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Enhancing tree performance through species mixing: review of a quarter-century TreeDivNet experiments revealing research gaps and practical insights

Authors:

Leen Depauw[1,*], Emiel De Lombaerde[1,*], Els Dhiedt[1,2], Haben Blondeel[1], Luis Abdala-Roberts[3], Harald Auge[4,5], Nadia Barsoum[6], Jürgen Bauhus[7], Chengjin Chu[8], Abebe Damtew[9,10], Nico Eisenhauer[11,12], Marina V Fagundes[13], Gislene Ganade[13], Benoit Gendreau-Berthiaume[14], Douglas Godbold[15,16], Dominique Gravel[17], Joannès Guillemot[18,19,20], Peter Hajek[21], Andrew Hector[22], Bruno Hérault[23,24], Hervé Jactel[25], Julia Koricheva[26], Holger Kreft[27], Xiaojuan Liu[28], Simone Mereu[29,30], Christian Messier[31, 32], Bart Muys[9], Alain Paquette[33], John D. Parker[34], William C Parker[35], Gustavo B Paterno[27], Michael P Perring[2,36], Quentin Ponette[37], Catherine Potvin[38], Peter B. Reich[39,40], Boris Rewald[16], Michael Scherer-Lorenzen[21], Florian Schnabel[7,41], Rita Sousa-Silva[42,43], Martin Weih[44], Delphine Clara Zemp[45], Kris Verheyen[1§], Lander Baeten[1§]

*shared first authorship, corresponding authors: leen.depauw@ugent.be, emiel.delombaerde@ugent.be

[§] shared senior authorship

Affiliations:

1 Forest & Nature Lab, Campus Gontrode, Ghent University, Geraardsbergsesteenweg 267, BE-9090 Melle-Gontrode, Belgium

2 UKCEH, Environment Centre Wales, Deiniol Road, Bangor, Gwynedd, LL57 2UW, UK

3 Departamento de Ecología, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Km. 15.5 Carretera Mérida-Xmatkuil Mérida, Yucatán, 97000, México

4 Helmholtz Centre for Environmental Research - UFZ, Theodor-Lieser-Strasse 4, 06120 Halle, Germany

5 German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, 04103 Leipzig, Germany

6 Forest Research, Alice Holt Lodge, Farnham, Surrey, GU10 4LH, UK

7 Chair of Silviculture, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacherstr. 4, 79106 Freiburg, Germany

8 State Key Laboratory of Biocontrol, School of Ecology, Shenzhen Campus of Sun Yat-sen University, Shenzhen, 518107, China

9 Division of Forest, Nature and Landscape, Department of Earth & Environmental Sciences, KU Leuven

10 Department of Land Resources Management and Environmental Protection, Mekelle University, Ethiopia

11 German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig; Puschstrasse 4, 04103 Leipzig, Germany

12 Institute of Biology, Leipzig University; Puschstrasse 4, 04103 Leipzig, Germany

13 Department of Ecology, Centre for Bioscience, Federal University of Rio Grande do Norte, UFRN, Lagoa Nova, CEP:59.072-970, Natal, RN, Brazil

14 Institut des Sciences de la Forêt tempérée (ISFORT), Université du Québec en Outaouais, Gatineau, Quebec, Canada

15 Institute of Forest Ecology, Universität für Bodenkultur, 1180, Vienna, Austria

16 Department of Forest Protection and Wildlife Management, Mendel University, 613 00 Brno, Czech Republic

17 Département de biologie, Université de Sherbrooke, 2500 Boul. Université, Sherbrooke, Canada

18 CIRAD, UMR Eco&Sols, Montpellier, France

19 Eco&Sols, Univ. Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France

20 Department of Forest Sciences, ESALQ, University of São Paulo, Piracicaba, São Paulo, Brazil

21 University of Freiburg, Faculty of Biology, Geobotany, Schaenzlestr. 1, D-79104 Freoburg, Germany

22 Department of Plant Sciences, University of Oxford, Oxford, UK

23 CIRAD, UPR Forêts et Sociétés, F-34398 Montpellier, France

24 Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France

25 INRAE, Université de Bordeaux, Cestas, France

26 Department of Biological Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX, United Kingdom

27 Biodiversity, Macroecology and Biogeography, University of Göttingen, Germany

28 State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, the Chinese Academy of Sciences, 100093 Beijing, China

29 National Research Council of Italy, Institute of BioEconomy, Traversa La Crucca 3, 07100, Sassari.

30 National Biodiversity Future Center S.c.a.r.l., (NBFC), Palazzo Steri, Piazza Marina 61, Palermo, 90133, Italy

31 Institut des Sciences de la Forêt tempérée (ISFORT), Université du Québec en Outaouais, Gatineau, Quebec, Canada

32 Département des sciences biologiques, Université du Québec à Montréal, Montréal, Quebec, Canada

33 Centre for Forest Research, Université du Québec à Montréal, Montréal, Canada

34 Smithsonian Environmental Research Center, Edgewater, Maryland, USA

35 Ontario Ministry of Natural Resources and Forestry, Sault Ste. Marie, ON, Canada

36 The UWA Institute of Agriculture, The University of Western Australia, Perth, WA 6001, Australia

37 UCLouvain, Earth & Life Institute, Louvain-la-Neuve, Belgium

38 Department of Biology, McGill University, Montreal Quebec Canada and Smithsonian Tropical Research Insitute Panama

39 Institute for Global Change Biology and School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA

40 Department of Forest Resources, University of Minnesota, St. Paul, MN, USA

41 Systematic Botany and Functional Biodiversity, Leipzig University, Johannisallee 21, 04103 Leipzig, Germany

42 Young Academy for Sustainability Research, Freiburg Institute for Advanced Studies, University of Freiburg, Albertstraße 19, 79104, Freiburg im Breisgau, Germany

43 Institute of Environmental Sciences, Leiden University, P.O. Box 9518, 2300 RA Leiden, The Netherlands

44 Department of Crop Production Ecology, Swedish University of Agricultural Sciences, 750 07 Uppsala, Sweden

45 Laboratory of conservation biology, University of Neuchâtel, Switzerland

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Abstract:

Purpose of review

International ambitions for massive afforestation and restoration are high. To make these investments sustainable and resilient under future climate change, science is calling for a shift from planting monocultures to mixed forests. But what is the scientific basis for promoting diverse plantations, and what is the feasibility of their establishment and management? As the largest global network of tree diversity experiments, TreeDivNet is uniquely positioned to answer these pressing questions. Building on 428 peer-reviewed TreeDivNet studies, combined with the results of a questionnaire completed by managers of 32 TreeDivNet sites, we aimed to answer the following questions: (i) How and where have TreeDivNet experiments enabled the relationship between tree diversity and tree performance (including productivity, survival, and pathogen damage) to be studied, and what has been learned? (ii) What are the remaining key knowledge gaps in our understanding of the relationship between tree diversity and tree performance? (iii) What practical insights can be gained from the TreeDivNet experiments for operational, real-world forest plantations?

Recent findings

We developed a conceptual framework that identifies the variety of pathways through which target tree performance is related to local neighbourhood diversity and mapped the research efforts for each of those pathways. Experimental research on forest mixtures has focused primarily on direct tree diversity effects on productivity, with generally positive effects of species and functional diversity on productivity. Fewer studies focused on indirect effects mediated via biotic growing conditions (e.g. soil microbes and herbivores) and resource availability and uptake. Most studies examining light uptake found positive effects of species diversity. For pests and diseases, the evidence points mostly towards lower levels of infection for target trees when growing in mixed plantations. Tree diversity effects on the abiotic growing conditions (e.g. microclimate, soil properties) and resource-use efficiency have been less well studied to date. The majority of tree diversity experiments is situated in temperate forests, while (sub)tropical forests, and boreal forests in particular, remain underrepresented.

