BIOLOGY LETTERS

rsbl.royalsocietypublishing.org

Research

Cite this article: Jactel H, Gritti ES, Drössler L, Forrester DI, Mason WL, Morin X, Pretzsch H, Castagneyrol B. 2018 Positive biodiversity–productivity relationships in forests: climate matters. *Biol. Lett.* **14**: 20170747.
http://dx.doi.org/10.1098/rsbl.2017.0747

Received: 6 December 2017
Accepted: 13 March 2018

Subject Areas:
ecology

Keywords:
biodiversity, ecosystem functioning, overyielding, precipitation, meta-analysis

Author for correspondence:
H. Jactel
e-mail: herve.jactel@inra.fr

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4041431.

THE ROYAL SOCIETY PUBLISHING

Community ecology

Positive biodiversity–productivity relationships in forests: climate matters

H. Jactel[1], E. S. Gritti[2], L. Drössler[3], D. I. Forrester[4], W. L. Mason[5], X. Morin[6], H. Pretzsch[7] and B. Castagneyrol[1]

[1]BIOGECO, INRA, University of Bordeaux, 33610 Cestas, France
[2]UMR System, Montpellier Supagro, 2 place Viala, 34060 Montpellier, France
[3]Institute of Ecology, ISU, Cholokashvili avenue 3/5, 0162 Tbilisi, Georgia
[4]Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
[5]Forest Research, Northern Research Station, Roslin, Midlothian EH25 9SY, UK
[6]CEFE UMR 5175, CNRS, 1919, route de Mende, 34293 Montpellier, France
[7]Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

HJ, 0000-0002-8106-5310

While it is widely acknowledged that forest biodiversity contributes to climate change mitigation through improved carbon sequestration, conversely how climate affects tree species diversity–forest productivity relationships is still poorly understood. We combined the results of long-term experiments where forest mixtures and corresponding monocultures were compared on the same site to estimate the yield of mixed-species stands at a global scale, and its response to climatic factors. We found positive mixture effects on productivity using a meta-analysis of 126 case studies established at 60 sites spread across five continents. Overall, the productivity of mixed-species forests was 15% greater than the average of their component monocultures, and not statistically lower than the productivity of the best component monoculture. Productivity gains in mixed-species stands were not affected by tree age or stand species composition but significantly increased with local precipitation. The results should guide better use of tree species combinations in managed forests and suggest that increased drought severity under climate change might reduce the atmospheric carbon sequestration capacity of natural forests.

1. Introduction

It is widely acknowledged that forest biodiversity contributes to many ecosystem services, from the provision of material and energy [1] to the regulation of abiotic and biotic disturbances [2]. In particular, several recent studies have reported a positive effect of tree species diversity on forest productivity at the global scale [3,4]. However, there is increasing evidence that tree species diversity–ecosystem functioning relationships are dependent on environmental conditions. Specifically, climatic conditions can change biodiversity–productivity relationships (BPRs), as shown by reports of their large variation across forest biomes in Europe [5,6] and globally [4].

In forest ecosystems, studies focusing on the comparison between two-species mixtures with their respective monocultures showed a positive BPR when tree species interactions improved the mobilization of the limiting resource, such as water [7]. In addition, studies using large-scale datasets found that BPRs were more likely to be stronger under colder or drier environments [4,8–11], suggesting that the productivity of mixed-species forests can be affected by climatic conditions. However, it is still difficult to discern clear response patterns of BPRs to climatic gradients [12], especially as the size of climatic effects on BPR was small, not significant, or varied between regions

