i> ) [53]

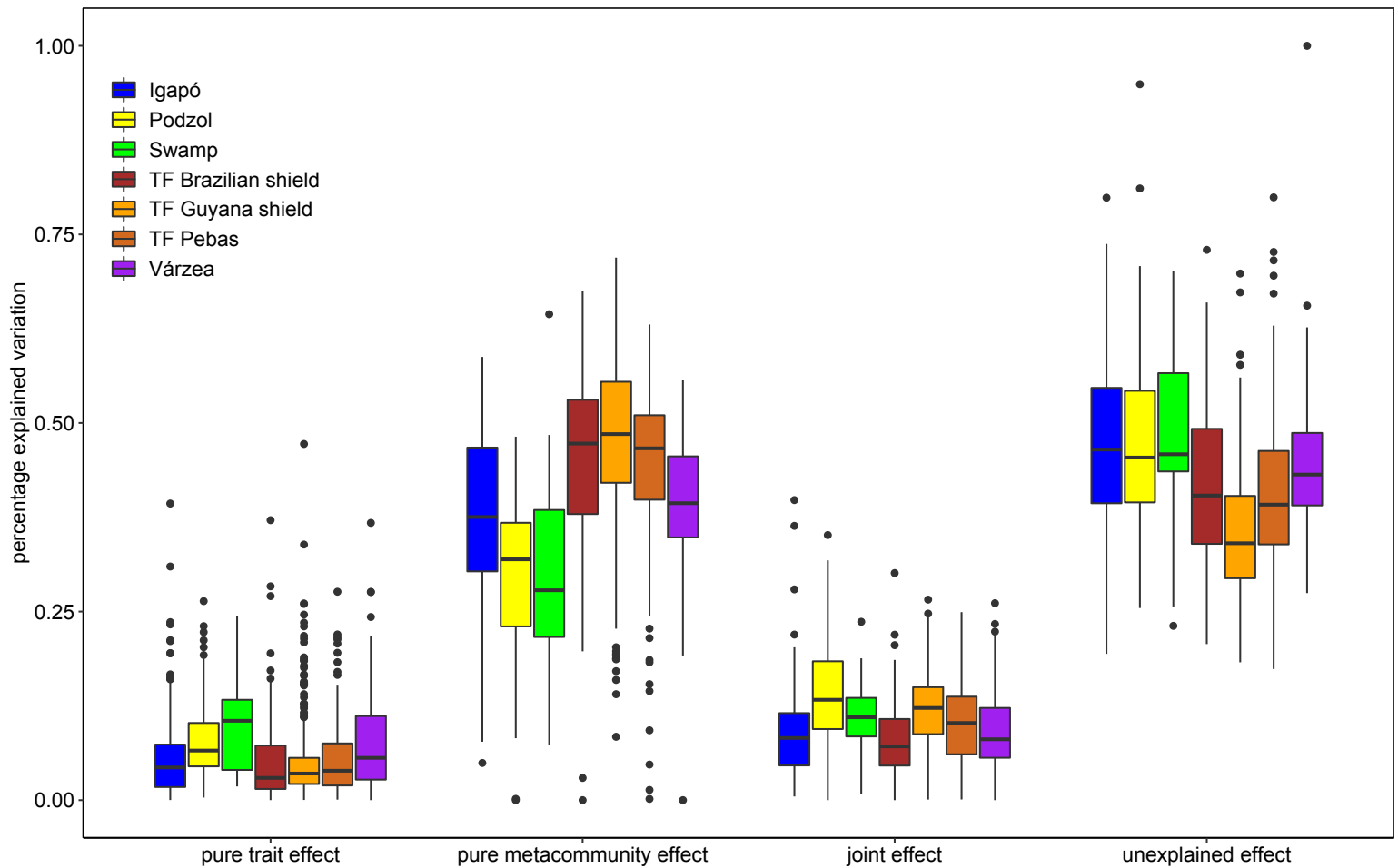
**Table 1. Overview of used functional traits.** Mean and standard deviation (SD) are calculated after predictive mean matching (percentage of estimated values is given by Est (%)). Associated challenge indicates different aspects of life history and selective environment related to specific functional traits, sources are given in the footnote. For specific methodology of measurement protocols and calculation for each trait we refer to the original sources of the data: Chris Baraloto (TRY), Adalardo de Oliveira (unpublished data), L. Poorter (unpublished data), J. Lloyd (TRY), Van der Sande and Mazzei (unpublished data), Van der Sande and Poorter (unpublished data), [54–62]

FIGURE 1



**Fig. 1. Schematic depiction of the MEF procedure.** Left panel shows a genus abundances per site and a functional trait matrix per genus, bottom half outlines calculations. Middle and right panel show different scenarios of neutral and deterministic dynamics under infinite or limited migration. Dashed and solid lines indicate local and regional abundance distributions respectively.

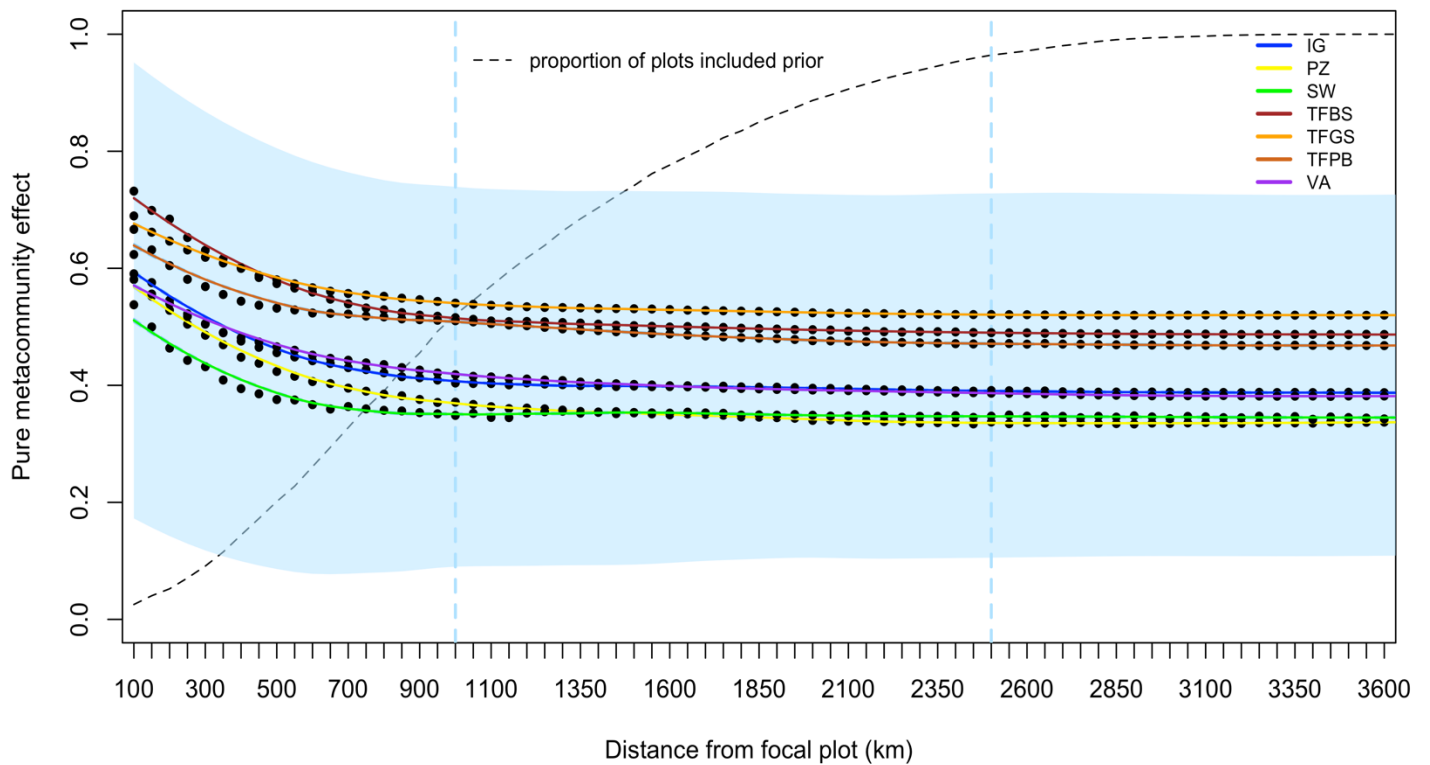
FIGURE 2



**Fig. 2. Visual representation of pure trait, pure metacommunity, hybrid model and the remaining unexplained information for each separate forest type.**

Abbreviations indicate different types: igapó (IG), podzol (PZ), swamp (SW), Brazilian shield terra firme (TFBS), Guiana Shield terra firme (TFGS), Pebas terra firme (TFPB) and várzea (VA). Boxplots show median value of pure effects over all samples, with lower and upper hinges corresponding to 25th and 75th percentiles. Whiskers extends from hinge to largest or smallest value no further than  $1.5 * IQR$  from hinge. Points beyond this range are plotted individually.