Summary

TreeDivNet provides evidence in favour of mixing tree species to increase tree productivity while identifying a variety of different processes that drive these diversity effects. The design, scale, age, and management of TreeDivNet experiments reflect their focus on fundamental research questions pertaining to tree diversity-ecosystem function relationships and this scientific focus complicates translation of findings into direct practical management guidelines. Future research could focus on (i) filling the knowledge gaps related to underlying processes of tree diversity effects to better design plantation schemes, (ii) identifying optimal species mixtures, and (iii) developing practical approaches to make experimental mixed plantings more management oriented.

Main text:

Introduction

Forest landscape restoration and afforestation are receiving wide international attention as they are considered key nature-based solutions to mitigate several global crises, including climate change, biodiversity loss, and rural poverty [1–5]. This importance has been reflected in highly ambitious global initiatives such as the 2011 Bonn Challenge [6], the 2014 New York Declaration on Forests, which pledged to restore 350 million ha of forest globally by 2030, the UN Decade on Restoration, China’s Grain-for-Green Program [7] and many more [e.g. 8–10]. Also in the Global South forest restoration interest is high with AFR100, for instance, a country-led effort to afforest 100 million hectares of land in Africa by 2030. Thirty-one African governments have signed up to AFR100, with each country pledging to afforest an explicit target area (https://afr100.org).

Forest plantations provide an increasingly large share of global wood products, which can be used as substitutes for more greenhouse gas-intensive materials like concrete [11]. High-yielding plantations can also contribute to land sparing for biodiversity conservation by reducing land-use pressure on natural forests [12, 13], depending on policy and economic context [14]. However, climate change is putting forests under pressure through the increasing frequency and severity of stress and disturbances like droughts and biotic infestations such as insect outbreaks [15]. This compromises the ability of forests to act as carbon sinks and provide numerous key ecosystem services [16, 17]. Therefore, the ability of forests to provide ecosystem services in the long run will depend on how well trees perform and can maintain ecosystem functioning under predicted future global change.

There is considerable evidence from experiments and observations that greater diversity leads to greater forest productivity and resiliency, in natural and plantation systems, and in many different biomes [18–20]; hence the question arises of whether we can deploy the underlying mechanisms in plantation forestry. A growing body of evidence suggests that mixed forest plantations, i.e. plantations where multiple tree species (or varieties) are growing together at the patch or individual scale and interact, can be more efficient in biomass accumulation compared to monocultures [21–26]. Moreover, mixed forests can also better cope with climate change-related stress and other disturbances, such as droughts, pests, diseases, fires and windstorms [27, 28].

Mixed plantations could thus represent a valuable tool to attain multifunctional, resilient, and productive forests for the future. Yet, monocultures still dominate forest plantations across the globe [29]. Forest owners and managers have identified multiple constraints that are still hindering a wide adoption of mixed plantations, including logistical (e.g. requirement of highly trained workers and specialized machinery), economic (e.g. costs of more complex management operations), and cultural and historical (e.g. professional and public perceptions, prejudices) challenges [30–32]. However, the most important constraint, which is likely at the root of landowner's and stakeholder's reluctance to adopt mixed plantations, is the lack of information and evidence regarding benefits of mixtures and how they can be successfully established and maintained [23]. Hence, scientific research should not only assess the benefits or disadvantages of diverse plantations in terms of ecosystem services and their sustained provision under global change [e.g. 33], but also the feasibility and costs to establish, manage, and harvest them [22, 32]. Moreover, the multifunctional benefits of biodiverse tree plantations as well as the underlying mechanisms at play may depend on the environmental context [34], in addition to the plantation layout in terms of density and species composition.

TreeDivNet is a global network of tree diversity experiments with sites in various environmental contexts and testing a wide range of species compositions. It provides a unique platform to respond to the need for a science-based understanding of the benefits and drawbacks of mixed forest plantations [23]. Findings from the first 15 years of TreeDivNet on the consequences of diversity for tree growth, tree survival, and tree damage by pests and pathogens were reviewed by Grossman et al. (2018) [21]. Here, we reviewed all 428 studies originating from more than 20 years of research within TreeDivNet, aiming not only to reveal diversity effects on tree performance, but also to reveal the different mechanistic pathways enabling these diversity effects, and which of these pathways remain understudied. Moreover, in addition to earlier TreeDivNet reviews [21–23], we aimed to uncover the main challenges related to bridging theoretical knowledge with practical implementation in real-world operational forest plantations. Our review will answer the following questions:

(i) How and where have TreeDivNet experiments enabled the relationship between tree diversity and tree performance to be studied, and what has been learned?

(ii) What are the remaining key knowledge gaps in our understanding of the relationship between tree diversity and tree performance?

(iii) What practical insights can be gained from the TreeDivNet experiments for operational, real-world forest plantations?

While we focus our review and research questions on individual tree performance, representing local scale effects, we consider that good individual tree performance is a prerequisite for healthy, resilient, and productive plantation stands at larger spatial scales.

In our review, we first introduce the conceptual framework around which our synthesis is built. Next, we elaborate on TreeDivNet and data collection (literature review and questionnaire). Finally, we present and discuss our findings structured around our three research questions.

Conceptual framework: how does tree diversity alter tree performance?

Healthy and productive trees are the basis of well-functioning forests and thus the provisioning of ecosystem services. Therefore, we focus our review on the influence of tree species mixing on tree performance. In order to systematically synthesize the TreeDivNet studies, we developed a comprehensive framework identifying various pathways through which the performance of a target tree is related to the diversity or composition of the local tree neighbourhood (Fig. 1). We focus the framework on effects occurring at the local scale, i.e. between a target tree and its directly neighbouring trees, assuming that for relatively young plantations, with limited mortality, diversity effects at the larger plot or stand level are the combined result of local scale tree level interactions [35]. This way, both studies at the community or plot level, which were initially the main focus of TreeDivNet, and studies on the individual scale, which have increased in recent years, could be mapped on our conceptual framework and included in this review to investigate tree diversity effects. However, we should recognize that while studying tree-level interactions can improve our understanding, it does not fully explain stand-level behaviour, and vice versa [see [36]]. TreeDivNet studies have typically evaluated tree performance as tree productivity, survival, and damage level due to herbivory or infestation by pests or diseases. The specific interpretation of tree performance within the framework depends on the context of each study, but, in general, the framework assumes that good tree performance is a prerequisite for healthy, resilient, and productive trees.

The framework identifies three key components that regulate the effect of local neighbourhood diversity on tree performance: growing conditions, resources, and functional traits (Fig. 1). Both aboveground and belowground **growing conditions** will alter tree performance. We made a distinction between abiotic growing conditions, including soil pH, carbon content, soil texture or structure (belowground) and microclimate (aboveground), and biotic growing conditions, including the herbivore community (aboveground) and the soil and leaf microbial community (below- and aboveground). In addition to suitable growing conditions, a tree needs **resources**: water, nutrients, and light. Its performance will depend on three factors related to resources: (i) resource availability is the amount of a resource available to the target tree, (ii) resource uptake is the amount of a resource that the tree can take up, and (iii) resource-use efficiency defines how efficiently a tree can invest these resources into its growth [37]. The third and final linking component between tree diversity and tree performance are **functional traits**. Adapting the framework by Suding et al. [38], we distinguish functional effect traits from functional response traits. The neighbouring trees can mediate the growing conditions and resources for the target tree via their *functional effect traits*.

For instance, the height of neighbouring trees can influence the probability of the target tree being found by herbivores [39]. The shade-casting ability of trees in the local neighbourhood can affect light availability for the target tree, hence altering its growth [40]. The target tree can then, in turn, respond differently to growing conditions and resources, depending on its own *functional response traits*. For instance, plant metabolite and leaf elemental concentrations of the target tree may affect the level of infestation by herbivores and pathogens [41]. Fine-root traits such as root diameter and specific root length can alter the ability of the target tree to take up nutrients and water [42].

