

Spatial complementarity in tree crowns explains overyielding in species mixtures

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Deciphering the mechanisms that link biodiversity with ecosystem functions is critical to understanding the consequences of changes in biodiversity. The hypothesis that complementarity and selection effects drive relationships between biodiversity and ecosystem functions is well accepted, and an approach to statistically untangle the relative importance of these effects has been widely applied. In contrast, empirical demonstrations of the biological mechanisms that underlie these relationships remain rare. Here, on the basis of a field experiment with young trees, we provide evidence that one form of complementarity in plant communities—complementarity among crowns in canopy space—is a mechanism, related to light interception and use, that links biodiversity with ecosystem productivity. Stem biomass overyielding increased sharply in mixtures with greater crown complementarity. Inherent differences among species in crown architecture led to greater crown complementarity in functionally diverse species mixtures. Intraspecific variation, specifically neighbourhood-driven plasticity in crowns, further modified spatial complementarity and strengthened the positive relationship with overyielding—crown plasticity and inherent interspecific differences contributed near equally in explaining patterns of overyielding. We posit that crown complementarity is an important mechanism that may contribute to diversity-enhanced productivity in forests.

Biomass overyielding in diverse plant communities is well documented^{1,2}, but few studies provide experimental evidence of the biological mechanisms that underlie these diversity–productivity relationships^{3–7}. In forest ecosystems, characteristics of the crowns of individual trees and how they fit together to form the forest canopy may be key determinants of productivity^{8,9}. Light often limits individual tree growth in forests¹⁰, and light interception is determined by canopy structure—the density and distribution of leaves—which, in turn, is determined by the characteristics and arrangement of individual tree crowns. Morphological and physiological differences among interacting trees may enhance the filling of canopy space, leaf area index (LAI), and light capture and use—all crucial factors for explaining productivity^{6,9,11,12} and potential reasons for why more diverse forests tend to be more productive^{2,13,14}.

Explanations of the relationships between biodiversity and ecosystem function are grounded in theory developed to explain species coexistence¹⁵. Within the species coexistence literature¹⁶ and early biodiversity–ecosystem function literature¹⁷, the word ‘complementarity’ was used to describe niche or resource partitioning; however, the operational difficulty of untangling niche complementarity from other positive species interactions led Loreau and Hector¹⁸ to use ‘complementarity’ to describe positive effects attributable to mixing species, including facilitation, within their widely adopted^{19–21} statistical approach of untangling selection from complementarity effects. Here, we use the term ‘complementarity’ in a literal sense—the extent to which two or more parts are complementary or fit together without overlap—that aligns more closely with its earlier use.

Complementarity in space may explain biodiversity–productivity relationships by characterizing how much an assemblage can exploit resources such as light^{12,15}. In theory, complementarity is measurable among any interacting individuals²². Functional traits, which reflect and determine resource use, vary both among and within species, and help link community-scale properties (like complementarity) and function. Plants may express different trait values in different neighbourhoods²³, affecting complementarity and ecosystem function—often enhancing both^{4,20,24,25}. Notably, plasticity in plant architectural traits has been shown to increase canopy packing²⁴, LAI²⁶ and light capture²⁵.

In this study, we examined how crown architecture differs among trees during the early stages of stand development, and examined the consequences of the resulting spatial complementarity of tree crowns on stem biomass overyielding (Fig. 1). Here we define stem biomass overyielding as the difference in stem biomass between a mixture and the average of its constituent monocultures (equivalent to the net biodiversity effect¹⁸, see Methods). In addition to being a useful model system for testing theory that links individuals to communities and ecosystems, developing stands influence future forest composition and function, making their dynamics important to investigate. To better understand the functional underpinnings of our results, we also examined how crown complementarity relates to variability in the maximum growth rate among species. In one study, single functional traits were found to be poor predictors of young tree growth worldwide²⁷, and there is some evidence to suggest that multiple traits better reflect the ecological strategies and realized performance of plants in different environments^{28–30}. Maximum growth rate can be considered an

