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Trade-offs between ecosystem services along gradients of tree species diversity and values

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ABSTRACT

Trade-offs between incommensurable values of services are a challenge to the implementation of the ecosystem services framework. The International Platform of Biodiversity and Ecosystem Services (IPBES) recommends pluralistic valuations of ecosystem services that include intrinsic, instrumental, and relational values. To understand how value pluralism may affect trade-offs between ecosystem services, we conducted a study quantifying ecosystem service proxies along a tree species diversity gradient in plantation forests in the coastal Pacific Northwest, USA. Further, we developed four frameworks emphasizing different bundles of ecosystem services based on how the services clumped within a matrix of value types and level of social organization at which benefits are likely to accrue. We then determined tree species compositions that optimized ecosystem services emphasized under the four frameworks. Some ecosystem services responded in sync, but we found trade-offs between provisioning services with primarily instrumental value and cultural services with relational values. Most single ecosystem services were maximized by monocultures. In contrast, high levels of tree species diversity supported the largest variety of value types. We hypothesized that biodiversity may be important not just for increasing ecosystem functions and services, but also for value pluralism.

1. Introduction

Ecosystem services (ES), or the benefits people receive from nature, can be a useful, although not uncontested (Schröter et al., 2014), conceptual framework for policy makers, natural resource managers, and conservationists (Chan et al., 2017; Daily, 1997). The ES framework is often used to support resource management decisions and to communicate the importance of the natural world. However, it can ignore intra-generational justice and neglect marginalized groups (Lele, 2013; Schröter et al., 2017), particularly those with non-instrumental understanding of human nature relationships including interdependence, responsibility, care, and reciprocity (Jax et al., 2013; Jax et al., 2018; Whyte, 2018). Further, management actions often result in trade-offs between different ecosystem services (Bradford and D'Amato, 2012; Langner et al., 2017). While the values of many ecosystem services are clearly commensurable (reducible to a single common measure, e.g. commodity goods like timber or grain production), others may be only weakly comparable (comparable without reducing to a single type of value) or incommensurable and are best assessed using multiple criteria (Martinez-Alier et al., 1998; O'Neill, 1993). Navigating trade-offs between incommensurable values of services in a way that is helpful for decision makers and stake holders with diverse objectives, priorities, and perspectives is a core challenge to the implementation of the ES framework (Rodríguez et al., 2006) and for natural resource management in general.

Within the context of forests, more ecosystem services are being demanded from plantations (FAO, 2010). Increasing the tree species diversity of plantations has been proposed as a way to meet the growing general demand for different ES from these systems which have traditionally been managed almost exclusively to produce wood fiber (Verheyen et al., 2013). Since wood fiber is strongly commensurable with other commodities via common monetary units, trade-offs with other ecosystem services are easily monetized as opportunity costs with little consideration for other values attributed to them that might not be (as easily) commensurable. Because of this, non-monetary values of ES produced from plantations are at a heightened risk of being ignored, and benefits of managing for species compositions other than monocultures may be missed or undervalued.

Therefore, incorporating multiple domains of value articulation in ES assessments is integral to navigating trade-offs (Martín-Lópeza et al., 2014). The recent International Platform on Biodiversity and Ecosystem Services (IPBES) conceptual framework recognized that the benefits

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people receive from nature and the relative importance of these benefits are context specific and vary with different cultural and institutional settings (Dıaz et al., 2015; Pascual et al., 2017). The IPBES recommended pluralistic valuations of ecosystem services that include intrinsic, instrumental, and relational values to better communicate to decision makers the complex ways the value of ES are understood and articulated by people. Many ES valuations are criticized for over dependence on monetary methods (mostly eliciting/capturing instrumental values) which tend to ignore non-instrumental languages of valuation and neglect power asymmetries, thus failing to acknowledge and address issues of epistemic as well as environmental injustice (Himes and Muraca, 2018; Jax et al., 2013; Martinez-Alier, 2001). This is not only ethically questionable, but also problematic as a basis for policy interventions, as it does not adequately represent the social-ecological complexity of a case (TEEB, 2010). Pluralistic valuation methods are a more holistic way of assessing ES and help resolve these criticisms (Berbés-Blázquez et al., 2016). Also, pluralistic valuations of ES that include relational values increase the transparency of trade-offs between ES (Cundill et al., 2017; Himes and Muraca, 2018) and are more likely to capture non-instrumental ways of relating to nature (Arias-Arévalo et al., 2017).

In this paper we use an observational field study to identify ranges of tree species composition and diversity that minimize ES trade-offs while optimizing priority ES under four frameworks in plantations in the coastal Pacific Northwest of the USA. We selected nine ES for this study to represent each of the four widely adopted ES types described in the Millennium Ecosystem Assessment, regulating services, provisioning services, cultural services and support services (MEA, 2005). We assigned each of the ES to a framework based on where they fit in a values matrix depicting relevant social scale and value types. Each framework emphasized a different value domain. This methodology highlights that interactions between management priorities, values, and biodiversity can change the co-production of ecosystem services.

The aim of our study was to explore four key questions. 1.) What trade-offs exist between ecosystem services in relation to species composition and diversity? 2.) Do more diverse mixtures of tree species relate to higher levels of multiple ecosystem services? 3.) Is there a relationship between biodiversity and value domains? 4.) Does monistic value articulation increase trade-offs between ES?

2. Materials and methods

2.1. Field study

The study was in the Lewis and Clark Timberlands, approximately 70,000 ha of industrial plantation forest in the Coast Range of Northern Oregon and Southern Washington USA near the mouth of the Columbia River. We sampled forest conditions in multiple plantations of even-aged trees between 35 and 39 years of age. All plantations were established and managed similarly. Across the sampling area 43 ten-meter radius plots were established with the intent of replicating all combinations of Douglas-fir (*Psuedotsuga menziesii)*, red alder (*Alnus rubra*) and western hemlock (*Tsuga heterophylla)* in roughly even mixtures. The presence or absence of the three tree species in this setting was likely due to a combination of past management, seed bed conditions following the previous harvest and chance (Himes and Puettmann, 2019*)*. Western hemlock (WH), Douglas-fir (DF) and red alder (RA) were selected because they have similar harvest costs and market opportunities in the region and their growth in the first forty years is comparable (Himes and Puettmann, 2019). Efforts were made to sample plots of each species composition evenly across the range of known environmental variation, and plots were placed randomly in areas at least 10 m from openings where stem density ranged from 700 to 987 trees/ha (Himes and Puettmann, 2019). We established six plots of each of the species combinations shown in Table 1, plus one extra plot of red alder monoculture. Diameter at breast height (DBH) of all

Table 1
Description of species composition criteria (Himes and Puettmann (2019)).

	WH	DF	RA	WHDF	WHRA	DFRA	WHDFRA
Tree species in plot	Western hemlock	Douglas-fir	Red alder	Western hemlock and Douglas-fir	Western hemlock and red alder	Douglas-fir and red alder	Western hemlock, Douglas-fir, and red alder
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

trees larger than 10 cm in each plot was measured and a subset of three trees of each species were measured for total height, height to live crown, and stem diameter at 25–35% of the total tree height. Damage was also noted for the bottom, middle, and top third of all trees in every plot with a code describing the type and severity of damage following Arney (2015). Understory vascular plant species composition and cover were also sampled in four subplots in each plot. Details on the study area, plot selection, plot installation, tree measurements, and understory sampling were further described in Himes and Puettmann (2019).

In addition to tree and understory data collection, digital photographs of each plot were taken with an i-phone 6 s using the True Horizon ap. The following controls were used to ensure unbiased representation of the scenery: Photographs were taken from two locations on opposites sides of the plot boundary looking into the plot center and perpendicular to the predominant slope in landscape. Gridline and bubble level display in the True Horizon ap ensured photographs were consistently taken on level with the plot centered horizontally at the bottom third of the display. The same individual took all photographs while holding the i-phone 6 s at eye height. All photographs were taken during full light, avoiding dusk or dawn light conditions, furthermore since all plots were taken under forest canopy and buffered from large openings, the images had relatively consistent diffuse lighting.