In TreeDivNet experiments, tree communities are manipulated in experimental plots with a gradient of tree diversity. We distinguished the following four facets of diversity: (i) **species diversity** or taxonomic diversity (e.g. species richness, Simpson index, Shannon-Wiener index and evenness); (ii) **functional diversity**, i.e. the diversity of functional effect traits; (iii) **genetic diversity** (including both phylogenetic diversity and genetic variation within tree species originating from different seed provenances); (iv) finally, **identity effects** are known to play a key role in the impact of the neighbourhood community on target tree performance. This is defined as the effect of the presence of a specific species within a species mixture, or the effect of the composition of a certain mixture.

Within our framework, we define structural diversity as variation in height or crown structural complexity as an expression of a tree species' functional traits, and therefore group this with functional diversity. We acknowledge that structural diversity can also emerge from staggered planting using different aged trees. However, given that this is not generally applied in the TreeDivNet experiments (with exception of the BEF-Agroforestry experiments [43]), structural diversity as an independent gradient is not included in our framework. Note that the experiments vary to some degree in planting densities, species mixing patterns, and developmental stages, but this variation is only found *across* experiments, while the focus of the conceptual framework is to capture tree performance responses to treatments *within* experiments, i.e. principally tree diversity gradients. Therefore, cross-experiment mediators such as planting density and development stage are not included in the conceptual framework of this study, despite their potential to alter tree performance responses to mixing. Note that the recently established TWIG experiment (2017) applies a planting density gradient, which will allow to explore density effects also *within* experiments in the future.

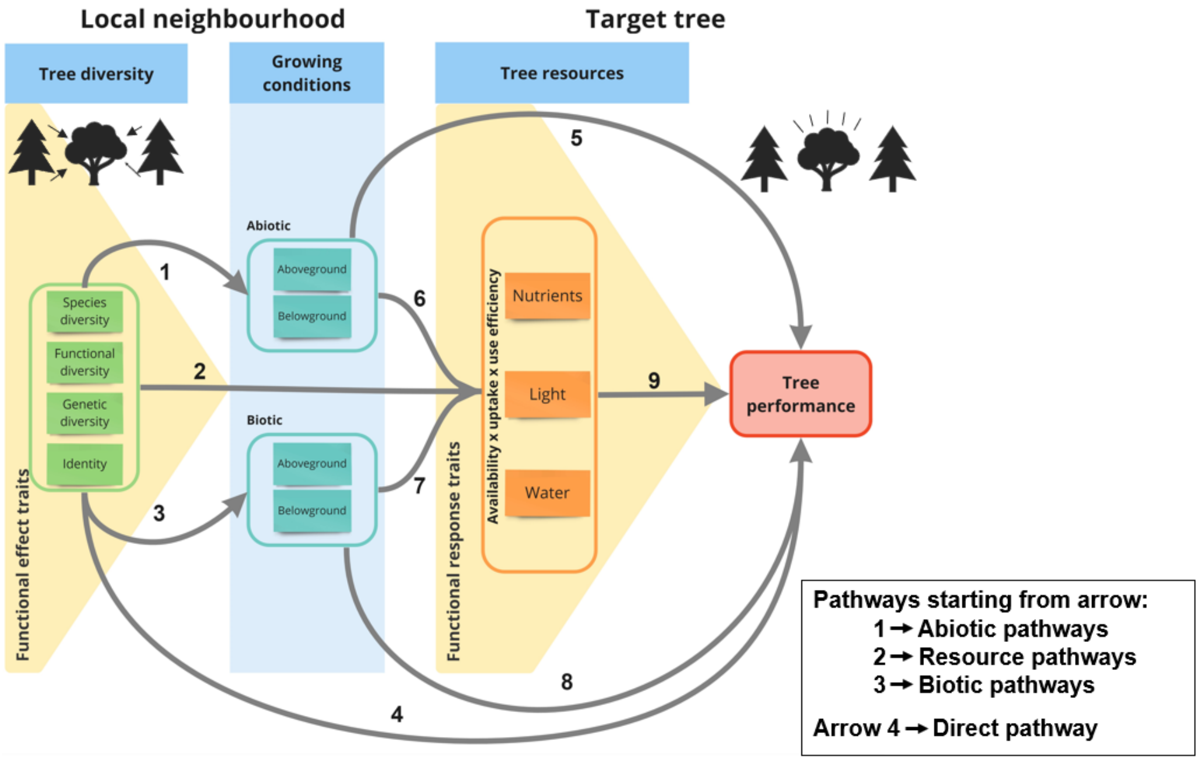

Figure 1. Conceptual framework identifying three key components that regulate the effect of local neighbourhood diversity on tree performance: functional traits, growing conditions, and resources. Both aboveground and belowground **growing conditions** will alter tree performance. In addition, the availability, uptake and use-efficiency of **resources** will alter tree performance. **Functional traits** represent the third and final linking component between tree diversity and tree performance. Neighbouring trees can mediate the growing conditions and resources for the target tree via their *functional effect traits*. The target tree can respond differently to growing conditions and resources, depending on its own *functional response traits*. Four different groups of pathways through which local neighbourhood diversity can affect target tree performance can be distinguished in the framework. (i) Abiotic pathways, comprising arrow 1, and combinations of arrow 1 with subsequent arrows (arrow 1+5, arrow 1+6 and arrow 1+6+9); (ii) biotic pathways, comprising arrow 3, and

combinations of arrow 3 with subsequent arrows (arrow 3+8, arrow 3+7 and arrow 3+7+9); (iii) resource pathways, comprising arrow 2, and arrow 2+9; and (iv) the direct pathway (i.e. without considering the underlying biological processes behind any effects), arrow 4. Yellow triangles represent the underlying influence of effect and response traits.

Data collection and extraction

TreeDivNet

TreeDivNet is the largest global network of tree diversity experiments (treedivnet.ugent.be) [22]. At present, it consists of 29 experiments, spread across 21 countries and 6 continents, in the boreal, temperate, and (sub)tropical ecoregions [44]. The oldest experiment was planted in 1999 (Satakunta, Finland), and the most recent experiment was established in 2022 (BEF-Agroforestry, Bolivia). To allow testing the effects of diversity, the unifying characteristic of all experiments is that tree species are grown in both monoculture and mixture plots, and that tree diversity levels up to a minimum of three species are replicated in a randomized design at the community scale. In this way, TreeDivNet provides a unique platform to investigate the benefits and drawbacks of mixed species plantations. Notably, The International Diversity Experiment Network with Trees (IDENT) is a sub-network consisting of nine diversity experiments in North America, Europe and Africa. The focus of IDENT is on early successional stages of stand development thus the trees are planted in high density, i.e., 40 to 60 cm apart, to accelerate species interactions [45].

Here, we tap into the TreeDivNet network using two different approaches. First, we reviewed all studies that were published in scientific journals and based on one or multiple TreeDivNet experiments, to obtain an overview of what can be learned from 23 years of tree diversity experiments, in terms of tree, plot, and stand level performance. Second, we asked the site managers from each experiment to complete an in-depth survey about their insights and experiences, in particular with regard to the practical challenges related to managing mixtures vs.

monocultures. The main goal of this survey was to complement the literature review with insights from a management perspective that are often not considered in scientific publications.

Scientific literature review

We started the review with a pool of 428 studies originating from the TreeDivNet experiments actively archived on the network's web page (https://treedivnet.ugent.be/), all published in peer-reviewed international journals before October 2022. To check whether the TreeDivNet output covers a representative share of the experimental research on tree diversity, we did a literature search on Web of Science using the following search string: Tree AND diversity AND experiment AND (plantation OR "planted forest" OR afforestation). This did not yield any additional experiments meeting the criteria of TreeDivNet (see treedivnet.ugent.be/mission), suggesting that the 428 TreeDivNet studies are highly representative of the scientific knowledge gained from tree diversity experiments. We only included studies that reported effects of one or more diversity metrics on either target tree performance directly, or on the growing conditions or resources for the target tree. Meta-analyses, review papers, perspectives, experimental design papers, and research papers that did not assess tree diversity effects were excluded. This resulted in a list of 215 relevant papers for our review. We then mapped each study onto the conceptual framework, extracting the investigated diversity metric(s), mechanistic pathway(s), and response variable(s). Response variables were grouped into logical categories, depending on the pathway. For instance, for the resource pathway, response variables were grouped into light, nutrients and water, and within each of these resources, into availability, uptake and use-efficiency, resulting in nine response categories for the resource pathway. These categories are explained in detail in the results section, and shown in Table 1.