FIGURE 3



**Fig. 3. Distance decay of pure metacommunity effect.** X-axis represents radius of metacommunity prior. Dashed line indicates mean number of plots for that distance included as metacommunity prior. Y-axis represents information unique to metacommunity prior taken relative to model bias. Solid lines indicate predictions from loess regression based on all points with different colours indicating forest types with abbreviations as in main text. Blue shading reflects minimum and maximum loess regression predicted values.

## BOX S1

**Entities:**

*The basic unit of the MEF model can exist in different states. If the system under study is a collection of genera existing at a site, then each entity is a single genus.*

**States:**

*Classification of different ways any entity can exist. In the same collection of taxa, states of each entity (i.e. genus) are their specific abundance at that site. Microstates are the exact arrangement in time and space for the states of the entities in the system. Macrostates are the description of entities among the possible states in the system under study without regard to the spatial or temporal arrangement of these entities. I.e. observing a relative abundance distribution, but not the actual dispersal and germination of individuals.*

**Traits, attributes or properties:**

*Each entity possesses measurable properties whose values will probably differ between states. For example, genera differ in average wood density, seed mass, height etcetera.*

**Maximally uninformative prior:**

*All the information concerning states before constraints are introduced. Called maximally uninformative as preferably all empirical information is introduced in the form of constraints as to have the maximal gain of information regarding the different traits.*

**Prior distribution:**

*Prior distribution of expected states for the entities which can be incorporated as a constraint in addition to the traits, being either the observed relative abundance of each entity in the summed sample (i.e. the metacommunity) or a maximally uninformed (uniform) distribution. The former would be a neutral prior (expected local abundance is equal to the abundance in the larger metacommunity).*

**Community-weighted means:**

*The average trait value (i.e. measurable property such as wood density) of entities (such as genera) weighted by the relative abundance of each entity at a specific site*

**Box S1. Different ingredients necessary for analyses using MEF.** Definitions of the most important terms used in the MEF analyses and throughout the main text to provide the necessary framework of understanding.

BOX S2

<p>The Maximum Entropy Formalism works on the basis of a conceptual model called the CATS (<i>Community Assembly by Trait Selection</i>) and makes use of three inputs:</p> <p>i) A <b>trait matrix</b> containing the measured functional traits of each of the <math>S</math> total genera in the total regional pool, these can be of either discrete or continuous form.</p> <p>ii) A <b>vector of <math>n</math> community weighted trait values</b>, estimating the average trait value over all individuals in the local community for each of the traits</p> <p>iii) A <b>prior probability distribution</b> specifying the regional abundance distribution, quantifying potential contributions of the regional pool of recruits to the structure of local communities.</p> <p>Using these three sources of information, the model predicts relative abundances (<math>p_i</math>) in the form of Bayesian probabilities for each genus in each local community without assuming any a priori relations or processes. This is achieved by finding the vector of relative abundances maximizing entropy:</p> $1) RE = - \sum_{i=1}^S p_i \ln \left( \frac{p_i}{q_i} \right)$ <p>with <math>q_i</math> the regional species pool abundance of species <math>i</math> and <math>RE</math> (Relative Entropy) subject to the known constraints for <math>j</math> traits and <math>i</math> species:</p> $2) \bar{t}_j = \sum_{i=1}^S o_i t_{ij} \text{ and } 3) \sum_{i=1}^S p_i = 1$ <p>The solution is a generalized exponential distribution where the <math>\lambda</math> values measure the importance of each trait when all other traits are constant:</p> $4) p_i = \frac{q_i e^{\sum_{j=1}^n \lambda_j t_{ij}}}{\sum_{i=1}^S q_i e^{\sum_{j=1}^n \lambda_j t_{ij}}}$ <p>Note that when all <math>\lambda</math> values are zero, i.e. there is no trait based selection, <math>p_i = q_i</math></p>	<p>The final step is to measure the proportion of total deviance accounted for between observed and predicted relative abundances for each of the four-step solution. These are the <math>R^2_{KL}</math> values, a generalization of the classic <math>R^2</math> index of maximum likelihood estimation using the Kullback-Leibler index [16]:</p> <p>i) <math>\bar{R}^2_{KL}(\mathbf{u})</math>: fit of model bias, the model null hypotheses given a uniform prior (i.e. equal distribution in the regional pool of recruits).</p> <p>ii) <math>R^2_{KL}(\mathbf{u}, \mathbf{t})</math>: fit using again a uniform prior but including traits as constraints.</p> <p>iii) <math>\bar{R}^2_{KL}(\mathbf{m})</math>: fit using the metacommunity prior but excluding traits as constraints</p> <p>iv) <math>R^2_{KL}(\mathbf{m}, \mathbf{t})</math>: fit using the metacommunity prior and including traits as constraints</p> <p>The general form of the <math>R^2_{KL}</math> divergence is calculated by:</p> $5) R^2_{KL} = 1 - \frac{\sum_{k=1}^c \sum_{i=1}^S O_{ik} \ln \left( \frac{O_{ik}}{P_{ik}} \right)}{\sum_{j=k}^c \sum_{i=1}^S O_{ik} \ln \left( \frac{O_{ij}}{Q_{i,0}} \right)}$ <p>With the following parameters:</p> <p><math>O_{ik}</math> as the observed relative abundances of the <math>i^{th}</math> genus in the <math>k^{th}</math> community,</p> <p><math>P_{ik}</math> the accompanying predicted values for the specific model of the four solution step as described in the main text and,</p> <p><math>Q_{i,0}</math> the predicted relative abundances given only the maximum uninformative prior.</p> <p>Further details on the calculation of all separate <math>R^2_{KL}</math> values and accompanying pure trait, pure metacommunity, joint information and biologically unexplained information can be found in the SOM (box S2).</p>
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**Box S2. Mathematical description of the Maximum Entropy Formalism for the four-step solution.** Left panel shows the necessary ingredients and basic formulation of the Maximum Entropy Formalism. Right side panel shows decomposition of the proportion of total deviance accounted for between observed and predicted relative abundances for each of the four-step solution.

The purpose of using MEF is to decompose the deviance between observed and predicted relative abundances using the four-step solution as described in the main text. The values generated are described below. The  $R^2_{KL}$  value is a generalization of the classic  $R^2$  index of maximum likelihood estimation using the Kullback-Leibler index for a non-linear regression including a multinomial error structure [16–18]. In essence, it is a way of measuring the proportion of total deviance accounted for by that specific model from one of the four steps:

$\bar{R}^2_{KL}(\mathbf{u})$ : fit of model bias, the model null hypotheses given a uniform prior and permuted traits

$R^2_{KL}(\mathbf{u}, \mathbf{t})$ : fit using a uniform prior but including observed traits as constraints

$\bar{R}^2_{KL}(\mathbf{m})$ : fit using the metacommunity prior but excluding observed traits as constraints

$R^2_{KL}(\mathbf{m}, \mathbf{t})$ : fit using the metacommunity prior and including observed traits as constraints

1) The increase in the explained deviance due to traits can be calculated either by

$$\Delta R^2_{KL}(\mathbf{t}|\boldsymbol{\varphi}) = R^2_{KL}(\mathbf{u}, \mathbf{t}) - \bar{R}^2_{KL}(\mathbf{u})$$

Increase in explained deviance due to traits beyond that due solely to model bias

$$\text{or } \Delta R^2_{KL}(\mathbf{t}|\mathbf{m}) = R^2_{KL}(\mathbf{m}, \mathbf{t}) - \bar{R}^2_{KL}(\mathbf{m})$$

Increase in explained deviance due to traits beyond contributions made by the meta-community

2) The increase in explained deviance due dispersal mass effects via the metacommunity can be calculated by either:

$$\Delta R^2_{KL}(\mathbf{m}|\boldsymbol{\varphi}) = \bar{R}^2_{KL}(\mathbf{m}) - \bar{R}^2_{KL}(\mathbf{u})$$

Increase in explained deviance (if any) due to the metacommunity beyond that due to model bias

$$\text{or } \Delta R^2_{KL}(\mathbf{m}|\mathbf{t}) = R^2_{KL}(\mathbf{m}, \mathbf{t}) - R^2_{KL}(\mathbf{u}, \mathbf{t})$$

Increase in explained deviance due to the meta-community given traits, relative to the explained deviance due only to the traits: i.e. information unique to neutral prior