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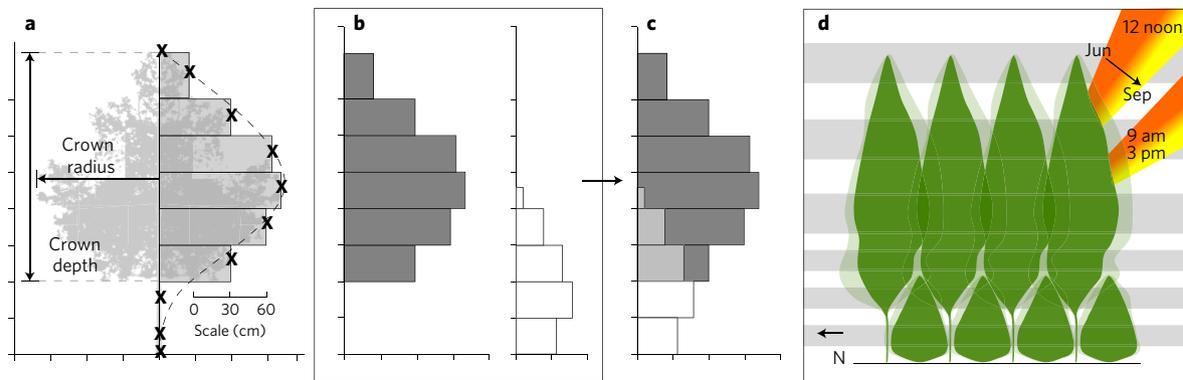


Figure 1 | Crown measurements and crown complementarity. **a**, Crown radii were measured in strata from ground to treetop to characterize crown size and shape. **b, c**, Using these radii, crown complementarity was calculated for pairs of trees and subsequently averaged to give plot-level crown complementarity indices (CCI; equations (1) and (2) in Methods section). Crown complementarity was calculated for tree pairs by modelling each tree as a stack of elliptical cylinders (**b**; simplified as rectangles), and calculating the difference between trees in terms of their crown volume within each stratum (**c**; dark grey or white; light grey is the volume shared by both trees) and summing those differences across all strata before expressing this total difference in strata occupation as a proportion of the combined volume of the pair of trees. **d**, An east-facing view of a *Betula papyrifera* and *Pinus strobus* mixture (size and spacing of one row of trees to scale; mean north and south crown radii in dark green, standard deviation in light green) showing the approximate range in solar elevation through the growing season; depicted for noon, 9 am and 3 pm (Eastern Standard Time) from 21 June (orange) to 21 September (yellow).

integrated performance trait³¹ that is associated with shade tolerance (Supplementary Fig. 1) and the suite of functional traits that influence both a plant's resource strategy and its performance in different environments³².

We hypothesized that tree crown size and shape would differ both between species and within species across different neighbourhoods, leading to variation in crown complementarity among species mixtures. We predicted that greater variation in maximum growth rate among species would be associated with greater crown complementarity and, moreover, that mixtures with greater variability in maximum growth rate would show greater crown complementarity, even when holding species richness constant. Finally, we expected that crown complementarity would help explain stem biomass overyielding, with the relationship mostly determined by inherent differences in crowns across species, but strengthened by neighbourhood-driven plasticity.

To assess these hypotheses, we characterized individual tree crowns and applied a series of novel crown complementarity indices (CCIs; see Methods, Fig. 1 and Supplementary Fig. 2) across a high-density tree diversity experiment in southern Quebec, Canada. This experiment is composed of 12 common temperate-boreal tree species planted in monocultures and 25 functionally diverse mixed-species communities (see Methods). Since diversity in functional traits and species richness tend to covary closely^{33,34}, their relative importance can be difficult to untangle^{15,33,35}. In this experiment, we untangled their relative importance by establishing gradients of species richness and functional diversity along orthogonal axes^{19,36}. CCIs quantify vertical partitioning of strata within canopy space. This is probably the main axis on which trees partition light in our high-density system with evenly spaced trees and relatively low solar elevation (Fig. 1d), and links the CCIs with the well-recognized ecological importance of canopy stratification³⁷. By comparing three CCIs for each mixture—(1) the complementarity observed in the mixture (CCI_{obs}), (2) the complementarity predicted for the mixture on the basis of the crown size and shape of constituent species in monoculture (CCI_{pred}), and (3) the arithmetic mean of the complementarity of constituent species observed in monocultures (CCI_{mono})—we examined how variation among and within species contributes to crown complementarity and its relationship with stem biomass overyielding (see Methods and Supplementary Fig. 2).

Results

We found that crown size and shape differed within and among species four years after the experiment was planted (Supplementary Tables 1 and 2), and led to differences among mixtures in crown complementarity. Within species, considerable variation was observed both within and among neighbourhoods (Supplementary Table 2). As a result of these differences in crowns, crown complementarity observed in species mixtures (CCI_{obs}) ranged from 0.20 to 0.68 (Supplementary Fig. 3), covering much of the potential range from zero to complete ($CCI = 1$) complementarity.