2.2. Selecting and calculating ecosystem service proxies

Provisioning of nine ecosystem service proxies were quantified based on the field data (table 2). We selected services based on the availability of relevant field data and to cover a broad spectrum of ecosystem services. In an effort to include different ways that nature benefits people we selected services to represent all four categories of ecosystem services defined by the Millennium Ecosystem Assessment: provisioning services (products obtained from ecosystems), regulating services (benefits of regulated ecosystem processes), cultural services (nonmaterial benefits of ecosystems like spiritual enrichment and recreation), and support services (ecosystem benefits that are necessary for the production of all other ecosystem services) (MEA, 2005). It was important to include diverse service types covering all four categories to represent, as much as possible, the plethora of importance this system may have for people. However, the services selected were limited to those which were feasible to quantify proxies for given the resources and expertise of the researchers.

We estimated Merchantable Wood using the Forest Projection and Planning System™ (FPS). FPS is a commercially available fully integrated software and database system for managing working forests. It is commonly used by industrial forest managers to simulate the volume and grade of logs that can be cut from trees and is based on diameter at breast height, tree height, and stem taper (derived from stem diameter at 25–35% of the total tree height) measurements. Additional FPS input data included a measure of potential tree productivity (i.e., site index (King, 1966) provided by the plantation managers) and defect for the bottom, middle, and top third of all trees (0%, 5%, 10%, 20%, and 30% corresponding to damage severity ratings 0–4). Details on FPS are available in Arney (2015), but specific equations used by FPS are proprietary. We estimated merchantable volume and log grade of every tree in every plot. We used the sum of FPS net merchantable volume (total merchantable volume deducted for defect) of all trees in each plot as the response variable for the Merchantable Wood ES proxy. This proxy was an estimate of the volume of wood fiber that would be commercially utilized from each plot following a clear-cut harvest. Merchantable Wood was considered a provisioning service.

We calculated Timber Revenue by multiplying the FPS output merchantable volume in each log grade by the corresponding average log price delivered to the mill as reported for western Washington by the Washington Department of Natural Resources (WDNR) between 2014 and 2018 ("Timber Sale Query/Log Prices|WA – DNR," n.d.). We summed the delivered log revenue for each plot. The WDNR prices were used because they were publicly available and significantly overlapped with the sales region of the property. Since monetary valuation was not the objective of the study and the property owner's operating costs were proprietary, gross revenue was the most reasonable proxy for commercial value.

Carbon Stock was estimated as the carbon content of the aboveground portion of the trees following International Panel on Climate Change (IPCC) Good Practice Guidance for Land Use, Land-Use Change and Forestry (Penman et al., 2003). First, we estimated the total aboveground biomass (AGB) in the trees of each plot using species specific allomeric equations (Chojnacky et al., 2014). Next, we estimated the carbon content as the biomass multiplied by a factor of 0.5 (Ross, 2010).

We derived Pollinator Supporting Understory, Fire Re-sprouting Understory, Climate Change Resistant Understory, and Herbivore Forage ES proxies from functional traits of understory species as categorized by Neill and Puettmann (2013). Herbivore Forage included fruit bearing understory plants and those with moderate or high palatability. Pollinator Supporting Understory included all insect pollinated plant species. Fire Re-sprouting Understory species were those with moderate or high fire tolerance. Climate Change Resistant understory were all plant species that had moderate or high rates for drought tolerance or heat tolerance. We used the average cover (m^2 total understory vegetation foliage cover/ m^2 ground) of species in each category as an ES proxy.

We determined understory species with potential human uses including medicinal, edible, and decorative application based on descriptions in Pojar and MacKinnon (2004) or their inclusion in the U.S. Department of Agriculture (USDA) list of Special Forest Products for the Pacific Northwest (Vance et al., 2001). If a plant species appeared in the USDA list or the entry for a species in Pojar and MacKinnon specified that the plant was or had been used for medicine, food, or in the preparation of food we categorized it as an Edible/Medicinal/Decorative Plant. The plot average of the cover (m^2/m^2) of all Edible/Medicinal/Decorative Plants was used as the ES proxy.

We estimated Scenic Beauty as perceived by recreation permit holders, i.e., people who registered online for a free recreation permit which was required prior to entering the study area. Recreation permit holders use the property for hunting, hiking, running, dog walking, mountain biking, fishing, and other forms of non-motorized recreation. The survey instrument was an online Qualtrics survey that displayed plot photographs and asked respondents to rate the images. The two pictures of each plot were used, except for 9 of the 43 plots in which one of the pictures was out of focus, flagging or a person were prominent in the background, or there was substantial brush in the foreground blocking the view which may have influenced viewers' interpretations of the photographs. In total there were 11 photographs of each combination of tree species. A similar number of photographs was deemed to be a large enough sample to provide reasonable reliability in similar forest ecosystems (Ribe, 2009). The order of the photographs in the survey instrument was randomly assigned. The survey instrument asked respondents to rate the images on a scale of −5 to +5 where −5 indicated very ugly, +5 indicated very beautiful, and 0 indicated neither ugly nor beautiful following Ribe (2009). A link to the survey instrument was sent out by e-mail to 3487 people who signed up for a free recreation permit for Lewis and Clark Timberlands. Partially finished surveys were not used for analysis. In total, we received 331 complete responses (9.5% response rate). Responses were shifted to a 1–11 scale and the average of the 331 responses to each photograph were calculated. Often this type of psychophysical scaling uses some form of rating protocol like the scenic beauty estimation method (SBE) to standardize the dispersion, skewness and central tendency of various respondents' scenic beauty ratings to a common interval scale (Daniel and Boster, 1976; Ribe, 2009). However, results using SBE have been shown to correlate with direct use of semantic differential scale, like the one used here, at the 0.99 level (Stamps, 1999). The average response for each

Table 2
Description of the nine ecosystem service proxies analyzed.

Service	Type	Data	ES Description	Values Category
Scenic Beauty (1–11 scale)	Cultural	Survey Instrument	Indicator of aesthetic value, a commonly recognized cultural service.	Primarily Relational, eudemonic. Significant mostly to the individual for itself.
Edible/Medicinal/Decorative Plants (m^2/m^2)	Cultural/ Provisioning	Understory functional traits	May be considered provisioning services but also a cultural service because in this system non-commercial uses are of great significance and the primary benefit to people is the recreational or historic/cultural significance of gathering and using small quantities.	While instrumental in so far as collected goods are consumable, we consider non-subsistence foraging as primarily Relational, eudemonistic. Foraging is tied to sense of individual and cultural identity, heritage, and living a good life (Hall, 2013; Nugent and Beames, 2017). Significant mostly to the individual or groups for itself, especially under the management conditions of the area1
Herbivore Forage (m^2/m^2)	Supporting/ Provisioning/ Cultural	Palatability (moderate or high) and fleshy fruit	Indicator of habitat suitability for herbivores, habitat being the supporting ecosystem service. Animals like deer and elk provide cultural and provisioning services through hunting and recreation.	Primarily relational/eudemonistic. Important to people for whom non-subsistence hunting and/or wildlife viewing is integral to their relationship with nature (Peterson et al., 2010). As an indicator of wildlife in a specific place it is not easily substitutable.
Merchantable Wood (m^3/ha)	Provisioning	DBH, HT, upper stem diameter	Merchantable portions of the log are used as raw material of human used consumptive goods.	Primarily Instrumental. A commodity that is easily substitutable and globally exchanged. Not very significant to the individual for itself.
Timber Revenue (USD/ha)	Provisioning	DBH, HT, Upper stem diameter, market data	Indicates direct product revenue which drives many benefits to people both direct (employing foresters and loggers) to indirect (injects capital into local economy).	Primarily Instrumental. A commodity that is easily substitutable and globally exchanged. Not very significant to the individual for itself.
Carbon Stock (Mg/ha)	Regulating	DBH, HT	Important for regulation of global climate	Fundamental-relational. Impacts global atmospheric conditions that are essential to the persistence of human life.
Climate Change Resistant Understory (m^2/m^2)	Supporting	Drought and Heat Tolerance (moderate or high)	Indicator of ability of the plant community to persist in hotter or drier conditions expected under climate change scenarios. The persistence of the plant community is a supporting service providing habitat for animals, aesthetic quality, and regulating services like soil health and stability.	Primarily fundamental-relational. Impacts the ability of the system to adapt to climate change and perpetuate conditions that support regional life. Not easily substitutable.
Fire Re-sprouting Understory (m^2/m^2)	Supporting	Ability to sprout after fire	Indicator of the plant community ability to persist following the disturbance of fire, which is expected to increase in frequency and severity as the climate changes. Supporting service ensuring continued habitat for animals, recovery of aesthetic quality and perpetuation of regulating services like soil health and stability.	Primarily fundamental-relational. Impacts the ability of the system to adapt to climate change and perpetuate conditions that support regional life. Not easily substitutable.
Pollinator Supporting Understory (m^2/m^2)	Regulating	Insect pollinated	Supports insect populations which provide the regulating service of plant and crop pollination in the region.	Primarily fundamental-relational. Integral to integrity of natural systems the life they support. Not easily substitutable.

