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Diversity-Carbon Flux Relationships in a Northwest Forest

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Abstract: While aboveground biomass and forest productivity can vary over abiotic gradients (e.g., temperature and moisture gradients), biotic factors such as biodiversity and tree species stand dominance can also strongly influence biomass accumulation. In this study we use a permanent plot network to assess variability in aboveground carbon (C) flux in forest tree annual aboveground biomass increment (ABI), tree aboveground net primary productivity ($ANPP_{tree}$), and net soil CO_2 efflux in relation to diversity of coniferous, deciduous, and a nitrogen (N)-fixing tree species (*Alnus rubra*). Four major findings arose: (1) overstory species richness and indices of diversity explained between one third and half of all variation in measured aboveground C flux, and diversity indices were the most robust models predicting measured aboveground C flux; (2) trends suggested decreases in annual tree biomass increment C with increasing stand dominance for four of the five most abundant tree species; (3) the presence of an N-fixing tree species (*A. rubra*) was not related to changes in aboveground C flux, was negatively related to soil CO_2 efflux, and showed only a weak negative relationship with aboveground C pools; and (4) stands with higher overstory richness and diversity typically had higher soil CO_2 efflux. Interestingly, presence of the N-fixing species was not correlated with soil inorganic N pools, and inorganic N pools were not correlated with any C flux or pool measure. We also did not detect any strong patterns between forest tree diversity and C pools, suggesting potential balancing of increased C flux both into and out of diverse forest stands. These

data highlight variability in second-growth forests that may have implications for overstory community drivers of C dynamics.

1. Introduction

Forests of the Pacific Northwest (PNW) can be highly productive [1-4], and as temperate forests they may store more biomass carbon (C) per unit area than most other ecosystems [1,5-8]. Second-growth forest productivity can also be highly variable, and understanding reasons for this variability is an important research priority with implications for ecosystem C dynamics and global C cycles. While a large portion of variability in forest C flux (both above- and belowground) occurs in response to abiotic variation [9-19], biotic gradients in plant community composition and diversity may be especially important as drivers of patterns in C cycling and productivity even at fine scales [4,7,20-23]. Stand diversity (richness, evenness, and diversity of dominant species), species biomass dominance, and presence/absence of soil modifying organisms (such as nitrogen [N]-fixing plants) could all represent major biotic influences on ecosystem C flux. A better understanding of how ecosystem C dynamics are affected by biotic factors such as these could lead to a better understanding of C dynamics of the global climate system [24].

Productivity-diversity and diversity-ecosystem function experiments (especially in grassland systems), generally show that more diverse plots are more productive [4,25,26], and have suggested positive relationships between ecosystem C-uptake and species diversity [25-28], and recent research spanning PNW forests also suggest positive relationships between productivity and diversity in natural forested ecosystems [4]. In fact, studies across productivity gradients have suggested the reverse relationship where productivity predicts forest tree diversity in large-scale regional datasets [16,29]. Forests may exhibit positive productivity-diversity relationships even though peaks in forest diversity across gradients in site quality have often shown intermediate productivity [16,21,30]. However, when productivity and diversity are related within a site, it is unclear whether productivity-diversity relationships are due to the influence of hyper-productive species (*i.e.*, sampling effects) or complementarity in resource acquisition [21,31,32]. There is also a general need for more studies examining biodiversity-ecosystem function patterns in natural systems [33] where site-quality variation is constrained.

Undoubtedly, presence of dominant plant species can play a major role in determining the C flux in ecosystems [34]. Although biomass stand dominance by abundant species can influence productivity [4], species differences in functional traits are also important as drivers of ecosystem productivity and are well-recognized as important controls on ecosystem processes (e.g., [35,36]). It is also possible that different species achieve similar net C uptake rates via different trait suites. For example, *Alnus rubra* Bong., a deciduous species in the PNW with a symbiotic association with an N-fixing bacteria, may maintain high productivity during the regular growing season that is matched by consistently lower (comparatively) productivity by coniferous evergreen species like *Pseudotsuga*

menziesii (Mirb.) Franco., which accumulate biomass over a greater portion of the year [37]. Thus it has been hypothesized that mixtures of these N-fixing and non-N-fixing species could yield more productive forests [38-40]. Presence of *A. rubra* may be especially important in increasing forest productivity (e.g., [16,38-44]) via N additions to soils [37,45-47]. This is important because low levels of soil N can limit growth in many PNW, USA forests (but see Binkley *et al.* [44]).

