ARTICLE

# Tree species diversity and composition relationship to biomass, understory community, and crown architecture in intensively managed plantations of the coastal Pacific Northwest, USA

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**Abstract:** Trends in land cover and the demand for ecosystem services suggest that plantation forests will be expected to provide a larger quantity and diversity of ecosystem services. We identified three measures indicative of diverse ecosystem services (aboveground biomass, understory biodiversity, and crown length) and compared their relationships to tree species composition in intensively managed forest plantations of the Coast Range mountains of the Pacific Northwest, United States. This study was conducted in stands of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and red alder (*Alnus rubra* Bong.), as well as in mixtures of the three species that were 35–39 years old. In this operational setting, we did not observe the positive relationship between species diversity and productivity observed in other studies, which we attributed to management practices that minimize interspecific interaction during most of the rotation. Crown length and understory species diversity were greater in mixtures of tree species than in (monospecific) monocultures. When multiple ecosystem components were considered simultaneously, mixtures of tree species outperformed monocultures. The observed relationships of the three responses to tree species composition and diversity are likely explained by differences in tree phenology, shade tolerance, disease susceptibility, and management interventions. Based on the results, management that is solely fixated on wood production homogeneously throughout the plantation may miss opportunities to provide other ecosystem services.

*Key words:* biodiversity, plantations, mixed species, ecosystem services.

**Résumé :** Les tendances en matière de couverture terrestre et la demande pour des services de l'écosystème indiquent que les plantations forestières devront fournir une plus grande quantité et diversité de services de l'écosystème. Nous avons identifié trois mesures indicatives de divers services de l'écosystème (biomasse aérienne, biodiversité du sous-bois et longueur de la cime) et comparé leurs relations avec la composition en espèces arborescentes dans des plantations forestières sous aménagement intensif situées dans la chaîne Côtière du Pacific Northwest américain. Cette étude a été réalisée dans des peuplements de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.), de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) et d'aulne rouge (*Alnus rubra* Bong.) ainsi que des peuplements mélangés comprenant ces trois espèces âgées de 35 à 39 ans. Dans ce cadre opérationnel nous n'avons pas observé de relation positive entre la diversité des espèces et la productivité qui a été observée dans d'autres études, ce que nous avons attribué aux pratiques d'aménagement qui minimisent l'interaction interspécifique durant presque toute la durée de la période de rotation. La longueur de la cime et la diversité des espèces de sous-bois étaient plus grandes dans les peuplements mélangés que dans les monocultures (monospécifiques). Lorsqu'on tenait compte simultanément de plusieurs composantes de l'écosystème, les peuplements mélangés avaient une meilleure performance que les monocultures. La relation des trois réactions à la composition et à la diversité des espèces arborescentes qui a été observée s'explique vraisemblablement par les différences dans la phénologie, la tolérance à l'ombre, la susceptibilité aux maladies et les interventions d'aménagement. Sur la base des résultats, l'aménagement axé uniquement sur la production de bois de façon homogène partout dans une plantation peut réduire les opportunités de fournir d'autres services de l'écosystème. [Traduit par la Rédaction]

*Mots-clés :* biodiversité, plantations, espèces mélangées, services de l'écosystème.

## 1. Introduction

The demand for ecosystem services provided by forests (e.g., genetic resources, wood production, and habitat for terrestrial flora and fauna) is projected to dramatically increase in the coming decades (Alcamo et al. 2005). Rapid human population growth and increased pressures on natural resources over the last century have led to more native forests becoming degraded, with an associated decline in the ability of native forests to provide various ecosystem services (Millennial Ecosystem Assessment 2005). In contrast, the area of forest plantations has increased by >100 Mha globally since 1990, and consequently, forest plantations provide an expanding quantity of selected ecosystem services (Payn et al. 2015). Given the historical and ongoing trends in forest cover, coupled with the projected increase in demand for ecosystem

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services from forests, the role of plantation forests in providing a diversity of ecosystem services is likely to considerably increase in the future.

In the 20th and 21st centuries, plantation forests of the European and Euro-American tradition have been primarily managed for provisioning wood fiber with the assumption that most other services benefit from "good" timber management, an idea called "Kielwassertheorie" or "wake theory" (Schuler 1998). Ecosystem services that do not benefit from timber production have often been viewed as constraints. However, increased societal demand for a wider array of goods and services has led to incentives for managers to focus on benefits besides timber (Robert and Stenger 2013). For example, carbon markets, wetland mitigation banking, water quality trading, and conservation easements have the potential to offset the opportunity costs of management decisions that result in suboptimal timber production but cultivate or protect other values (Deal et al. 2012). Regulations and voluntary certification programs like the Forest Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification (PEFC) also require explicit consideration of nontimber services (Fernholz et al. 2011). However, the demand for services beyond the provisioning of wood fiber often results in trade-offs and the need for forest managers to balance the outflow of multiple ecosystem services (Bauhus et al. 2010).

Increasing tree species diversity in plantations established for timber production has been suggested as one way to increase the potential provision of ecosystem services (Verheyen et al. 2016). Ecosystem processes and structures related to the provisioning of ecosystem services can vary between mixed stands and (monospecific) monocultures. Notably, studies in many systems have found that mixtures of plant species can be more productive than expected when compared with monocultures, a phenomenon known as overyielding (Hector 2006). Experimental studies that compared productivity (measured as biomass or harvestable wood accumulation over time) of monocultures and mixed species in intensively managed plantations have had varied results. In temperate plantations, Amoroso and Turnblom (2006) found that stand density mediates the impact of mixing tree species on stand productivity. In contrast, in tropical plantations, Bouillet et al. (2008) found that mixtures of species were more productive than monocultures on some sites but not on others. The authors attributed this to facilitation (interactions between plants species in which at least one species benefits and neither is harmed) in conjunction with the stress-gradient hypothesis, which states that facilitation is more likely to occur under conditions of high abiotic stress (see Forrester and Bauhus (2016) for detailed discussion and further references on mechanisms affecting species mixing effects on forest productivity).

Mixing species in plantations can affect trees and associated vegetation relative to those in monocultures. For example, differences between mixed species and monoculture stands have been found in height of the crown base (Grotta et al. 2004), total height, length of the crown (Bauhus et al. 2004), and tree allometry (Forrester et al. 2017). Understory plant diversity is also influenced by tree species composition because of variation in light infiltration, water availability, and soil chemistry (Barbier et al. 2008). Few studies on mixed-species plantations have considered multiple responses or more than two species, even though high plant diversity is needed to support multiple ecosystem services (Isbell et al. 2011). Mixed-species forests generally provide a greater amount of multiple ecosystem services than monocultures, but the specific species mixture and biogeographical context are important for assessing trade-offs, justifying regional studies of biophysical responses to tree species composition and diversity in plantation forests (Felton et al. 2016).

We conducted an exploratory study in even-aged, intensively managed plantations in the coastal Pacific Northwest, United States (USA), to investigate (*i*) how aboveground biomass (AGB) of trees, mean live crown length (LCL), and diversity of understory plants (DUP) respond to tree species composition and (*ii*) what trade-offs may exist among these measures of ecosystem components in operational settings. Exploratory studies are a type of observational study and an efficient hybrid of planted experiments and inventory studies for analyzing ecosystem properties in tree species mixtures and comparing them with monocultures in which existing mature stands with comparable environmental conditions and management regimes are explicitly selected to represent a gradient of tree species diversity (Bauhus et al. 2017). The plantations we focused on were 35–39 years old, regenerated from clear-cut harvest, and included monocultures and all species combinations of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and red alder (*Alnus rubra* Bong.). We focused on tree AGB, mean LCL, and DUP because these measures are responsive to growing conditions and can be related to several ecosystem services. Also, these ecosystem measures can be derived from forest inventory data commonly collected by plantation forest managers. As such, they can be used by managers to make practical assessments of potential ecosystem service response to management decisions. Furthermore, because the stands in this study were managed as working plantations, the results may be more representative of real-world operational conditions than those of planted experiments.