[1]Under the current property managers harvest of any non-timber forest products is prohibited. However, the prohibition is generally not enforced for people who have signed up for free permits and harvest small quantities for personal use. Commercial foraging is strictly prohibited and enforced by patrols.

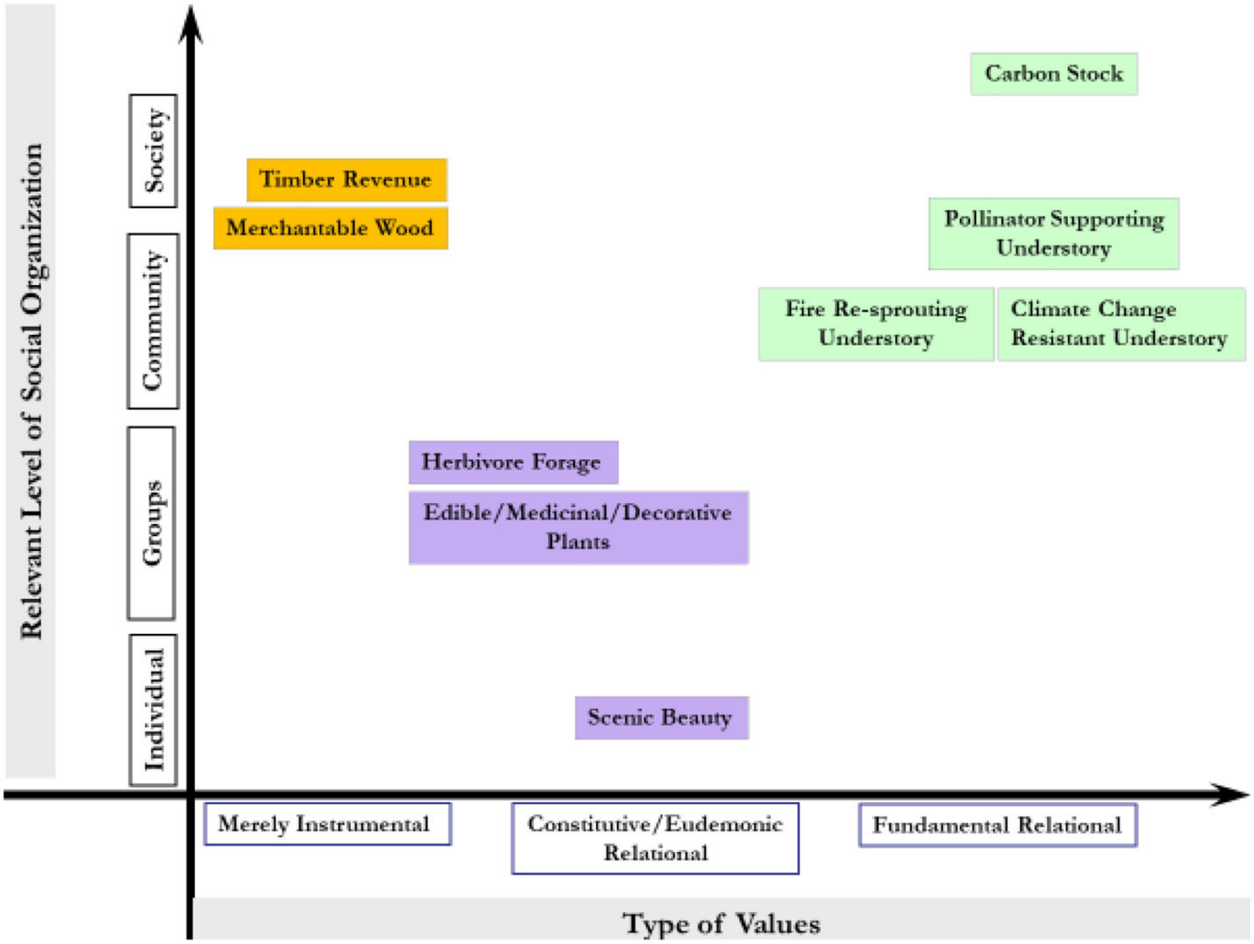

Fig. 1. Values Matrix. The x-axis of the value matrix represents a continuum of human nature relationships as described in Muraca (2011) in so far as those relationships correspond to the content of ecosystem service valuation (Himes and Muraca, 2018). Near the origin are solely instrumental values of ecosystem services, i.e. those that are easily substitutable in principle (although not always in practice) and commensurable. Further along the x-axis are values whose substitutability is barely possible or ethically problematic because they are specific to a place, constitute a sense of identity, are essential components of a "good life" (Constitutive/Eudemonic Relational) or are fundamental to the conditions that make human habitation and life as we know it possible (Fundamental Relational). The y-axis represents the relevant scale corresponding to ES beneficiaries that ranges from individuals to society adapted from Small et al. (2017). The placement of ES proxies within the matrix of value type indicate the authors' interpretation of the value articulation best suited to each ES and the primary level of social organization at which the ES benefits represented by the measured proxies are likely to be accrued with specificity to the study area. The different colored boxes correspond to different management frameworks (purple = local conservation, yellow = production, green = preserving the future).

plot was used as the Scenic Beauty ES proxy.

2.3. Categorizing ecosystem services within a matrix of values

The nine ES proxies were placed in a values matrix as shown in Fig. 1. Arranging the ES in this matrix facilitated the logical grouping of ES into different frameworks and made assumptions inherent in the ES proxies more transparent. The x-axis of the matrix represented a continuum of human nature relationships that ranges from instrumental to fundamental relational following (Muraca, 2011). The y-axis represented the relevant scale of social organization corresponding to the presumed beneficiaries of the ES specific to the study area and scale of measurement (Small et al., 2017). The exact placement of the ES on the proposed matrix is ultimately subjective, but we believe the logical clustering of the nine ES into three groups, as we proposed, remains plausible even if individual ES were shifted. The language of valuation (instrumental, relational or intrinsic) mirrored the significance attributed to specific human-nature-relationships. There is nothing inherent in a thing, in and of itself, that justifies an instrumental or relational language of valuation (Himes and Muraca, 2018). However, forcing heterogenous languages of valuation, especially non-instrumental ones, into an instrumental framework "leaves them ill-defined and neglects the complexity and specificity of relations articulated by the people in their own terms" (Himes and Muraca, 2018:5). In our matrix we attempted to represent diverse languages of valuation in their own terms, while also acknowledging gradients across different languages of valuation. Furthermore, by specifying the relevant social level at which the ES that we identified are likely to benefit people, we intended to increase the transparency of benefit distribution (i.e. who receives benefits from ecosystem services and if benefits can be transferred away from the place they were generated). Including the relevant social level of benefits with value type in a single matrix also enabled the investigation of interactions between the distribution of benefits and value articulation as both can shape the management decisions of different stakeholders.