3) And finally the joint information and the biologically unexplained information:

$$\Delta R^2_{KL}(\mathbf{m}+\mathbf{t}) = \Delta R^2_{KL}(\mathbf{m}|\boldsymbol{\varphi}) - \Delta R^2_{KL}(\mathbf{m}|\mathbf{t}) = \Delta R^2_{KL}(\mathbf{t}|\boldsymbol{\varphi}) - \Delta R^2_{KL}(\mathbf{t}|\mathbf{m})$$

Joint information gain, or increase in explained deviance due to both the metacommunity prior and the constraints based on the traits

$$1 - \Delta R^2_{KL}(\mathbf{m}, \mathbf{t})$$

Biologically unexplained variation

*From these values the pure trait, pure metacommunity, joint effect and biologically unexplained variation can be calculated by the following calculations:*

$$\text{Pure trait effects: } \Delta R^2_{KL}(\mathbf{t}|\mathbf{m}) / (1 - \bar{R}^2_{KL}(\mathbf{u}))$$

$$\text{Pure metacommunity effects: } \Delta R^2_{KL}(\mathbf{m}|\mathbf{t}) / (1 - \bar{R}^2_{KL}(\mathbf{u}))$$

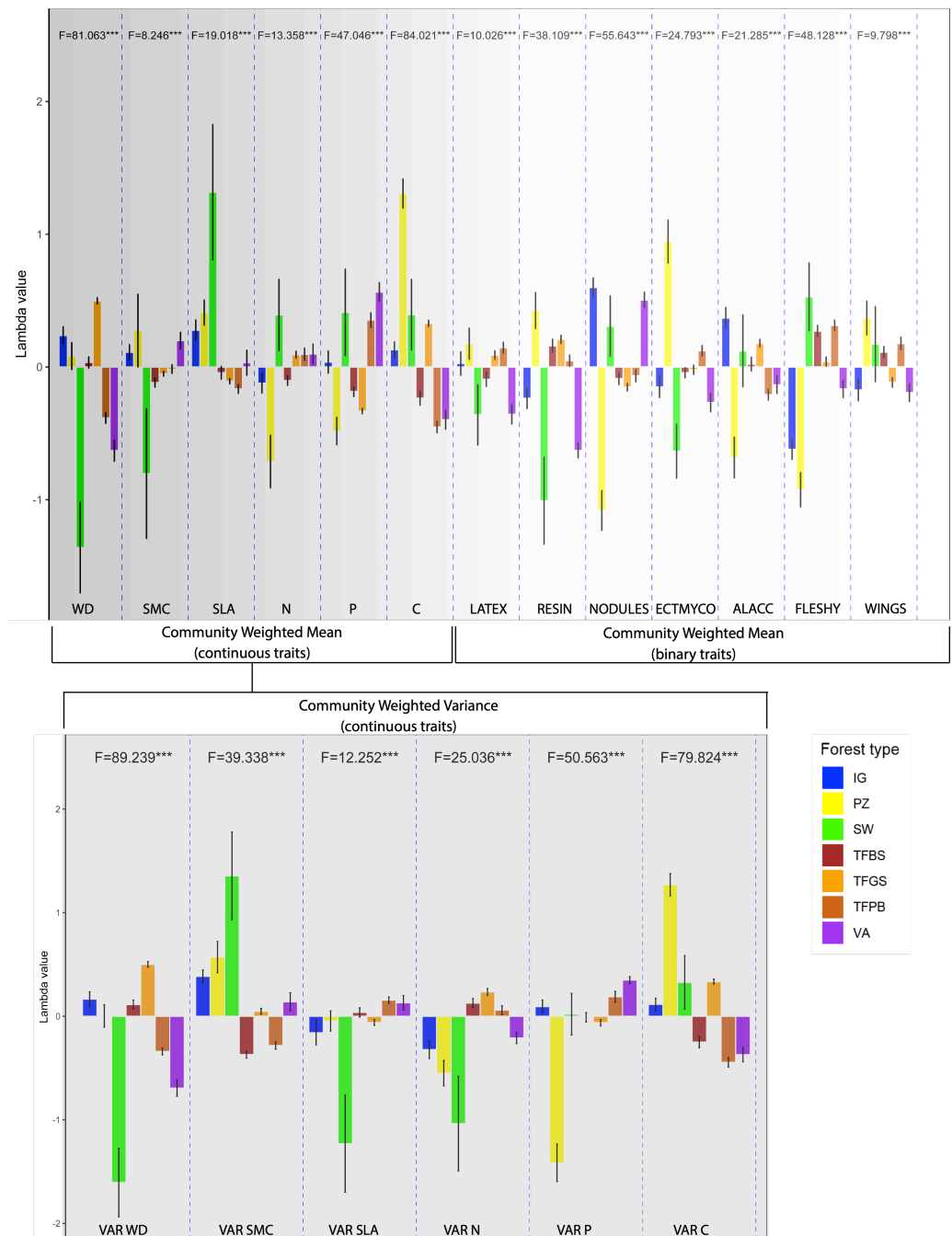
$$\text{Joint metacommunity and trait effects: } \Delta R^2_{KL}(\mathbf{m}+\mathbf{t}) / (1 - \bar{R}^2_{KL}(\mathbf{u}))$$

$$\text{Unexplained effects: } 1 - \Delta R^2_{KL}(\mathbf{m}, \mathbf{t}) / (1 - \bar{R}^2_{KL}(\mathbf{u}))$$

**Box S3. Detailed decomposition of the four-step solution from the MEF.** Mathematical description of the decomposition based on the constraints and prior distributions (both uniform and neutral) for each of the steps from the four-step solution to measure the proportion of total deviance accounted for by each specific model from one of the four steps.