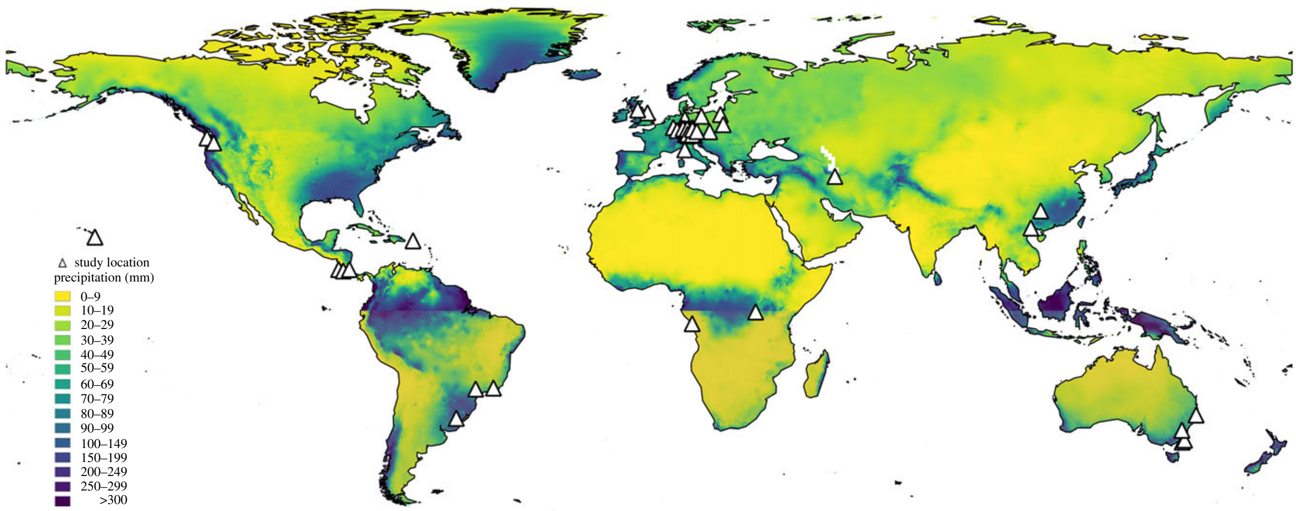

Figure 1. Location of the study sites according to global variation in precipitation. *Precipitation* corresponds to the sum of precipitation in the second winter month, the best correlated variable with PCA_2 coordinates used as moderator in the meta-analyses.

and forest types [3,8,13–15]. One main reason for such idiosyncratic effects is that large-scale BPR studies have been mainly based on forest inventories [4,5,8,14] or empirical studies [6,9] where the mixtures and monocultures of a given species combination have not been sampled at the same site, leading to potential confounding factors, such as mixed forest growing in better local climatic conditions [13]. Owing to these uncertainties, it remains difficult to predict how climate change will interact with tree species diversity to influence productivity in forests.

To circumvent this drawback, we used a meta-analytical approach to combine the results of long-term growth and yield experiments where forest mixtures and corresponding monocultures were compared at the same time on the same site. We calculated the mixing effect at the stand level using overyielding (OY) and transgressive overyielding (TOY) estimates for each mixture and tested whether this mixing effect changed along global gradients of temperature and precipitation.

Table 1. Summary of meta-analytical model values for the effects of temperature, precipitation and mixture type on overyielding (OY) in old forests. Parameter estimates (*b*) in italics show significant effects.

models	parameters	*b* [−CI; +CI]
$OY_i \sim$ precipitation	intercept	0.13 [0.05; 0.21]
	precipitation	*0.16 [0.05; 0.27]*
$OY_i \sim$ mixture type + precipitation	intercept	0.1 [0.01; 0.19]
	mixture type: EE	0.08 [−0.07; 0.23]
	precipitation	*0.18 [0.07; 0.28]*
$OY_i \sim$ N-fixing + precipitation	intercept	0.08 [−0.02; 0.19]
	precipitation	0.12 [−0.01; 0.26]
	N-fixing: present	0.11 [−0.1; 0.33]
$OY_i \sim$ temperature + precipitation	intercept	0.12 [0.05; 0.20]
	precipitation	*0.14 [0.02; 0.26]*
	temperature	0.05 [−0.05; 0.14]

2. Material and methods

We surveyed all studies published up to 2016 on the effect of tree species diversity on forest productivity at the stand level using the Web of Science, Agritrop and CAB Abstracts with the combinations of the following terms: 'mixed or mixing or mixture or intercropping or diversity' and 'monoculture or pure or single species' and 'productivity or production or yield or performance or growth' and 'tree or forest'. We also looked at the references cited in the articles we retrieved.

We retained studies where: (i) all component tree species of mixed-species stands (e.g. A + B) were grown as monocultures (e.g. A and B) of the same age and in the same pedoclimatic conditions and were measured in the same year; (ii) the mean, variance and sample size (if >3) were reported for response variables in the text or available from tables or figures; (iii) a precise geographical site location was provided allowing the retrieval of local climatic conditions. We used stand biomass, volume or basal area as response variables to estimate productivity. We discarded studies focusing only on height as height growth is mostly driven by site index and thus cannot accurately reflect BPRs. When stand productivity was reported for several years in the same study, we only used data from the last measurement.