Realized differences in crown size and shape among trees led to greater crown complementarity being observed in 23 of 25 mixtures, versus the average in their constituent monocultures ($CCI_{obs} > CCI_{mono}$; Supplementary Fig. 3). Crown complementarity was predicted to be, on average, 29% greater in mixtures—purely due to inherent interspecies differences—than crown complementarity in constituent monocultures ($CCI_{pred} > CCI_{mono}$ in all mixtures). Plasticity caused observed crown complementarity to be significantly greater than that predicted from monoculture-grown trees ($CCI_{obs} > CCI_{pred}$) in four of the 25 mixtures and significantly less than predicted ($CCI_{obs} < CCI_{pred}$) in five mixtures ($P < 0.05$).

Mixtures composed of species with greater differences in their maximum growth rates had greater crown complementarity. Functional dispersion (FDIs) of the maximum growth rate among species, which is a measure of how much the species within a mixture functionally differ, explained 64% of the variation in CCI_{obs} among mixtures (coefficient of determination $r^2 = 0.64$, regression coefficient $b = 0.29$, $t_{23} = 6.43$, $P < 0.001$; Fig. 2). The number of species (two or four) within a mixture did not affect CCI_{obs} (variance ratio $F_{1,22} = 0.014$, $P = 0.91$).

Furthermore, this crown complementarity was positively and strongly associated with patterns of stem biomass overyielding. Plots ranged from modest net underyielding for stem biomass (-6.7 Mg ha^{-1}) to considerable net overyielding (33.4 Mg ha^{-1}). CCI_{obs} explained 61% of variation among all species mixtures in stem biomass overyielding ($r^2 = 0.61$, $b = 65.43$, $t_{23} = 6.01$, $P < 0.001$; Fig. 3). No interaction with species richness was observed, and the strong positive relationship held when two- and four-species mixtures were considered alone (two species: $r^2 = 0.61$, $b = 66.10$, $t_{12} = 4.34$, $P = 0.001$; four species: $r^2 = 0.60$, $b = 55.96$, $t_8 = 3.45$, $P = 0.009$; Fig. 3). We statistically separated stem biomass overyielding

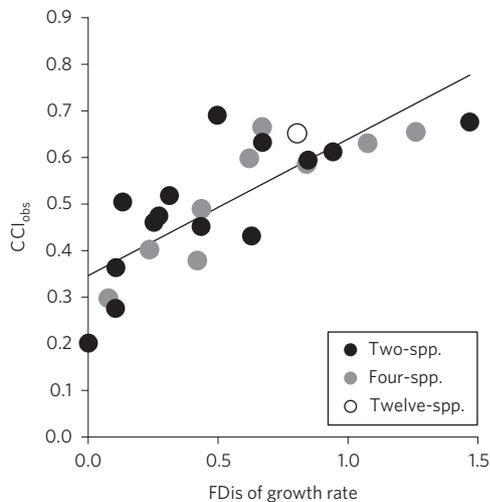


Figure 2 | Functional dispersion of maximum growth rate and crown complementarity. Across all mixtures (two-, four- and twelve-species; $n = 25$), functional dispersion (FDIs; see Methods) of the maximum growth rate was positively associated with variation in the observed crown complementarity (CCI_{obs} ; $r^2 = 0.64$, $b = 0.29$, $t_{23} = 6.43$, $P < 0.001$).

into what have been labelled ‘selection effects’ (SEs) and ‘complementarity effects’ (CEs)¹⁸, both of which are underpinned by biological interactions³ (see Supplementary Note). Note, as discussed above, this usage of the word complementarity is not directly parallel to how we use the term in defining ‘crown complementarity’. Both SEs and CEs contributed to the overall patterns of stem biomass overyielding¹⁹ and its relationship with CCI_{obs} ; with SEs tending to be stronger (Supplementary Fig. 4 and Supplementary Note).

The relationship between CCI_{obs} and stem biomass overyielding was explained, but only in part, by overyielding in crown size (difference between the mean crown volume of trees in a mixture and the mean crown volume of trees in constituent monocultures; because trees in the mixtures were planted in equal abundance and <1% of stems had died, this approximates overyielding in crown volume at the plot level—see Methods). CCI_{obs} remained a significant predictor of stem biomass overyielding even after accounting for crown volume overyielding ($t_{22} = 4.41$, $P < 0.001$). Crown volume overyielding and CCI_{obs} together explained 75% of variation in stem biomass overyielding, and hierarchical partitioning (see Methods) revealed that 56% of the variation explained was attributable to CCI_{obs} with the remaining 44% attributable to crown volume overyielding. Thus, crown complementarity probably contributed to stem biomass overyielding both through larger crowns and through greater production per unit crown.