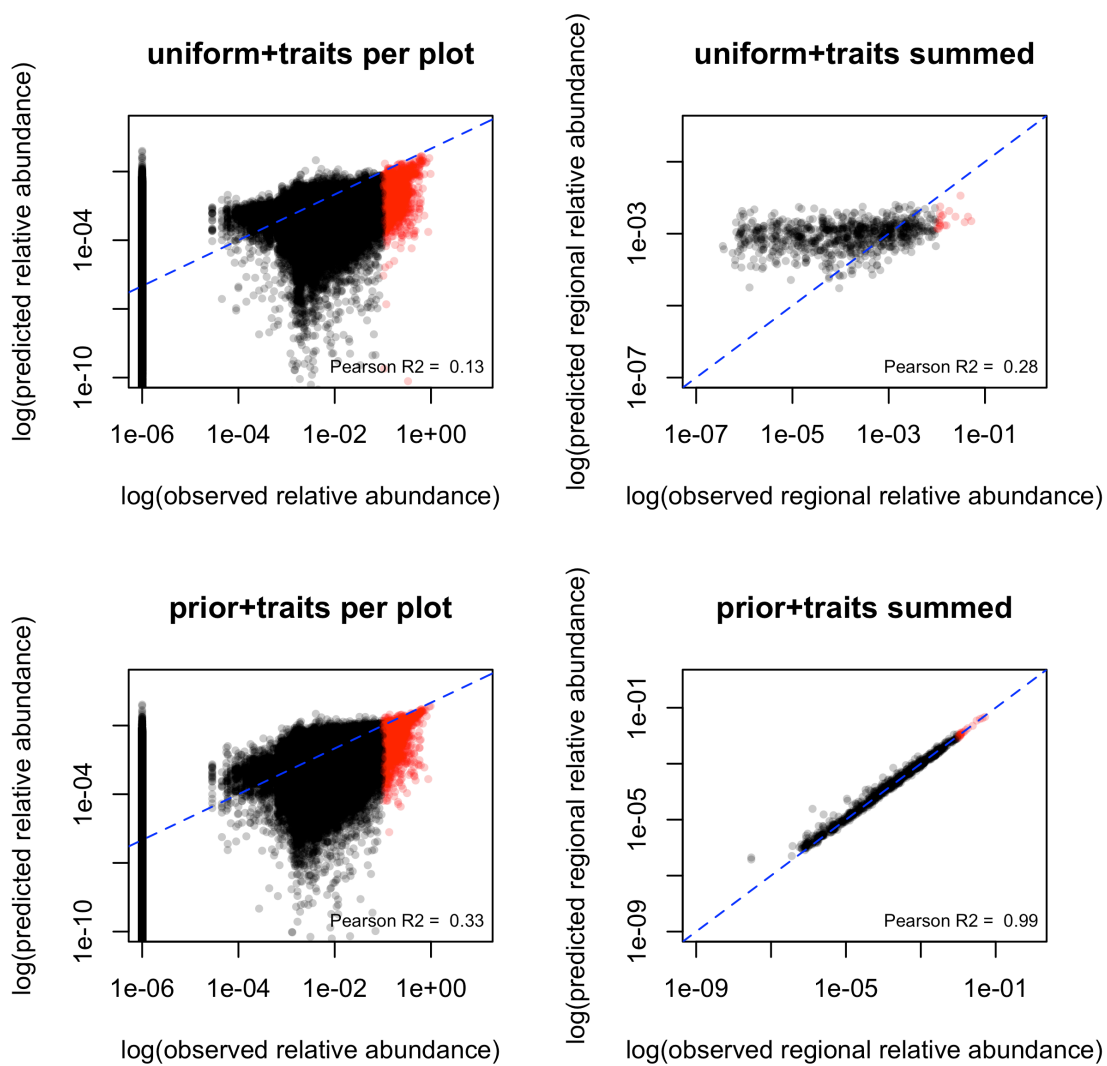


FIGURE S1



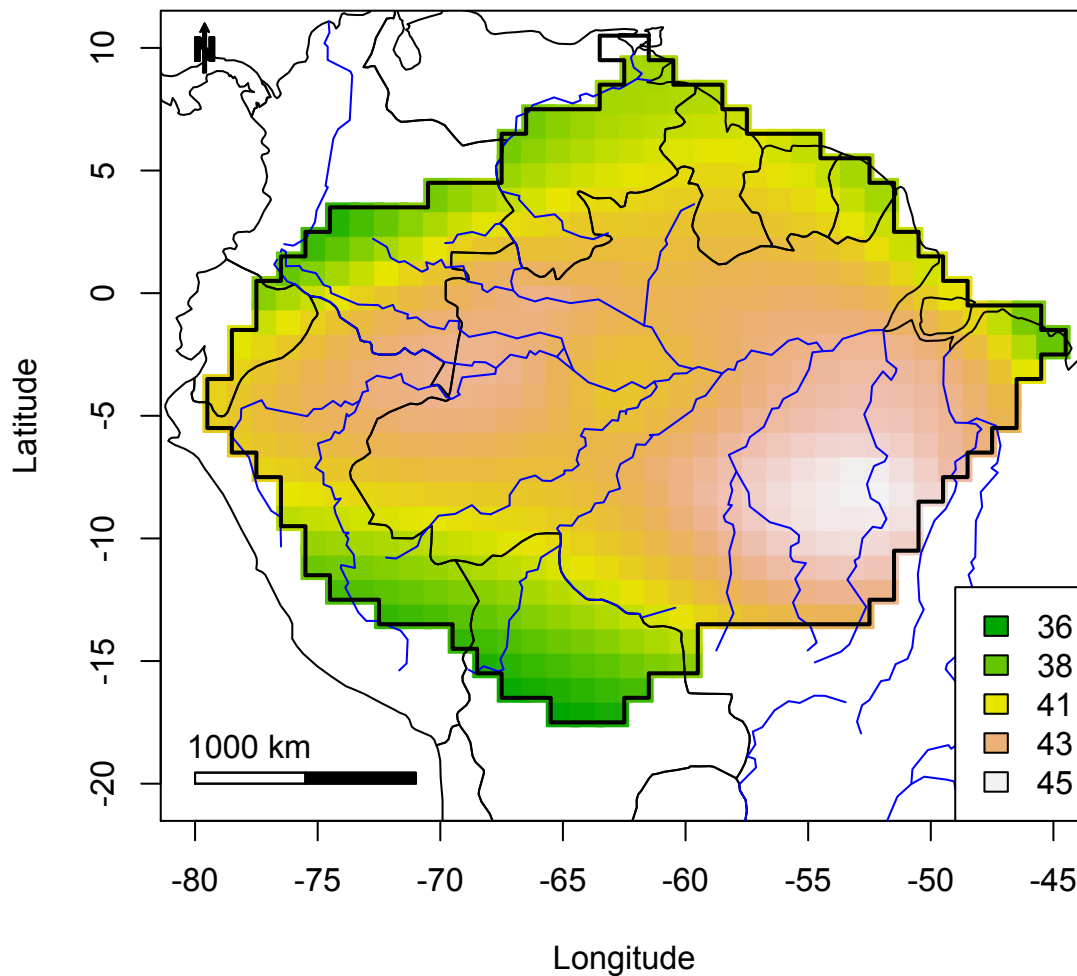
**Fig. S1. Mean lambda values with standard error bars for each functional trait and compared between forest types.** Forest types are *igapó* (IG), podzol (PZ), swamp (SW), Brazilian shield *terra firme* (TFBS), Guiana Shield *terra firme* (TFGS), Pebas *terra firme* (TFPB) and *várzea* (VA). Differences were tested with a one way analysis of variance with significance levels corresponding to: ns non-significant, \*  $p < .05$ , \*\*  $p < .01$  and \*\*\*  $p < .001$ . Traits used were wood density (WD), seed mass class (SMC), specific leaf area (SLA), nitrogen (N), phosphorus (P) and carbon (C) leaf content with the prefix of VAR for the variance of continuous traits. Latex, Resin, Nodules, Ectomycorrhiza (EctoMyco), the ability to accumulate aluminum (AlAcc), and the presence/absence of fleshy fruits (Fleshy) and winged seeds (Wings) were all binary traits.

FIGURE S2



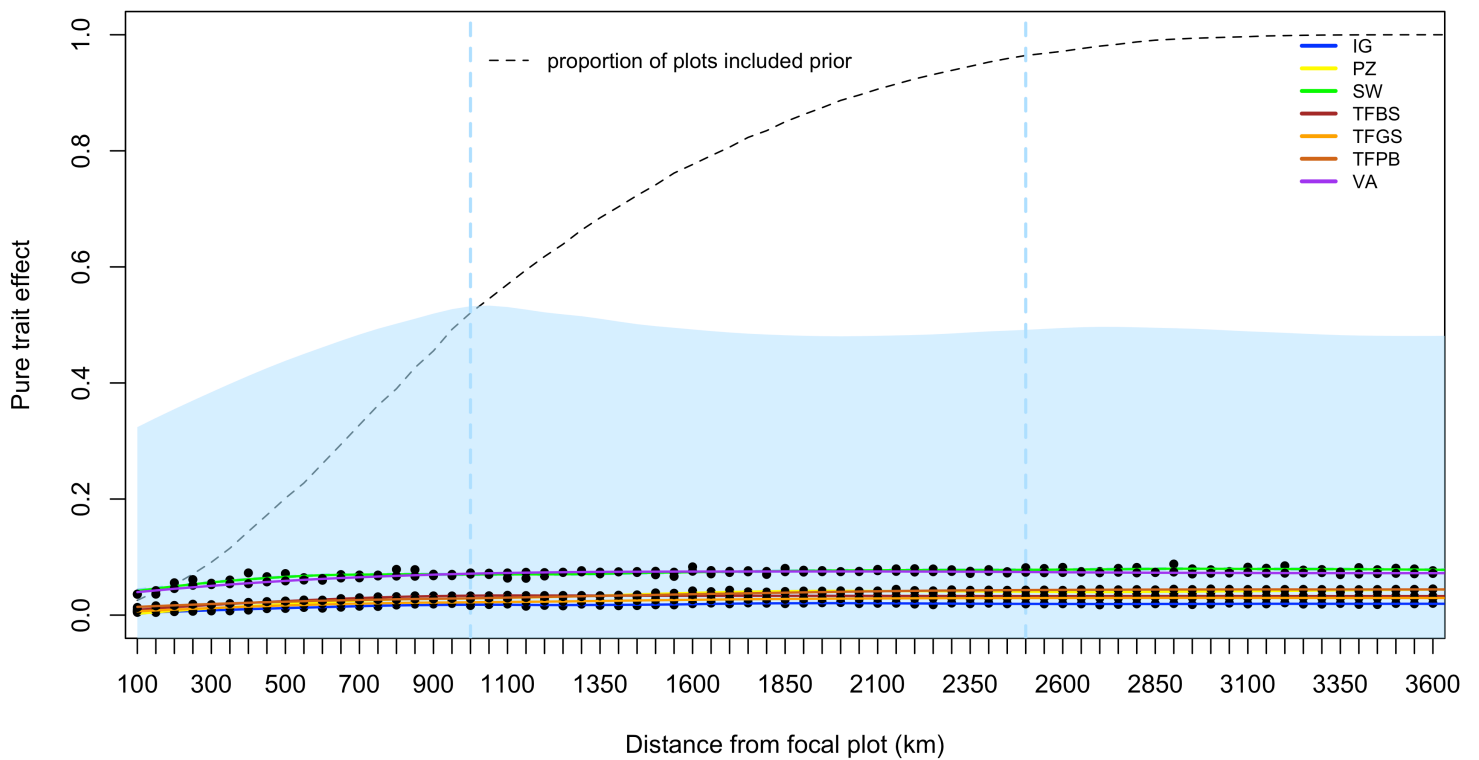
**Fig. S2. Observed relative abundances for each genus in all plots plotted against predicted relative abundance per plot (left) and summed (right) using only the traits as constraints in combination with a uniform prior (top) or the hybrid model using both traits and the metacommunity relative abundance as prior (bottom) on a log-log scale. Top figures show predictions using only a uniform prior, left separate for all plots and right for all genera summed over all plots. Bottom figures show predictions using the regional prior, again separate for all plots and genera (left) and summed over all plots for each genus (right). Red points indicate taxa with observed relative abundances over  $1e-1$ . Lines show the  $x=y$  prediction and  $R^2$  values correspond to the Pearson's correlation coefficient. Reported  $R^2$  value is equal to the Pearson correlation coefficient ( $R$ ) between the observed and predicted relative abundances defined as one minus the ratio of the error sum of squares to the total sum of squares.**