We considered each set of diversity metric, pathway, and response variable as an individual *case*. This means that one study can contain multiple cases, for instance when exploring multiple measures of diversity, multiple pathways or response variables, or when investigating more than one TreeDivNet site and reporting separate results for each site. For each case, we extracted the sign of the effect that was found (i.e., positive or negative) or noted if no significant effects were found or if effects were multidirectional. A multidirectional effect occurred, for instance, when effects of tree diversity on tree performance were dependent on the identity (species) of the target tree, or when tree diversity effects in herbivore abundance differed among herbivore groups. We did not assign any direction to identity effects, but only reported whether identity effects were significant or not. Below, we report how many cases represent each pathway and assign a direction of the relationship between the response category and tree diversity based on the results of the considered studies. We provide readers with a systematic overview of where research efforts have been focused (what processes and mechanisms), where evidence of the presence of diversity effects has been found and under which conditions, and which pathways have received little attention. We want to stress that we did not perform a quantitative analysis (*sensu* meta-analysis), thus no statistical conclusions should be drawn from the results we present.

Questionnaire

Complementary to the literature review, we developed a questionnaire that was sent out to the managers of all TreeDivNet sites (N = 39; see Appendix S3 for an overview of experiments and sites), to uncover the main challenges related to bridging theoretical knowledge with practical implementation. The aim of this questionnaire was to learn from hands-on experience and gain insights into transfer of results to forest management. Managers of TreeDivNet experiments are mostly academics, who typically do not have the same constraints, barriers, and objectives of “real-world” forest managers. Consequently, this questionnaire did not aim at drawing general guidelines regarding the management of mixed species plantations at a large scale, but rather to evaluate to what extent the TreeDivNet experiments reflect real-world plantations and can produce transferable knowledge. The questions referred to four development stages in tree plantations, as challenges can depend on the age of the plantation. First, the *design stage* entails all decisions and interventions done before planting, such as species selection, and choice of planting design and tree density. Second, the *establishment stage* covers the time between planting and canopy closure. Third, when the closed-canopy stage starts, this is a period of intense height growth where aboveground tree interactions become more and more apparent. Fourth, the *stem-exclusion stage* has been reached when mortality increases due to intense inter-tree competition and self-thinning. This is typically the stage in which, from a silvicultural point of view, stands need to be thinned for the first time. A mature and final harvesting stage was not considered since the vast majority of TreeDivNet experiments are still too young.

Our questionnaire was completed by the managers of 34of the 42 experimental sites. Two of these 34 sites have been terminated, and 32 were still active at the time of this review. The mean age of the experiments was approximately ten years. Thirteen experiments have entered the stem-exclusion stage (six excluding IDENT experiments which use very dense planting schemes close to those found following natural regeneration but far from typical tree spacings used in plantation management to mimic early interactions among seedlings following stand-replacing disturbance), and eleven experiments are currently fully in the closed-canopy stage (six excluding IDENT experiments) and will reach the stem-exclusion stage in the near future.

In broad terms, the questionnaire can be divided into four major parts. For a list of actions and decisions in the **design stage**, we asked the managers if and how choices were influenced by planting mixtures instead of monocultures. For each of the **next three development stages**, we inquired about (i) challenges encountered, (ii) possible causes of the challenges, (iii) actions taken in response to the challenges, and (iv) the outcome of the response to the challenges. To achieve some level of standardization, challenges were categorised into major dieback events, reductions in tree health, reductions in tree quality, and other challenges. Next, we asked for **future perspectives** for the experimental site, including the long-term ambitions, expected future challenges and their possible causes, and planned management actions in order to reach the long-term ambitions and tackle the expected challenges. Finally, we asked site managers whether they could identify **best-performing mixtures** in their stands. The full questionnaire can be found in Appendix S4.

Results and Discussion

How and where have TreeDivNet experiments enabled the relationship between tree diversity and tree performance to be studied, and what has been learned?

We synthesized a total of 215 studies, comprising 635 cases (for an overview see Appendix S2). We only present and discuss the pathways in Fig. 1 that start from tree diversity effects, as this effect was a prerequisite for including a study in this synthesis. Hence, arrows 5, 6, 7, 8 and 9 by themselves will not be discussed, unless they are part of a combined pathway, such as the much-investigated pathway 3+8 (see further).

Tree diversity effects on biotic growing conditions (pathway 3 in Fig. 1) were the most represented in the TreeDivNet literature with a total of 211 cases investigated, followed by the direct pathway of diversity to tree performance (pathway 4 in Fig. 1) with a total of 180 cases investigated. The diversity effect on resources (pathway 2 in Fig. 1) was investigated in 99 cases, and the diversity effect on tree performance via biotic conditions (pathway 3+8 combined in Fig. 1) in 91 cases. These four most investigated pathways (Fig. 2) are discussed later in detail.

Only 12 studies (29 cases) investigated the effect of tree diversity on abiotic growing conditions (pathway 1 in Fig. 1). This mainly involved studies on diversity effects on soil conditions, such as bulk density, soil carbon, and soil pH [46–51], but also two studies on diversity effects on microclimate [52, 53], and a few studies on how soil erosion is affected by tree diversity [54–56]. While the effect of diversity on tree resources (pathway 2 in Fig. 1) was well-studied, only a few studies also looked at how this could alter tree performance (pathway 2+9). For example, Dillen et al. [57] investigated diversity effects on growth via differences in shade-casting ability of the neighbouring trees, and thus via light availability for the target tree. Schnabel et al. [58] assessed how functional diversity of drought-tolerance traits impacts growth and growth stability. One study investigated diversity effects on resources via biotic conditions (pathway 3+7 in Fig. 1): Koczorski et al. [59] investigated P availability in the soil, via the effect of tree diversity on P-solubilizing fungi.

The temperate biome was best represented within all cases (N=326 out of 635 cases). The number of cases per pathway for temperate forests followed the same trend as when looking at all biomes together, although the pathway on tree performance via biotic conditions (arrow 3+8) was slightly more represented in temperate forests than the resource pathway (arrow 2) (Fig. 2). The tropical biome was second best represented (N=149), but for tropical forests (unlike in temperate forests), there was a stronger focus on the direct diversity effects on tree performance (arrow 4) than on diversity effects on biotic conditions (arrow 3). The effect on tree performance via biotic conditions (arrow 3+8) was much less represented in tropical forests compared to temperate forests, where TreeDivNet research has focused very strongly on this aspect of tree diversity effects. In subtropical forests (N=97), dominated by cases from the BEF-China experiment, the focus was mainly on diversity effects on biotic growing conditions (arrow 3). Boreal (N=53) and Mediterranean (N=8) forests were strongly underrepresented within the TreeDivNet studies.