Inherent interspecies differences and plasticity together drove the relationship between CCI_{obs} and stem biomass overyielding. This is revealed by how stem biomass overyielding was related to differences between the three crown complementarity indices (Supplementary Fig. 2). The net difference in crown complementarity between monoculture- and mixture-grown trees ($CCI_{obs} - CCI_{mono}$), a measure that represents the effects of both plasticity and inherent interspecies differences, had a strong relationship with stem biomass overyielding ($r^2 = 0.70$, $b = 74.79$, $t_{23} = 7.25$, $P < 0.001$; Fig. 4a). Considered alone, crown complementarity attributable to interspecies differences ($CCI_{pred} - CCI_{mono}$) was positively associated with stem biomass overyielding ($r^2 = 0.31$, $b = 63.90$, $t_{23} = 3.19$, $P = 0.004$; Fig. 4b); crown complementarity attributable to plasticity ($CCI_{obs} - CCI_{pred}$) was also positively associated with stem biomass overyielding ($r^2 = 0.34$, $b = 76.09$, $t_{23} = 3.46$, $P = 0.002$; Fig. 4c) and further strengthened the overall relationship.

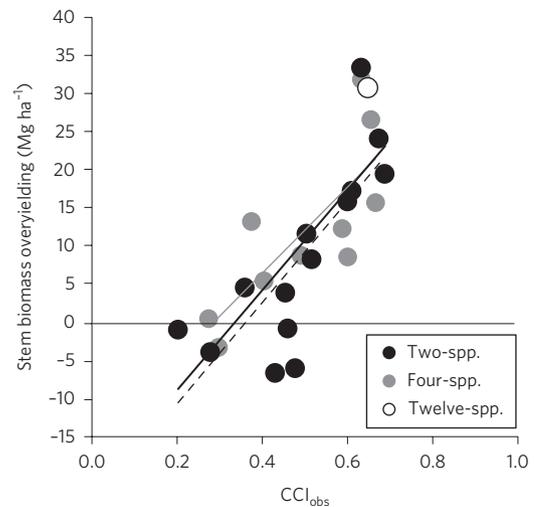


Figure 3 | Crown complementarity and stem biomass overyielding.

Observed crown complementarity (CCI_{obs}) was positively associated with overyielding of stem biomass across all species mixtures (thick black line; $n = 25$, $r^2 = 0.61$, $b = 65.43$, $t_{23} = 6.01$, $P < 0.001$), and when two-species mixtures (dashed line; $n = 14$; $r^2 = 0.61$, $b = 66.10$, $t_{12} = 4.34$, $P = 0.001$) and four-species mixtures (grey line; $n = 10$; $r^2 = 0.60$, $b = 55.96$, $t_8 = 3.45$, $P = 0.009$) were considered alone.

Discussion

In this study of young experimental tree communities where a gradient in functional diversity was established orthogonally to species richness, spatial complementarity of tree crowns in mixtures was strongly and positively related to functional diversity (functional dispersion among species in maximum growth rate) and to stem biomass overyielding. This provides novel evidence for a mechanism—spatial complementarity—by which functional diversity links with complementarity and enhances productivity, building on past studies that show greater spatial complementarity causes greater resource capture^{5,6,25,38}. Overall, these findings suggest that spatial partitioning within canopies, as captured by crown complementarity, is important in enhancing the productivity of these young tree communities, and could be a mechanism contributing to the global trend of diversity enhancing productivity within forests².

Here, among communities of equal species number, we found patterns of overyielding were explained by crown complementarity, and crown complementarity, in turn, was explained by the functional diversity of mixtures (Fig. 3). Previous studies of mature forest have found that species richness does²⁴ or does not³⁹ explain canopy filling. The latter study also found no relationship between species richness and patterns of productivity. Taken together, these results leave open the prospect of crown complementarity acting as a mechanism in the many cases where relationships between diversity (as captured by numbers of species or functional traits) and productivity are observed².

The foundation for crown complementarity in mixtures was variation within and among species in crown size and shape, including the influence of neighbourhood-driven plasticity within species. Plastic contributions to crown complementarity were nearly equal to the contributions of interspecies differences in their strength of association with stem biomass overyielding. Plasticity did not always enhance crown complementarity—reflecting the poor ecological combining ability of certain species in this experimental context¹⁹—but plastic shifts in complementarity, overall, were positively associated with biomass overyielding.

