

Nature Ecology & Evolution Comment

1 **A million and more trees for science**

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15 **TreeDivNet is the largest network of biodiversity experiments worldwide, but needs to expand.**16 **We encourage colleagues to establish new experiments on the relation between tree species**17 **diversity and forest ecosystem functioning, and to make use of the platform for collaborative**18 **research.**

19

20 Forests now cover approximately 30% of the Earth's land surface (FAO State of the World's
21 Forests 2012), support high levels of biodiversity, and provide essential ecosystem services to
22 humanity (Millennium Ecosystem Assessment 2005). About 30% of the world's forests were lost
23 during the last 5000 years following human population growth, and forest cover is still being
24 reduced at unprecedented rates, through deforestation and conversion to agriculture (FAO 2012).
25 Reforestation and afforestation programs exist in many countries to compensate for the loss of
26 forest cover, with China's Grain-for-Green Program being the largest.

27

28 It is predicted that >50% of industrial timber will come from plantations by around the middle of
29 this century ¹. While planting restores tree cover, virtually all industrial plantations are single-
30 species monocultures, most often of fast-growing cultivars or hybrids of pine, eucalypt, acacia,
31 spruce, poplar or larch. Foremost among the many reasons for this are the high yields normally
32 achieved with intensive, high-input silviculture, under a predictable and stable climate, low
33 disturbances and minimal pests and diseases. However, with increasing recognition of the
34 environmental costs of high-input systems, a changing climate, increasing exotic pests and
35 diseases, and the increasing importance given to other ecosystem services provided by forests,
36 the historical arguments in favour of monocultures is becoming less persuasive ².

37

38 Indeed, over the last quarter century, research demonstrated a general trend for ecosystem
39 functioning and the provisioning of ecosystem services to increase with higher levels of diversity ³.
40 This research was generally conducted with herbaceous plants that are more convenient
41 experimental systems, but forests are now one of the main areas of research in this field despite
42 the challenges they present.

43

44 **Linking tree diversity and forest ecosystem functioning**

45 Whether biodiversity is positively related to ecosystem functioning has been a controversial idea,
46 and particularly difficult to test for in arboreal systems for several reasons, including the large size
47 of trees, slow growth, and long lifespans. Observational approaches compare ecosystem
48 functioning in existing forests of different tree diversity, while statistically controlling for other
49 drivers of productivity⁴.

50

51 Observational studies have provided perhaps the strongest support for a positive effect of forest
52 diversity on productivity, culminating with a recent study that included data from all forested
53 biomes of the world⁵. Such studies are relatively easy to perform and have high relevance to real-
54 world systems, but potential confounding factors (species identity, climate, soil, management
55 history) may limit their ability to isolate the effect of tree diversity. A second possibility is to
56 remove species from established communities while monitoring impacts on functioning⁶. While
57 these removal experiments bring greater control than observational studies, the disturbance
58 incurred can confound the results.

59

60 A third approach is to experimentally manipulate tree diversity (and identity) by planting trees in
61 well replicated designs⁷. In tree diversity experiments, plots of different levels of diversity are
62 established to monitor the impacts on ecosystem functioning and stability. Experiments have the
63 advantage of greater control of confounding factors as well as species composition and stem
64 density, but they take time to develop whereas evidence has shown that diversity effects tend to
65 strengthen through time⁸. This could in part explain why so far, and contrary to expected,
66 observational studies have repeatedly shown larger diversity effects than did experiments³. In
67 summary, there is no perfect approach: observational (comparative) studies, removal

68 experiments and tree diversity experiments all have strengths and weaknesses. Some
69 compromises (or hybrid solutions) are also possible such as improved observational studies that
70 aim at better controlling exogenous factors through a careful plot selection process⁹.

71

72 **The Tree Diversity Network**

73 TreeDivNet (www.treedivnet.ugent.be) is a global network of tree diversity experiments which
74 provides a unique platform for research on the relationship between tree diversity and ecosystem
75 functioning in all major forest types around the world⁷. TreeDivNet is the largest network of
76 biodiversity experiments worldwide - of any group of organisms - and one of the largest research
77 facilities in ecology in general. Many of the experiments are large-scale and long-term (planned to
78 run for decades), whereas others work at smaller or shorter scales. To date, more than 1,115,000
79 trees have been planted in 25 experiments, covering a total area of more than 820 ha (Figure 1).
80 Key strengths of the network include a pool of 230 tree species, the wide biogeographic gradient
81 covered, and the diversity and complementarity of the research teams involved.