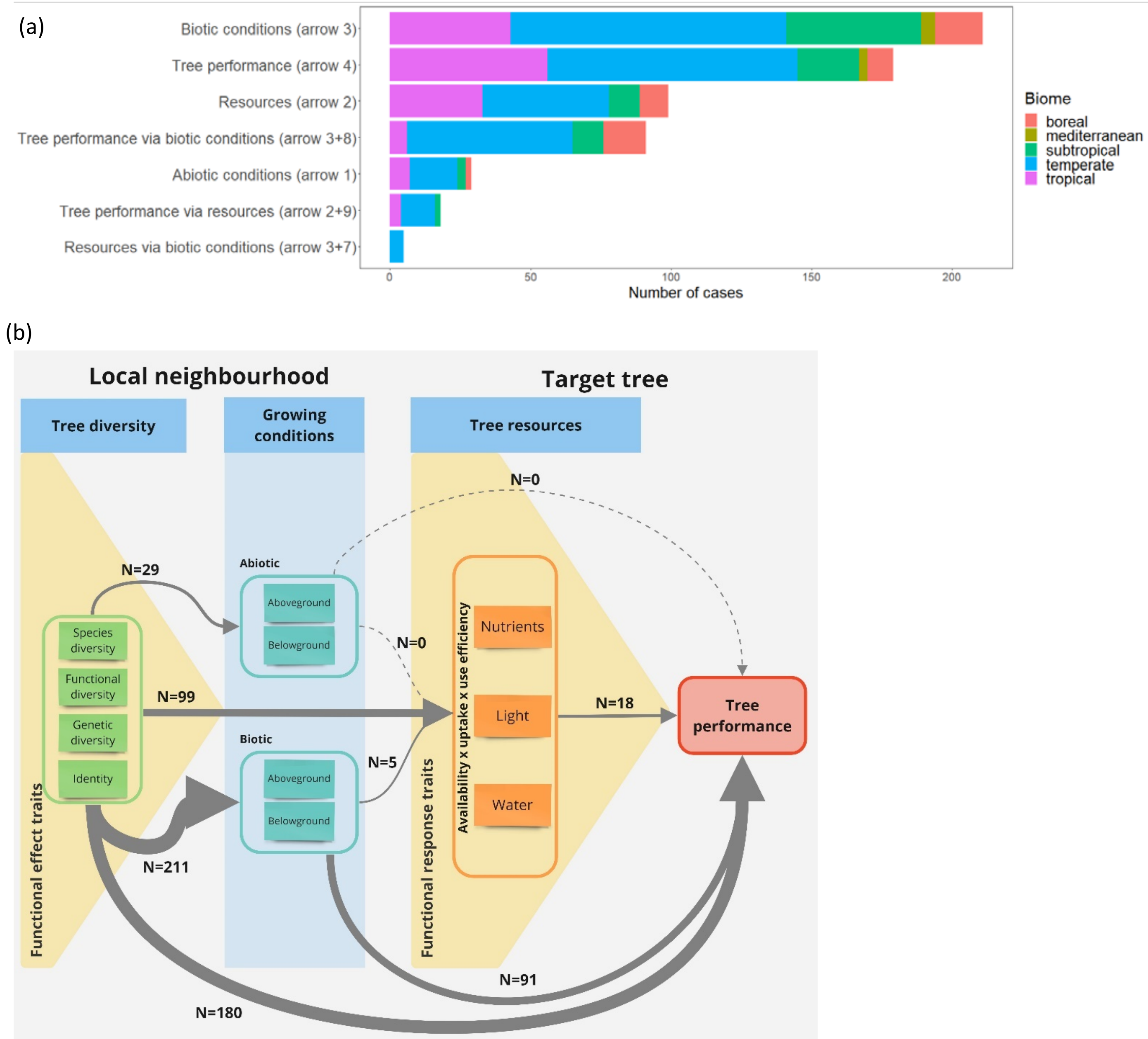

Figure 2. Number of investigated cases per pathway of the conceptual framework. (a) Pathways are ranked according to their number of cases within the TreeDivNet literature. Colours indicate how the pathways and cases are spread across different biomes. (b) Conceptual framework (see Fig. 1) with the width of the arrows indicating the number of cases within the TreeDivNet literature; dashed lines indicate no cases.

Pathway	Category	Species diversity		Functional diversity		Genetic diversity		Identity	
		N	Direction	N	Direction	N	Direction	N	Frequency
2	Light availability	2		1		0		0	
2	Light uptake	12	↗	2		0		5	
2	Light use efficiency	2		0		0		0	
2	Nutrients availability	8		1		2		9	
2	Nutrients uptake	9		0		2		8	
2	Nutrients use efficiency	3		0		0		3	
2	Water availability	1		0		0		0	
2	Water uptake	11	↻	0		1		10	
2	Water use efficiency	5		0		0		2	
2,9	Productivity via light	8		1		0		6	
2,9	Productivity via nutrients	1		0		0		0	
2,9	Productivity via water	1		1		0		0	
3	Birds	2		0		0		0	
3	Decomposition	12	↻	2		3		10	
3	Herbivore predation and resistance to herbivory	11	✕	0		2		5	
3	Invertebrates	25	✕	10	✕	8		10	
3	Microbiota	45	↻	7		26	↻	21	
3	Plants	6		1		0		5	
3,7	Nutrient availability via biotic conditions	0		0		3		2	
3,8	Herbivory damage	28	✕	5		12	✕	12	
3,8	Pests and diseases	20	↘	2		3		9	
4	Productivity	77	↗	23	↗	14	↻	47	
4	Survival	11	✕	1		0		6	

↗ Majority of the studies reported a positive effect of species diversity

↘ Majority of the studies reported a negative effect of species diversity

✕ Multidirectional across studies: similar amounts of positive and negative effects

↻ Lack of statistical clarity: majority of the studies found no evidence of any diversity effect

Identity effect absent

Identity effect present

Table 1. Overview of the key results from the systematic literature review. Pathway numbers refer to Fig. 1. For pathways and response categories with more than 10 cases in the literature (N ≥ 10), we indicate (i) the main direction of the relationship that can be drawn on diversity effects on tree

performance from reviewing all the studies, and (ii) the frequency of studies that have reported the absence/presence of identity effects. In Appendix S1, we provide a larger table showing the frequencies of different effects found within the studies for all pathways and categories. Per pathway, responses were assigned to different categories. For pathway 2, i.e. the resources pathway, responses are categorized into light, nutrients and water, and three resource-related features, availability, uptake and use efficiency. To incorporate the wide variety of studies, often investigating these resources indirectly via proxies, strong assumptions were often required (see main text). Pathway 2+9 comprises studies that have looked at how diversity effects on resources have altered tree performance, and is categorized according to resources (light, water and/or nutrients). For pathway 3, i.e. the biotic pathway, results are divided into effects of tree diversity on four taxonomic groups (microbiota, invertebrates, plants and birds), decomposition of organic matter, and herbivore control through herbivore predation and defensive tree traits. For the taxonomic groups, responses can represent abundances, diversity measures or functioning (e.g. stability of trophobiotic networks). For herbivore control, responses could represent different types of indicators of herbivore predation (predation rates on fake caterpillars, number of spiderwebs, etc.) or defensive traits (e.g. concentration of phenols, volatile organic compounds or condensed tannins). For pathway 3+8, i.e. the pathway on diversity effect on tree performance via biotic conditions, results are shown for studies investigating tree damage by herbivores, and by pests and diseases. A positive (negative) effect on herbivory damage indicates more (less) damage to the target tree caused by herbivores with increasing levels of diversity. Similarly, a positive (negative) effect on pests and diseases indicates higher (lower) levels of infection for the target tree with increasing levels of diversity. For pathway 4, i.e. the direct performance pathway, results are divided into diversity effects on productivity and survival. N represents the number of investigated cases within TreeDivNet.

Tree diversity effects on biotic conditions (pathway 3)

Over all biomes together, pathway 3 (Fig. 1) was the most represented with N=211 cases investigating diversity effects on biotic growing conditions (Table 1). Many studies investigated the effect of tree diversity on the species diversity, abundance, and/or functioning of other taxonomic groups, which we categorized into birds, plants, invertebrates, and microbiota. We included the effect of tree diversity on this “associated” diversity in our framework assuming that these organisms influence the growing conditions of target trees, irrespective if this influence is positive or negative as this is not researched in these studies. Bird abundance and diversity was investigated in only two studies [60, 61]. Diversity effects on plants (i.e. herbs and shrubs) were assessed in 12 cases [62–67]. Invertebrates were much more often investigated within TreeDivNet, with a total of 53 cases investigating a wide variety of features related to invertebrate communities, such as the occurrence and stability of trophobiotic networks [e.g. 68, 69], abundance and diversity of arthropods [e.g. 70–73], earthworms [74], and insects such as leafhoppers [75], beetles [e.g. 76], wasps [e.g. 77] and ants [e.g. 78]. Effects of both species diversity and functional diversity on invertebrate features were multidirectional across studies (Table 1). With 99 cases, microbiota were by far the most investigated taxonomic group within TreeDivNet, including studies on fungal and bacterial communities both in the soil [e.g. 79, 80] and on the tree leaves [e.g. 81, 82], soil respiration [e.g. 83, 84], soil enzymatic activity [e.g. 47, 85], and mycorrhizal communities [e.g. 86–88]. However, for microbiota, we found the relationship with both species diversity and genetic diversity to be unclear (Table 1). The majority of cases reported the presence of identity effects on different features of plants, invertebrates, and microbiota (Table 1), indicating the importance of tree species composition.

