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Biodiversity

Complementary canopies

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Old (with your corrections): Physical complementarity among trees in the use of vertical space increases productivity due to species-specific differences and plasticity in crown architecture,

A large number of biodiversity experiments have shown positive effects of plant species richness on plant biomass production[1]. This has been theoretically explained by differences among species in the use of resources such as light and soil nutrients, but empirical evidence for such niche complementarity or division of labor among plant species has rarely been found, and even then solely in grassland ecosystems[2]. Writing in this issue of *Nature Ecology & Evolution,* Williams et al.[3] demonstrate physical complementarity among trees in the use of vertical space, confirming that crown complementarity is an important mechanism for enhancing primary productivity in forests

The hypothesis that complementarity among species causes positive biodiversity effects at the ecosystem level rests on the assumption that no single species is able to acquire all resources in the environment as efficiently as an assemblage of different species can. For example, even though a single species can grow leaves in different canopy layers, it is likely that another species better adapted to low light can fill lower canopy layers. This occupation of different niches becomes possible when the range of available leaf adaptations to different light levels is greater in mixed species stands than in monocultures. Even though it seems obvious that physical complementarity among trees should be greater in mixed-species communities, there have been very few experimental tests of this effect[5] and no tests of whether such physical complementarity indeed promotes ecosystem functioning. One reason for this lack of evidence is that biodiversity experiments typically compare a limited number of different species combinations with a given species richness, making it difficult to separate the effects of physical complementarity from the effect of species richness. In contrast, the study of Williams et al. focused on a larger number of species combinations at two levels of species richness (2- and 4-species mixtures). They were thus able to demonstrate that physical complementarity does indeed promote ecosystem functioning.

In order to do so, Williams et al first established dense experimental stands of young trees with two or four species. Importantly, they also created a gradient in the degree of differences among species within communities of equal species richness. This approach allowed Williams et al. to show that biomass overyielding in mixtures compared with the average monoculture of the species making up the mixtures can be predicted from *a-priori* differences between species in crown architecture and thus vertical space use. Plasticity of species in response to interspecific competition in mixture can increase or decrease physical crown complementarity and this is associated with corresponding modifications of stand biomass (Fig. 1). Direct analysis of physical complementarity between species, before (in monoculture) and after plastic adjustment (in mixed plots), can move biodiversity–ecosystem functioning research beyond the statistical description of species richness and complementarity effects[4] and beyond modeling[5] to a more predictive science, permitting better design of forests that can promote biomass production, carbon storage and thus contribute to climate change mitigation.

In their analysis, Williams et al. performed a systematically designed experiment with monoculture and mixed communities rather than studying natural tree communities. Such “artificiality” is crucial to reveal mechanisms because one of the basic assumptions of plant biodiversity experiments is that — without interspecific competition — all species could reach constant final yield in mixed plots, in the same way as they could at lower density in monocultures[6] (dashed frames in Fig. 1). Physical complementarity can be calculated by averaging pairwise vertical crown overlap between trees (independent of whether they are direct neighbours or not). This allows derivation of crown complementarity indices within

(CCI_{mono}) and between species as predicted without plasticity (CCI_{pred}) and as observed with plasticity (CCI_{obs}). Williams et al. found that CCI_{pred} and CCI_{obs} were positively correlated with aboveground biomass overyielding, demonstrating that physical crown complementarity determined the degree to which mixed experimental stands exceeded biomass production of monocultures (solid frames in Fig. 1).

The mechanisms underlying overyielding have often been analysed statistically, attributing effects to "complementarity effects" and "selection effects"[4]. Interestingly, Williams et al. found that the effect of crown complementarity on overyielding was related mostly to selection effects rather than to complementarity effects[3]. This suggests that in this case the statistical selection effect included a strong "trait-dependent complementarity effect"[7], i.e. large trees benefitted from reduced competition from small neighbours, but these smaller trees suffered less than the larger ones benefitted. As hypothesized above, large trees were thus unable to fill all vertical space available to small trees. Another recent study showed that plasticity increased crown overlap (and decreased statistical complementarity effects) in mixed stands of young trees where species were similar in size but decreased crown overlap (and increased statistical complementarity effects) when they differed in size[8]. This might help to explain why Williams et al. found that crown plasticity sometimes decreased and sometimes increased CCI_{obs} relative to CCI_{pred}.