82

83 Unlike traditional forestry trials, monitoring productivity between a monoculture and the same
84 species mixed with a companion species, experiments within TreeDivNet typically have longer
85 diversity gradients and investigate the effects of tree diversity (and not only the effect of mixture)
86 on multiple forest ecological functions. In addition, many experiments within TreeDivNet
87 manipulate not only tree species richness, but also other components of diversity such as species
88 identity (plots of the same diversity level but using different combinations of species),
89 intraspecific genetic diversity, functional or phylogenetic diversity, and evenness. The ultimate
90 goal is to identify the multiple and complex mechanisms through which trees, and species at
91 other trophic levels such as microbes and insects, interactively influence ecological dynamics to

92 promote coexistence, resilience, facilitation and complementary resource use^{10, 11, 12}. In addition,
93 the network translates that knowledge into relevant guidelines to foster the use of well-designed,
94 diverse tree plantations that are more resilient and productive, while maximizing synergies with
95 other forest functions (recreational, environmental) and biodiversity conservation¹³.

96

97 **Key findings**

98 TreeDivNet has already produced some key findings on the relationships between tree diversity
99 and several forest functions¹⁴. Tree diversity often improved the survival and growth of trees,
100 and the mechanisms involved variation in species traits, and included both selection and
101 complementary effects^{12, 15, 16}. However the effect of tree diversity on herbivory damage is still
102 elusive as positive, negative, and neutral responses have been observed, whereas the
103 mechanisms involved included changes in concentration, frequency, and apparency of hosts,
104 herbivore breadth, the spatial scale of interactions, and natural enemies¹⁷. This highlights the
105 importance of environmental context for biodiversity research and the need for system-specific
106 analyses¹⁸. TreeDivNet is also playing a key role in highlighting the importance of other trophic
107 levels, such as microbes, in mediating diversity effects in tree communities^{11, 19}.

108

109 **Real world applications**

110 The potential applications of the research conducted within the TreeDivNet platform are broad
111 and varied:

112 (1) Industrial plantations. Almost all fast-growing forest plantations are monocultures. Few
113 polycultures exist and yet the potential benefits in terms of yield, increased stability and
114 decreased risk in productivity, increased social acceptance and ecosystem services to
115 other users are high.

116 (2) Forest landscape restoration. Large areas of degraded land, especially in the tropics and
117 subtropics, are in need of restoration and global political initiatives such as the Bonn
118 Challenge (www.bonnchallenge.org) are under way to improve human well-being through
119 multifunctional landscapes. In many situations, new forests will have to be created with
120 the opportunity to use specific mixtures to optimize resilience and the provision of
121 multiple ecosystem services.

122 (3) Agroforestry. A traditional use of trees that is gaining popularity is in agricultural fields.
123 Again, most agroforestry systems use only one tree species, although the benefits of
124 mixtures of arboreal species nested within a broader design including other plant growth
125 forms could be high.

126 (4) Urban forest planning. Trees are often planted alone or in small groups along streets or in
127 parks, with no consideration for the possible benefits that a greater diversity of tree
128 species could provide, if only to reduce the risks associated with global change factors
129 such as introduced pests and diseases. To acknowledge that, TreeDivNet millionth tree
130 was planted at IDENT-Cité in spring 2015, in Montreal (Canada). This installation - a double
131 spiral with increasing diversity as the visitor moves toward the center - serves as
132 educational link between the science developed in TreeDivNet and the public.

133

134 **Outstanding questions and research priorities**

135 The extension of biodiversity - ecosystem functioning research into forests is improving ecologists'
136 capacity to understand the mechanistic bases sustaining diversity effects, and presents
137 opportunities for novel research¹⁴. Since tree experiments enable measurements at individual,
138 neighborhood and plot levels, they allow asking some key questions such as the scale at which
139 diversity matters, and whether relationships and mechanisms change through time. Tree

140 experiments also provide ample opportunities to use remote sensing and spectral approaches to
141 study community dynamics, integrate belowground and aboveground processes, and scale-up the
142 consequences of individual physiology and plasticity for ecosystem functioning. Fueled by mixed
143 results from observational studies ²⁰, some of the more recent additions to the network are
144 asking whether and how diversity may buffer against climate change driven stresses, such as
145 increased drought through manipulating water availability.