Tree AGB was selected as a variable because it is representative of the cumulative productivity of the trees and is integral to multiple ecosystem services such as the provisioning of wood fiber and forest carbon storage (Chojnacky et al. 2014). DUP was selected as a variable because many ecosystem functions and services are mediated by nontree species (Gamfeldt et al. 2013). For example, the understory plant community provides critical habitat and forage for a wide variety of animal species and can directly contribute to numerous cultural and provisioning ecosystem services derived from medicinal and edible species (Whigham 2004). Furthermore, the cover of understory species with functional traits such as tolerance to drought and heat may increase the stability and resilience of understories, as well as the services they provide (Neill and Puettmann 2013). Biodiversity itself is considered an ecosystem service, and the understory plant community represents a large portion of the overall biodiversity of forest systems (Duguid and Ashton 2013). We selected LCL as a variable because it has many attributes that make it an attractive and feasible indicator of multiple potential ecosystem services. It is already widely used in silviculture because it is easy to measure in the field (Maguire and Kanaskie 2002). It is a predictor of tree growth, leaf area, and tree photosynthetic capacity (Gilmore et al. 1996; Maguire and Bennett 1996; Wykoff 1990). LCL is also a surrogate for the distribution of branch biomass, which correlates to the abundance of arthropods (Halaj et al. 2000), an important food source for wildlife (e.g., bats) that feed on insects (Kalcounis et al. 1999). Crown structure also affects wildlife use of canopy habitat, and larger crowns provide more area for some species of birds to nest and forage in the region (Hayes et al. 1997). Therefore, LCL is a suitable proxy for multiple aspects of the ecosystem (future growth potential, foundational trophic level, and critical structures) and the potential services that they support (wildlife habitat and future wood production or carbon capture).

Our objectives were to determine (*i*) if tree AGB, mean LCL, and DUP individually have positive or negative relationships with tree species diversity; (*ii*) if tree AGB, mean LCL, and DUP increase or decrease with one another when there are changes in tree species diversity and composition; and (*iii*) if mixed-species stands can support higher levels of all three measures simultaneously compared with monocultures. We collected field data to estimate the three measures and then assessed their relationships to tree species composition and diversity using a response surface model.

**Table 1.** Description of species composition criteria for field selection of plots, with proportions based on stem counts.

| Composition criterion | WH | DF | RA | WHDF | WHRA | DFRA | WHDFRA |
|---|---|---|---|---|---|---|---|
| Maximum proportion of a single species | 1.00 | 1.00 | 1.00 | 0.70 | 0.70 | 0.70 | 0.50 |
| Minimum proportion of a single species | NA | NA | NA | 0.30 | 0.30 | 0.30 | 0.25 |

**Note:** WH, western hemlock; DF, Douglas-fir; RA, red alder; NA, not applicable.



## 2. Materials and methods

### 2.1. Study area description

The study was located within the Lewis and Clark Timberlands, a 70 000 ha industrial plantation forest in the Coast Range mountains of northern Oregon and southern Washington, USA, near the mouth of the Columbia River. The area is mountainous, with elevation ranging from sea level to just over 1000 m above sea level. The forests are part of the western red cedar (*Thuja plicata* Donn ex D. Don) zone near the coast and transition into the western hemlock zone eastward into the mountains (Franklin and Dyrness 1973). The mean annual rainfall is 180–320 cm·year$^{-1}$, but summers can be dry. Mean annual temperatures are 7–11 °C, and daily low temperatures frequently fall below freezing during the winter. The soils are igneous and sedimentary in origin and tend to be very well drained, with very high water-holding potential (Soil Survey Staff 2018). The area is characterized as having the most productive temperate forests in the world (Franklin and Dyrness 1973).

Most of the property has been managed for commercial timber production for at least two rotations. Because ownership of the property has changed multiple times in recent decades, precise management records for all study stands were not available; however, based on typical management practices, we can assume that all study stands were planted within 1 year of harvest at a density of 890–1075 trees·ha$^{-1}$. Planted species included western hemlock, Sitka spruce (*Picea sitchensis* (Bong.) Carrière), and Douglas-fir. Both monocultures and mixed-conifer stands were planted. Vegetative competition was typically controlled chemically within the first 2 years following harvesting. Based on current spacings, it is likely that most stands were precommercial thinned around age 15 years to maintain the density of 890–1075 trees·ha$^{-1}$ following natural regeneration of western hemlock and red alder from windblown seed. During precommercial thinning, the largest defect-free trees were retained, regardless of species. Thus, naturally regenerated trees may have been retained at precommercial thinning if they were able to achieve dominant or codominant positions in the canopy.

As a result of past management, the landscape is a mosaic of even-aged stands with similar stocking but species compositions that range from monocultures to mixtures of multiple tree species. For this study, we selected the three predominant species of abundance and economic importance: western hemlock, Douglas-fir, and red alder. Limiting the study to only three tree species was necessary because inventory data indicated that mixtures of four tree species or more were too rare to adequately replicate. These three species also provide the greatest functional contrast by including deciduous (red alder), shade-tolerant conifer (western hemlock), and shade-intolerant conifer (Douglas-fir) trees. All three species are native to the area, grow on the same sites, occur within a single canopy layer in the sample stands, can be commercially harvested on the same rotation lengths, and have similar harvest costs and market opportunities in the region. Western hemlock likely regenerated through a combination of planting and naturally seeded trees, Douglas-fir were likely all planted, and all red alder were naturally seeded. Microsite factors may have contributed to the locations where naturally seeded trees established and persisted, with the most significant factor being conditions of the seed bed. Specifically, western hemlock is more likely to establish in duff or on woody debris, whereas red alder is more likely to establish on exposed mineral soil (Gray and Spies 1997; Harrington et al. 1994). The conditions of the forest floor at the time of establishment were likely the result of previous harvest. For example, skid trails, landings, burns, and areas on which trees were dragged may expose mineral soil, whereas areas on which equipment did not travel are more likely to retain intact forest litter and residual rotting wood. The result of standard harvest practices in the area is a mosaic of exposed mineral soil, down woody debris, and intact forest floor. It is rare for advanced regeneration to survive harvest and site preparation in this system. Both western hemlock and red alder are well adapted to the conditions throughout the study area and are known to commonly grow in mixture with each other and with Douglas-fir (Harrington et al. 1994). Another factor that potentially affects natural seeding of red alder is areas where herbicide was not applied during site preparation, which would have also retained "competing" non-tree vegetation.

Management objectives may have influenced the locations of where Douglas-fir and western hemlock were planted. For example, Douglas-fir on the plantations tends to be impacted by the endemic pathogen *Phaeocryptopus gaeumannii* (T. Rohde) Petr., which causes Swiss needle cast and reduces growth. Swiss needle cast is more severe close to the coast; thus, many managers now avoid planting Douglas-fir near the coastline. However, management decisions on planting are not easily predictable or uniform across ownerships or from forester to forester. For example, many of the stands with Douglas-fir that were selected for this study are very close to the coastline. Douglas-fir foliage was sampled from 21 of the 24 plots by felling three trees and collecting branches from the whorl closest to the midpoint of the live crown. In all cases, visual estimates indicated that mean needle retention was <3 years, and *Phaeocryptopus gaeumannii* presence was confirmed by DNA sequencing using polymerase chain reaction (PCR), indicating that Swiss needle cast disease was ubiquitous within the study (Shaw et al. 2011).