Our method of characterizing crown complementarity is simple, yet its positive relationship with stem biomass overyielding was robust. The relationship was stronger than the relationship between

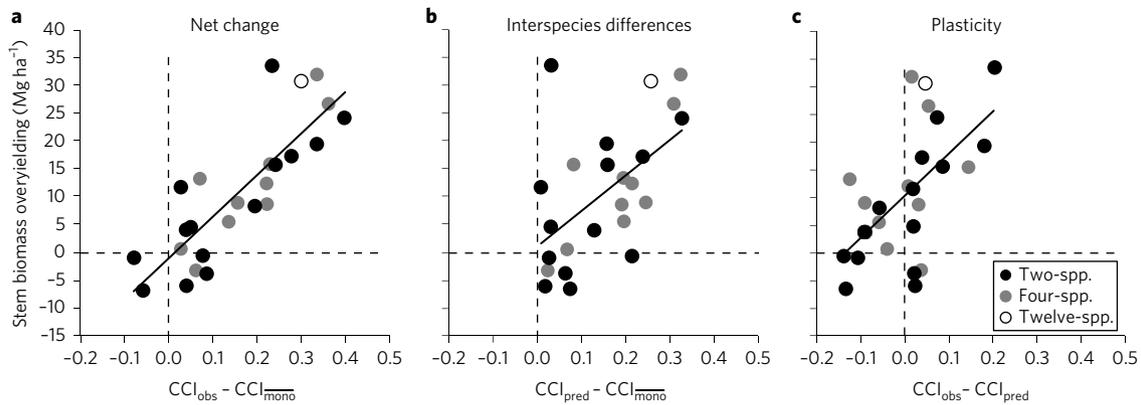


Figure 4 | Differences between three indices of crown complementarity and stem biomass overyielding. **a–c**, Across all species mixtures (two-, four- and twelve-species; $n = 25$), stem biomass overyielding was positively associated with the net difference in crown complementarity between mixture- and monoculture-grown trees (**a**; $CCI_{obs} - CCI_{mono}$; $r^2 = 0.70$, $b = 74.79$, $t_{23} = 7.25$, $P < 0.001$), the contribution of interspecies differences to complementarity (**b**; $CCI_{pred} - CCI_{mono}$; $r^2 = 0.31$, $b = 63.90$, $t_{23} = 3.19$, $P = 0.004$) and the contribution of plasticity to complementarity (**c**; $CCI_{obs} - CCI_{pred}$; $r^2 = 0.34$, $b = 76.09$, $t_{23} = 3.46$, $P = 0.002$).

crown complementarity and crown volume overyielding. Moreover, positive relationships were observed with stem biomass overyielding when crown complementarity was calculated using only the volume (Fig. 3), the volume weighted by leaf area or mass (Supplementary Fig. 5), or an independent dataset of LAI (Supplementary Fig. 6 and Supplementary Methods).

Light capture and use probably underlie the positive relationship between crown complementarity and stem biomass overyielding. Crown complementarity might lead to overyielding in mixtures by increasing overall light interception (because more canopy space is occupied allowing more leaf area to intercept light) and/or light-use efficiency (because plants throughout the canopy differ in their light response curves). Both probably matter^{6,7,11,12,24,25,38}.

We found variability in maximum growth rate, a measure of functional diversity, was strongly and positively associated with crown complementarity in mixtures. Variation among trees in growth rate may first generate vertical partitioning within the canopy, especially in even-aged stands like ours, and increase light interception. Variation in growth rate may subsequently enable effective partitioning of light environments within the canopy—because growth rate aligns with shade tolerance and traits indicative of a tree's resource strategy³² (Supplementary Fig. 1)—and increase overall light-use efficiency. These findings, gleaned from young stands, appear consistent with the long-standing observation that mixing fast-growing shade-intolerant species with slow-growing shade-tolerant species can enhance productivity in forests^{40,41}.

Interactions among trees in young stands are of foremost importance in shaping forests. Since our results come from even-aged stands, they may be especially relevant for plantation forestry or regenerating forests following stand-replacing disturbance, and provide a strong empirical basis for developing forestry practices that favour diversity⁴², such as multi-species plantations that may be more productive and resilient⁴³. As stands develop, the relationship between diversity and productivity probably changes²¹ as do attributes of species that contribute to complementarity, but we anticipate the underlying principles of complementarity, and resultant effects, will remain⁴⁴.

