A million and more trees for science

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

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

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

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

Linking tree diversity and forest ecosystem functioning

Whether biodiversity is positively related to ecosystem functioning has been a controversial idea, and particularly difficult to test for in arboreal systems for several reasons, including the large size of trees, slow growth, and long lifespans. Observational approaches compare ecosystem functioning in existing forests of different tree diversity, while statistically controlling for other drivers of productivity [4].

Observational studies have provided perhaps the strongest support for a positive effect of forest diversity on productivity, culminating with a recent study that included data from all forested biomes of the world [5]. Such studies are relatively easy to perform and have high relevance to real-world systems, but potential confounding factors (species identity, climate, soil, management history) may limit their ability to isolate the effect of tree diversity. A second possibility is to remove species from established communities while monitoring impacts on functioning [6]. While these removal experiments bring greater control than observational studies, the disturbance incurred can confound the results.

A third approach is to experimentally manipulate tree diversity (and identity) by planting trees in well replicated designs [7]. In tree diversity experiments, plots of different levels of diversity are established to monitor the impacts on ecosystem functioning and stability. Experiments have the advantage of greater control of confounding factors as well as species composition and stem density, but they take time to develop whereas evidence has shown that diversity effects tend to strengthen through time [8]. This could in part explain why so far, and contrary to expected, observational studies have repeatedly shown larger diversity effects than did experiments [3]. In summary, there is no perfect approach: observational (comparative) studies, removal experiments and tree diversity experiments all have strengths and weaknesses. Some compromises (or hybrid solutions) are also possible such as improved observational studies that aim at better controlling exogenous factors through a careful plot selection process [9].

The Tree Diversity Network

TreeDivNet (www.treedivnet.ugent.be) is a global network of tree diversity experiments which provides a unique platform for research on the relationship between tree diversity and ecosystem functioning in all major forest types around the world [7]. TreeDivNet is the largest network of biodiversity experiments worldwide - of any group of organisms - and one of the largest research facilities in ecology in general. Many of the experiments are large-scale and long-term (planned to run for decades), whereas others work at smaller or shorter scales. To date, more than 1,115,000 trees have been planted in 25 experiments, covering a total area of more than 820 ha (Figure 1). Key strengths of the network include a pool of 230 tree species, the wide biogeographic gradient covered, and the diversity and complementarity of the research teams involved.

Unlike traditional forestry trials, monitoring productivity between a monoculture and the same species mixed with a companion species, experiments within TreeDivNet typically have longer diversity gradients and investigate the effects of tree diversity (and not only the effect of mixture) on multiple forest ecological functions. In addition, many experiments within TreeDivNet manipulate not only tree species richness, but also other components of diversity such as species identity (plots of the same diversity level but using different combinations of species), intraspecific genetic diversity, functional or phylogenetic diversity, and evenness. The ultimate goal is to identify the multiple and complex mechanisms through which trees, and species at other trophic levels such as microbes and insects, interactively influence ecological dynamics to promote coexistence, resilience, facilitation and complementary resource use [10, 11, 12]. In addition, the network translates that knowledge into relevant guidelines to foster the use of well-designed, diverse tree plantations that are more resilient and productive, while maximizing synergies with other forest functions (recreational, environmental) and biodiversity conservation [13].

Key findings

TreeDivNet has already produced some key findings on the relationships between tree diversity and several forest functions [14]. Tree diversity often improved the survival and growth of trees, and the mechanisms involved variation in species traits, and included both selection and complementary effects [12, 15, 16]. However the effect of tree diversity on herbivory damage is still elusive as positive, negative, and neutral responses have been observed, whereas the mechanisms involved included changes in concentration, frequency, and apparency of hosts, herbivore breadth, the spatial scale of interactions, and natural enemies [17]. This highlights the importance of environmental context for biodiversity research and the need for system-specific analyses [18]. TreeDivNet is also playing a key role in highlighting the importance of other trophic levels, such as microbes, in mediating diversity effects in tree communities [11, 19].

Real world applications

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

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

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

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

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

Outstanding questions and research priorities

The extension of biodiversity - ecosystem functioning research into forests is improving ecologists' capacity to understand the mechanistic bases sustaining diversity effects, and presents opportunities for novel research [14]. Since tree experiments enable measurements at individual, neighborhood and plot levels, they allow asking some key questions such as the scale at which diversity matters, and whether relationships and mechanisms change through time. Tree experiments also provide ample opportunities to use remote sensing and spectral approaches to study community dynamics, integrate belowground and aboveground processes, and scale-up the consequences of individual physiology and plasticity for ecosystem functioning. Fueled by mixed results from observational studies [20], some of the more recent additions to the network are asking whether and how diversity may buffer against climate change driven stresses, such as increased drought through manipulating water availability.