### 2.2. Study design

The study approximates a replacement series design with all combinations of three tree species, including monocultures. Replacement series biodiversity experiments, sometimes called substitutive designs, retain the same level of plot density with all levels of plant species diversity (Jolliffe 2000). Thus, the operational reality of this industrial plantation approximates a replacement design because density is carefully managed, but species composition varies. The study design required identifying multiple plots that represent seven different species compositions and cover the entire study area. As the study was conducted in existing mature stands instead of planted experimental plots, the species composition reflects a combination of management choices and environmental conditions that allowed for the establishment and persistence of the tree species present. The target species compositions represented all possible combinations of the three selected tree species and their monocultures, as described in Table 1. The target species compositions also represent the vertices, midpoints, and centroid of a three-dimensional simplex, facilitating response surface analysis (Cornell 2002).

Plots were considered monoculture if the proportion of all trees (by stem number) of a single species was at least 0.90. Two-species plots needed to have a proportion of 0.30–0.70 for each target

**Table 2.** Mean potential annual direct incident radiation (PDIR), heat load, manager-reported 50-year site index, elevation, and density of plots with different species compositions.

| Species composition | PDIR ($MJ·cm^{-2}·year^{-1}$) | Heat load | Site index | Elevation (m) | Density ($trees·ha^{-1}$) | Latitude (°N) | Longitude (°W) |
|---|---|---|---|---|---|---|---|
| WH | 0.82 (0.56–0.93) | 0.85 (0.67–0.95) | 134 (120–148) | 177 (37–392) | 844 (732–987) | 45.989 (45.603–46.348) | 123.898 (123.752–124.007) |
| DF | 0.90 (0.87–0.95) | 0.86 (0.71–0.92) | 128 (107–154) | 251 (70–459) | 759 (700–828) | 46.011 (45.577–46.383) | 123.710 (123.578–123.914) |
| RA | 0.85 (0.65–0.95) | 0.82 (0.71–0.92) | 136 (115–154) | 296 (235–459) | 878 (764–955) | 45.936 (45.577–46.027) | 123.727 (123.576–123.912) |
| WHDF | 0.78 (0.60–0.91) | 0.76 (0.60–0.91) | 118 (108–125) | 257 (76–443) | 817 (732–891) | 46.036 (45.937–46.279) | 123.742 (123.621–123.816) |
| WHRA | 0.81 (0.56–0.92) | 0.85 (0.70–0.92) | 134 (119–154) | 199 (37–459) | 822 (732–891) | 46.038 (45.898–46.347) | 123.824 (123.578–124.006) |
| DFRA | 0.84 (0.56–0.95) | 0.83 (0.71–0.92) | 146 (126–154) | 253 (37–459) | 822 (732–923) | 45.957 (45.566–46.298) | 123.694 (123.578–123.914) |
| WHDFRA | 0.77 (0.56–0.90) | 0.77 (0.60–0.91) | 127 (108–152) | 266 (45–443) | 891 (859–923) | 45.954 (45.872–46.019) | 123.746 (123.623–123.924) |

**Note:** Ranges (minimum to maximum values) are indicated in parentheses. WH, western hemlock; DF, Douglas-fir; RA, red alder.



species, and a proportion of nontarget species <0.05 was permitted. Three-species plots needed to have a proportion of 0.25–0.50 for each target species, and a proportion of nontarget species <0.05 was permitted. Only trees with diameter at breast height (DBH; breast height = 1.30 m) > 10 cm were counted. Selected plots contained similar overstory densities, around 800 trees·ha$^{-1}$ (ranging 700–987 trees·ha$^{-1}$), and were all in stands with similar stand history and age. The age range of 35–39 years was selected because it was close to final rotation age and therefore allowed the maximum time for tree and species interactions within intensively managed plantations.

We identified candidate stands likely to meet the composition, density, and age specifications from inventory data. The latitude, longitude, mean elevation, mean slope, average aspect, and 50-year site index (when available) of candidate stands were also retrieved from the database. We calculated the potential annual direct incident radiation (PDIR) and heat load index for each candidate stand as indicators of environmental variability. PDIR and heat load index were calculated using latitude, slope, and aspect data (McCune et al. 2002). PDIR is the amount of solar radiation energy received on a given surface over 1 year and is the maximum amount of energy that plants can intercept for photosynthesis. Heat load varies from PDIR because energy intercepted in the afternoon has a larger effect on heating than energy intercepted in the morning and consequently results in a different potential rate of photosynthesis. A final subset of 142 candidate stands was selected to maximize the range of PDIR, heat load, elevation, and site index across all target species compositions. The final subset of stands was investigated in the field, and 43 plots were installed in 25 stands in which conditions fell within the target density range and species composition. No two plots with the same species composition were included in the same stand, and no more than three plots were included in any single stand. Plots located in the same stand were at least 20 m from one another. Within stands, plot centers were selected to meet parameters of density and species composition. Mean, minimum, and maximum values of PDIR, heat load, site index, elevation, density, latitude, and longitude for plots of each species composition are shown in Table 2.

Plots were circular, with radii of 10 m (area of 314 m$^2$). Choice of plot size was guided by previous studies on tree species interaction in the Pacific Northwest (Canham et al. 2004; D'Amato and Puettmann 2004). Plots were buffered by a distance ≥ 10 m from openings, roads, or streams.

### 2.3. Data collection

Field data were collected during the summer of 2017. DBH was measured for all trees in the plot with DBH > 10 cm. We also measured total tree height and height to live crown for the three trees of each target species closest to the plot center. Height to live crown was defined as the vertical distance between the bottom of the crown and the top of the crown. The bottom of the crown was defined as the lowest point of live green branches that comprise one-third or greater of the bole's projected circumference and was measured from the point that those branches attached to the bole of the tree. The top of the crown was defined as the top of the terminal leader or highest point of the tree (U.S. Department of Agriculture Forest Service 2018). Measurements were taken using the Haglof Vertex IV hypsometer (Haglöf Sweden AB, Långsele, Västernorrland, Sweden). Understory species were defined as all vascular plant species <3 m in height. All vascular plants observed in the study were either trees or understory plants, as intermediate canopy plants are virtually absent from this system. Understory species were surveyed in four 1 m$^2$ sampling frames located at 2 and 6 m from the plot center in both directions along a transect running uphill to downhill. The identity, total height, and percent cover of all vascular plant species in the sampling frame were recorded.

### 2.4. Response variable estimation

AGB was estimated using species-specific allometric equations for each tree and summing the individual tree AGBs for each plot (Chojnacky et al. 2014). Because mixture-specific allometric equations are not available for the study stands and destructive sampling of all plots was not feasible in the operational setting, we assumed that the generic equations applied to trees on our study sites and that deviations due to genetics, stand history, site quality, or species mixtures were minor within the scope of this study (Forrester et al. 2017).

The DUP for each plot was estimated with Shannon's diversity index based on the mean percent cover in subplots, as shown in eq. 1 (Shannon 1948). Shannon's diversity index is one of the most widely used indices of species diversity (Spellerberg and Fedor 2003). Cover of understory plants is assumed to correlate to understory biomass but is more commonly collected in forest inventories and does not require destructive sampling. Other studies have used understory species cover to characterize ecosystem functions of the understory community in similar forests (Neill and Puettmann 2013). Shannon's diversity index ($H$) is calculated as follows:

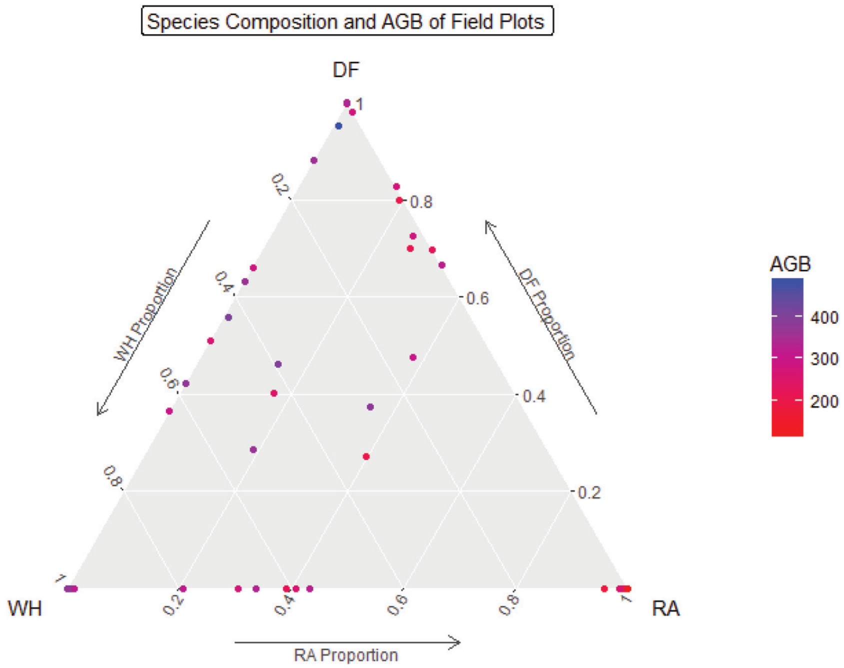
$$(1) \qquad H = -\sum_i \left[\frac{n_i}{N} \times \ln\left(\frac{n_i}{N}\right)\right]$$

where $n_i$ is the relative abundance of species $i$ based on cover in all understory sampling frames within a plot, and all $n_i$ sum to $N = 1$.