This resulted in the selection of 30 publications, published from 1997 to 2016, which accounted for 126 case studies, i.e. individual comparisons of mixed stands with monocultures of component species (electronic supplementary material, table S1 and references in appendix S1), in 60 sites across five continents (figure 1).

For the meta-analyses, we calculated two effect sizes as the log-ratios between productivity of mixtures and mean productivity of component species monocultures (overyielding or underyielding, OY) or productivity of the most productive component species (i.e. transgressive overyielding or underyielding, TOY) [16].

We tested the effect of five covariates (hereafter termed 'moderators') on the magnitude of BPR: stand age, species composition, presence of N-fixing species, local temperature and precipitation (see electronic supplementary material, appendix S2 for details on calculation). We used multi-level meta-analytic models [17] to estimate heterogeneity from multiple sources (detailed in electronic supplementary material, appendix S2), and tested the effects of moderators in an information theory framework (using Akaike information criterion for small sample size, AICc). Publication bias was assessed with cumulative meta-analyses [18]. Meta-analyses were made with the 'metafor' package 1.9-8 version in R 3.2.3 [19].

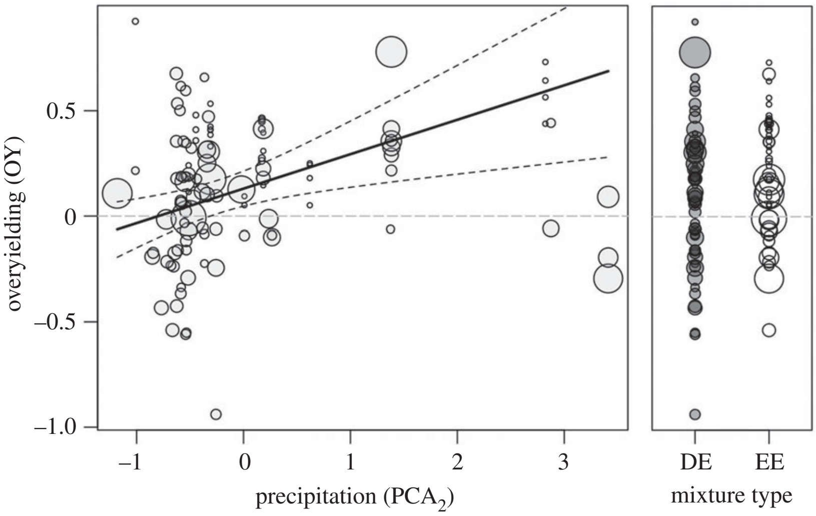

Figure 2. Effect of precipitation (coordinates on PCA_2) and type of tree species mixture (D, deciduous; E, evergreen) on overyielding in old forests (older than half of the rotation age). The diameter of a bubble is proportionate to the weight (inverse of variance) of the corresponding study in the meta-analyses.

3. Results

Overall, mixed-species forests exhibited a significant overyielding (OY) regardless of stand age. The overyielding was 16% [−CI = 1%; +CI = 32%] in young forests and 15% [3%; 28%] in old forests (with percentage calculated from model coefficient parameter estimates as $100 \times (e^{OY} - 1)$). There was neither transgressive overyielding nor transgressive underyielding as the grand mean estimate (TOY) was not significantly different from zero, its confidence interval bracketing the zero value (−13% [−32%; 5%] in young forests and −4% [−20%; 9%] in old forests).

Model comparisons for overyielding in young forests and transgressive overyielding in both young and old forests identified the null model as the best one, indicating that none of the tested moderators contributed to explaining heterogeneity among effect sizes (electronic supplementary material, table S2).

In old forests, three models for overyielding were in the range of 2 units of ΔAICc from the best model and included precipitation, temperature and stand composition as moderators (electronic supplementary material, table S2). However, coefficient parameter estimates for the effect of mixture type and temperature were not different from zero (table 1). The best model only retained precipitation as a significant moderator (electronic supplementary material, table S2). The overyielding in old forests increased (slope: 0.16 ± [0.05; 0.27]) with higher precipitation (figure 2), whereas temperature had no significant effect on overyielding, nor did the interaction between precipitation and temperature (electronic supplementary material, table S2). The presence of nitrogen-fixing species never explained the overyielding of old mixed forests (table 1). These results were unlikely to be affected by a publication bias (electronic supplementary material, figure S1 and appendix S2)