Aboveground C stocks and aboveground productivity (especially aboveground net primary productivity (ANPP)) have been thoroughly investigated using numerous metrics in multiple experimental systems [48], but soil CO_2 efflux responses to biotic variation in forest ecosystems are less well-studied [8,17,49]. Significant variation in belowground C flux exists alongside variation in dominant plant diversity [18], and this could be driven by the influence of hyper-productive (or nutrient-cycle altering) species (e.g., [21,32,49]).

In this study, we hypothesized that stand diversity, species biomass dominance, and presence/absence of an N-fixing tree species were all major biotic influences related to ecosystem C flux. We focused on three key measurable C flux measures in a natural second-growth PNW forest: net changes in aboveground tree C pools (hereafter; aboveground biomass increment (ABI), aboveground net primary productivity of trees ($ANPP_{tree}$)), and net soil CO_2 efflux. While not an exhaustive list of potential C fluxes in forests, these variables (ABI, $ANPP_{tree}$, and soil CO_2 efflux) may be indicative of major above- and belowground shifts in C flux associated with biotic variation in forests. All three of these variables can be responsive to both biotic and abiotic changes, and are important to quantify in order to understand whole ecosystem C flux. Our primary goal was to identify variation in aboveground C flux and net soil CO_2 efflux co-varying with stand diversity at a relatively homogeneous site. We examined C flux with regard to influences of: (1) overstory richness and diversity; (2) biomass-based stand dominance of overstory tree species; and (3) soil nutrient pools.

We prioritized these examinations in regards to four, more specific, hypotheses. First, we hypothesized aboveground productivity (ABI and $ANPP_{tree}$) would increase with an increase in forest tree richness and diversity. Second, we hypothesized stands containing the N-fixing species, *A. rubra,* would have higher aboveground productivity (ABI, and $ANPP_{tree}$) driven by high values in inorganic N pools. We expected lower productivity in sites dominated by slow-growing coniferous species such as *Thuja plicata* Donn ex D. Don and *Tsuga heterophylla* (Raf.) Sarg. Third, we hypothesized stands with higher stand diversity would also have higher soil CO_2 efflux. And finally, if C flux predictably varies with stand diversity, then we should expect total standing C stocks to be higher where aboveground productivity is higher, as long as aboveground C uptake is not overcome by high soil CO_2 efflux, and all sites have had a similar recovery time post-disturbance. This is important because sites with similar recovery times since disturbance are likely to have similar establishment dates and may be similarly aged. Thus with similarly ages stands we hypothesized C pools would increase with stand diversity and *A. rubra* presence.

2. Materials and Methods

2.1. Study Area

This study was conducted adjacent to the Puget Sound, Washington, USA in the Evergreen Ecological Observation Network, a long-term permanent plot network of 44 permanent ecological monitoring plots located throughout a 380 ha forest reserve owned and managed by The Evergreen State College. The ecosystem is a second-growth temperate forest that was clear-cut in 1937-39 using cable techniques. Our site has an average temperature of 10 °C and receives approximately 100 cm of annual rainfall [50]. All plots were located on similar Alderwood gravelly loam soils [51].

The forest overstory is dominated by a mixed canopy of *P. menziesii* and four primary codominant species: *Acer macrophyllum* Pursh, *A. rubra*, *T. heterophylla* and *T. plicata*, with an understory dominated primarily by *Polystichum munitum* (Kaulf.) C. Presl and *Gaultheria shallon* Pursh. The plot network was established in 2005 using a systematic 250 m spaced grid placed with a random start point using circular 20 m-diameter plots (Figure 1).