146

147 **Calling out to fellow scientists**

148 The oldest experiments in TreeDivNet are approaching two decades, but many are planned to run
149 for much longer, and the network offers a unique infrastructure for long-term ecological research.
150 A large number of publications have already been published (175; 158 peer-reviewed papers and
151 16 PhD thesis; Figure 1), and more research is underway. However, huge potential exists for
152 further work, especially in areas outside the expertise of the current TreeDivNet teams. We
153 encourage colleagues worldwide to suggest collaborative research making use of the TreeDivNet
154 platform. Additional experiments in underrepresented forest biomes are also much needed in
155 order to foster and strengthen synthesis studies as well as enable transfer of well-founded
156 knowledge to stakeholders worldwide ⁵. The network needs to expand conceptually, for example
157 by developing designs for the next generation of experiments that may better isolate the
158 mechanisms that lead to diversity effects. We should also address the new questions and
159 challenges posed to forest ecosystems by global changes, such as an increased frequency of
160 severe droughts, floods and storms. Also, to be successful at turning the tide on the use of
161 monocultures in plantation forestry, the network needs to foster operational scale experiments to
162 demonstrate not only the benefits of diversity at scales that matter to managers, but their

163 feasibility as well ^{21,22}. In short, additional (long-term) data collection in existing experiments and

164 the set-up of new experiments are needed to further increase the impact of the network.

165

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246

247 **Author Contributions**

248 The concept was developed at the plenary TreeDivNet meeting in Bordeaux, February 2017. The
249 first draft was written by AH and AP, with later input from BC, MV, KV, JK, MSL, and all TreeDivNet
250 members⁷.

251

252 **Declaration of Financial Competing Interests**

253 The authors declare no competing financial interest.

254

255 ⁷ **Members of the TreeDivNet are:**

256 Abdala-Roberts, Luis; Auge, Harald; Barsoum, Nadia; Bauhus, Jürgen; Baum, Christel; Bruelheide,

257 Helge; Castagneyrol, Bastien; Cavender-Bares, Jeannine; Eisenhauer, Nico; Ferlian, Olga; Ganade,

258 Gislene; Godbold, Douglas; Göransson, Hans; Gravel, Dominique; Hall, Jefferson; Hector, Andy;

259 Hobbs, Richard; Hoelscher, Dirk; Hulvey, Kristin B.; Huxham, Mark; Jactel, Hervé; Koricheva, Julia;

260 Kreft, Holger; Liang, Jingjing; Mereu, Simone; Messier, Christian; Montgomery, Rebecca; Muys,

261 Bart; Nock, Charles; Paquette, Alain; Parker, Bill; Parker, John; Parra-Tabla, Victor; Perring, Mike;

262 Ponette, Quentin; Potvin, Catherine; Reich, Peter; Rewald, Boris; Scherer-Lorenzen, Michael;

263 Smith, Andy; Standish, Rachel; Vanhellefont, Margot; Verheyen, Kris; Weih, Martin; Wollni,

264 Meik; Zemp, Clara

265

266

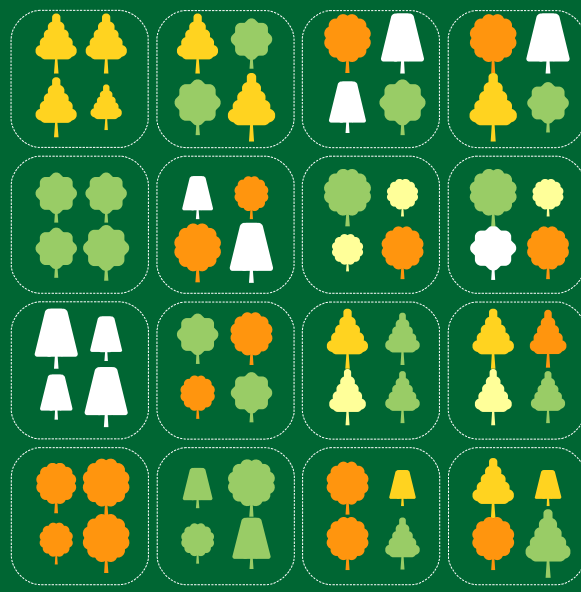
267 Figure 1. TreeDivNet in winter 2018.