4. Discussion

Our meta-analysis confirmed that trees are generally more productive when growing in mixed-species stands than in the corresponding monocultures, but the most striking result was that overyielding varied at the global scale and increased with precipitation. The stress gradient hypothesis (SGH) posits that facilitation processes replace competition between species under increasing levels of stress [20], which should result in more positive BPR in forest with more limited water supply [5,21]. However, the SGH is more relevant at the species level and stressful conditions are difficult to define for all component tree species of forest mixtures [10]. In addition, many of the interactions in mixed forests, especially light-related interactions, are more likely to involve competitive reduction than facilitation [22,23]. As water availability increases, competition for light or nutrients may increase, so any interactions that improve light or nutrient availability, uptake or use efficiency will become more evident and the complementarity effect will increase [7,24]. Therefore, the increasing overyielding with precipitation suggests that light- or nutrient-related mechanisms are likely dependent on water-related interactions in mixed forests.

There was no significant effect of temperature on overyielding in our models, suggesting that temperature was not a growth-limiting factor, as opposed to light, water or nutrients. Studies using forest inventory data revealed higher diversity effects on productivity in mixed forests growing under harsher temperature conditions [4,8,11], which could be due to higher complementarity effects under environmental stress. It might also account for temperature being a key driver of tree functional diversity [11], a process that was controlled in the silvicultural studies included in our meta-analysis.

The inclusion of a nitrogen-fixing species in a mixture did not significantly influence the mixing effect, as already observed [3]. The absence of a nitrogen-fixing effect in that large-scale review and the present one may indicate that mixtures containing nitrogen-fixing species were often located on sites where nitrogen was not the main limiting factor. Alternatively, the classification of nitrogen-fixing species may need to be adapted to reflect the occurrence of positive nutritional interactions with mycorrhizae present in mixed stands [25].

Taking into account a large bioclimatic gradient, we estimated the overyielding of mixed-species forests at around 15%. This finding is consistent with earlier large-scale studies showing a positive and moderate effect of mixing tree species on tree growth in both Mediterranean [14] and temperate and boreal forests [8,26]. A previous meta-analysis [3] found a higher estimate of overyielding, with an increase of 24% in productivity. However, as we only used published studies that provided information on sample size and variance, we could model multi-level error structure and estimate the confidence interval of mixing effect size more confidently. Our figure of $15 \pm 12\%$ thus provides a more conservative estimate of overyielding in mixed forests.

We further demonstrated for the first time to our knowledge that there was, on average, no transgressive underyielding in mixed-species forests, which means that mixed-species forests are not significantly less productive than the best monoculture of the component species at the same site. This outcome is of great interest as it implies that carefully designed mixed-species stands could provide a wide range of ecosystem services (e.g. [1]), with a lower vulnerability to disturbances (e.g. [3]), without negatively affecting wood production.

Data accessibility. Table S1 in the electronic supplementary material reports all data used for statistical analyses. They have also been deposited in Dryad: (http://dx.doi.org/10.5061/dryad.6d57c) [27].

Authors' contributions. H.J. and E.S.G. collected data with the help of all other co-authors. B.C., E.S.G. and H.J. performed the meta-analyses and wrote the first draft of the manuscript. E.S.G., B.C., X.M. and H.J. analysed output data. All authors contributed substantially to editing and revising the manuscript. All authors approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

Funding. This research was funded by the Meta Programme on Adaptation of Agriculture and Forest to Climate Change of INRA and the European Commission FP7 via the Project BACCARA (GA no. 226299).

Acknowledgements. We are grateful to the authors who kindly provided original data.