In the context of ecosystem services, instrumental and relational values are both rooted in the relationships people have with nature and distinguishable because instrumental values are substitutable in principle, while relational values are not (Himes and Muraca, 2018). Relational values help articulate the value of those human-nature relationships that would be misrepresented if reduced to only instrumental language. They refer to "preferences, principles, and virtues associated with relationships, both interpersonal and as articulated by policies and social norms" (Chan et al., 2016: 1462). In our matrix they encompassed *constitutive/eudemonic* and *fundamental* relationships. The former refers to relationships that are essential components of someone's identity (as individual or as community) or of a life of flourishing and dignity, i.e. a good human life (Muraca, 2016, 2011; Nussbaum, 2009). The latter refer to necessary, basic conditions for life in general. Framing such conditions merely in terms of means to human ends neglects the relationship of fundamental dependence upon them for human life.

Intentionally absent from the matrix were intrinsic values. Intrinsic values, in the sense of inherent moral values, could have been included as a third axis to the matrix scaling moral obligation justifications for value (similar to Muraca, 2011). Inherent moral values refer to the attribution of rights or dignity (Callicott, 2003; Regan, 2004; Taylor, 1986) to nonhuman entities and include direct moral obligations towards them as ends in themselves (this language of valuation is used for example to argue for the protection of polar bears or whales and is articulated regardless of its relationships to human interests, needs, or preferences). Although intrinsic values are important for biodiversity conservation (Brockerhoff et al., 2017), we decided to leave out the category because it is difficult to represent within an ES-based study design. Given the framework analysis proposed here, we believed that including an intrinsic dimension would not substantively change the grouping of the selected ES.

The first group of ES we identified was Scenic Beauty, Edible/Medicinal/Decorative Plants, and Herbivore Forage. These ES were best represented by constitutive/eudemonic relational values. Although both Edible/Medicinal/Decorative Plants and Herbivore Forage have aspects of instrumental value, the multi-faceted ways that these types of activities can contribute to a good life constituted more than instrumental benefits of the goods foraged, or meat acquired (Kaltenborn et al., 2017). As a result, we categorized the primary (but not sole) value of these ES as eudemonic/constitutive relational (Chan et al., 2018; Himes and Muraca, 2018). Similarly, scenic beauty is widely accepted as an aesthetic value that belongs in the relational domain because of its being constitutive for a good quality of life (Arias-Arévalo et al., 2017). They were all also categorized as cultural ecosystem services.

All three of these values were positioned lower on the y-axis because the benefits of these service as measured are likely to accrue at the level of individuals or groups. For example, Scenic Beauty was quantified as the average of individual responses to photographs inside of forest stands. The pool of survey participants consisted of individuals who have experience or interest in being on the property where the research was conducted as evident by their participation in the free permit program. Thus, the Scenic Beauty response likely reflected the place-based values that individuals or groups who visit or intend to visit the study area associate with it. The goal of the survey was not to elicit abstract aesthetic preferences with respect to forests in general, but the specific way in which people, who had already manifested some level of relationship with that particular place, express their sense of Scenic Seauty. Other ways of measuring Scenic Beauty, like responses of the general populations to landscape views of the Oregon Coast Range may represent the same type of service, but the benefit would be accrued at a higher level of social organization. Scenic Beauty accrued to the individual or group in a local context is likely to be more important for the current land managers, while Scenic Beauty accrued to higher levels of social organization may be more relevant to state wide or national level policy makers.

The second group included Timber Revenue and Merchantable Wood. These two ES proxies were commodities. They were easily substitutable and were means to other ends, i.e. building shelter or buying shelter, thus clearly their value was primarily instrumental (Himes and Muraca, 2018). As commodities, (quantified as the volume of wood and dollar value of that wood) the benefits of these ES were largely determined by markets, traded globally, and ultimately distributed to millions of dispersed individuals, hence they were positioned high on the Y-axis. Alternative measures of potential benefits, like contribution to local economy or volume of timber milled at regional facilities would be positioned lower on the Y-axis and be more or less relevant to different stake holders or managers. Timber Revenue and Merchantable Wood are both provisioning ecosystem services.

Fire Re-sprouting Understory, Climate Change Resistant Understory, Carbon Stock, and Pollinator Supporting Understory were considered as supporting and regulating services all positioned in the upper right in the matrix. These ES proxies were all important for the ecosystem's resistance and resilience in the face of future change. The first two were indicators of the plant community's ability to persist in the face of expected climate change. Carbon Stock was an indicator of the systems contribution to mitigating carbon emissions and global warming. Pollinator Supporting Understory was indicative of the system's ability to support native pollinating insects which in turn support the perpetuation of many plant communities and are increasingly important for the pollination of agricultural crops as honey bee colonies decline (Kremen et al., 2004). All four of these ES contributed to the ecosystems' ability to perpetuate the conditions critical to human habitation and were therefore fundamental-relational (Muraca, 2011). Carbon Stock is significant for global atmospheric greenhouse gas concentrations and therefore is positioned highest of all the ES on the Y-axis. Although some individuals and groups may benefit disproportionately from the other three ES, their contributions to system resistance and resilience will contribute to the livability of the region and therefore benefit the entire community.

2.4. Defining frameworks

These three groups of ES conceptually aligned with different management frameworks. These frameworks were selected to emphasize extremes and are not necessarily reflective of existing management objectives. For example, most industrial forest managers in the region are voluntarily certified to a sustainable forestry standard that requires consideration of many values including aesthetics and continued forest cover of the land.

Framework 1*, Local Conservation,* prioritized Scenic Beauty, Edible/Medicinal/Decorative Plants, and Herbivore Forage ES (purple boxes in Fig. 1). The management objectives in this framework may align with a local conservation strategy focused on the preservation of the local system so that its natural beauty can be enjoyed by recreationalists. Constitutive/Eudemonic relational values were the primary consideration[1].

Framework 2, *Production,* prioritized Timber Revenue and Merchantable Wood production ES (yellow boxes in Fig. 1). The management objectives in this framework may be aligned with timber industry. The priority was to optimize return on investment or timber production to support manufacturing. Instrumental values were the primary consideration.

Framework 3, *Preserving the Future,* prioritized Climate Change Resistant Understory, Fire Re-sprouting Understory, Pollinator Supporting Understory, and Carbon Stock ES (green boxes in Fig. 1). The management objectives in this framework may be aligned with large international environmental NGOs investing in climate change mitigation and adaptation. Managers may be interested in conserving the study region as a sink for atmospheric carbon and a climate change refuge. Fundamental-relational values were the primary consideration.

Framework 4, *Value Pluralism,* considered all ES and weighed them equally. This was a multi-objective framework that may roughly align with selected government agencies or small private

[1] Although we did not consider intrinsic values in our survey, it is likely that they might also fit in this framework, as well as in framework 4.

landownerships. This framework indiscriminately emphasized a plurality of values. This was a tractable compromise at simulating management where value pluralism would be embraced. In practice, management based on value pluralism would have to consider and integrate different methods of eliciting values where different languages of valuation could be expressed in their own terms and the values of different ES could be possibly classified in instrumental, intrinsic, and relational terms. For example, qualitative interviews, ethnographic approaches or deliberative processes could be used (Kenter et al., 2011).

2.5. Analytical model

The analytical approach was similar to the one used in Himes and Puettmann (2019) and is briefly described here. Our study design approximated a simplex centroid design (Cornell, 2011) and we used a special cubic mixture model, i.e., a polynomial model (see Appendix A) that fits a response surface to three component mixtures with a centroid (Scheffe, 1963).

We quantified the mixture proportions of each species (x) based on aboveground biomass of trees for each plot. Aboveground biomass was chosen because of its simplicity and its suggested indication of the ability of each species to access resources (Pretzsch and Forrester, 2017). The species proportions and total AGB of all 43 plots are depicted in Fig. 2.