230
Tree species

1 116 247
Planted trees

Initiated in
1999

Now covering
821
hectares



3 diversity gradients
genetic, functional, species

4818
experimental
plots



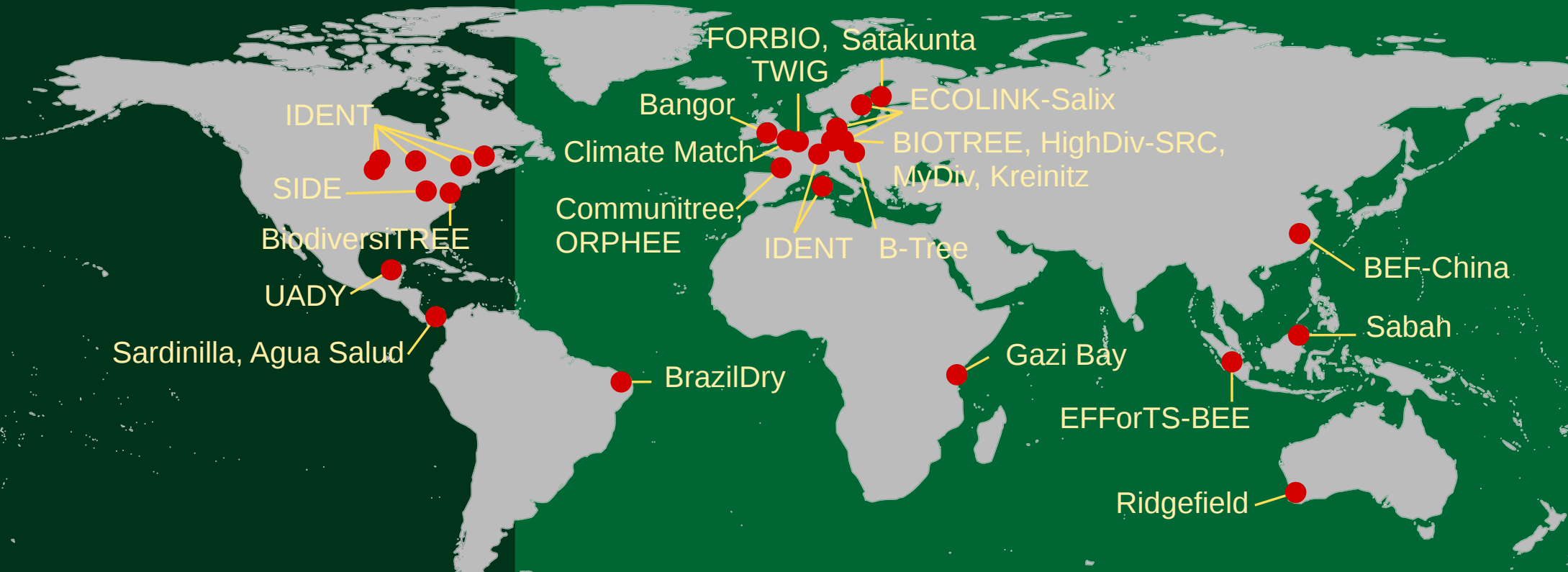
Tree
species
richness

Forest biodiversity and
ecosystem functioning

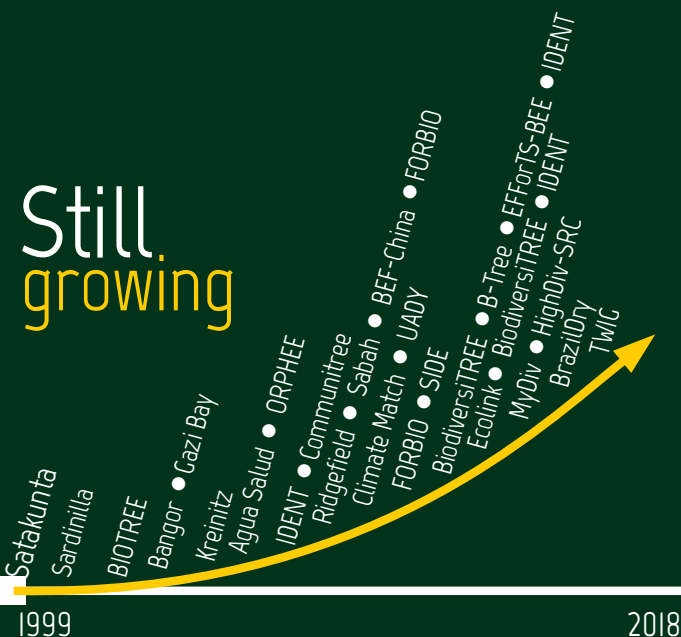
TreeDivNet

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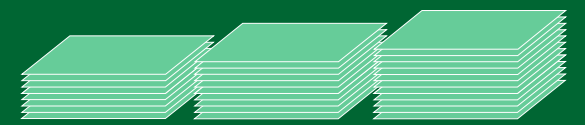
25 experiments • **45** sites • **6** continents



Still
growing



43 partners



175 publications

158 papers, 1 book chapter
16 PhD theses