Figure 1. Map of study area depicting circular 10 m radius permanent plots along a 250 m grid with a random starting point: **(A)** Historical (1939) photo of the study area showing part of a clear-cut which took place from 1937-39. Blue dots depict the subset of 11 plots measured for soil CO_2 efflux and leaf litter, white dots depict the subset of 21 plots measured for aboveground biomass increment (ABI), and yellow dots depict 6 of the 44 plots measured for aboveground biomass pools only. **(B)** Locations of all 44 permanent plots measured for aboveground biomass pools only. For reference The Evergreen State College is located at the center of the image.
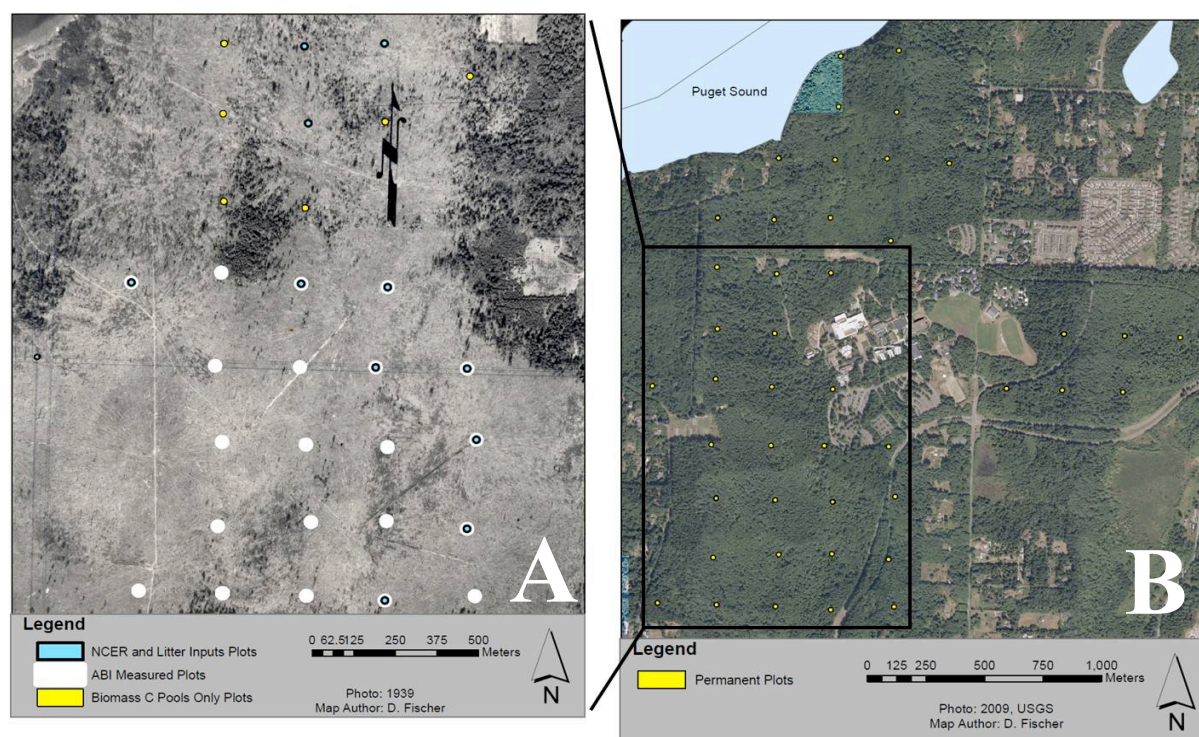
For this study we utilize 44 plots to estimate C pools in live and dead standing biomass, coarse woody debris (CWD), and understory vegetation. A subset of 21 plots were used to measure aboveground biomass increment (ABI), sampled once in 2006 and again in 2008. These years were expected to be average growth years based on data from an on-site weather station [50]. A smaller subset of 11 plots was intensively measured between 2006–2008 for estimates of leaf litterfall and aboveground net primary productivity of trees (ANPP$_{tree}$). Another subset of 10 intensive plots was independently selected in 2008 for the measurement of fine woody debris (FWD), and net soil CO_2 efflux (see Section 2.7; *Net Soil CO_2 Efflux Rate*). All intensive plots were chosen haphazardly from a subset of plots that could be determined to have similar site histories (similarly cleared) based on a 1939 orthophoto showing the last logging operation to take place at our study site.