We defined LCL for the plot as the mean LCL (difference between total tree height and height to live crown) of the three trees of each target species closest to the plot center.

AGB, DUP, and LCL were the response variables in the analytical model described in section 2.5. However, this was not a planted experiment in which all potentially confounding factors are controlled; therefore, identified relationships between the response variables and tree species composition should be considered corollary and not necessarily causal.

**Fig. 1.** Species mixture based on aboveground biomass (AGB) of 43 field plots. Total plot AGB, represented by shading, is in megagrams per hectare. Each corner for the tertiary plots represents a monoculture (DF, Douglas-fir; WH, western hemlock; RA, red alder), the edges of the plots represent two-species mixtures, and the interior of the triangle represents mixtures of all three species. The proportion of each species can be determined at any point by the corresponding value on each of the three axes. [Color online.]






### 2.5. Analytical approach

Substitutive or replacement series designs are similar to mixture experiments in which the response is a function of the proportion of multiple components that sum to 1. Thus, we analyzed the data using response surface methodology described for mixtures (Myers and Montgomery 1995). Our study design approximates a simplex centroid design (Cornell 2002), so we used a special cubic mixture model (i.e., a polynomial model that fits a response surface to three component mixtures with a centroid) as shown in eq. 2 (Scheffe 1963):

$$(2)\qquad Y_k = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_{12} x_1 x_2 + \beta_{13} x_1 x_3 + \beta_{23} x_2 x_3 + \beta_{123} x_1 x_2 x_3 + \varepsilon_k$$

where $Y_k$ is the estimated ecosystem function from plot $k$ ($k$ = 1–43); $x_1$, $x_2$, and $x_3$ are the proportions of western hemlock, Douglas-fir, and red alder, respectively, in mixture; $\beta_1$, $\beta_2$, and $\beta_3$ are the parameters for the pure mixtures of $x_1$, $x_2$, and $x_3$, respectively; $\beta_{12}$, $\beta_{13}$, and $\beta_{23}$ are the parameters for the mixtures of $x_1$ and $x_2$, $x_1$ and $x_3$, and $x_2$ and $x_3$, respectively; $\beta_{123}$ is the parameter for the mixture of $x_1$, $x_2$, and $x_3$; and $\varepsilon_k$ is the random error of plot $k$ ($\varepsilon_t \sim N(0,\sigma_r^2)$). The sum of $x_1$, $x_2$, and $x_3$ must always equal 1. The model assumes that residuals are independent and normally distributed and have constant variance.

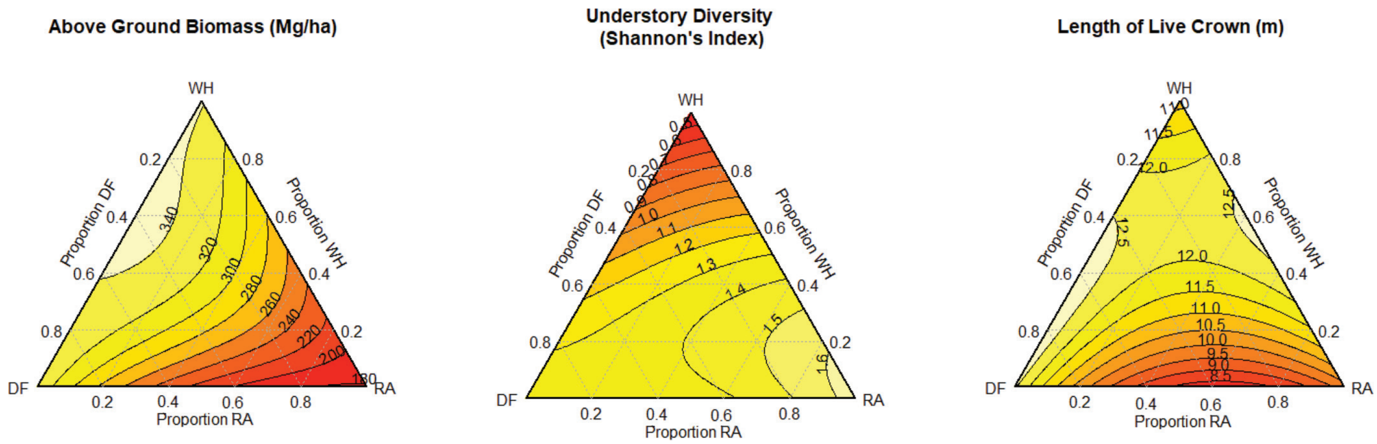
For the analysis, mixture proportions were quantified based on AGB. AGB was chosen because of its simplicity and its suggested indication of the ability of each species to access resources (Pretzsch and Forrester 2017). In some plots, there were tree species not included in the study design. Specifically, Sitka spruce or western red cedar occurred in nine of the plots but represented a proportion of <0.10 of the total biomass (in most cases, <0.02). Sitka spruce and western red cedar were grouped with the most functionally similar study species: western hemlock. The species proportions and total AGB of all 43 plots are depicted in Fig. 1. These proportions vary from the plot-selection criteria in Table 1 because the Table 1 criteria used stem count instead of biomass to estimate species proportion. Biomass estimates of species were not available a priori, and stem counts were a feasible alternative for plot selection in the field. The analytical procedure does not distinguish between monocultures and mixtures; it can utilize the full data set because it views monocultures as mixtures with 0% of one or two species and 100% of the third species.

The special cubic model was fit in R statistical software using the package mixexp (Lawson and Willden 2016; R Core Team 2016). Visual inspection of residuals plots indicated that model assumptions were adequately met. Results were considered statistically significant if the mean of monocultures, weighted by their respective proportion in mixture, was not included in the 95% confidence interval of the response surface.

### 2.6. Procedure for simultaneously optimizing several responses

The species composition that supported the highest levels of each of the three response variables described in section 2.5 was determined using a procedure for simultaneously optimizing several responses in mixture experiments (Cornell 2002). The areas of the response surface for each response variable representing species compositions that equaled or exceeded the best-performing monoculture in each respective variable were graphed and overlaid upon one another. If there was no overlap of species composition that simultaneously performed as well as or better than the best monoculture for each response variable, then the process was repeated with species compositions that equaled or exceeded 99% of the best-performing monocultures. This process was repeated iteratively in lock-step increments of 1% of the best-performing monoculture in each respective response variable until all three overlapped one another. Once there was overlap in species composition that achieved relatively equal levels of all three response variables (within the same percentile relative to the respective best-performing monoculture), one response variable at a time was increased by increments of 1% of the respective best-performing monoculture while keeping the other two response variables constant until the three response surfaces no longer

**Fig. 2.** Response surfaces of aboveground biomass, understory plant species diversity, and live crown length to mixtures of Douglas-fir (DF), western hemlock (WH), and red alder (RA) (corrected multiple coefficients of determination ($R^2$) = 0.51, 0.66, and 0.27, respectively). Triangle layout is as described in Fig. 1. The isolines are at intervals of 20 Mg·ha⁻¹, 0.1 Shannon's diversity index, and 0.5 m for aboveground biomass, understory plant species diversity, and live crown length surfaces, respectively. Color indicates surface values from low (dark red) to high (light yellow). [Color online.]




overlapped. In this way, we estimated the species composition that predicted the greatest levels, relative to each respective best-performing monoculture, of each response variable without causing either of the other two to decrease.