FIGURE S3



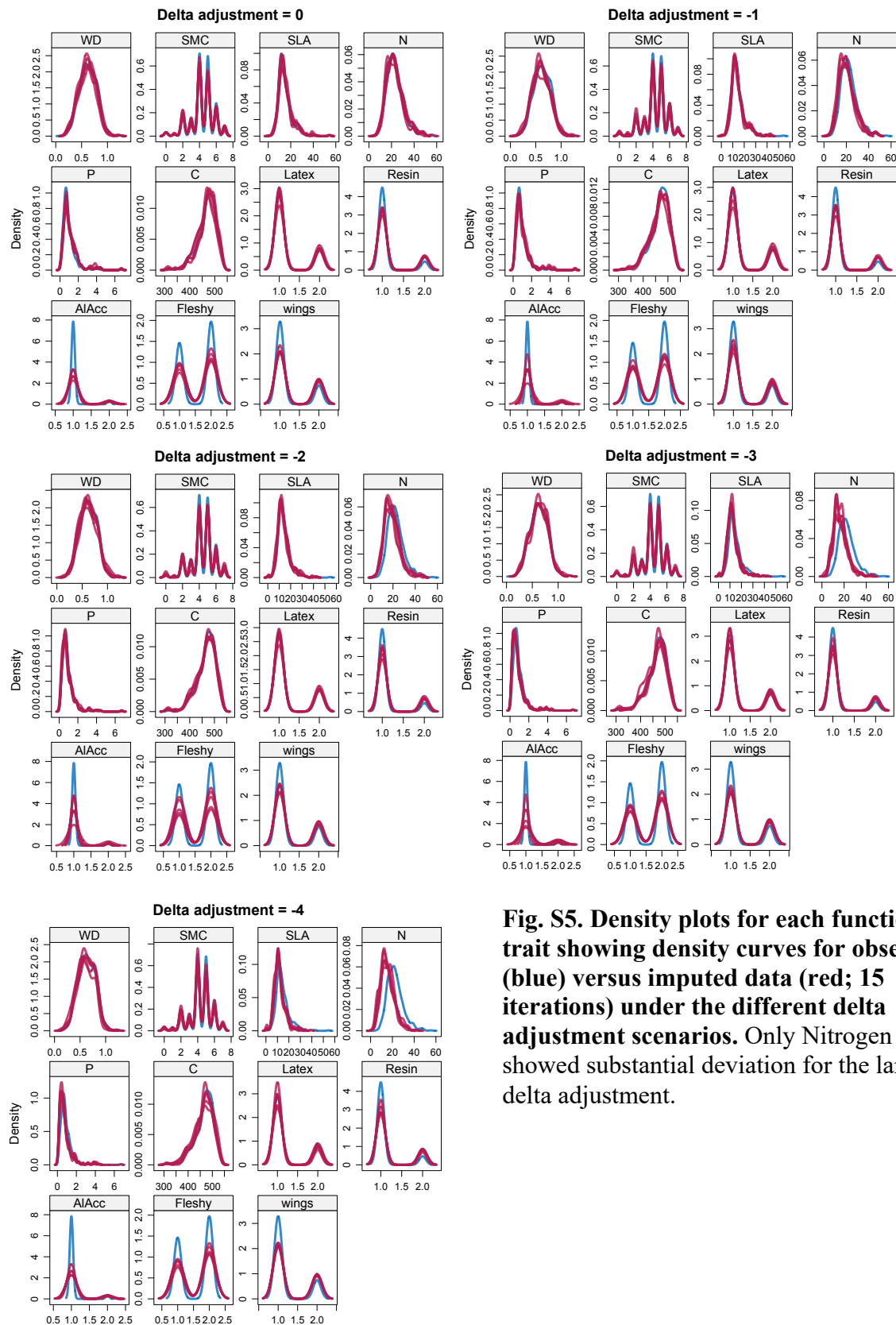
**Fig. S3. Spatial gradient in pure trait relative to pure metacommunity effect.** Map showing the ratio between the pure metacommunity effect and the pure trait effects for each plot. Ratio was calculated per plot by dividing the pure metacommunity effect by  $(10 \times \text{pure trait effects} + 1)$ . Values for projection on the map using a loess regression were multiplied by 1000 to allow clearer differentiation. Squares show the predictions from loess regression (color depending on value). Map shows interior of the Amazon having weaker trait effects relative to metacommunity effects whereas on the edges of the Amazon this pattern is reversed.

FIGURE S4



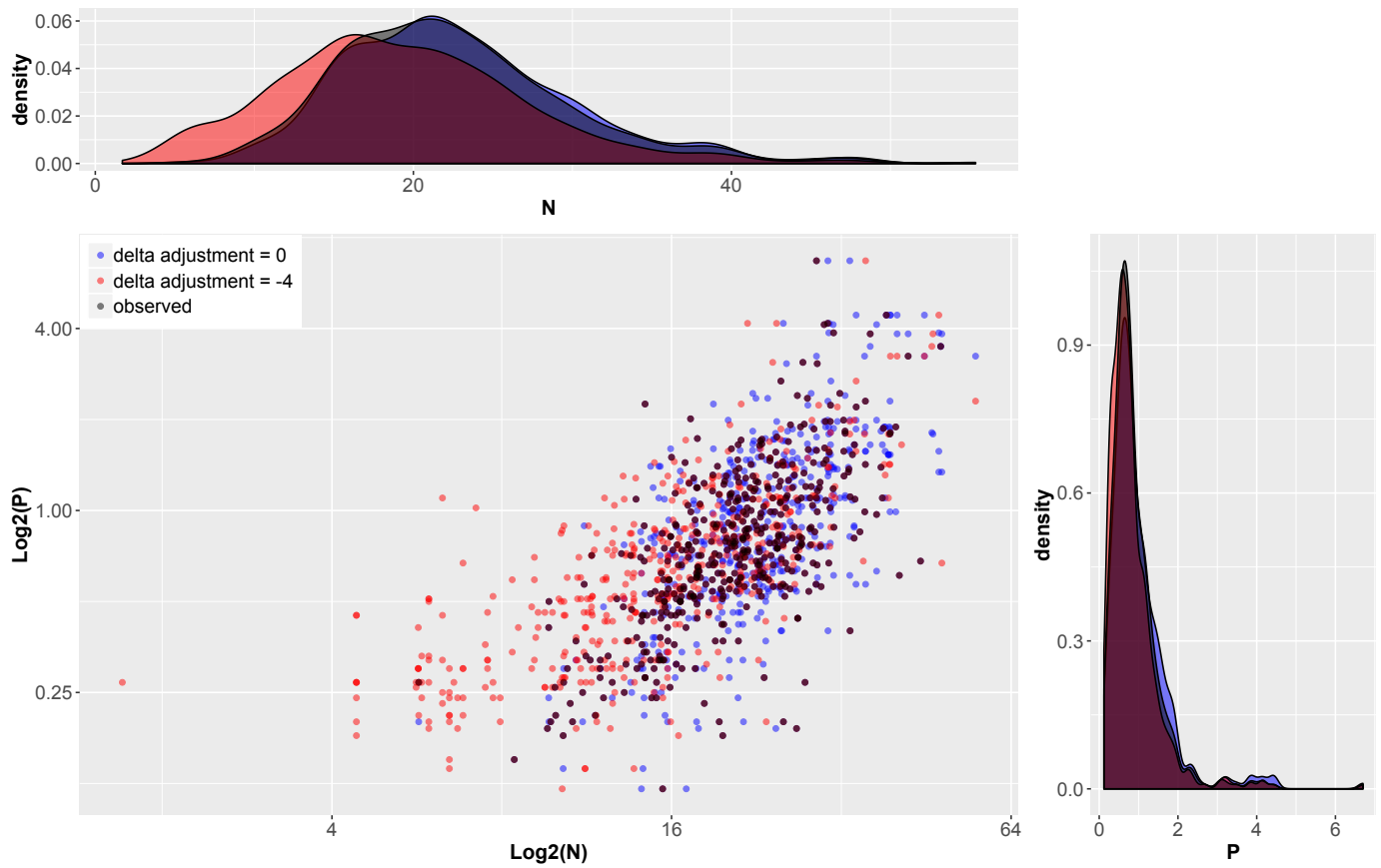
**Fig. S4. Distance decay of pure trait effect for each forest type separately and the overall dataset.** X-axis represents the radius of the metacommunity prior; i.e. the first 100 km consists of just a few plots and at 3800 km all plots are taken into account. Y-axis represent the pure trait effect, i.e. the increase in explained deviance due to traits beyond contributions made by the meta-community and relative to the model bias (see also Box S2). Colors indicate the different forest types with abbreviations as in main text. Lines indicate the predictions following from the loess regression based on all points. Blue vertical lines indicate the 1000 and 2500 km boundary points. Blue shading reflects maximum values for that distance of the whole dataset.