Additional dimensions of physical complementarity could conceivably have contributed to biomass overyielding in Williams et al.'s study, for example complementarity in belowground resource use. Furthermore, at least the plastic component of crown complementarity could have been affected by the biomass overyielding itself[5]. Unfortunately, it is impossible to differentiate between such primary and secondary effects. A decisive test would require a set of species that differ in crown architecture only, which cannot reasonably be expected because of the inherent correlations of morphological and physiological traits that emerge from fundamental trade-offs. One might maintain that only effects that cannot be explained by other variables (including biomass overyielding) are causal effects[5], but this extremist perspective ignores that the opposite may equally be true, i.e. the same reasoning could be applied to these other variables.

To understand the biological mechanisms that drive overyielding in mixed communities, experimental research must move from pure species richness manipulations and the assessment of statistical selection and complementarity effects to manipulations of physical complementarity and the analysis of why at a given species richness some mixtures overyield considerably whereas others do not. Manipulations of functional diversity and trait-based approaches have been leading the way, but are usually focused on static species traits that are then used to derive community-weighted trait means and functional diversity measures. It will be interesting to see to what extent plastic responses of species to variation in the diversity and structure of their environment will relate to statistical selection and complementarity effects, even if the conclusion might be that the statistical approach is of limited use and novel approaches will have to be developed to better understand the fundamental mechanisms underlying biodiversity–ecosystem functioning relationships.

Williams and colleagues' work has important implications for agriculture and forestry as well, where current production systems mostly consist of monocultures. It may now be possible to identify particular phenotypes that optimally complement each other in the use of resources, allowing the design of forest plantations that deliver higher yields. It is likely that the full potential of such systems of mixed species or provenance up to now has not been recognized and that opportunities to promote desirable ecosystems services such as carbon sequestration are therefore missed.

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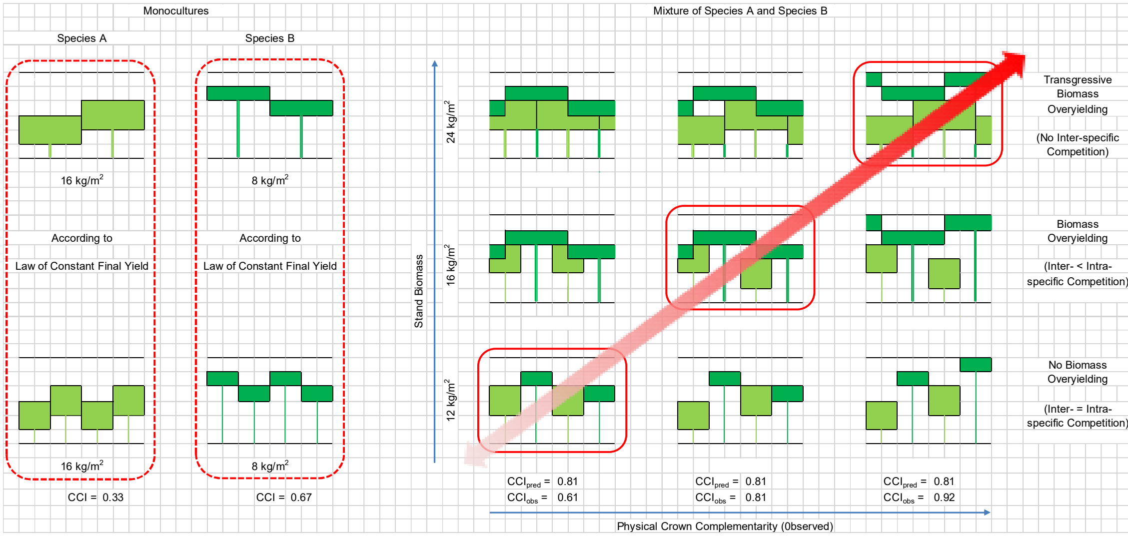

Figure 1 | Illustration of potential effects of crown complementarity between two species in vertical space on stand biomass. The vertical extent of the tree crowns in the pictures is used to calculate crown complementarity indices (CCIs)[3] whereas the green crown areas illustrate biomass. The total number of trees planted in monocultures (shown on the left) and mixed stands (shown on the right) is kept constant and therefore the individual density of each species in two-species communities is half the one of monocultures. However, in the absence of interspecific competition each species would produce a biomass equal to monocultures (law of constant final yield) and as a consequence the mixture would produce a total biomass equal to the sum of the two monocultures (top row). With identical inter- and intra-specific competition, the community biomass of the mixture would equal the average biomass of the monocultures (bottom row). The study by Williams et al.[3] showed that with reduced vertical overlap, i.e. increased crown complementarity, biomass overyielding in mixtures increased as indicated by the stands in the solid red frames. Plasticity either decreased (first column with mixtures) or increased (third column with mixtures) observed crown complementarity and as a consequence decreased or increased stand biomass.