## 3. Results

### 3.1. AGB

The western hemlock (WH) monoculture had the greatest AGB, closely followed by Douglas-fir (DF), whereas red alder (RA) had much less AGB (see Fig. 2). As the number of tree species in a mixture increased, mean plot AGB also increased, but the increase was not statistically significant (see Fig. 3). As highlighted in Fig. 4, the weighted mean AGB of the monocultures was viewed as a reference level for the biomass of two-species mixtures (i.e., the sum of each respective monoculture multiplied by its proportion in mixture). The total biomass of the mixture of western hemlock and Douglas-fir (WHDF) was similar to the weighted mean of the two monocultures, and the biomass of each species in mixed plots was proportional to that of its respective monoculture. The AGB in the mixture of western hemlock and red alder (WHRA) was also similar to the weighted mean of the monocultures at the plot level, but RA AGB tended to be greater in mixture than in monoculture, which was offset by WH AGB, which was lower in the mixture. The AGB in the mixture of Douglas-fir and red alder (DFRA) was less than the weighted mean of the monocultures, but this difference was not statistically significant. In the DFRA mix, like in the WHRA mix, RA consistently had an AGB that was higher than expected based on the monoculture performance, and DF consistently had a lower AGB, with the effect of DF outweighing the RA.

Weighted mean AGBs of monocultures and species mixtures did not differ significantly, suggesting that overyielding, the phenomenon of species mixtures producing more than the proportionally weighted mean of their component species grown in monocultures, did not occur or we were unable to detect it in this study. The response surface predicted the greatest AGB with a mixture of mostly DF and WH and a small component of RA. The greatest AGB was predicted to be 342.7 Mg·ha⁻¹, with proportions of 0.61 WH, 0.35 DF, and 0.04 RA, but it was not statistically or substantively different from the weighted mean of the monocultures (overyielding) or the best-performing monoculture (transgressive overyielding) as shown in Table 3.

### 3.2. DUP

In total, 41 understory vascular plant species were identified, and plot understory species richness ranged from 1 to 14. Mean DUP of plots with one, two, or three tree species did not differ significantly ($\alpha$ = 0.05); however, the mean DUP did increase from one to two species and from two to three species (Fig. 3). DUP, as estimated by Shannon's diversity index, was greatest under RA monocultures, with a mean of 1.65, and least under WH monocultures, with a mean of 0.40 (Fig. 2). DUP was projected to be higher than the weighted monoculture means in all mixtures containing WH and statistically significantly higher for selected mixtures of WH and RA and mixtures of all three species (Fig. 5). These results show that including other tree species with WH was related to higher DUP, more than would be expected from the weighted mean of the species monocultures.

### 3.3. LCL

Trees in the DF monoculture had the longest mean LCL at 12.6 m; however, even mixtures of both WHRA and WHDF had LCLs equal to or greater than that of the DF monoculture at 12.6 m and 12.7 m, respectively. RA had the smallest LCL of all the monocultures at 9.7 m, but DFRA had the lowest overall LCL at 8.4 m (Fig. 2). Mean LCL was greater on average in plots with two species than in monocultures but was the same for plots with two or three species. The difference between plots with one species and plots with two or three species was not statistically significant at $\alpha$ = 0.05 (Fig. 3). In species mixtures with WH, predicted LCL tended to be longer than the weighted mean of the monocultures. The trend was driven by increased WH LCL in mixtures compared with LCL of the WH monoculture; however, not all mixtures showed positive mixing effects of LCL. The response surface indicated that DFRA mixtures had smaller LCL than the weighted mean of the monocultures, driven by reductions of LCL in both species (Fig. 6).

### 3.4. Optimal conditions for a combination of the three response variables

The best-performing monoculture was different for each of the three response variables. The gradients of AGB and DUP were almost directly opposed along the mixture gradient (i.e., AGB was highest in mixtures composed predominantly of WH with little or no RA, whereas DUP was highest for pure RA plots and lowest for WH monoculture). In contrast, LCL was high for DF monocultures but also relatively high in even mixtures of WHDF, WHRA, and the three-species mixtures. Consequently, no species mixture re-

**Fig. 3.** Mean aboveground biomass of trees, understory diversity (Shannon's diversity index), and live crown length with 95% confidence interval for plots with one, two, and three tree species.

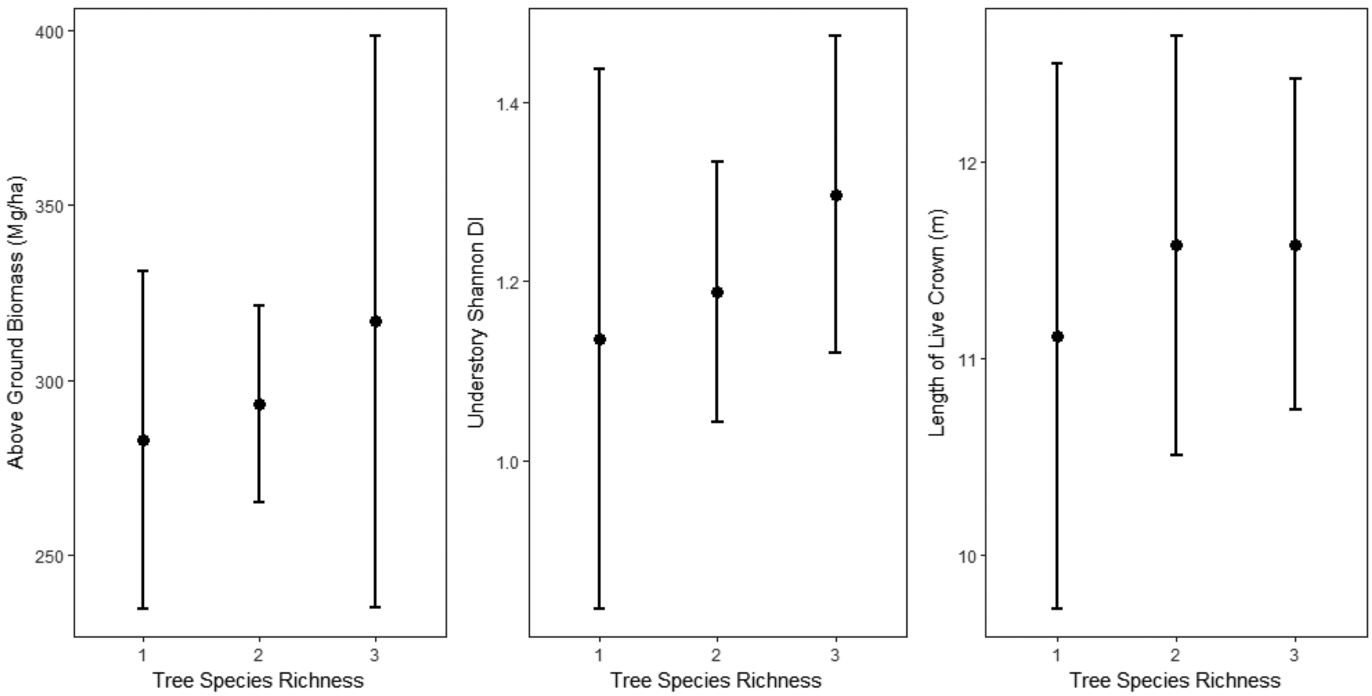
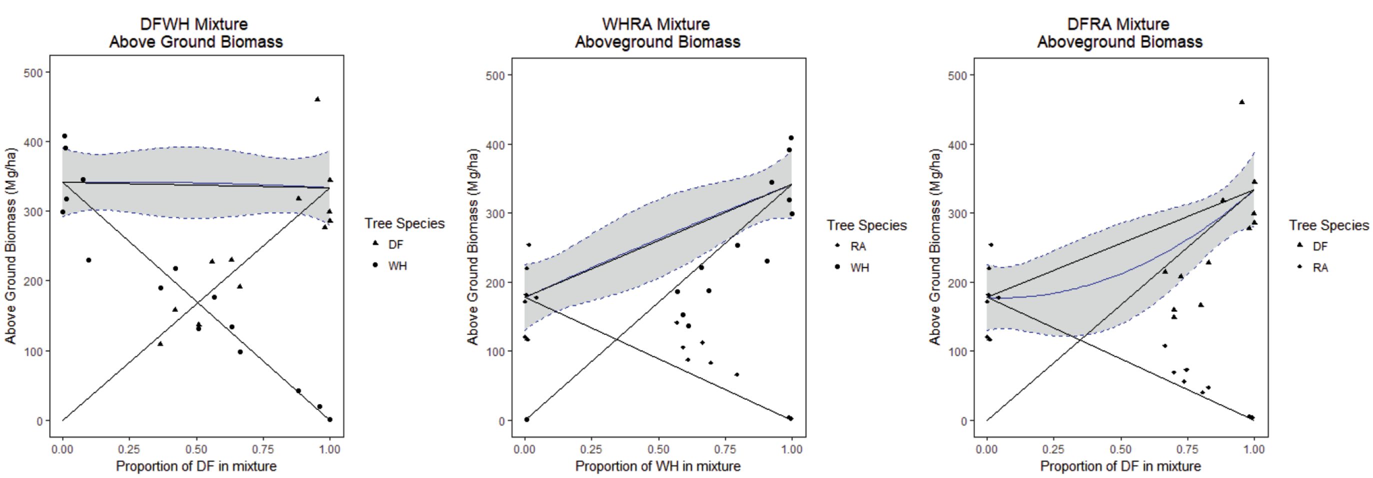



