Tree species diversity and forest productivity

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Scientists and policy makers have looked at Mediterranean forest biodiversity mainly from a conservation point of view. But biodiversity is increasingly considered an important aspect of ecosystem functioning. In this presentation, we review more specifically diversity-productivity relationships in forests. But it's not an easy task, because the problem is that forest condition and growth are determined by many interacting environmental and management factors. In this context, developing an international network of such experiments, including Mediterranean sites, would be very useful.

Introduction

Primary productivity as a result of photosynthesis and respiration is an important life support function, contributing largely to the provisioning services of wood and other forest products and to the climate regulating services of carbon sequestration and storage (MEA 2005). Sustainable forest management aims at co-optimizing for stock functions (biomass and carbon), rate functions (growth, sequestration) and stability of stocks and fluxes (PACALA & KINZIG 2002). At least since the 19th century foresters have wondered whether mixed forests would be more productive than monocultures (PRETZSCH 2005), but so far without conclusive answers. During the last decade strong positive diversity/productivity relationships have been reported from experimental grassland species assemblages (TILMAN *et al*. 2001, LOREAU *et al*. 2001). They were at least partly explained by species complementarity in accessing below-ground resources (e.g. VERHEYEN *et al*. 2008). In this contribution we further explore if diversity/productivy research in forests could reveal similar patterns.

Evidence for biodiversity /productivity relationships in forests

Many stand-level observations worldwide on important timber species like spruce, Douglas fir, pine or Eucalypt reported higher productivity in monocultures compared to mixed stands including the same species (Pretzsch 2005). But a few studies with these species also report positive effects of species mixture on productivity of up to 10 to 20%. Such positive diversity/productivity relationships were mainly observed on rich soils while, on poor soils, mixtures showed an often negative effect on productivity (Körner 2005). A synthesis of tropical stand-level studies showed an overall better diameter growth in mixed forest plantations over monocultures (Piotto 2008). Mölder *et al.* (2008) found a positive relation between herb-layer biomass and tree-layer diversity in deciduous forests in Germany.

So far, very few studies tested diversity/productivity relationships at larger than stand scale. A first attempt to test the biodiversity-productivity hypothesis with regional forest inventory data was made by Vila *et al.* (2007) in Catalonia, see figure 1. They found increased stand stemwood production with tree species richness before canopy closure in sclerophilous forest, less so in conifer forests and not in deciduous forests. This would suggest that in Mediterranean forests this relationship can be observed in early successional forests or on marginal sites. Ever since, some analyses of national inventory data to deduct effects of mixed forests are ongoing in France and Germany (e.g. Morneau *et al.*, 2008). Analysing a global NPP database analysis, Luyssaert *et al.* (2007) showed that the net carbon balance of forests is rather similar over the world because, for average annual temperatures and precipitation above the optimum of 10°C and 1500 mm, photosynthesis is increasingly compensated by higher respiration rates. Global variation between forest sites is not so much the effect of climatic differences but is rather due to factors such as forest age, management and history of disturbance which, among others, influence the tree species composition.

This short review suggests that results from observational studies on the diversity/productivity relationship in forests are not univocal. Observed diversity/productivity relationships seem context specific and strongly confounded by environmental factors and management practices. This finding underlines the need for well-designed unconfounded synthetic community experiments.

In recent years methodological advances are debated in recent literature (Scherer-Lorenzen *et al.* 2007, Leuschner *et al.* 2009) and have led to the establishment of large-scale long-term tree species assemblages to explore the functional significance of tree diversity for forest productivity in Germany, Finland, Belgium, France, Panama, Malaysia, China and Canada (see figure 2). Unfortunately no experiments have been established in the Mediterranean biome so far. Next to an experimental platform, the FP7 project FunDivEurope[1] also includes an exploratory platform, where plots with different tree species diversity levels were selected within areas of existing mature forest with homogeneous environmental conditions. Six such exploratory sites have been established in Europe, of which two of them