Calling out to fellow scientists

The oldest experiments in TreeDivNet are approaching two decades, but many are planned to run for much longer, and the network offers a unique infrastructure for long-term ecological research. A large number of publications have already been published (175; 158 peer-reviewed papers and 16 PhD thesis; Figure 1), and more research is underway. However, huge potential exists for further work, especially in areas outside the expertise of the current TreeDivNet teams. We encourage colleagues worldwide to suggest collaborative research making use of the TreeDivNet platform. Additional experiments in underrepresented forest biomes are also much needed in order to foster and strengthen synthesis studies as well as enable transfer of well-founded knowledge to stakeholders worldwide [5]. The network needs to expand conceptually, for example by developing designs for the next generation of experiments that may better isolate the mechanisms that lead to diversity effects. We should also address the new questions and challenges posed to forest ecosystems by global changes, such as an increased frequency of severe droughts, floods and storms. Also, to be successful at turning the tide on the use of monocultures in plantation forestry, the network needs to foster operational scale experiments to demonstrate not only the benefits of diversity at scales that matter to managers, but their feasibility as well [21, 22]. In short, additional (long-term) data collection in existing experiments and the set-up of new experiments are needed to further increase the impact of the network.

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Author Contributions

The concept was developed at the plenary TreeDivNet meeting in Bordeaux, February 2017. The first draft was written by AH and AP, with later input from BC, MV, KV, JK, MSL, and all TreeDivNet members[7].

Declaration of Financial Competing Interests

The authors declare no competing financial interest.

[7] **Members of the TreeDivNet are:**

Abdala-Roberts, Luis; Auge, Harald; Barsoum, Nadia; Bauhus, Jürgen; Baum, Christel; Bruelheide, Helge; Castagneyrol, Bastien; Cavender-Bares, Jeannine; Eisenhauer, Nico; Ferlian, Olga; Ganade, Gislene; Godbold, Douglas; Göransson, Hans; Gravel, Dominique; Hall, Jefferson; Hector, Andy; Hobbs, Richard; Hoelscher, Dirk; Hulvey, Kristin B.; Huxham, Mark; Jactel, Hervé; Koricheva, Julia; Kreft, Holger; Liang, Jingjing; Mereu, Simone; Messier, Christian; Montgomery, Rebecca; Muys, Bart; Nock, Charles; Paquette, Alain; Parker, Bill; Parker, John; Parra-Tabla, Victor; Perring, Mike; Ponette, Quentin; Potvin, Catherine; Reich, Peter; Rewald, Boris; Scherer-Lorenzen, Michael; Smith, Andy; Standish, Rachel; Vanhellemont, Margot; Verheyen, Kris; Weih, Martin; Wollni, Meik; Zemp, Clara

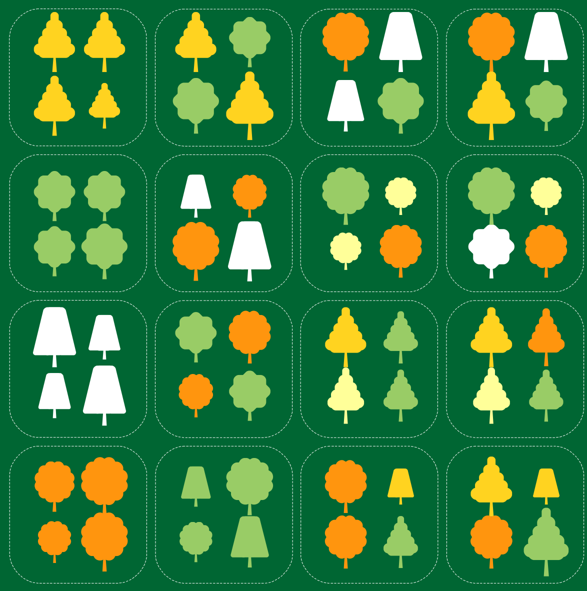
Figure 1. TreeDivNet in winter 2018.