**Fig. 4.** Cross plots of two-species mixtures. Cross plots show the expected aboveground biomass of two-species mixed plots (blue line with shaded 95% confidence interval) with the weighted mean of the monocultures as a reference (top black line). Points indicate the biomass of each species estimated in the actual plots. The crossed black lines represent the expected aboveground biomass of each component species based on its respective monoculture at a given proportion. Proportions for which the blue line is above or below the top black line are predicted to overyield or underyield, respectively. The distribution of the points representing each species around the corresponding crossed line indicates if individual species performed better (above the line), worse (below the line), or the same (on the line) in mixture as in monoculture. WH, western hemlock; DF, Douglas-fir; RA, red alder. [Color online.]




sulted in as much or more of all three variables as the respective best-performing monocultures. The "optimal" level of all three ecosystem variables resulted in 86%, 85%, and 89% of AGB, DUP, and LCL, respectively, of the best-performing monocultures and was achieved with roughly equal mixture proportions of all three species (0.30 WH, 0.29 DF, and 0.41 RA) (Fig. 7).

## 4. Discussion

Correlations between tree species composition and diversity differed for the three ecosystem measures considered in this study. The variation in relationships suggests that multiple mechanisms were likely behind the observed patterns, and some of those mechanisms may play out differently in intensively managed systems compared with typical research installations. Those responses may provide insight relevant to plantation managers interested in increasing or maintaining high levels of ecosystem functions.

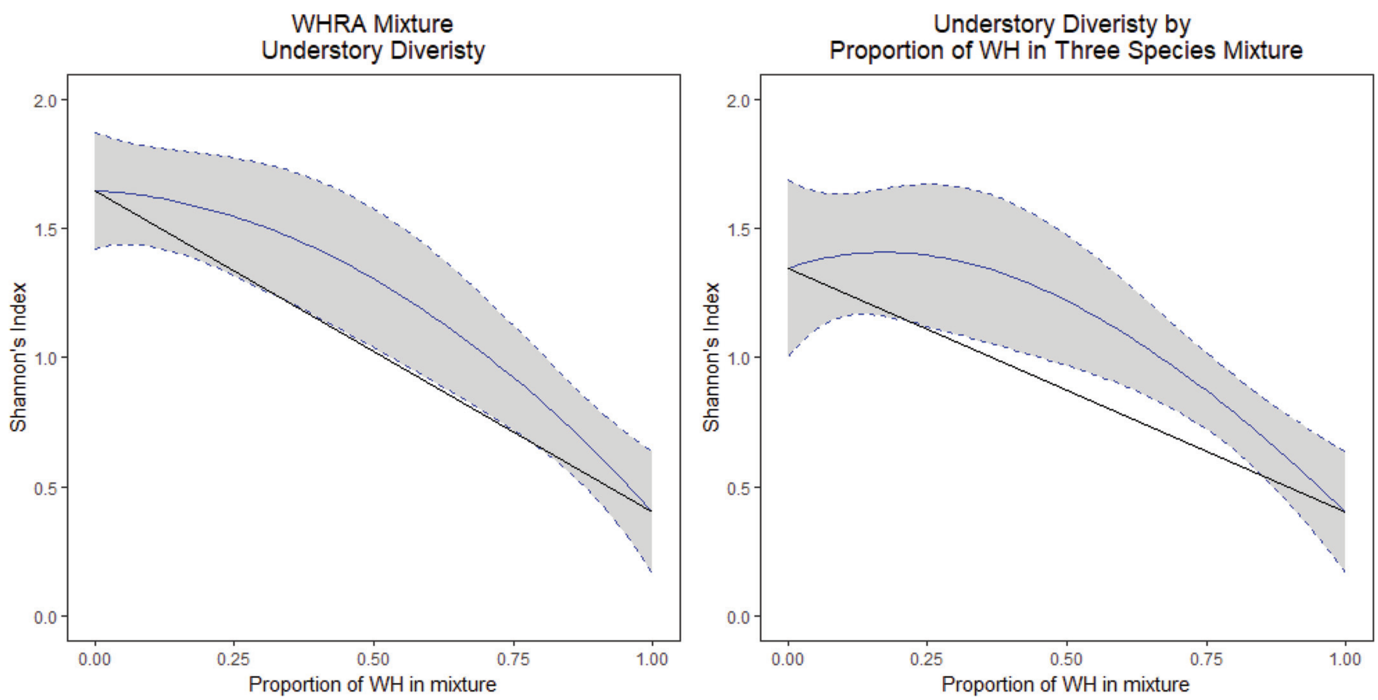
The lack of statistically significant overyielding in our study, as evidenced by the fact that mixtures did not produce more AGB than was expected from their constitutive monocultures, may be partially due to past management actions (Schulze et al. 2018). For example, managers commonly employ techniques intended to reduce tree interactions (and thus species interactions) such as planting at relatively low densities and precommercial thinning. These practices were designed to minimize competition, but they

**Table 3.** Predicted aboveground biomass (AGB) of trees in monocultures and species mixtures of western hemlock (WH), Douglas-fir (DF), and red alder (RA) with 95% confidence intervals (CIs) and the weighted (based on species proportions) mean AGB of the respective monocultures.

| Species composition | Predicted AGB (Mg·ha$^{-1}$) | 95% CI (Mg·ha$^{-1}$) | Mean AGB of monocultures (Mg·ha$^{-1}$) |
|---|---|---|---|
| WH monoculture | 341.6 | 292.1–391.2 | NA |
| DF monoculture | 334.1 | 280.3–387.9 | NA |
| RA monoculture | 177.7 | 130.0–225.3 | NA |
| WHDF (0.5:0.5 mixture) | 341.1 | 289.9–392.3 | 337.9 |
| WHRA (0.5:0.5 mixture) | 262.8 | 205.9–319.7 | 259.7 |
| DFRA (0.5:0.5 mixture) | 212.0 | 139.1–285.0 | 255.9 |
| WHDFRA (0.33:0.33:0.33 mixture) | 309.9 | 248.7–371.0 | 284.5 |