FIGURE S5



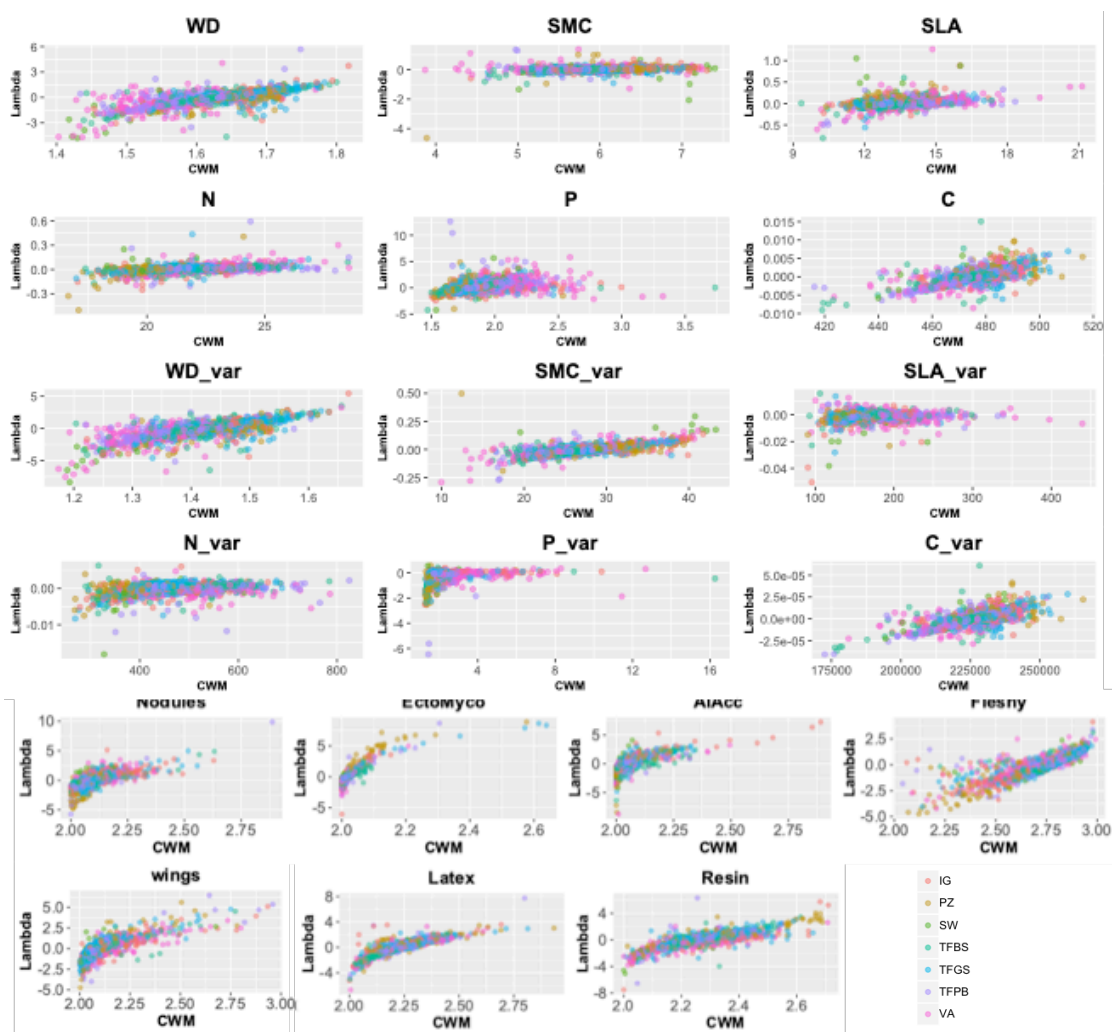
**Fig. S5. Density plots for each functional trait showing density curves for observed (blue) versus imputed data (red; 15 iterations) under the different delta adjustment scenarios. Only Nitrogen showed substantial deviation for the larger delta adjustment.**

FIGURE S6



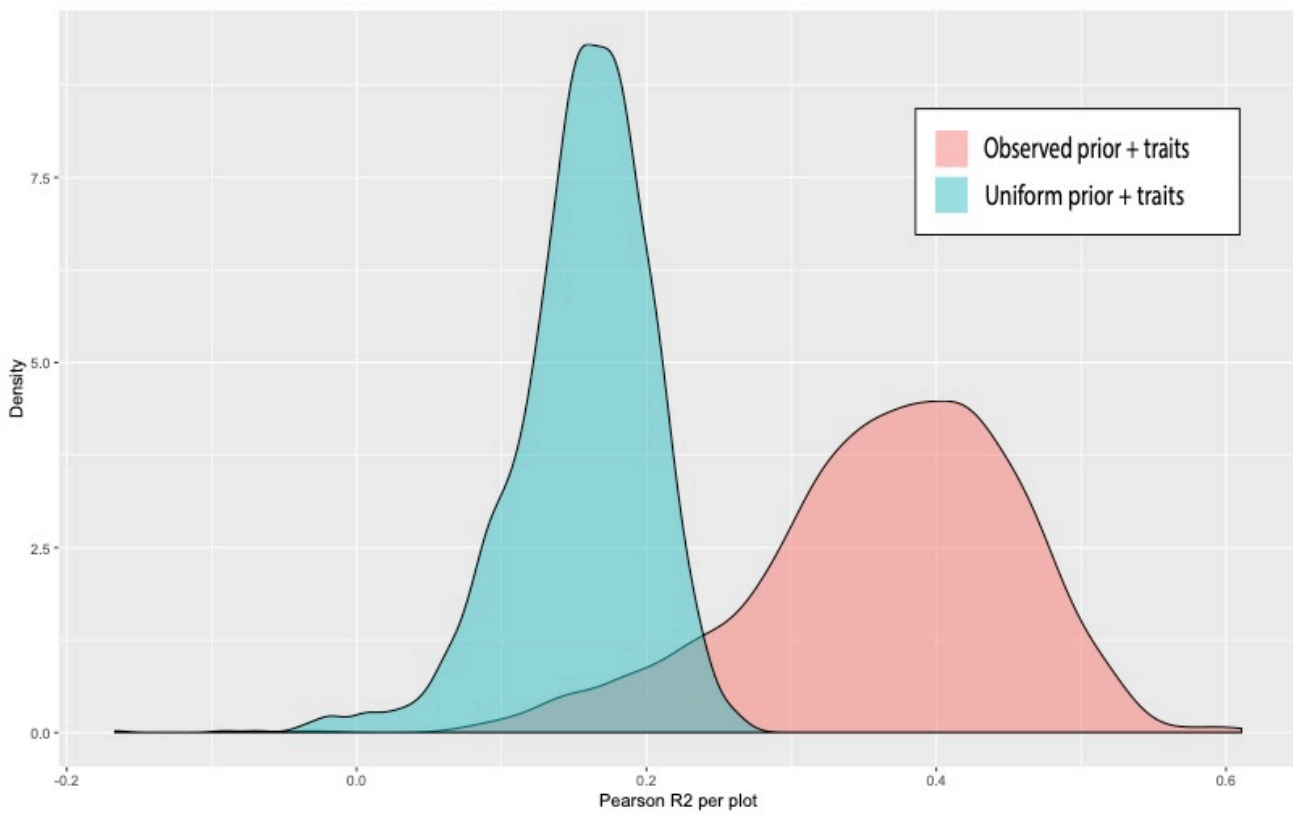
**Fig. S6. Scatterplot of observed vs. imputed leaf nitrogen and phosphorus content under different delta adjustment scenarios.** As Leaf Nitrogen content showed substantial deviation in the larger delta adjustment scenario it was here plotted versus Leaf Phosphorus content, which showed hardly any deviation.