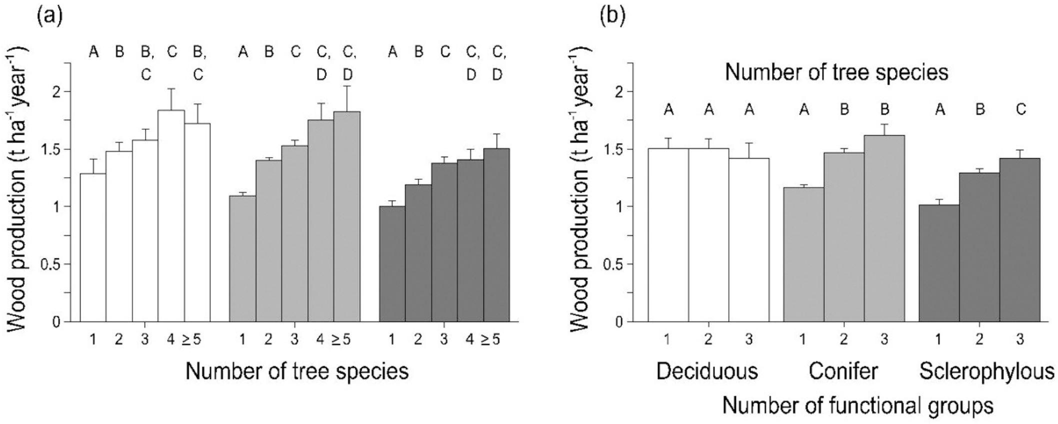

Figure 1: Analysis of the Catalan forest inventory revealed positive relationships between number of tree species and wood production, and also between number of functional groups and wood production in evergreen sclerophylous forests, but less pronounced in broadleaved deciduous and conifer stands (capital letters above graphs reveal significant differences between groups). The results suggest a stronger complementarity effect in early successional stages on marginal sites, which seems contradictory to findings in cold temperate climate.
From Vila et al. 2007

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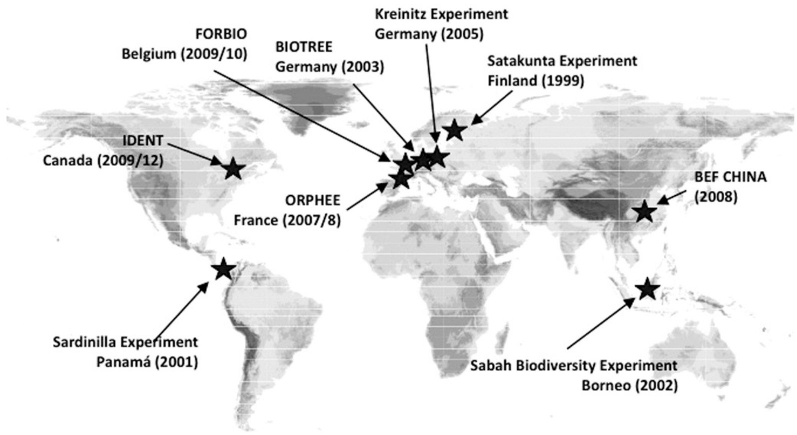
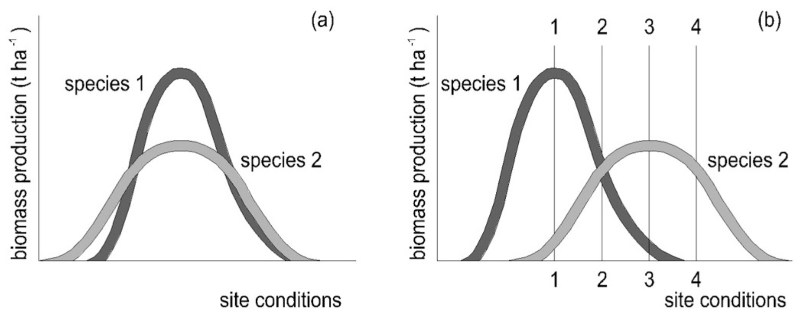
in the Mediterranean Region (Alto Tajo Natural Park in Spain and Berignone-Tatti and Belagaio forests in Italy with sub-mediterranean climate).

Attempts for mechanistic explanation

Tree species can show different types of interactions depending on the abiotic conditions. When two species occupy more or less the same ecological niche, one being more productive than the other, then introduction of the second species would lead to productivity loss (see figure 3a). Such situation, where competition occurs between functionally similar species is common in forests and explains the multitude of studies where negative diversity/productivity relationships are observed. But, when different species with clearly distinct niches occur together (fsee igure 3b), then productivity will depend on the complex interaction between the two and can lead to different outcomes, depending on the species/site interaction (see figure 4).