The special cubic model was fit in R statistical software using the package *mixexp* (Lawson and Willden, 2016). Visual inspection of residuals plots indicated that model assumptions were adequately met except for the assumption of normality in Climate Change Resistant Understory, which showed signs of multi-modality, and Edible/Medicinal/Decorative Plants, which showed signs of symmetrical deviation from the normal distribution. In addition, variance was very small around WH monoculture plots for all variables derived from the understory because most WH plots had very little understory cover. However, linear models are robust against the assumption of normality and the small variance around WH plots should only result in conservative standard error estimates.

2.6. Procedure for optimizing several ecosystem services simultaneously

The goal of the procedure was to determine the species composition that provided the highest level of all the prioritized ES in each framework. Conceptually, the objective was to find the efficient solution for the simultaneous production of the two or more ES prioritized in each framework. This is the same as finding the species composition that produces the most of each priority ES in a framework with minimal reduction to the amount of any of the other priority ES. We accomplished this objective using a procedure for optimizing several responses simultaneously in mixture experiments (Cornell, 2011). The area of each priority ES response surface that represented 99% of its maximum were graphed and overlaid on one another. Then each ES was decreased in lockstep by intervals of 1% of their respective maximum output until the graphs overlap, signaling a region of the response surface (a range of species composition) that produced the greatest equal percent of each ES simultaneously. Next, model predictions for the range of species compositions indicated in the overlapping area were compared for each of the priority ES. The species composition with the largest combined priority ES output was determined to be best for that framework.

2.7. Ecosystem service trade-off analysis

To better understand the relationship between the investigated ES, two-way comparisons of the predicted responses of each ES to all 1% incremental combinations of WH, DF, and RA were plotted against each other (a total of 5151 combinational proportions of the three species). A smoothed line was drawn along the top of the resulting scatter plot by dividing the range of values into 100 equal sized bins and connecting the point with the greatest value in each bin to the point with the greatest value in adjacent bins. The resulting lines approximated the maximum values of one ES for any given value of the other. If the resulting line had a negative slope or primarily negative slope with

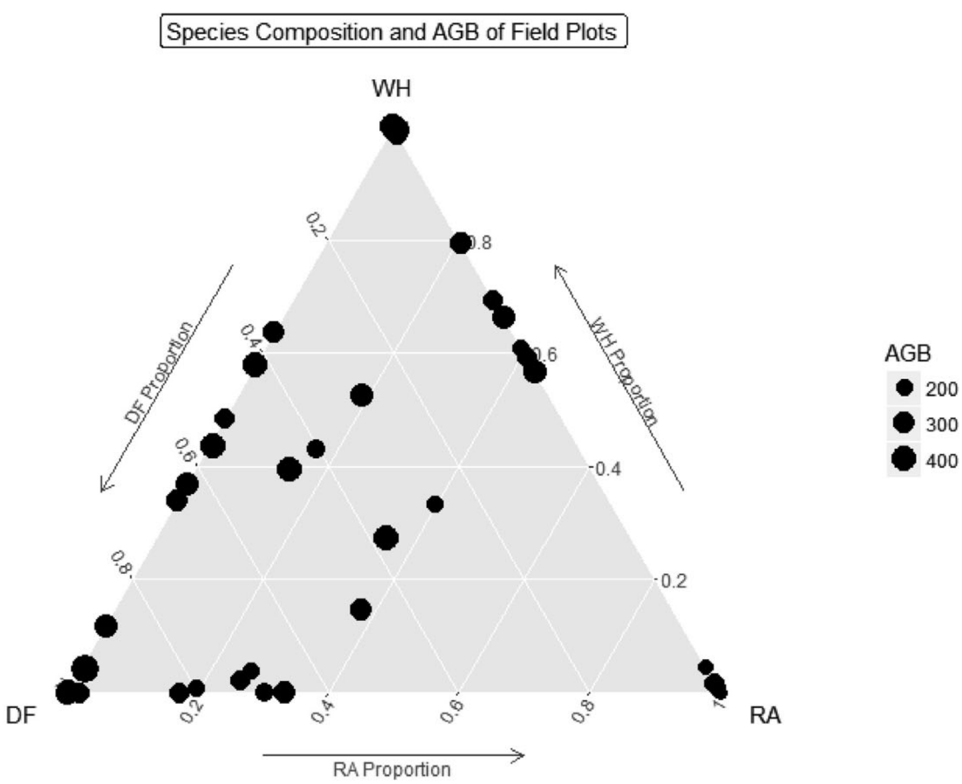

Fig. 2. Modified from Himes and Puettmann (2019). Species composition of 43 plots with proportions determined by aboveground biomass (AGB). Total plot AGB represented by relative size. Each corner for the plot represents a different monoculture (DF = Douglas-fir, WH = western hemlock, RA = RA), the edges of the plots represent two species mixtures and the interior of the triangle represents all proportional combinations of all three species.

intermittent flat regions, the two ES were considered to have a negative relationship (i.e. as one ES increases in response to changing tree species composition, the other ES decreases or does not change). If the slope was consistently positive or positive with intermittent flat regions the relationship between the two ES was considered positive (i.e. as one ES increases in response to changes in tree species composition, the other ES either increases or does not change). If the line had humps or U-shaped patterns, the relationship between the two ES was considered inconsistent (i.e., interactions allowed one ES to increase as the other ES increases for some range of values and decreases at some other range of values of the first ES).

2.8. Framework comparisons

Frameworks were compared based on the predicted output of all nine ecosystem services, reported in Table 2. In addition, because we were interested in understanding possible relationships between the biodiversity and the value types represented in the four frameworks, we calculated the Shannon Diversity Index for the tree species composition that optimized each framework. Shannon Diversity Index is commonly used as an index of species diversity (Spellerberg and Fedor, 2003). It is a measure of both the number and evenness of species. Shannon Diversity Index is calculated as follows:

$$H' - \sum_i \left(\frac{n_i}{N} * \ln\left(\frac{n_i}{N}\right)\right)$$

where n_i was the relative abundance of species i based on cover in all understory sampling frames within a plot and all n_i sum to $N = 1$ (Shannon, 1948).

3. Results

3.1. Ecosystem services relationship to tree species composition

The response surfaces for all nine ES proxies and corresponding R^2 are shown in Fig. 3. The R^2, which describes the proportion of variation explained by the model, ranged from 0.30 to 0.68. The response surfaces for ES variables derived from understory plant species (Edible/Medicinal/Decorative Plants, Herbivore Forage, Climate Change Resistant Understory, Fire Re-sprouting Understory, and Pollinator Supporting Understory) tended to be greatest near the RA vertex, decreased toward the WH vertex, and had mixed responses toward the DF vertex. ES proxies derived from tree properties (Volume of Merchantable Wood, Timber Revenue, and Carbon Stock) had a similar but opposite pattern with the greatest values near the WH vertex, decreased values toward the RA vertex and more variable values near the DF vertex. Scenic Beauty, on the other hand peaked around the centroid of the response surface but declined sharply toward the WH vertex.

3.2. Trade-offs between ES

The shape of the response surfaces showed trade-offs between ES derived from the understory community and those derived from trees, particularly near the RA and WH vertices representing the monocultures of those species. However, there was substantial curvature in many response surfaces leaving open the possibility for positive relationships between selected understory ES and overstory ES at selected ranges of tree species composition.

The two-way trade-offs between different ES are summarized in Fig. 4. ES derived from the trees tended to have positive or inconsistent relationships with each other but negative or inconsistent relationships with ES derived from understory plants. In inconsistent relationships, ES were positively related to each other in portions of the variable range and negatively correlated in other portions. ES derived from understory plants also had positive or inconsistent relationships with each other. Scenic Beauty, on the other hand had inconsistent relationships with all other ES. Some climate related ecosystem services had trade-offs, such as Carbon Stock and climate resistant understory. ES within and between frameworks had inconsistent relationships. For example, the ES prioritized in the *Production* framework were positively related to each other but had negative or inconsistent relationships with all other ES except for Carbon Stock. The ES prioritized in *Local Conservation* had positive or inconsistent relationships with one another and negative or inconsistent relationships with the ES prioritized in *Production*. The priority ES in *Preserving the Future* had a mix of positive, negative, and inconsistent relationships and as such, some ES aligned with the first two frameworks and others did not. The difference of ES within and between *Production* and *Local Conservation* highlighted that ES with primarily instrumental values in this study were positively related to each other but tended to be negatively related to ES with constitutive/eudemonic relational values.