FIGURE S7



**Fig. S7 Scatterplots of the CWM values against lambda values, colored according to forest type.** Titles are abbreviations for functional traits as used in the main text. Plots show in some cases these are clearly correlated (e.g. wood density, seedmassclass and C) but for many others not (e.g. SLA, Latex or Nodules).

FIGURE S8



**Fig. S8 Density plot of the per-plot-Pearson correlation coefficient between predicted relative abundances of each genus.** Models either used a uniform prior and functional traits (blue) or the actual observed prior and functional traits (red), results show a large increase in accuracy for the latter.



FIGURE S9

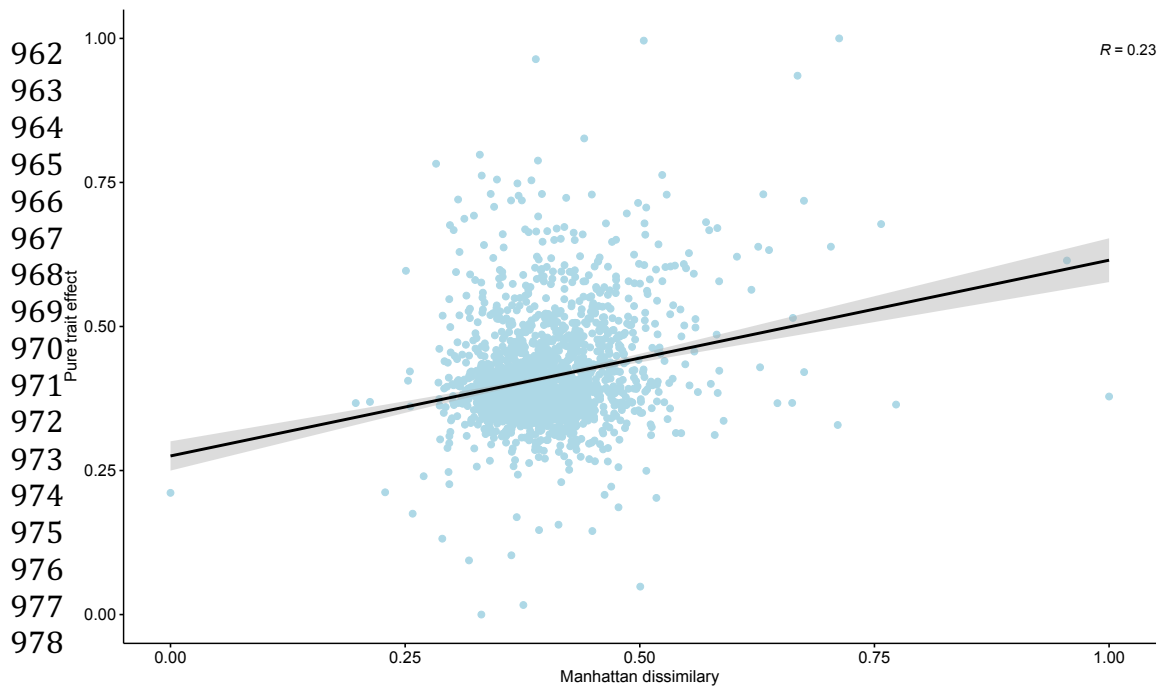


FIGURE S10

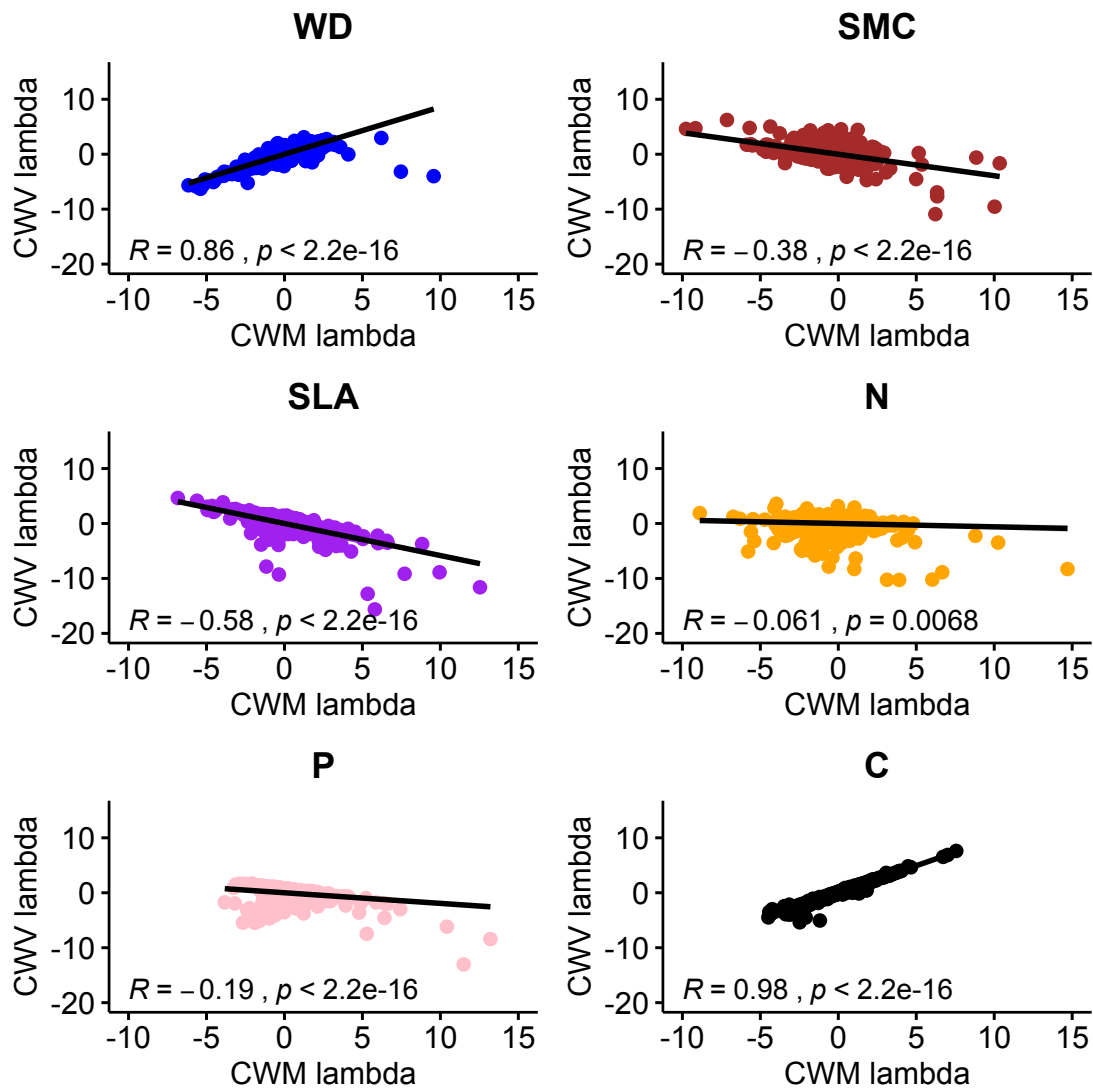


TABLE S1

**Table S1. Decomposition of results from the various maximum entropy models, combined and separated by forest type (PZ podzol, IG igapó, VA várzea, SW Swamp, TF terra firme with subregions BS (Brazilian Shield), GS (Guyana Shield) and PB (Pebas formation)).** Top rows indicate estimated proportions ( $R^2_{KL}$ ) of total information reflective of variation in local relative abundance explained for by the various models. Middle rows indicate the specific information gain from any one of the used models relative to the model bias. Bottom rows show the actual effects of traits, the metacommunity and the joint information relative to the model bias.