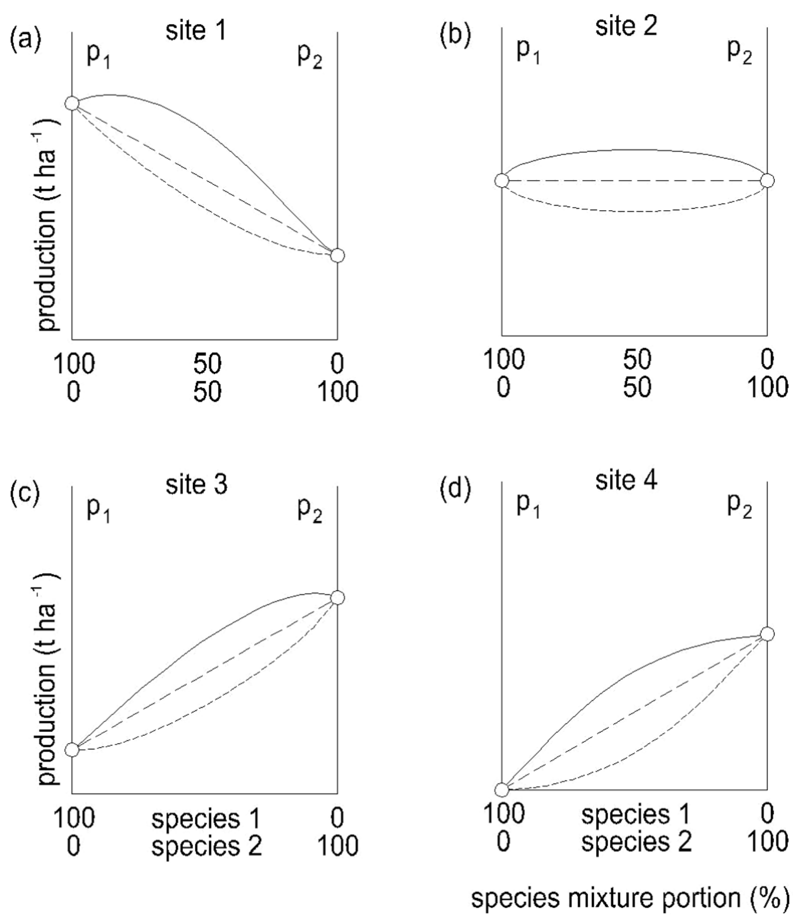


Figure 2:
The global network of synthetic community experiments evaluating tree species diversity function consists of more that 2900 plots covering more than 600 hectares and more than 600,000 planted trees (www.treedivnet.ugent.be). Background map of vascular plant diversity, Barthlott *et al.* 2005

Figure 3:
Biomass production in relation to site for two tree species. a) species with similar ecological niche. B) species with different ecological niche. (Pretzsch 2005). Sections 1-4 refer to species interactions explained in figure 4.

Figure 4:
Biomass production for two tree species in monocultures and mixed stands under different site conditions (conditions 1-4 from figure 3b). When two species with strongly different niche co-occur their productivity will theoretically depend on the complex interaction between 3 types of species interaction (positive interaction, continuous line; negative interaction, dotted line; neutral interaction, dashed line) at 5 site types (growing range of species A but outside growing range of species B (not in figure), growth optimum for species A (fig 4a), same growth potential for both species (fig 4b), growth optimum for species B (fig 4c), growing range for species B but outside range of species A (fig 4d) (Pretzsch 2005).

These possible interactions between species can be tested in the field by comparing the productivity or any other performance indicator of monoculture plots/patches versus mixed plots/patches situated on the same site. As explained above the interaction between species can have a negative (competition) effect, a neutral effect or a positive effect. But not all positive effects imply species complementarity, i.e. demonstrated patterns of niche differentiation and facilitation between the species (HOOPER *et al.*, 2005). It is also possible that there is simply a selection/insurance effect. It means that the higher species diversity leads to a higher probability of presence for high performing species (example: admixture of an N-fixing tree species on poor soil) or to a higher probability of alternative pathways (example: ash and alder filling the gaps of elm in a riverine forest damaged by dutch elm disease). The simple tests to identify the kind of interaction are given in the following equations.

[1] *Net diversity effect (NDE) = [observed productivity]– [expected productivity]*

where the expected productivity is the area weighted average productivity of the monocultures of species in the mixture.

[2] *Transgressive overyielding (Dmax) = [observed prod.] – [max. single species prod.]*

where the maximum single species productivity is the productivity of the best performing monoculture of species in the mixture.