230 Tree species

1 116 247 Planted trees

Initiated in **1999**

Now covering **821** hectares



3 diversity gradients
genetic, functional, species

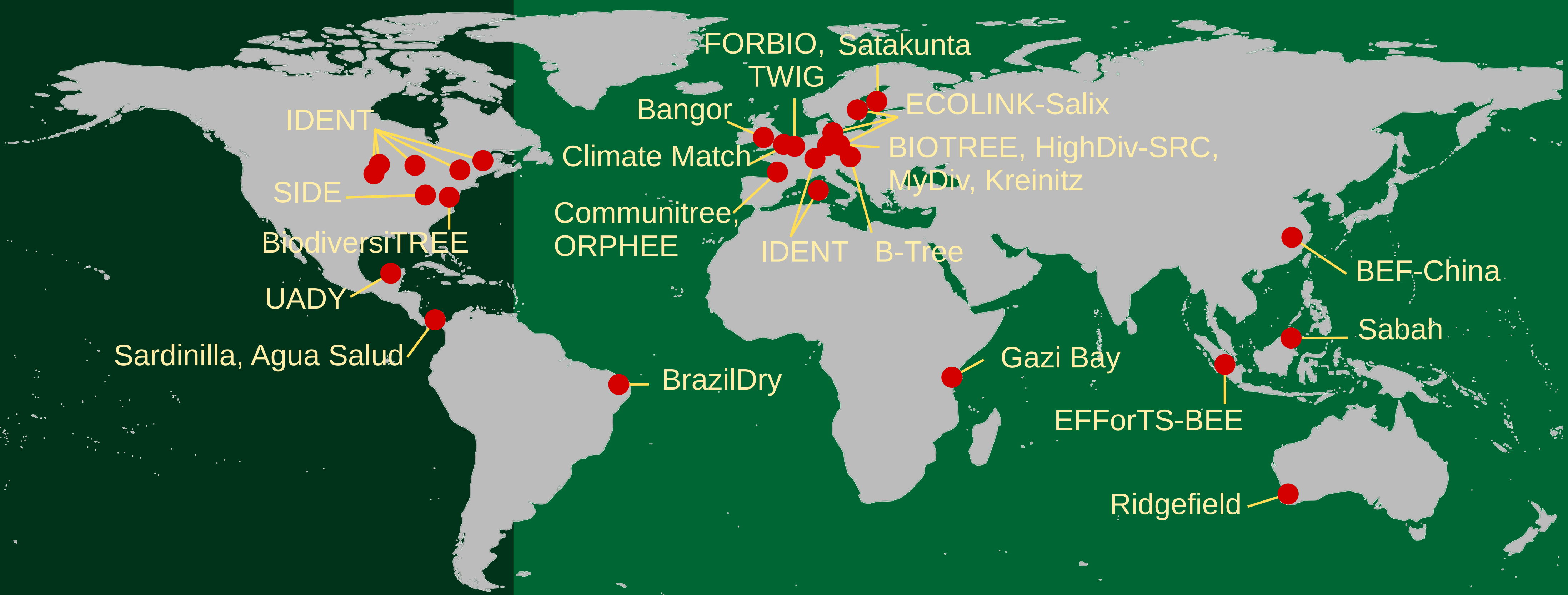
4818 experimental plots

Forest biodiversity and ecosystem functioning

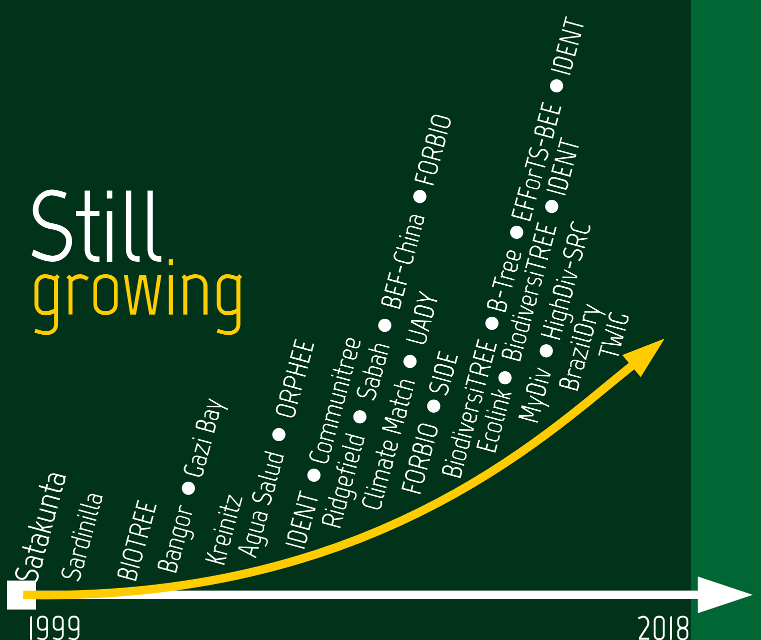
TreeDivNet

Tree Diversity Network • www.treedivnet.ugent.be

25 experiments • 45 sites • 6 continents



Still growing



43 partners

175 publications

158 papers, 1 book chapter
16 PhD theses