Partitioning of canopy space and light are general mechanisms for enhancing productivity that are likely to be widespread. However, many other factors such as other limiting resources, community assembly processes, direct and indirect anthropogenic influences, and architectural constraints may influence whether the effects of these mechanisms would be observed as clearly in other systems. More work is needed to assess the strength of

these mechanisms across different systems and at different developmental stages. Finally, it is also possible that stem biomass overyielding could increase crown complementarity and/or that the direction of causation could vary through time. However, there are plausible mechanisms by which functional diversity can increase crown complementarity and in turn increase stem biomass overyielding; therefore, this interpretation appears more parsimonious than the reverse, which needs to invoke some other latent driver of overyielding.

This study experimentally demonstrates that the spatial complementarity of tree crowns, attributable to both intraspecific and interspecific differences in crown morphology and physiology (maximum growth rate and associated light response), explains patterns of stem biomass overyielding across functionally diverse, young tree communities. Alongside mechanisms such as spatial partitioning of belowground resources⁵, facilitation⁴⁵ and plant–soil feedbacks^{46,47}, spatial partitioning of the canopy may be a general biological mechanism by which diversity can enhance productivity in tree communities.

Methods

Experimental design. This study uses a high-density tree-diversity experiment established as part of the International Diversity Experiment Network with Trees (IDENT)³⁶. The design is described in detail in ref. ¹⁹. In brief, the experiment was established at Ste-Anne-de-Bellevue (Quebec, Canada, 45°26'N, 73°56'W, 39 m above sea level) in spring 2009 on a flat, high-input agricultural field with sandy soil (approximately 70 cm deep, overtopping clay). The mean annual temperature is 6.2 °C and precipitation is 963 mm (<http://www.climate.weatheroffice.gc.ca>).

Seedlings of 12 common North American temperate-boreal tree species were planted 0.5 m apart in a grid pattern within plots 4 × 4 m in size (64 trees per plot). Plots were spaced 1 m apart. In total, we examined 37 plots: 12 monocultures, 14 two-species mixtures, 10 four-species mixtures and 1 twelve-species mixture. Given the small size of the plots, we use the term 'neighbourhood' interchangeably with 'plot'.

The combinations of species planted in two- and four-species mixtures were chosen at random using a stratified design intended to untangle functional diversity from species richness by including plots of the same species richness varying in functional diversity, thus creating two orthogonal gradients. To do this, functional dispersion (FDIs)⁴⁸ was calculated for all possible mixtures of two and four species using a range of functionally important traits, these mixtures were binned into classes representing the entire gradient of FDIs, and mixtures were randomly chosen from within each class (for details, see refs ^{19,36}). Seven gymnosperm species, *Abies balsamea* (L.) Mill, *Larix laricina* (Du Roi) K. Koch, *Picea glauca* (Moench) Voss, *Picea rubens* Sarg., *Pinus resinosa* Aiton, *Pinus strobus* L. and *Thuja occidentalis* L., and five angiosperm species, *Acer rubrum* L., *Acer saccharum* Marsh., *Betula papyrifera* Marsh., *B. alleghaniensis* Britt. and *Quercus rubra* L. were planted. Within plots, an equal number of trees

of each species was planted, and species were arranged at random with restrictions to avoid clumping (for details, see ref. ¹⁹). Seedlings were one-year (all deciduous species except *Quercus rubra*) or two-years (all evergreen species and *Q. rubra*) old at the time of planting. The site was fenced to exclude large herbivores, and volunteer understorey plants were hand-weeded regularly.

Field measurements. To minimize edge effects, all measurements excluded trees in the outermost row or column on the four sides of each plot, and focused on the interior 36 trees where species were planted in equal proportions. Measurements were taken four years after planting, by which time the canopy had closed on almost all plots.

Height and basal diameter (0.05 m above the ground) of each tree was measured at the end of the growing season. Stem volume for each tree was estimated as basal diameter squared multiplied by height (D^2H), and was multiplied by literature-derived values of wood density¹⁹ to estimate stem biomass.

Focal trees for crown measurements were selected at random from the 36 interior trees of each plot. Six trees were measured in each monoculture, four per species in each two-species mixture, three per species in each four-species mixture and two per species in the 12-species mixture, for 328 trees in total. If a selected tree was unrepresentative of trees on the plot (for example, it was damaged, or substantially smaller or larger than conspecifics), another was selected at random.