Explained proportions	Forest types							Combined
	PZ	VA	IG	SW	TFB S	TFGS	TFPB	
$\bar{R}^2_{KL}(u)$ <i>model bias fit</i>	0.20	0.14	0.15	0.23	0.11	0.11	0.09	0.12
$\bar{R}^2_{KL}(m)$ <i>pure neutral model fit</i>	0.54	0.53	0.54	0.57	0.56	0.63	0.56	0.58
$R^2_{KL}(u,t)$ <i>pure trait model fit</i>	0.36	0.25	0.23	0.34	0.20	0.24	0.21	0.23
$R^2_{KL}(m,t)$ <i>hybrid model fit</i>	0.60	0.59	0.56	0.60	0.60	0.66	0.60	0.62
<b>Increase in explained deviance</b>								
$\Delta R^2_{KL}(m \phi)$ <i>metacommunity effect beyond model bias</i>	0.34	0.39	0.39	0.34	0.45	0.52	0.47	0.45
$\Delta R^2_{KL}(t \phi)$ <i>trait effect beyond model bias</i>	0.15	0.11	0.08	0.11	0.10	0.13	0.11	0.11
$\Delta R^2_{KL}(t m)$ <i>trait effect beyond metacommunity effect</i>	0.06	0.06	0.02	0.03	0.04	0.03	0.05	0.04
$\Delta R^2_{KL}(m t)$ <i>metacommunity effect relative to trait effects</i>	0.24	0.34	0.33	0.27	0.40	0.43	0.40	0.38
$\Delta R^2_{KL}(m+t)$ <i>joint effect of metacommunity and traits</i>	0.09	0.05	0.06	0.07	0.06	0.10	0.07	0.07
$1 - \Delta R^2_{KL}(m,t)$ <i>unexplained effects</i>	0.40	0.41	0.44	0.40	0.40	0.34	0.40	0.38
<b>Biologically relevant information</b>								
Pure trait effect <i>Information from traits, relative to bias</i>	0.08	0.07	0.03	0.05	0.05	0.04	0.05	0.05
Pure metacommunity effect <i>Information from metacommunity, relative to bias</i>	0.30	0.39	0.38	0.33	0.45	0.48	0.44	0.43
Joint effect <i>Information from joint effect, relative to bias</i>	0.12	0.06	0.07	0.10	0.06	0.11	0.07	0.08
Unexplained information <i>Left over information not explained, relative to bias</i>	0.50	0.48	0.52	0.52	0.45	0.38	0.44	0.44

TABLE S2

**Table S2. Summary statistics overview for the linear models of the various scenarios under the delta adjustment technique as described in the main text.**

Rows indicate the different delta adjustments used with the columns representing the standard summary statistics of the linear model comparing the imputed versus observed trait values. Results showed similar patterns with each imputation scenario, indicating a robust imputation procedure.

Scenario	Summary statistics linear model $lm(\text{imputed} \sim \text{observed})$						
	Intercept	Std. error	T value	Pr.	R <sup>2</sup>	Adj. R <sup>2</sup>	Sigma
<i>Delta 0</i>	-.33	.07	-4.85	1.42e-06	.32	.33	.63
<i>Delta -2.5</i>	-.34	.06	-5.93	4.31e-09	.37	.37	.58
<i>Delta -5</i>	-.16	.04	-3.57	3.77e-04	.40	.40	.53
<i>Delta -7.5</i>	.64	.09	-7.33	5.18e-13	.42	.42	.88
<i>Delta -10</i>	0.09	.04	3.17	1.57e-03	.47	.47	.48

979

980

981

## 982 S-A Ecological interpretation of the MEF results

983

984 A number of functional traits associated with low nutrient conditions (e.g.  
985 ectomycorrhiza) and life history strategies suited for protection against herbivores  
986 (e.g. latex and high leaf C content) were clearly positively associated with abundance  
987 in nutrient poor environments (podzols) in terms of community weighted mean  
988 values, indicated by the positive lambda values. In contrast, community weighted  
989 means for fleshy fruits and high leaf N and P content were negatively associated with  
990 abundance on these soils. Nodulation was also negatively associated with abundance  
991 on poor soils, supporting earlier results [1]. The ability to accumulate aluminium was  
992 positively associated with abundance on soils commonly associated with higher  
993 aluminium content such as *igapó* (strong positive effects) and *terra firme* soils (a  
994 minor, yet positive effect). In contrast, it was strongly negatively associated with  
995 abundance for podzol, *várzea* and swamp forests. Traits such as SLA or winged fruits  
996 also showed strong patterns dependent on forest type.

997

998 Signals of quantitative environmental selection were found to be highest for podzol  
999 forests, whereas its counterpart in the form of the dispersal mass effect from the  
1000 regional pool of genera had the lowest value. Podzol forests, having extremely  
1001 nutrient poor soils could reflect a much stronger selective environment than any of the  
1002 other forest types. *Terra firme* forests, presumably reflective of a less strong selective  
1003 environment in terms of resource availability, showed the opposite, with less than half  
1004 of the pure trait effect in comparison with podzol forests (even when rarefied to  
1005 accommodate for different sample sizes). Traits associated with protection against  
1006 herbivores such as latex [2] and high leaf carbon content showed higher values  
1007 associated with greater abundance and overall lower variance on podzol soils,  
1008 whereas traits indicative of investment in growth and photosynthetic ability such as  
1009 high foliar concentrations of P and N [3] showed strong negative associations on  
1010 nutrient poor soils for both community weighted means and variance. The ability to  
1011 accumulate aluminium was also strongly positively associated with relative  
1012 abundance on the more nutrient but also often aluminium enriched soils of *terra firme*  
1013 and in some cases aluminium rich *igapó* forests. Lambda values also showed strong  
1014 negative lambda values for wood density in swamp and forests in both community  
1015 weighted means and variance, fitting high tree mortality and many individuals  
1016 belonging to pioneer species in especially the western Amazonian swamp forests.  
1017 *Várzea* and Pebas *terra firme* forests showed a similar response. As the Pebas consists  
1018 mainly of Andean sediments it has higher nutrient content, promoting lower wood  
1019 density, supported by our results whereas *várzea* forests are also often flooded. There  
1020 were also traits that showed no specific (strong) signal of selection on certain forest  
1021 types (either positive or negative), such as latex on *igapó* and ectomycorrhiza on  
1022 *várzea* (see Fig. 1 for all lambda values). Plotting lambda values for CWM and CWV  
1023 constraints of the continuous traits showed WD and C were both strongly positively  
1024 correlated indicating strong directional selection for lower trait values accompanied  
1025 by a reduction in trait variance. SMC, SLA and leaf P content, however, showed a  
1026 negative correlation with higher lambda values for CWM values associated with  
1027 lower trait variance (Figure S11). None of the traits showed a reduction in variance  
1028 without a change in the CWM, suggesting directional selection is more likely than  
1029 stabilizing selection, even though the overall information yield remains low.  
1030 Interestingly, terra firme forests in general showed the smallest lambda values overall  
1031 (positive or negative).

1032

1033 This may be indicative of either more pronounced demographic stochasticity or  
1034 ecological drift eliminating the association between traits and relative abundance.  
1035 Lower effects of selection in general or more (random) variation due to the larger  
1036 species pool in comparison with other forest types, however, could also be the result  
1037 of mixing heterogeneous microenvironments into a single environmental class.  
1038 Support for such heterogeneity within terra firme forests having influence on  
1039 distribution of functional traits on valleys or plateaus has recently been found [4]. In  
1040 addition, natural but also anthropogenic [5] disturbance history affects biotic  
1041 community composition and can lead to changes in tree community through time,  
1042 blurring relationships between traits and relative abundances. It should further be  
1043 noted that, although for terra firme forests we were able to make a distinction by  
1044 subregion, true within forest type heterogeneity was not taken into account. This  
1045 might cause an underestimation of the deterministic effect but as of yet cannot be  
1046 corrected for on this scale and is worth to be investigated in future studies. In  
1047 addition, podzol forests have a smaller connected surface area and accompanying  
1048 smaller number of genera in comparison with terra firme forests, adding to the  
1049 calculated stronger trait effects [6,7]. When more detailed understanding and  
1050 knowledge of these functional traits would be provided, this would most likely  
1051 increase the explanatory power of the MEF. The fact, however, that we do not have a  
1052 very specific knowledge of these interactions and specific traits is precisely the reason  
1053 why the MEF can provide additional insight.

1054  
1055 It should be noted that for species level analyses any micro environmental gradients  
1056 might prove to also show (stronger) selection at local scales [8,9], as it has been  
1057 shown that most variation in community composition, due to selection in regard to  
1058 habitat filtering and niche conservatism, is found at lower taxonomic levels, such as  
1059 between species within genera [10,11]. In contrast, theoretically it has been shown  
1060 and tested that immigration numbers are actually very robust across taxonomic  
1061 scales [12], validating our results of the metacommunity importance using genus  
1062 level taxonomy. Spatial patterns of metacommunity effects, showing shallowest  
1063 declines in the centre, also support the suggestion that high diversity of the  
1064 Amazonian interior could be explained by influx of recruits due to large (overlapping)  
1065 ranges. This mid-domain effect [13], however, would also predict lower species  
1066 richness for the edges due to lower range overlap, assuming a closed community. This  
1067 is not the case, as there is a strong species richness gradient from West (rich) to  
1068 Eastern Amazonian forests (poor) [14]. The lower metacommunity effect for the  
1069 edges then is most likely not due to less absolute influx of genera, but rather less  
1070 influx from the Amazonian tree community. Influx from the species-rich Andes could  
1071 account for the high diversity [15], yet low Amazonian metacommunity effect for  
1072 Western Amazonian forests. In contrast, South Eastern parts of Amazonia receive  
1073 influx from tree species-poor biomes (i.e. the Cerrado) resulting in lower diversity but  
1074 also low metacommunity effect for Amazonian trees in this region.  
1075

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