3.3. Comparing ecosystem service results for frameworks

Predicted quantities and confidence intervals for all nine ES proxies under the four frameworks as well as the maximum predicted quantity of each ES are reported in Table 3. The largest trade-offs existed between *Local Conservation* and *Production*. For example, Timber Revenue and Merchantable Wood were less than half of their maximum value in *Local Conservation* compared to *Production* where both were maximized.

Under the *Production* framework, provision of Edible/Medicinal/Decorative Plants, Herbivore Forage, Climate Change Resistant Understory, Fire Re-sprouting Understory, and Pollinator Supporting Understory ES proxies were all very close to zero and Scenic Beauty was less than in any other framework. All ES prioritized in the *Local Conservation* framework except for Scenic Beauty were greater in that framework than any of the other frameworks. Scenic Beauty was slightly greater in the *Preserving the Future* framework than the *Local Conservation* framework because of trade-offs between it and Herbivore Forage when both ES proxies were maintained at high levels. Scenic Beauty was still at 95% of its maximum in the *Local Conservation* framework. All the ES prioritized in *Production* were greater in that framework than any of the other frameworks. In the *Preserving the Future* framework, all prioritized ES were maintained at 72% of their maximum or greater. The negative relationship of Carbon Stock with Climate Change Resistant Understory and Pollinator Supporting Understory drove their simultaneous output in *Preserving the Future* to a lower threshold than *Local Conservation* or *Production,* and as a result the four priority ES in *Preserving the Future* had greater values in different frameworks. The *Value Pluralism* framework resulted in moderate quantities of all ES.

The tree species composition that simultaneously optimized the priority ES for each framework are shown in Table 4 which further illuminates differences in ES response between the frameworks. *Local Conservation* was heavily weighted toward RA while the *Production* framework was optimized with WH monoculture. The countering trends of ES derived from understory plants and ES derived from trees between the RA and WH vertices was playing out between *Local Conservation* and *Production* resulting in the substantial trade-offs between them. On the other hand, *Preserving the Future* and *Value Pluralism* had more even mixtures of all three species and fewer extreme trade-offs compared to the other two frameworks. The *Production* framework had the lowest Shannon Diversity Index with zero, since a monoculture (Shannon Index = 0) resulted from the procedure to simultaneously optimized the ES prioritized in that framework. The next lowest was *Local Conservation*, which included all three species, but in very uneven mixture predominated by RA. *Preserving the Future* and *Value Pluralism* have substantially greater Shannon Diversity Index values for their corresponding optimal tree species mixtures. *Value Pluralism*'s mixture had the greatest Shannon Diversity Index driven by the more even mixture of the three species.

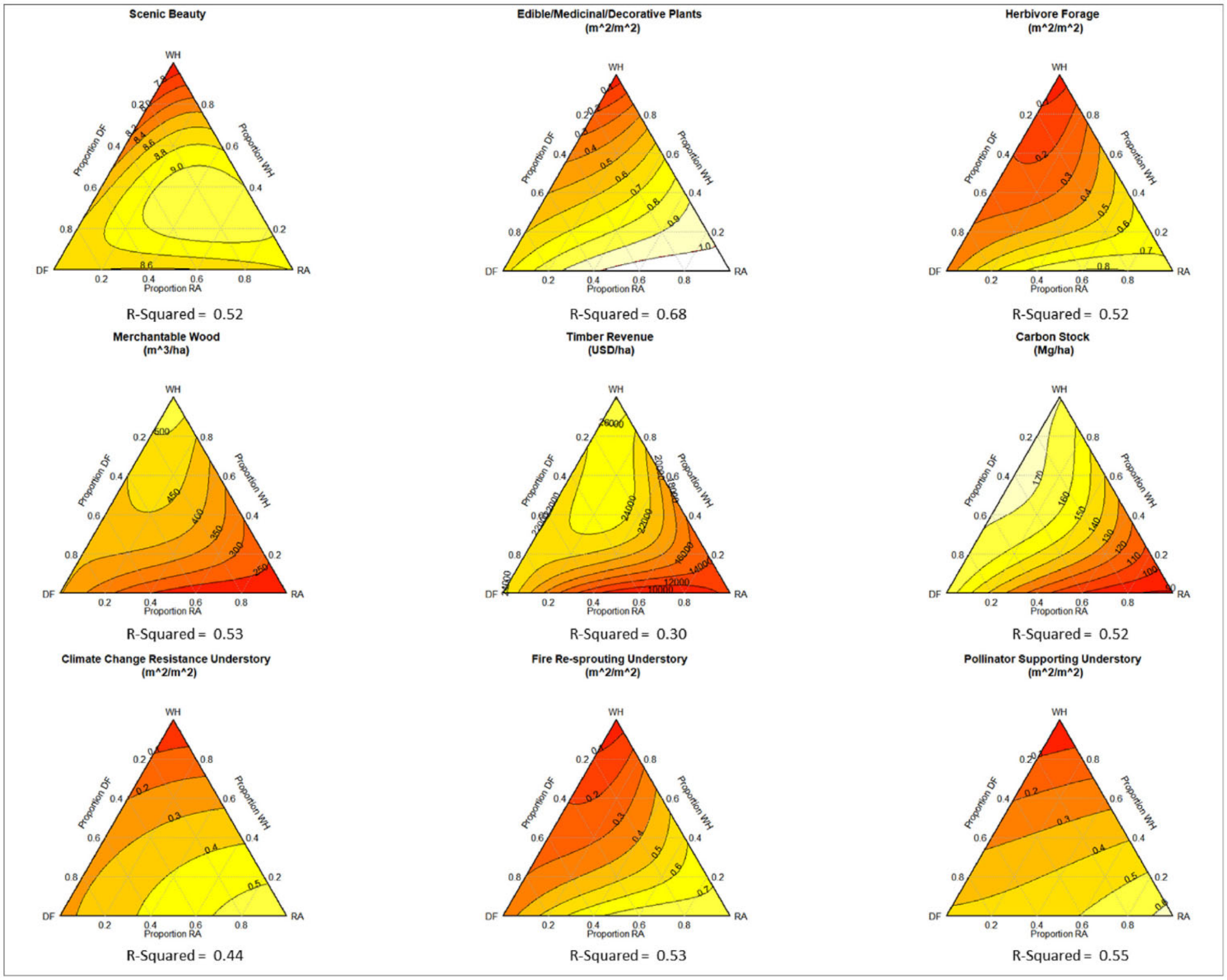

Fig. 3. Ecosystem Service Proxy response surfaces and corresponding R-squares. Red indicates lesser values and yellow/white greater.