Over two weeks during peak leaf area (12 to 25 July 2012), the crown dimensions of focal trees were measured (Fig. 1a). Trees ranged from 0.56 to 4.96 m in height with a mean height of 2.10 m across the 12 species. We considered each tree to be composed of a series of strata 0.30 or 0.60 m in height from the ground to the top of the tree; strata were 0.30 m in height from 0.00 to 2.10 m, and 0.60 m in height above 2.10 m due to the difficulty of measuring above this height. For each tree, we measured the maximum radius of the foliage horizontally from the centre of the tree's stem in each of the four cardinal directions (north, south, east, west) for each stratum. Together, these measurements provide an estimate of the outside dimensions of a crown analogous to a stack of boxes 0.30 m (or 0.60 m) in height fitted tightly around the crown.

Calculations of stem biomass overyielding. For each of the 25 mixed-species plots, a measure of stem biomass overyielding (equivalent to the net biodiversity effect¹⁸) was calculated as the stem biomass of trees observed in a mixture minus the stem biomass of trees of the same species grown in monoculture (weighted by the proportion of each species initially planted in the mixture, such that mortality was considered a treatment effect; in total, 9 of 1,332 trees died), and was expressed per hectare.

Characterizing crown size and shape. We characterized the size and shape of each focal tree using the crown-dimensions measurements (Fig. 1a). For crown size, we calculated crown volume (estimated as stacked elliptical cylinders), maximum crown radius (the mean radius at the widest point of the crown), and crown depth (expressed as a proportion of tree height).

For crown shape, the four sets of crown radius measurements (north, south, east and west) were averaged for each stratum to give each focal tree a mean profile. We fitted the beta distribution to these profiles using the *optim* function in R version 3.2.1 (ref. ⁵⁰), and extracted the two shape parameters (*a* and *b*) of the distribution⁵¹ (Supplementary Methods). The mean, mode, variance and skew of each estimated distribution were then calculated as estimators of crown shape.

For each size and shape measurement for each species, the phenotypic plasticity index (PI)⁵² was used to characterize variation among plots (monoculture and all mixtures; $PI_{\text{among plots}}$) and the mean variation among conspecific trees within plots ($PI_{\text{within plots}}$) (Supplementary Methods).

Characterizing crown complementarity. To assess the partitioning of canopy space, we introduce an index of crown complementarity that is based on the difference among trees in crown volume within strata from the ground to the top of the canopy (Fig. 1b,c). For each focal tree, crown volume was calculated from the crown dimensions measurements by treating each stratum as an elliptical cylinder. Crown complementarity (CC) was calculated for a pair of trees as the difference in crown volume (*V*) between the two trees (*i* and *j*) in each stratum (*k*) summed across all strata. The total difference in crown volume was expressed as a proportion of the combined volume of the pair of trees, as follows:

$$CC_{ij} = \frac{\sum |V_{ik} - V_{jk}|}{V_i + V_j} \quad (1)$$

The crown complementarity index (CCI) for a plot (*p*) was calculated by averaging the crown complementarity (CC) of all possible pairs of measured trees (*n*):

$$CCI_p = \frac{\sum (CC_{ij})}{n} \quad (2)$$

Note that measured trees were not necessarily adjacent, and pairs included trees of the same species. This reflects the random arrangement of species within plots and accounts for the possibility that variation among conspecific trees affects

the crown complementarity of an assemblage. CCI measures that remove the effect of conspecific variation were also calculated and showed that the relationship between crown complementarity and stem biomass overyielding held regardless of whether conspecific variation was included (data not shown).

Conceptually, CCI represents the extent to which trees in an assemblage occupy different strata. The index is designed to represent the partitioning of strata across the plot rather than to represent individual trees or tree pairs, and results (not shown) were very similar if calculated at the plot rather than tree level.