References

1. Gamfeldt L *et al.* 2013 Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun.* **4**, 1340. (doi:10.1038/ncomms2328)
2. Jactel H *et al.* 2017 Tree diversity drives forest stand resistance to natural disturbances. *Curr. For. Rep.* **3**, 223–243. (doi:10.1007/s40725-017-0064-1)
3. Zhang Y, Chen HYH, Reich PB. 2012 Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J. Ecol.* **100**, 742–749. (doi:10.1111/j.1365-2745.2011.01944.x)
4. Liang J *et al.* 2016 Positive biodiversity-productivity relationship predominant in global forests. *Science* **354**, aaf8957. (doi:10.1126/science.aaf8957)
5. Ratcliffe S *et al.* 2016 Modes of functional biodiversity control on tree productivity across the European continent. *Glob. Ecol. Biogeogr.* **25**, 251–262. (doi:10.1111/geb.12406)
6. Jucker T, Bouriaud O, Avacaritei D, Coomes DA. 2014 Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. *Ecol. Lett.* **17**, 1560–1569. (doi:10.1111/ele.12382)
7. Forrester DI. 2014 The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *For. Ecol. Manag.* **312**, 282–292. (doi:10.1016/j.foreco.2013.10.003)
8. Paquette A, Messier C. 2011 The effect of biodiversity on tree productivity: from temperate to boreal forests. *Glob. Ecol. Biogeogr.* **20**, 170–180. (doi:10.1111/j.1466-8238.2010.00592.x)
9. Ratcliffe S *et al.* 2017 Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecol. Lett.* **20**, 1414–1426. (doi:10.1111/ele.12849)
10. Ruiz-Benito P, Gómez-Aparicio L, Paquette A, Messier C, Kattge J, Zavala MA. 2014 Diversity increases carbon storage and tree productivity in Spanish forests. *Glob. Ecol. Biogeogr.* **23**, 311–322. (doi:10.1111/geb.12126)
11. Mori AS. 2018 Environmental controls on the causes and functional consequences of tree species diversity. *J. Ecol.* **106**, 113–125. (doi:10.1111/1365-2745.12851)
12. Paquette A, Vayreda J, Coll L, Messier C, Retana J. 2017 Climate change could negate positive tree diversity effects on forest productivity: a study across five climate types in Spain and Canada. *Ecosystems* **2017**, 1–11. (doi:10.1007/s10021-017-0196-y)
13. Vilà M *et al.* 2013 Disentangling biodiversity and climatic determinants of wood production. *PLoS ONE* **8**, e53530. (doi:10.1371/journal.pone.0053530)
14. Vilà M, Vayreda J, Comas L, Ibáñez JJ, Mata T, Obón B. 2007 Species richness and wood production: a positive association in Mediterranean forests. *Ecol. Lett.* **10**, 241–250. (doi:10.1111/j.1461-0248.2007.01016.x)
15. Pretzsch H, Schütze G, Uhl E. 2013 Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol.* **15**, 483–495. (doi:10.1111/j.1438-8677.2012.00670.x)
16. Hector A, Bazeley-White E, Loreau M, Otway S, Schmid B. 2002 Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. *Ecol. Lett.* **5**, 502–511. (doi:10.1046/j.1461-0248.2002.00337.x)
17. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith G. 2009 *Mixed effects models and extensions in ecology with R*. New York, NY: Springer Science and Business Media.
18. Nakagawa S, Noble DWA, Senior AM, Lagisz M. 2017 Meta-evaluation of meta-analysis: ten appraisal questions for biologists. *BMC Biol.* **15**, 18. (doi:10.1186/s12915-017-0357-7)
19. Viechtbauer W. 2010 Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* **36**, 1–48. (doi:10.18637/jss.v036.i03)
20. Maestre FT, Valladares F, Reynolds JF. 2005 Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *J. Ecol.* **93**, 748–757. (doi:10.1111/j.1365-2745.2005.01017.x)
21. Jucker T, Avăcăriei D, Bărnoaiea I, Duduman G, Bouriaud O, Coomes DA. 2016 Climate modulates the effects of tree diversity on forest productivity. *J. Ecol.* **104**, 388–398. (doi:10.1111/1365-2745.12522)
22. Forrester DI, Bauhus J. 2016 A review of processes behind diversity-productivity relationships in forests. *Curr. For. Rep.* **2**, 45–61. (doi:10.1007/s40725-016-0031-2)
23. Pretzsch H. 2014 Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For. Ecol. Manag.* **327**, 251–264. (doi:10.1016/j.foreco.2014.04.027)
24. Pretzsch H, Rötzer T, Matyssek R, Grams TEE, Häberle K-H, Pritsch K, Kerner R, Munch J-C. 2014 Mixed Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.]) stands under drought: from reaction pattern to mechanism. *Trees* **28**, 1305–1321. (doi:10.1007/s00468-014-1035-9)
25. Bauhus J, Forrester DI, Pretzsch H. 2017 From observations to evidence about effects of mixed-species stands. In *Mixed-species forests-ecology and management* (eds H Pretzsch, DI Forrester, J Bauhus), pp. 27–71. Berlin, Germany: Springer.
26. Pretzsch H *et al.* 2015 Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* **134**, 927–947. (doi:10.1007/s10342-015-0900-4)
27. Jactel H, Gritti ES, Drössler L, Forrester DI, Mason WL, Morin X, Pretzsch H, Castagneyrol B. 2018 Data from: Positive biodiversity–productivity relationships in forests: climate matters. Dryad Digital Repository. (http://dx.doi.org/10.5061/dryad.6d57c)