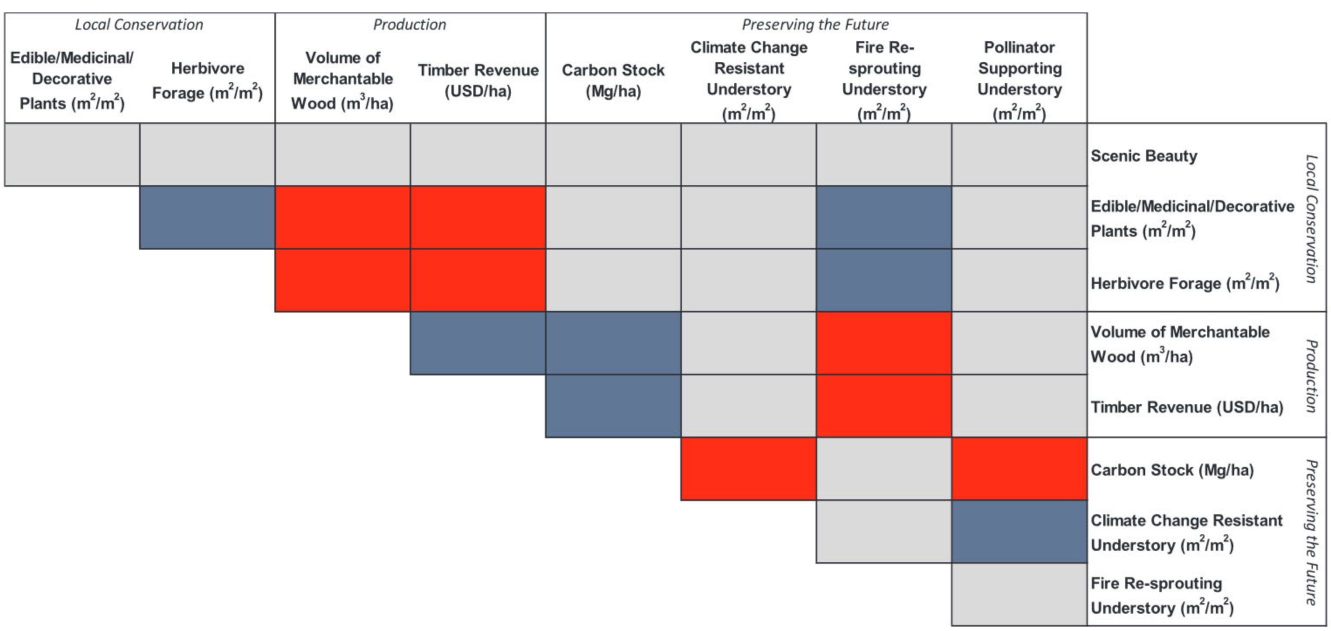

Fig. 4. Two-way relationships between individual ES proxies. Red indicates a negative relationship, blue indicates a positive relationship, and gray indicates relationships that were not consistently positive or negative but showed interactions such that for some range of values the relationship was positive and for a different range of values the relationship was negative.

Table 3
Maximum predicted output of ecosystem services proxies and output under the four frameworks. 95% CI in parenthesis.

	ES	Optimal	Local Conservation	Production	Preserving the Future	Value Pluralism
Local Conservation	Scenic Beauty (1–11 scale)	9.2 (8.8–9.6)	8.7 (8.3–9.1)	7.6 (7.2–8.0)	9.0 (8.7–9.4)	9.0 (8.7–9.4)
	Edible/Medicinal/Decrative Plants (m^2/m^2)	1.07 (0.82–1.31)	1.06 (0.85–1.26)	0.20 (0.0–0.21)	0.91 (0.74–1.09)	0.86 (0.67–1.06)
	Herbivore Forage (m^2/m^2)	0.82 (0.56–1.08)	0.79 (0.58–0.99)	0.03 (0.00–0.22)	0.58 (0.40–0.76)	0.53 (0.33–0.73)
Production	Merchantable Wood (m^3/ha)	551 (467–635)	213 (123–302)	551 (467–635)	316 (238–394)	342 (254–430)
	Timber Revenue (USD/ha)	$28,226 ($21,353-$35,100)	$10,654 ($3,353-$17,956)	$28,226 ($21,353-$35,100)	$17,604 ($11,221-$23,988)	$19,145 ($11,948-$26,342)
Preserving the Future	Carbon Stock (Mg/ha)	171.6 (151.5–191.8)	92.2 (65.9–118.4)	170.9 (146.1–195.6)	123.6 (100.7–146.6)	133.3 (107.4–159.1)
	Climate Change Resistant Understory (m^2/m^2)	0.57 (0.41–0.73)	0.53 (0.35–0.71)	0.00 (0.00–0.17)	0.46 (0.30–0.61)	0.43 (0.26–0.60)
	Fire Re-sprouting Understory (m^2/m^2)	0.78 (0.55–1.01)	0.77 (0.57–0.97)	0.02 (0.00–0.21)	0.59 (0.41–0.76)	0.53 (0.33–0.73)
	Pollinator Supporting Understory (m^2/m^2)	0.64 (0.49–0.78)	0.56 (0.40–0.72)	0.01 (0.00–0.16)	0.47 (0.33–0.61)	0.44 (0.28–0.60)

Table 4
Proportion of WH, DF, and RA that yielded optimal priority ES values for the four frameworks along with the corresponding Shannon diversity index.

Proportion of three tree species in the optimal mixture for each scenario				
Scenario	WH	DF	RA	Shannon Diversity Index
Local Conservation	0.01	0.19	0.8	0.54
Production	1.00	0.00	0.00	0.00
Preserving the Future	0.17	0.24	0.59	0.96
Value Pluralism	0.17	0.36	0.47	1.02

4. Discussion and conclusion

The approaches to assessing ecosystem service trade-offs in this study rely on the services being quantifiable and at least weakly comparable (Martinez-Alier et al., 1998). Thus, we could not accommodate other services that are likely affected by the tree species composition and diversity which do not fit these criteria. As the trade-offs between different frameworks emphasized, the choice of what services to include and by extension what values to give voice to can result in potentially undesirable results and favor the interests of some groups over others, creating or perpetuating environmental or epistemic injustice (Himes and Muraca, 2018; Muraca 2016). This study also assumes that the different priority ecosystem services within a given framework are equally desirable and their value scales linearly with the range of proxy responses observed. We mitigated the potential negative ramifications of these assumptions by targeting diverse ES representing all four MEA categories and a broad range of value types likely to appeal to different ways of knowing (Dıaz et al., 2015). The limitations of these assumptions could be minimized in future studies with direct policy implications by using deliberative methods of stakeholder engagement prior to selecting what ecosystem services to consider (Kenter et al., 2011), and recognizing the epistemic and technical uncertainties of the study (Ainscough et al., 2018). Stakeholder engagement and deeper ecological function assessments could also identify critical thresholds for ES (Fanny et al., 2015) and more nuanced understanding of the importance of increasing or decreasing percentage changes in the ES relative to each other to inform implementation of a weighting scheme in analysis.

Trade-offs between ecosystem services demonstrated the need to consider understory vegetation in conjunction with tree components when investigating the impacts of plant diversity on ecosystem services in forests. Forest understory vegetation has been linked to important aspects of ecosystem function in forest types around the world (Gamfeldt et al., 2013; Neill and Puettmann, 2013; Nilsson and Wardle, 2005). Understory species are typically light limited and closely tied to tree canopy structure (Barbier et al., 2008), which can result in trade-offs between understory plants and trees (Burton et al. 2013). Despite the high potential for such trade-offs a disproportional number of studies investigating relationships between biodiversity and ecosystem function or services in forests focus exclusively on tree biomass (Brockerhoff et al., 2017).

All ES proxies derived from understory species cover generally aligned positively with understory species diversity measured by Shannon diversity index (Himes and Puettmann, 2019; Shannon, 1948). This suggests a positive relationship between species diversity and ES, at least with regard to understory plants. For these services our results supported the hypothesis that there is a general positive relationship between biodiversity and ES proposed by others (Haines-Young and Potschin, 2010; Tilman et al., 2014). Similarly, ES derived from the overstory were well aligned with estimated aboveground biomass of trees in the same plot network reported previously by Himes and Puettmann (2019), supporting the supposition that tree productivity is a good proxy for many ecosystem functions and services (Balvanera et al., 2006). In contrast, Scenic Beauty—presumably a function of both understory and trees—was somewhat intermediary between aboveground biomass and understory species diversity. We believe this was because respondents simultaneously view the understory and overstory components of the plot when rating Scenic Beauty and other studies have shown that the basal area of trees and variability in understory both positively correlated to measures of scenic beauty (Ribe, 2009, 1989).