Using the CCI, crown complementarity was calculated in three ways for each mixed-species plot. These three indices allow us to untangle the contributions of inherent interspecies differences, neighbourhood-driven plasticity and conspecific differences to crown complementarity (Supplementary Fig. 2). First, we calculated the 'observed' crown complementarity (CCI_{obs}) by using the trees actually growing together in the mixed-species plot. This index includes the effects of interspecies differences, conspecific differences and neighbourhood-driven plasticity in crowns. Second, we calculated the 'predicted' crown complementarity (CCI_{pred}) by superimposing the sizes and shapes of monoculture-grown trees of the constituent species on to a hypothetical mixed-species plot, and calculating complementarity among these trees. This index represents how complementary trees would be in a mixture if they did not change in size or shape from when they were grown in monoculture. CCI_{pred} includes both interspecies differences and variation among conspecifics; we compared this measure with CCI_{obs} to quantify how neighbourhood-driven plasticity in crowns influences complementarity. Third, we calculated the 'mean monoculture' crown complementarity (CCI_{mono}) by calculating the observed crown complementarity for each of the constituent species in monoculture and taking the average across those complementarity values. We compared CCI_{mono} with CCI_{pred} to quantify how interspecies differences contributed to crown complementarity, and with CCI_{obs} to quantify how interspecies differences and plasticity together contributed to crown complementarity.

Note that unlike expected biomass production in mixtures, which is arithmetically calculated such that by definition it equals the mean biomass of its constituent species in monocultures and indicates nothing about overyielding, CCI_{pred} can be less than, equal to or greater than CCI_{mono} . Comparing CCI_{pred} with CCI_{mono} indicates whether crown complementarity in mixtures is expected to be greater than that in monocultures (whether overyielding in crown complementarity is expected) purely on the basis of interspecies differences.

Our index of crown complementarity implicitly assumes that leaves are distributed evenly throughout the volume occupied by the tree crown, which is unlikely to be true⁸. However, the vertical distribution of leaves—included by weighting the crown volume of each stratum with coarse estimates of leaf area or leaf mass—had little effect on patterns of crown complementarity among assemblages or on its relationship with overyielding (Supplementary Fig. 5 and Supplementary Methods). This indicates that our results are unlikely to be confounded by an uneven distribution of leaves through tree crowns.

Maximum growth rate. For each species, maximum growth rate was assigned according to the 90th percentile increase in stem biomass from 2009 to 2012 using all trees in the three blocks of the experiment not used in the present study. Maximum growth rate was strongly and negatively correlated with shade tolerance³³, as predicted from the literature^{54,55}, but angiosperms had a faster maximum growth rate for a given shade tolerance than gymnosperms (assessed with standardized major-axis regression⁵⁶; Supplementary Fig. 1). For each mixed-species plot, FD_{Dis} in the maximum growth rate was calculated as a measure of variation among species.

Statistical analyses. All trees measured for a given treatment—that is, species within a given monoculture or mixture—were located within the same plot. Therefore, any differences among treatments might be attributable to neighbourhood effects or any other spatially correlated difference. However, we expect little overestimation of neighbourhood effects because all plots are close and the site's topography is flat with little variation in soil texture or depth (further homogenized by decades of ploughing and disking).

One-way ANOVA was used to assess differences in crown size and shape among species and among neighbourhoods for each species, and to assess differences among the three indices of crown complementarity (CCI_{obs} , CCI_{pred} and CCI_{mono}) for each mixed-species plot. For analyses of the differences among the three indices the sequential Bonferroni procedure⁵⁷ was used to correct for multiple comparisons. Pairwise comparisons were assessed using Tukey's honest-significant-difference tests where significant differences were detected. We assessed whether variation among species in maximum growth rate explained CCI_{obs} using simple linear regression. Finally, the hypothesized relationship between CCI_{obs} and stem biomass overyielding was also tested with simple linear regression. To assess whether associations between CCI_{obs} and stem biomass overyielding simply reflected overyielding in crown volume, we calculated the independent and joint contribution of CCI_{obs} and crown volume overyielding to stem biomass overyielding using hierarchical partitioning⁵⁸.

To assess the contribution of interspecies differences and plasticity in crowns to the association between CCI_{obs} and biomass overyielding, we regressed stem biomass overyielding against $CCI_{obs}-CCI_{mono}$, $CCI_{pred}-CCI_{mono}$ and $CCI_{obs}-CCI_{pred}$.

For all analyses, assumptions of normality, homogeneity of variance and linearity, where relevant, were assessed using boxplots and residual plots. All calculations and analyses were implemented in R version 3.2.1 (ref. 50).

Data availability. Data that support the findings of this study are available from the corresponding author on reasonable request.

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Author contributions

A.P., P.B.R. and C.M. designed the broader IDENT study. L.J.W. designed the crown complementarity study and its link to overyielding, with help from all authors. L.J.W. and A.P. collected data. L.J.W. analysed the data with assistance from

P.B.R. and J.C.B., and wrote the first draft of the manuscript with editorial assistance from P.B.R. All authors contributed to further manuscript development.

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Competing interests

The authors declare no competing financial interests.