**Note:** NA, not applicable.

**Fig. 5.** Relationship of understory diversity and the percentage of western hemlock (WH) in mixture with red alder (RA) (left) and with RA and Douglas-fir (DF) maintained in equal proportion (right). The solid black line represents the expected value based on the weighted mean of the monocultures, the solid blue line represents the predicted values, and the shaded area within the dotted blue lines represents the 95% confidence interval of the predicted values. Where the shaded region is above the solid black line, the predicted value is significantly more than the weighted mean of the monocultures ($\alpha$ = 0.05). [Color online.]




also reduce opportunities for facilitation. By maintaining relatively low stand densities through planting and precommercial thinning in the study stands, interactions between trees and interactions between species were minimized for much of the trees' juvenile growth phase, influencing crown-, tree-, and stand-level growth trajectories (Garber and Maguire 2004). Furthermore, when managed at lower densities, the stand canopy may not have an opportunity to stratify, which is one of the primary mechanisms of overyielding in mixed-species forests (Kelty 2006). Thus, our results suggest that typical experimental studies, which tend to be established at higher density to encourage species interactions (e.g., Boyden et al. 2009), may overestimate impacts of species interactions found in intensively managed, real-world landscapes. Similarly, the inclusion of nitrogen-fixing species has been shown to contribute to overyielding (Piotto 2008), but we did not observe overyielding in species mixtures with red alder. However, the potential benefit of including nitrogen-fixing species in mixtures needs to be viewed in the context of nitrogen availability. Specifically, DFRA mixtures have been shown to overyield on low-nitrogen sites (Tarrant 1961) but are less productive on high-nitrogen sites typical of our study area (Binkley 2003). The hypothesis that past management aimed at minimizing competitive impacts on tree and stand productivity was at least partially responsible for our AGB results is also supported by the fact that other ecosystem measures not directly considered in past management of the study stands (i.e., understory diversity and live crown) were greater in mixed stands than expected from respective monocultures. Thus, our results suggest that management opportunities not commonly utilized in production plantations (e.g., cultivating mixed-species stands) may help meet more diverse objectives in terms of ecosystem services (Puettmann et al. 2009).

There is general agreement that species identity (as defined by a species' functional traits) may be useful for identifying underlying mechanisms for performance of species mixtures (Lorentzen et al. 2008). Our AGB results appear to be at least partially driven by differences among species in terms of light competition, canopy shape, and relative shade tolerance. For example, in the mixture of western hemlock and red alder, the LCL of western hemlock, combined with its higher shade tolerance, likely facilitated maintenance of western hemlock growth comparable with that of

**Fig. 6.** Relationship of live crown length to the proportion of Douglas-fir (DF) in mixture with red alder (RA) (left); the proportion of western hemlock (WH) in mixture with RA (center); and the proportion of WH in mixture, with DF and RA held in constant ratio (right). Solid black lines represent expected values based on weighted mean of monocultures, the points represent species means from each plot, the solid blue lines represent the predicted values, and the corresponding shaded areas are the 95% confidence intervals. Other colored lines are simple trend lines fitted to each species. [Color online.]

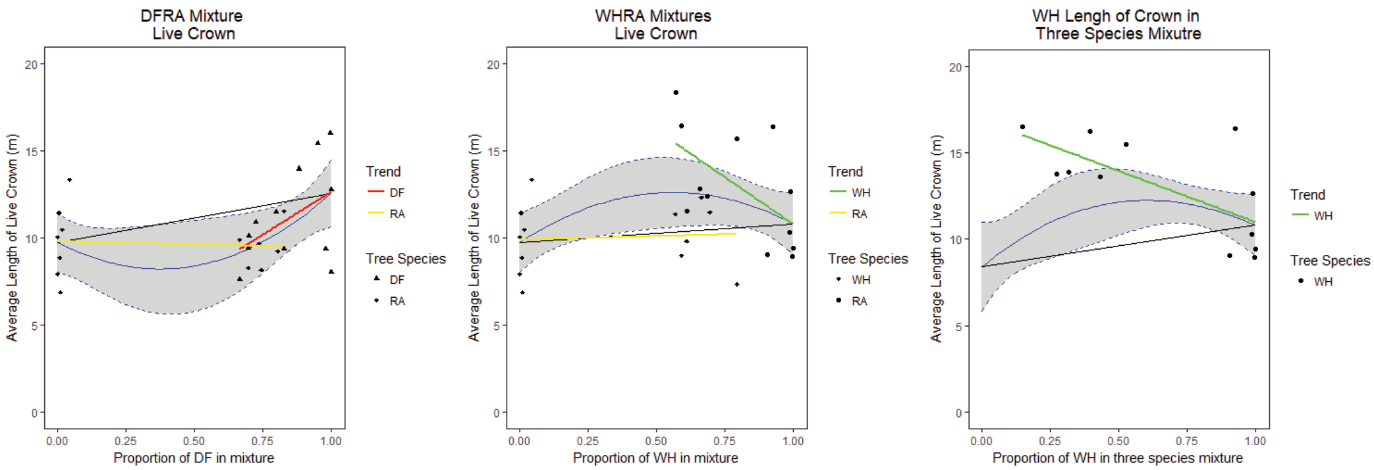
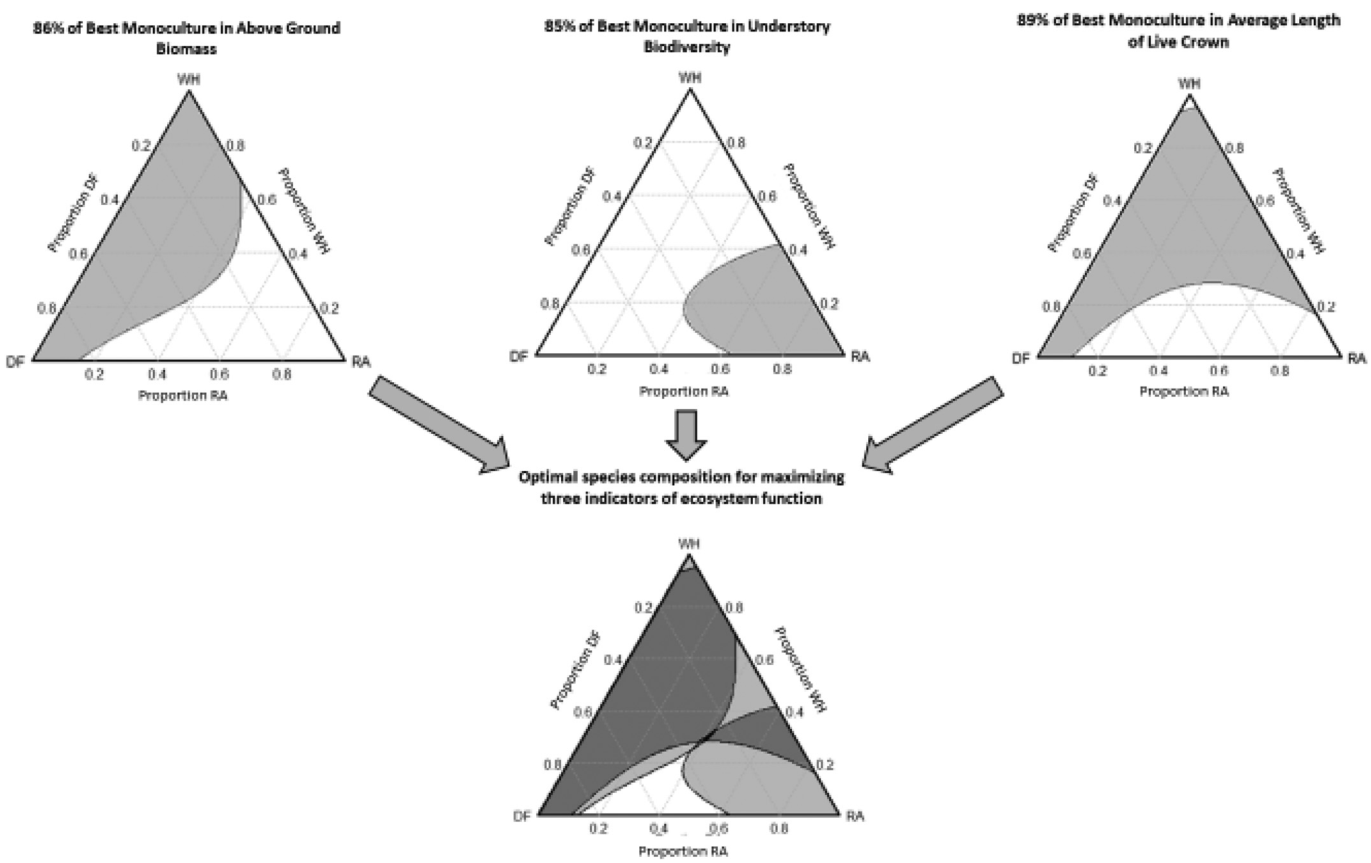