The outcome of equations [1] and [2] is compared with the following four equations to identify the type of species interaction:

NDE<0: antagonistic effect (competition) **[3]**

NDE=0: no effect **[4]**

NDE>0; Dmax<0: selection effect **[5]**

NDE>0; Dmax>0: complementarity effect **[6]**

In a study of tree growth of Scots pine and birch stands in the Netherlands, WIJDEVEN *et al.* (2000) observed higher productivity in mixtures than in monocultures of both species, with an increased effect of the mixture in stands with a higher basal area. Especially birch was more productive in mixture than in monoculture. The authors hypothesize resource complementarity, possibly through rooting in different soil layers, but do not dispose of measured proof for this hypothesis. PRETZSCH & SCHÜTZE (2009) were the first to prove resource complementarity between tree species in a mixture. While mixtures of beech and spruce on poor substrates always lead to dominance of spruce, without complementarity effects, they observed transgressive overyielding of 14-29% compared to monocultures on rich sites in Southern Germany, due to mutual growth stimulation of both species. This proven complementarity was assumed to be the consequence of more efficient nutrient uptake and distribution and a higher crown efficiency in the mixtures.

Conclusion

So far, little evidence for diversity/productivity has been reported from forests. Observational studies could not unequivocally find such relationships as they were possibly masked by confounding factors such as abiotic resource variability. Methodological challenges have seriously retarded the setup of experiments in forests, as these ecosystems are dominated by tall long-living organisms. Recently established experiments are expected to foster a breakthrough in understanding the role of biodiversity for forest productivity and carbon sequestration in the future. Meanwhile advanced statistical analysis of observational studies and inventory databases allows further testing the diversity/productivity hypothesis in forests. Where complementarity can be demonstrated, more process-based research is needed to understand the mechanisms behind it. Forest diversity function is a young science with a strong need for research results from the Mediterranean biome. Next to the exploratory plots of the FunDivEurope project in Italy and Spain, it is recommendable to consider establishing experimental tree diversity level assemblages with typical mediterranean species.

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Summary

Scientists and policy makers have looked at Mediterranean forest biodiversity mainly from a conservation point of view due to the status of the Mediterranean biome as a biodiversity hotspot. But biodiversity is increasingly considered an important aspect of ecosystem functioning, underpinning the supply of other ecosystem services (TEEB 2008). In temperate grasslands for example biodiversity-productivity relationships have been tested and discussed in detail. In Mediterranean forests, diversity-stability relationships would be of a higher interest considering the dry climatic conditions, and in a context of adaptation towards increasing drought. We suspect that many forest managers in the region consider that mixed forests are more stable against disturbances and even more productive in the long-term, but there is little scientific evidence for this.

In this presentation we first review some relevant theory of biodiversity function research. We compare complementarity and selection effects as possible mechanisms for biodiversity function and introduce the concept of overyielding as a measure of diversity function effect based on comparison of the mixed forest with the monocultures of its constituents. Then we highlight current and future research activities in Mediterranean forests. As a matter of fact, demonstrating diversity-productivity or diversity-stability relationships in Mediterranean forests is not an easy task. The problem is that forest condition and growth are determined by many interacting environmental and management factors, some of them having a much stronger influence than diversity. Controlling for these confounding factors would therefore require advanced statistical techniques or a very specific experimental design.

Vilà *et al.* (2007) made the most successful attempt so far to use national forest inventory data for testing biodiversity-productivity relationships in the Mediterranean forest. They used the inventory data from Catalonia, Northern Spain, wich includes high resolution spatial information on many environmental and management related co-variates. Basically, they found higher wood production with increasing tree species mixture in evergreen broadleaved forest, but not in deciduous broadleaved or conifers. This suggests a positive biodiversity-productivity relationship on more extreme or marginal sites.

More controlled observational studies will take place in the framework of the EU FP7 FunDivEUROPE project, where numerous ecosystem service indicators and associated biodiversity will be measured along tree species diversity gradients in areas selected for reduced variability of confounding factors. The two Mediterranean sites included are Alto Tajo Natural Park, in central Spain and the public-owned forest complexes of Berignone-Tatti and Belagaio in central-southern Tuscany, Italy.

Finally the need for specifically designed tree species diversity experiments that fully control for confounding factors will be discussed in the context of a developing international network of such experiments and the appropriateness for some Mediterranean sites to be included in this global effort will be argued.

Keywords : mixed forest, diversity-productivity relationship, diversity-stability relationship