In addition to the four taxonomic groups, two more categories of studies were included in biotic pathway 3. Decomposition of litter, wood, and roots was classified under the biotic pathway, as this will influence growing conditions for the target tree via its effect on nutrient and carbon cycling, as well as on tree regeneration, and on the functioning and composition of other taxonomic groups. Twenty-seven cases investigated diversity effects on decomposition, based on biomass loss in e.g. branches [e.g. 89, 90], litter bags [e.g. 91, 92], and tea bags [93]. The majority of the studies found no evidence of species diversity effects on decomposition, but identity effects were again important (Table 1). Finally, the sixth category in pathway 3 was 'herbivore control', comprising studies on herbivore predation and on tree defensive traits. Only studies that specifically measured predation levels, and not just, for instance, bird abundance, were included here. Several studies used model caterpillars made from plasticine to measure predation rates of arthropods and/or birds [e.g. 94–96], but also counts of spider webs [97], and assessment of mycophagy [98] were used to assess predation. In addition, survival of specific leaf herbivores was classified here [99, 100]. Also bottom-up control of herbivory, through assessing diversity effects on defensive traits of the target tree [101–103] were investigated in a few studies (five cases). Effects of species diversity on herbivore control were multidirectional across studies, with similar amounts of positive and negative effects. The impact of other diversity facets on herbivore control was not sufficiently studied to draw any conclusions (Table 1).

Diversity effect on tree performance via biotic conditions (pathway 3+8)

Studies that investigated diversity effects on tree damage by pests and diseases were classified under a pathway combining arrow 3 and 8 in the framework (91 cases; Fig. 1). The types of herbivory investigated ranged from moose browsing [e.g. 96, 104] and vole damage [105], to insect herbivory [e.g. 96] and damage by leaf miners, chewers, suckers, skeletonizers, rollers, galls, and webbers [e.g. 106–108]. Studies on infestation often examined foliar fungi [e.g. 98, 109, 110]. Some studies assessed damage in general, e.g. through defoliation and crown discoloration, or branch and shoot damage [e.g. 111].

For herbivore damage, the effects of species diversity and genetic diversity (functional diversity was not tested in a sufficient number of studies) are multidirectional as both positive and negative effects were regularly observed in studies (Table 1). Note that many studies on herbivory have investigated both herbivore abundance and damage, and that results for herbivore abundance is considered as a case within pathway 3, while results for herbivore damage is classified under pathway 3+8. For pests and diseases, the majority of evidence points toward a negative relationship with species diversity, indicating lower levels of infection for the target trees with increasing levels of diversity (Table 1). Effects of functional and genetic diversity on pests and diseases were not sufficiently tested to draw any conclusions. For both herbivore damage and pests and diseases, the majority of studies investigating identity effects confirmed their presence (Table 1).

Direct tree diversity effect on tree performance (pathway 4)

Studies investigating diversity effects on tree performance directly (N=179), i.e. without considering the underlying biological processes behind any effects, were divided into studies on productivity and studies on survival (Table 1). Studies on productivity were much more represented within the TreeDivNet literature (161 out of 179 cases), and comprised studies on a wide variety of measures of productivity, such as leaf area index [e.g. 112, 113], basal area [e.g. 25, 114], height [e.g. 115, 116], stem biomass or volume [e.g. 117, 118], shoot biomass [e.g. 119], crown width or volume [e.g. 120], and merchantable volume [121]. Several studies also looked at the temporal aspect, assessing the increment of these dendrometric variables over one or more years [e.g. 122, 123]. Also studies on litter production [92, 124, 125] and fruit production [126] were included here. Of the total number of investigated effects on productivity, 12% specifically explored belowground productivity, for instance in the form of fine root biomass and root length or productivity [e.g. 48, 116, 127, 128]. Wu et al. [112] assessed vegetation cover based on remote sensing as a proxy for productivity.

A small number of studies under pathway 4 examined diversity effects on tree survival (18 out of 179 cases). For instance, Van de Peer et al. [129] investigated cumulative sapling survival in mixtures. Tree mortality rates 2 to 7 years after planting were investigated by Mayoral et al. [130]. Survival was also assessed based on foliage discoloration and defoliation [131].

Both for functional diversity [e.g. 114, 122, 132] and species diversity [e.g. 25, 124] effects on productivity, more cases reported a positive effect than no effect, and only one case reported a negative effect of species diversity [101]. For genetic diversity, however, mostly no effect was reported [e.g. 75, 133, 134], one negative effect [135], and three positive effects have been shown [114, 136, 137]. Identity effects were also very important for productivity, with 42 cases finding a significant identity effect [e.g. 92, 117, 138], versus 6 cases reporting the absence of identity effects [e.g. 48, 133]. For survival, the few cases in the literature [e.g. 131, 139] are more evenly spread across the different possible outcomes (Table 1).

Diversity effect on tree resources (pathway 2)

Of the three main resources, diversity effects on nutrients were most often studied within TreeDivNet (45 cases), followed by effects on water (30 cases), and light (24 cases). We further distinguished between studies looking at resource availability (24 cases), uptake (60 cases), or use efficiency (15 cases) (Table 1). Most of these studies investigated these processes in an indirect way using proxies e.g. measuring $\delta^{13}C$ to estimate the influence of tree diversity on local water availability. We opted to incorporate these studies into our framework, but it is essential to acknowledge that they in part obscure the scarcity of research directly measuring and examining diversity effects via these processes.

Studies of diversity effects on nutrient availability included studies on soil N concentrations [e.g. 46, 48], but also on aboveground nutrients, such as N and P concentrations in branches and leaves [e.g. 140]. Studies on light availability investigated canopy cover [141] or light extinction profiles [142] in tree mixtures. Only one study investigated diversity effects on water availability: Jansen et al. [143] found increased water availability with increased species richness, and attributed this to either reduced competition and/or facilitation.

With regards to resource uptake, we classified studies on leaf trait variation [e.g. 144, 145], crown complementarity and plasticity [e.g. 146, 147], light interception [e.g. 148, 149], and light absorption

[150] under light uptake. We assumed that higher crown complementarity/plasticity and higher light interception resulted in a higher level of light uptake at the plot level, thus assuming on average higher light interception per target tree. In addition, we assumed that higher leaf trait variation invokes higher complementarity in resource acquisition and thus increased light uptake on the plot level. We classified studies on root morphology and architecture [e.g. 128, 151], vertical root distribution [e.g. 42, 152], and root productivity [e.g. 48, 153] under both water and nutrient uptake, as they impact the uptake of both resources. Here, we assumed that higher root lengths, higher root surface areas, higher root biomass, etc. will result in higher nutrient and water uptake, given that the availability of these resources remains constant. Effects on water uptake were also investigated based on isotopes [154, 155] or soil water fluxes [51], while effects on nutrient uptake were also investigated using labelled N15 [156]. Kunert et al. [157] investigated carbon allocation related to tree diversity, and found that trees in mixtures allocate a higher amount of carbon to their roots and leaves. This could potentially support species complementarity, both above-and belowground, and therefore we assumed that this will result in higher uptake of light via leaves and nutrients and water via roots.