**Fig. 7.** Overlapped response surface areas representing tree species mixtures that are equal to 86%, 85%, and 89% of the best-performing monocultures in terms of aboveground biomass, understory diversity, and mean live crown length, respectively. The overlap of the shaded regions has been minimized and shows the species composition that achieves the greatest levels predicted of all three variables while minimizing reductions to the others. WH, western hemlock; DF, Douglas-fir; RA, red alder.




monocultures when competing with the deciduous canopies of red alder. This was similar to many studies of mixed evergreen and deciduous species that showed complementary resource use when shade-intolerant deciduous species achieved dominant canopy position over more shade-tolerant evergreen trees (Kelty 2006; Puettmann and Hibbs 1996). The mixture of Douglas-fir and red alder showed a contrary pattern, with shorter LCL than either respective monoculture, and the predicted AGB for this mixture was less than the value expected from the weighted mean of the monocultures, with the reduction carried primarily by Douglas-fir. The impact of Swiss needle cast on Douglas-fir leaf area (Zhao et al. 2014) may have reduced the contrast in shade tolerance between the species and reduced the potential for complementary light use (Lu et al. 2016). The greater red alder AGB in mixtures with both conifers suggests that the canopy architecture of the conifers and deciduous red alder may have been complimentary, which has been observed in other forest communities (Pretzsch 2014). In the case of the two conifers mixing, the AGB of each component species was very similar to its respective monoculture, likely because of the low contrast in functional traits between the two species. Other studies of species mixtures with low contrasting functional traits (deciduous–deciduous mixtures) also did not show overyielding (e.g., Lu et al. 2016).

Tree species identity may also have influenced DUP. For example, our results suggest that mixing very shade-intolerant tree species with very shade-tolerant species such as western hemlock may be related to greater DUP than would be expected from the mean of the respective monocultures. This is because DUP can be affected by light infiltration (Hill 1979; Jennings 1999), and very shade-tolerant tree species tend to allow less light infiltration than intermediate shade-tolerant species (Canham et al. 1994). Conversely, shade-intolerant deciduous species such as red alder allow greater light infiltration when leaves are on and allow full penetration in early spring and late fall (Moore et al. 2011). The high levels of DUP associated with red alder suggest that the understory vegetation may have benefited from the same conditions that allowed red alder to become established (e.g., herbicide skips and skid trails) Also, the understory may have benefited from the impact of red alder nitrogen fixation (Hanley et al. 2006). The DUP results in this study generally align with previous research on other species in other systems, which supports the hypothesis that shade-intolerant deciduous species support higher levels of DUP than mixtures (Berger and Puettmann 2000). Generally, DUP tends to be greatest under deciduous monocultures, whereas conifer species tend to support lower DUP, and DUP is positively related to tree species diversity (Barbier et al. 2008). The exception to this pattern in our study was Douglas-fir, which supported a surprisingly high level of DUP in monoculture, presumably because of the presence of Swiss needle cast, which reduces Douglas-fir leaf area, thus permitting more light infiltration to support understory species (Hansen et al. 2000). This exemplifies how factors exogenous of species identity and diversity per se, for example, disease and management, can modify species interactions.

In addition to the mechanisms previously described, other factors may complicate the interpretation of the study results. For example, microsite edaphic factors may influence where naturally seeding western hemlock and red alder occur and the composition of the understory plant community. Similarly, areas missed by herbicide spray or areas where different herbicides were used may affect the likelihood of these species naturally seeding into an area and may affect tree growth and understory plant composition. Because this was an observational study and not a planted experiment, we were only able to indirectly control for these factors by choosing stands of similar age and management history from a representative range of environmental factors known to relate to soils and plant growth (e.g., elevation, aspect, and site index). The strength of the study design was that it allowed the rapid assessment of correlations between tree species composition and other ecosystem variables at any point in time in stand development. The study approach also enabled assessment across a relatively large geographic area under operational management without the expense, time, and restrictions required for planted experiments.

Regarding the first objective of the study, we found no statistically significant positive relationship between biomass of trees and tree species diversity, but DUP and mean LCL both had higher values than expected in some mixtures, based on the performance of monocultures. Regarding the second objective of the study, we identified trade-offs between different ecosystem responses as a result of tree species composition, namely that tree AGB and DUP showed opposite trends along a gradient of mixtures of western hemlock and red alder. Regarding the third objective of the study, we found that if high levels of multiple ecosystem functions as represented by tree AGB, DUP, and LCL are desired, then a near-even mixture of all three species was preferable to any monoculture alternative. This supports the theory that complementary effects are generally greatest in mixtures with relatively even proportions of species, as each individual is more likely to directly interact with individuals of a different species (Forrester and Bauhus 2016). Our results also support the theory that greater tree species diversity supports high levels of multiple ecosystem functions, even though monocultures produce higher levels of single functions (Gamfeldt et al. 2008; Isbell et al. 2011; van der Plas et al. 2016). Our results suggest that within intensively managed plantations, individual ecosystem responses may not be positively related to tree species diversity; however, when multiple indicators of ecosystem functions are simultaneously considered, mixed stands perform better than monocultures.

In determining the species composition that optimized all three ecosystem responses, each was considered equally desirable. In operational settings, it is much more likely that one or more ecosystem services will be important to specific managers based on their objectives. Managers can easily apply different weighting schemes to reflect their own preferences and objectives. Furthermore, certain ecosystem functions and services may have important thresholds such that reductions beyond a certain point are unacceptable to managers. If such thresholds are implemented, minimum values can be used to constrain the range of species composition that is acceptable. For example, investment-based managers may need to achieve positive cash flow or a minimum rate of return.

Nonetheless, it is important to recognize trade-offs implicit in managing to a single objective because myopic focus on the efficient provisioning of a single ecosystem service (e.g., timber) has the potential of undesired outcomes (Messier and Puettmann 2011). As society looks toward production plantations to provide a broader suite of ecosystem services, management strategies, including mixing tree species, that support multiple ecosystem functions are likely to become more important (Bauhus et al. 2010; Bauhus and Schmerbeck 2010), particularly in the face of uncertain future conditions (Messier et al. 2019). In areas with increasing population pressure, it is becoming less tenable to focus on one single ecosystem service and exclude all others, whether that focus is on timber, habitat, or wilderness (Sarr and Puettmann 2008). One size likely does not fit all for forest management, and the "Kielwassertheorie" (wake theory) that assumes that all social functions of forests are automatically provided in the wake of production management is clearly questionable (Schuler 1998).

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