Most of the individual ES proxies were maximized or very nearly maximized in monocultures. Scenic Beauty was a notable exception in which a high diversity mixture of all three tree species (31% WH, 22% DF, and 47% RA) rated most beautiful. All the other ES proxies are relatively simple services in comparison, i.e. derived from a small set of functional traits or physical parameters while Scenic Beauty is a multidimensional response to complex interactions in the ecosystem and between the physical world, social context, cognitive processes and values (Ford et al., 2014; Gundersen et al., 2017; Ribe, 1989). Our results suggest the hypothesis that ES derived from more complicated processes, i.e. those derived from interactions of multiple ecosystem functions, may be more reliant on higher levels of biodiversity. Examples from the literature support this hypothesis: the ecosystem service of pest control in organic coffee farms in Chiapas, southern Mexico depends on at least thirteen different species and multiple levels of interaction between them (Vandermeer et al., 2010), and simulations show that ES dependent upon multiple species will illicit higher levels of biodiversity conservation in economically optimal solutions (Dee et al., 2017). According to Hooper et al. (2005:4), there is certainty in the conclusion that, “more species are needed to insure a stable supply of ecosystem goods and services as spatial and temporal variability increases”. Thus it is reasonable to expect that ES affected by multiple factors or multiple levels of temporal and spatial scales may be more likely to have a positive relationship with biodiversity.

We observed trade-offs between ES represented by relational values with benefits specific to individuals and groups (*Local Conservation* framework) and ES which were primarily instrumental with near globally transferable benefits (*Production* framework). This is particularly concerning because a recent literature review of ecosystem services in mixed species forests found nearly 12 times as many publications on provisioning services derived from wood biomass as there were total papers on cultural ecosystem services (Brockerhoff et al., 2017). This differential in the literature heavily favors instrumental values. Our results suggest ES with primarily constitutive/eudemonic values likely to be specific to individuals and groups in the system region (*Local Conservation*) tended to be cultural services and were severely reduced in this system when globally transferable instrumental values were prioritized. Martín-Lópeza et al. (2014) recommend pluralistic valuation to avoid missing trade-offs between incommensurable value dimensions. Our results and the literature highlight the impetus for plural valuation frameworks that include relational values when making natural resource management decisions, particularly with regard to cultural ES (Fish et al., 2016; Himes and Muraca, 2018). Empirical evidence supported that cultural services and relational values can be associated with more biodiverse systems and tended to be more important for marginalized groups (Cáceres et al., 2015). Also, plural approaches to valuation more fully capture the importance of ES to people around the world (Arias-Arévalo et al., 2017; Klain et al., 2017). All of which support arguments that instrumental value monism in large scale land management or policy can perpetuate social/environmental injustice toward groups or individuals for whom other ways of valuing non-human nature are integral (Berbés-Blázquez et al., 2016; Jax et al., 2013; Temper and Martinez-Alier, 2013; Kosoy and Corbera, 2010).

The *Value Pluralism* framework, which prioritized all nine ES equally, was optimized with the most diverse tree species composition. This result supported findings from other forestry studies in which the importance of biodiversity increased when multiple ecosystem functions or services were considered (Gamfeldt et al., 2013, 2008; van der Plas et al., 2016). However, the selection effects of the specific tree species and not biodiversity per se, could also be affecting results (Hooper and Vitousek, 1997). The inclusion of red alder in our study may have impacted many of the ES indicators. Unlike the other two species, red alder is a deciduous species which fixes nitrogen. If red alder were replaced with another conifer in the study, there would likely be smaller difference between understory species diversity and composition which likely respond to the seasonal and persistent increased light availability under red alder canopies as well as likely higher available nitrogen levels (Deal et al., 2017). However, inclusion of red alder in the study provided a greater diversity of functional traits compared to a study with three similar conifer species, and the diversity of species traits may actually be a better (although harder to quantify) indicator of biodiversity than species richness and evenness (Hillebrand and Matthiessen, 2009).

The study results are derived from plots representing a relatively small spatial scale and a single point in time. The scale of the plots was selected to be most relevant for capturing interactions between different individual trees (D'Amato and Puettmann, 2004), which are theorized as the basis for the biodiversity ecosystem function relationship (Hooper et al., 2005) and resulting positive correlation between biodiversity and ecosystem services (Haines-Young and Potschin, 2010). This scale is also compatible with the scale of silvicultural decision making. However, the provisioning of the ecosystem services investigated and their relationship to tree species composition may change with stand age and is typically operationally assessed at larger spatial scales, such as ownerships or watersheds. Thus, ecosystem service trade-offs, including those identified in this study, can be at least partially accommodated by mosaic of monoculture stands with different ages, species and density placed strategically the landscape (Tittler et al. 2015). We recommend future research efforts investigate cross-scale interactions and feedbacks that may result in emergent properties governing the provisioning of ecosystem services from plantation forests across space and time (Puettmann and Messier 2019, Messier et al., 2019).

The observed relationships between species diversity and the different ecosystem service bundles aligned with different human values. Moving from left to right along the x-axis of the value matrix, the optimal tree species composition increases in diversity from *Production* to *Local Conservation* to *Preserving the Future*. Within the matrix, the *Value Pluralism* framework included the broadest range of values and social organization, most aligned with a value pluralist approach to managing ES and had the optimal mixture of trees that was the most species diverse as indicated by Shannon Diversity Index. This trend supports the following hypotheses: ES or ES bundles which support a plurality of values are related to higher levels of biodiversity than ES that primarily support a single type of value. This hypothesis aligns with the IPBES value framework (Pascual et al., 2017) and deserves further investigation.

5. Conclusion

We conclude by summarizing the findings and interpretation of the study with following four points:

)1) Trade-offs exist between selected ecosystem services while others are compatible. Trade-offs aligned biologically (understory vs. trees), and along value domains (solely instrumental vs. relational/eudemonic).

)2) Most of the ES were optimized, or nearly optimized, by monocultures except for Scenic Beauty. Scenic Beauty was derived from multiple dimensions of ecosystem function while the other ES were more simple in terms of quantification (i.e., reflecting only a small component of the vegetation). We hypothesize that the relationship between plant diversity and ES may be mediated by the degree of complexity inherent or quantified in the ES.

)3) Management frameworks prioritizing ES with primarily fundamental-relational value were optimized with higher levels of tree species diversity than those with primarily constitutive/eudemonic relational value or those with solely instrumental value. The highest level of tree species diversity supported the framework where a plurality of values was considered.

)4) Based on these results we suggest that when analyzing the correlation between biodiversity and ecosystem services, researchers should not only focus on ecological functions, but also include the value dimension and the different languages of valuation associated with ecosystem services (including cultural ES) by people affected at different scales. From our study we conclude that biodiversity was positively related to the range of value types and a variety of valuation languages associated with ecosystem services.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Polynomial model used to fit ecosystem service response surfaces to the three components of tree species mixtures (western hemlock, Douglas-fir, and red alder).

$$\mathbf{Y_t = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_{12}\, x_1\, x_2 + \beta_{13}\, x_1\, x_3 + \beta_{23}\, x_2\, x_3 + \beta_{123}\, x_1 x_2\, x_3 + \varepsilon_t}$$

where

$Y_{t,r}$	Is the estimated ES from the *t*th plot, t = 1–43
β_1	parameter for the x_1 pure mixture
β_2	parameter for the x_2 pure mixture
β_3	parameter for the x_3 pure mixture
β_{12}	parameter for the mixture of x_1 and x_2
β_{13}	parameter for the mixture of x_1 and x_3
β_{23}	parameter for the mixture of x_2 and x_3
β_{123}	parameter for the mixture of x_1, x_2 and x_3
x_1	proportion of western hemlock in mixture
x_2	proportion of Douglas-fir in mixture
x_3	proportion of red alder in mixture
ε_t	random error of the t^{th} plot, $\varepsilon_t \sim N(0,\sigma_r^2)$

By definition, the sum of x_1, x_2, and x_3 must always equal to 1. Residuals are assumed to be independent, normally distributed, and have constant variance.

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