Studies investigating nutrient use-efficiency include Zeugin et al. [158], who found identity effects on biomass per unit aboveground N or P, and Maxwell et al. [124], who found identity effects, no effects, or positive effects of diversity on nutrient-use efficiency, depending on the site (n=2), and expressed as the ratio between primary productivity and nutrient amounts in litterfall. Effects on light-use efficiency were only investigated by Pollastrini et al. [159] using chlorophyll fluorescence measurements. Effects on water-use efficiency were assessed using isotope analysis [154, 160, 161].

For the majority of the response categories related to resources, the number of cases were not sufficient to draw conclusions about the general effects of the different diversity metrics (Table 1). Many cases reported significant identity effects, especially in relation to resource uptake. Also for nutrient availability, several cases found identity effects, but a similar number of cases reported the absence of identity effects. For nutrient availability and uptake, as well as for water uptake, the majority of cases found no effect of any diversity metrics other than identity. The very similar results for nutrient and water uptake can be related to the fact that cases investigating root characteristics were classified under both water and nutrient uptake. For light uptake, most studies found positive effects of tree diversity (Table 1), and this can be attributed to the fact that tree diversity typically enhances crown complementarity and vertical stratification [162, 163], enabling trees to capture more light, assuming that average tree light uptake will increase even when light capture of individual trees may well be reduced.

What are the remaining key knowledge gaps in our understanding of the relationship between tree diversity and tree performance?

Abiotic pathways are underrepresented

Within the TreeDivNet research, diversity effects via abiotic conditions are strongly underrepresented (Fig. 2). As a result, we currently lack a proper understanding of how tree diversity and composition may alter, among others, soil and microclimatic conditions. Evidence on the importance of microclimate for forest functioning is gradually increasing (see [142] for a review), including evidence on how microclimate might impact tree performance [164, 165]. Similarly, it is expected that abiotic soil conditions, such as pH and carbon content are influenced by the tree community [166–168] and have, in turn, an impact on trees' growth and performance [169]. For instance, an observational study found that soil bulk density, cation exchange capacity, and pH were all influenced by tree species identity, and that soil carbon stocks were negatively affected by tree species diversity [167]. In a broadleaved mixed forest in Central Germany, higher soil pH and higher soil Ca and Mg stocks were found in mixed stands than in stands dominated by beech, and differences were mainly attributed to differences in leaf litter composition [168]. In addition, we found that while the effect of diversity on tree resources was well-studied, few studies linked altered resources to tree performance. Hence, future research should further investigate how tree mixing affects tree performance, both via altering the abiotic growing conditions and the available resources.

Biased representation of certain components within pathways

Within the well-investigated pathways, representation of different response categories was also strongly biased. For the resource pathway, diversity effects on nutrients were more frequently explored than those on water and light, and within each resource, the focus has mainly been on resource uptake, and much less on availability, except for nutrients (Table 1). Very few studies examined resource-use efficiency in relation to tree diversity, even though resource-use efficiency is commonly perceived as one of the main mechanisms linking biodiversity to ecosystem functioning [170]. For the studies on biotic conditions, it stands out that much attention has been given to microbiota and invertebrates (Table 1), the latter being related to the strong expertise of the research teams leading particular experiments (e.g. ORPHEE, UADY, BEF-China, Satakunta). The impact of tree diversity on bird and plant communities received very little attention. Yet, bird abundance and diversity can alter tree performance in insect herbivore control [171] and may also influence functioning through pollination and seed dispersal. Also, the forest understorey vegetation contributes to the ecological functioning of the forest, as herbs and shrubs compete with trees for light, nutrients and water, and affect tree regeneration, nutrient cycling and carbon cycling [172]. Hence, these taxonomic groups, but also others like small mammals, deserve more attention in future research.

Lack of survival analyses

Research in TreeDivNet experiments strongly focuses on different variables linked to productivity or damage to target trees, e.g. by herbivores, but how this translates to survival remains highly understudied (Table 1). TreeDivNet site managers reported major die-back events to be a problem in some experiments, but the causes or the mediating effect of mixing have been rarely researched [but see e.g. 129]. A global study by Blondeel et al. (submitted) using TreeDivNet data of saplings, demonstrated the role of tree diversity as insurance for sapling survival under drought during the initial years after planting, and site-specific studies have also found evidence for an insurance effect on survival [173]. Recently, Urgoiti et al. found lower self-thinning rates in more functionally diverse communities, explained by both an increase in tree growth and a reduction in density-related mortality [174]. Conversely, based on a large permanent sample plot network in temperate and boreal forests, Searle et al. (2022) showed that mortality probabilities increased with tree species diversity due to increased stand density and tree-size variation [175]. Also, Pretzsch et al. (2023) found increased mortality due to self-thinning in mixtures of Scots pine and European beech compared to monospecific stands [176]. These contrasting findings with regard to tree survival in mixed stands suggest that the impact of mixing on survival is context-dependent: in more favourable environments, tree diversity may cause an increase in competitive intensities through an increase in productivity, leading to higher density-related tree mortality [175]. On the other hand, in the face of climate change disturbances and catastrophic events (e.g. droughts, pest outbreaks), the benefits of mixing to reduce the impact of these events may outweigh the drawbacks of increased competition. Given these contrasting findings and the importance of survival in forest plantations, further (long-term) studies on survival in mixed forest plantations are recommended.

Unbalanced research across biomes

The distribution of studies across biomes is unbalanced (Fig. 2). This reflects the distribution of TreeDivNet sites across biomes, with 15 temperate sites (of which only 2 are Mediterranean), 7 tropical sites, 2 subtropical sites, and only one boreal site. Of the global forest area, 45% is tropical, 27% is boreal, 16% is temperate (including Mediterranean), and 11% is subtropical [177]. Hence, balancing geographic coverage and scientific coverage requires establishing more tree diversity experiments in (sub)tropical and boreal forest systems, as well as Mediterranean temperate forests.

In general, experimental sites in countries of the Global South are underrepresented within TreeDivNet. In these countries, wood is often the main domestic fuel in rural households, and consumption is growing at a rate close to that of population growth [178]. Meanwhile, political and financial commitments are rising to realize massive afforestation and reforestation in those areas of the world, both to meet the increasing demands and to enhance climate change resilience and mitigation. Interest in forest restoration is clearly high, also in countries of the Global South, and the momentum is there, but if we want to make these investments sustainable under future climate change, it is critical to shift from planting monocultures towards planting mixed forests [24]. Also from that perspective, we need to expand our knowledge base on mixed forest plantations in humid and semi-arid (sub)tropical forest biomes to study and demonstrate the benefits of planting (particular) mixtures in these regions.

Context-dependency of tree diversity effects

The importance of environmental context in biodiversity-ecosystem functioning relationships was demonstrated in mature forest plots across Europe, where researchers found stronger relationships in drier climates and in areas with longer growing seasons [34]. A meta-analysis combining the results of long-term experiments at 60 sites across five continents revealed that productivity gains in mixed-species stands increased with local precipitation [179]. The majority of TreeDivNet studies focuses on one experimental site, and therefore, offers little insight into such interplay between climatic or site conditions and tree diversity effects on ecosystem processes in young plantations.

A few experimental sites have applied drought or irrigation treatments (e.g. IDENT sites in Macomer, Outaouais and Sault-Ste-Marie, ORPHEE, MataDIV), addition of N and/or P (e.g. Ridgefield, IDENT site in Freiburg), or shading treatments (IDENT site in Ethiopia) to simulate the effects of altered climate or site conditions, or have observed natural variability in these variables within a site, such as changes in inter-annual climatic conditions. For instance, evidence on the role of tree diversity for productivity under drought remains mixed, which is consistent with similar conclusions from a recent review [180]. Within TreeDivNet, Belluau et al. [152] found that the positive functional diversity effect on biomass production was stronger under high water availability, which is contrary to the established stress-gradient hypothesis and the above results. On the contrary, Schnabel et al. [123] and Fichtner et al. [181] reported a strengthening of positive tree species richness effects on productivity under drought.

The design and global scale of TreeDivNet experiments provide a unique opportunity to scale up our understanding of tree diversity effects on tree performance across a large gradient of climatic conditions, from boreal forests in Finland, to tropical forests in Brazil and Panama, and temperate forests in Central Europe and North-America. For example, Poeydebat et al. [182] used data from 12 experimental sites to show that herbivory on birch decreased with tree species richness in colder environments, but this relationship faded when mean annual temperature increased. Cesarz et al. [83] used data from 11 TreeDivNet experiments to examine tree diversity effects on soil microbial biomass and respiration and found that context-dependent diversity effects were stronger in drier soils. Until now, however, the number of such large-scale studies using multiple TreeDivNet sites remains limited. Systematic analyses across multiple sites is a key next step to improve our understanding of the context-dependency of tree diversity effects on different forest functions and services. Such future meta-analyses across experimental sites will also allow to formally test the importance of other cross-experiment mediators that were not considered in our conceptual framework (Fig. 1), such as planting densities, species mixing patterns, and development stages.

What practical insights can be gained from the TreeDivNet experiments for operational, real-world forest plantations?

To complement our literature synthesis, we conducted a questionnaire to gather insights from the practical experiences of TreeDivNet experiment site managers. Below, we highlight the most significant findings, including practical insights as well as challenges encountered, that can help bridge the gap between theory, scientific understanding, and practical implementation.

Development stages and (future) challenges

During the design stage of the experiments, choices on species selection, planting density, and spatial plantation design were the criteria most often (c. 85, 45, 48% of managers, respectively) noted to have made setting up the experimental plantations more difficult when mixing instead of planting monocultures. Responses indicate a stronger focus on scientific purposes rather than practical management considerations: (i) species selection was often based on multiple, often scientific research goals (functional trait dissimilarity, mycorrhizal type, native vs exotic tree species, different growing strategies, etc.) and not commercial, silvicultural species mixtures, (ii) high planting densities were applied to accelerate species interactions, as the focus was on the early successional stage of stand development (e.g. the design of IDENT experiments with spacing of 40-60 cm) and (iii) planting patterns (e.g. planting in small mono-specific cells or patches) were often designed to avoid early de-mixing, i.e. an early, competition-driven loss of species. However, planting trees in patches is also a practical consideration in operational plantations, albeit at a somewhat larger scale, to reduce the efforts associated with tending [183].

Multiple challenges leading to die-back events, reduced health and quality of trees in the three stages after design (i.e., establishment, closed-canopy and stem exclusion stage) were identified. During all three stages, main reported causes were climate variability, especially drought, pathogens and herbivory. Major dieback occurred most often during the establishment stage (64% of managers indicated this was a challenge). A challenge most important to this initial stage is competition by surrounding vegetation. Managers responded to these different challenges by manual weeding or slashing of the competing vegetation, exclusion of herbivores, and replanting. During the closed-canopy stage, similar but fewer, less impactful challenges were reported. During this stage, the spontaneous establishment of non-target tree species influenced growth of target trees. Removal of these non-desired trees was the sole response implemented during this stage and reported in five of the experiments. From the stem-exclusion stage, self-thinning arises, which results in the need for thinning treatments if plantations want to remain relevant for operational management.

None of the experiment managers reported that responding to these challenges was more difficult in mixtures than in monocultures. Looking at these stages, challenges and design, the fact that these experiments are set up from a scientific perspective becomes particularly evident. Furthermore, management interventions in the experiments such as weeding, replanting, fencing, irrigation after planting (as a singular measure, not a treatment as mentioned earlier) are carried out in an unsystematic way among experimental sites strongly driven by context and funding availability, and implications of such interventions are not tested in a formal way. Due to this science-oriented perspective, it remains difficult to translate practical insights from these experimental plantations to guidelines for real-world, operational plantations.

Best performing mixtures

It is clear from the multitude of identity and composition effects observed in the TreeDivNet studies that certain mixtures perform better or worse than others in a specific environmental context. When TreeDivNet site managers were asked to identify the best performing mixtures, based on their observations, most managers (60%) could nominate a certain mixture. Site managers indicated that mixtures composed of species with complementary or contrasting growth strategies seemed to perform best, i.e., combinations of coniferous and deciduous species, of fast-growing light-demanding and slow-growing shade-tolerant species, but also the inclusion of drought tolerant species in a mixture. Other managers reported that at present it is hard to identify a best performing mixture (20%) or too early to make a clear choice (20%), and that this would depend on the desired outcome or goal, such as maximizing productivity, resilience to stress (especially drought), economic value or all these criteria together. Given the large number of species combinations (from species pools of 3 to 40 species per experiment), levels of mixing (from 2 to 24 species per mixture), and environmental contexts, it is currently not possible to deduce general guidelines on best performing mixtures. The identification of optimal species mixtures based on multiple criteria across the different contexts and species pools within the TreeDivNet experiments should therefore be a future scientific goal. Future climate change projections, particularly expected changes in the intensity and frequency of drought events, should be taken into consideration when identifying such optimal mixtures.

Take-home messages for experimental and real-world managers

Our synthesis exercise and questionnaire have provided clear evidence of the extensive knowledge amassed by TreeDivNet research and allowed us to identify current knowledge gaps and key lessons for management, in spite of the focus on basic science research in many of the experiments.

TreeDivNet research provides ample evidence in favour of mixing tree species. The majority of diversity effects found were positive for tree productivity, many were neutral, yet few negative effects were reported. Overall, these findings suggest that in most cases mixing improves productivity and that there should be no significant compromise on tree performance when adopting a strategy of mixing tree species. Moreover, we found clear evidence that mixing tree species decreases the level of infestation by pests or diseases within the stand. In light of future increases in pest or pathogen outbreaks due to climate change or unintended species introductions, this is of utmost importance [184, 185].

We showed that a variety of processes are at play that drive these diversity effects, both biotic and abiotic, the latter being understudied. We urge researchers to close these gaps. We also encourage setting up experiments in the (sub)tropical, Mediterranean, and boreal biomes (which are currently underrepresented) given the large pledges to reforest. Due to this mix of processes driving diversity effects and context specificity, choosing best-performing species mixtures remains challenging, also in large-scale studies in mature forest [186]. We therefore encourage operational managers to experiment with planting different species combinations using mixtures of tree species which are known to be complementary while including some drought resistant species and monitor these mixtures across spatial and temporal scales applied in operational tree plantations. At the same time, research should further focus efforts on identifying optimal species mixtures, but also on revealing trade-offs and synergies between ecosystem functions/services in mixtures in general.

Furthermore, through combining the literature review with our questionnaire, we highlighted that current foci of TreeDivNet have been predominantly centred on fundamental research questions pertaining to the mixing of tree species. Currently, translation of this fundamental knowledge to provide guidelines for the management of tree mixtures remains difficult, e.g. due to the design, scale, age, and operations of TreeDivNet experiments. Research of TreeDivNet has mainly focused on the early stages of tree plantations but now many experiments will transition into the critical stem-exclusion stage in the near future. Experimental managers will have to opt between focussing on scientific goals and maintaining the original experimental design as much as possible vs. shifting towards more management-oriented questions when applying thinning treatments, if required. Especially in case of the latter trajectory, timely decisions on thinning strategies will have to be made to make sure these experiments remain relevant for management.

As researchers and experiment managers, we commit to carefully consider the future of these tree diversity experiments and determine if continuing to focus on fundamental questions is most important or if the time has come to make experimental mixed plantations more management oriented.

Declarations

Ethical Approval

Not applicable.

Competing interests

Authors declare no competing interests.

Authors' contributions

EDL, LD, KV, LB, HB and ED conceived and designed the study; EDL, LD and ED collected the data from the literature; EDL and LD performed the analysis; EDL and LD wrote the paper and created the figures and tables; JG, JB, MSL, ED, LB, HB & KV commented on the first draft. All co-authors contributed to the questionnaire, commented and approved the final manuscript. KV and LB supervised the project and helped designing the conceptual framework.

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Availability of data and materials

All data is available in appendix.

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