2.2. Soil Nutrients

Variation in soil nutrient status could underlie any observed co-variation in forest diversity and C flux. In order to address potential variation in plot nutrient status, we analyzed cation exchangeable pools of mineral soil PO_4^{3-}, K^+, Ca^{2+}, NH_4^+, NO_3^- from a spring 2011 survey of the intensively measured plots. Briefly, for measurement of soil cation exchangeable PO_4^{3-}, K^+, and Ca^{2+}, we collected soils at 10 cm depths on north and south borders of each plot. Sieved (4 mm) soil samples were freeze-dried and powdered in a SPEX ball mill. Aliquots of 0.2 to 0.5 g of each soil were leached in 5 mL of 1M NH_4Cl solution for 20–24 h at room temperature in an agitator to separate the cation-exchangeable fraction of ions (*sensu* Nezat *et al.* [52]). Solutions were centrifuged to separate the supernatant and the remainder of the sample was rinsed 2 times in DI water to quantitatively collect the NH_4Cl leach. Leach solutions were analyzed for PO_4^{3-}, K^+, and Ca^{2+}, by Inductively-coupled Plasma Mass Spectrometry (ICP-MS; Perkin-Elmer DRC-e). For inorganic soil N (NH_4^+, NO_3^-), a 10 g aliquot of sieved (4 mm) soil was extracted in 100 ml of 2M KCl and hand-agitated (2 min) prior to leaching overnight (12 h; *sensu* Robertson *et al.* [53]). Suspensions were vacuum-filtered (grade 50 cellulose filter paper) and stored at 4°C until analyzed by University of Idaho Analytical Sciences Laboratory for colorimetric analysis utilizing flow injection analysis.

2.3. Changes in Aboveground Standing Carbon

To estimate net changes in aboveground C in forest plots, we rely on tree biomass estimation equations, and do not include sapling or understory biomass in changes of aboveground carbon stocks because trees dominate the system and aboveground portions of trees tend to reliably represent the majority of plant mass in most temperate forest ecosystems [48,54]. Changes in CWD C were also not included in calculation of aboveground C stocks as changes in CWD C are usually measured over decades rather than years (but see Section 2.4; *Coarse and Fine Woody Debris*). Death of trees and recruitment of new trees were accounted for on an individual tree basis as suggested in Clark *et al.* [48].

Aboveground tree biomass was estimated using independent allometric relationships based on stem diameter at 1.37 m (diameter at breast height; DBH) and tree height (HT). All trees within plot boundaries with DBH ≥ 5 cm were tagged and measured. We measured tree DBH in 2006 and again in 2008 at a tagged location on the tree trunk. Tree HT measurements were taken in 2007 and applied to

both 2006 and 2008 allometric biomass equation estimates of tree mass. Measurement of tree HT was obtained using a laser range finder and clinometer, and validated using estimates of tree HT generated from aerial LiDAR and processed in the program FUSION [55,56]. For mass estimation, we used species-specific biomass estimation equations from published studies compiled in the BIOPAK software package [57,58]. We primarily used biomass equations from Standish *et al.* [57] with the exception of the equation for *A. macrophyllum* biomass. For this species we compiled an equation from Gholz [59] using summation of individual equations for five separate components of the tree: total foliage biomass, stem wood biomass, live branch biomass, dead branch biomass, and stem bark biomass. In instances where a tree species did not have an associated biomass equation, the biomass equation for *A. rubra* [57] was substituted since it produced allometric predictions intermediate to other equations. This substitution was applied to the species *Salix scouleriana* Barratt ex Hook., *Frangula purshiana* (DC.) Cooper, *Corylus cornuta* Marsh., *Cornus nuttallii* Audubon ex Torr. & A. Gray, and *Ilex aquifolium* L. Across all species, aboveground C was assumed to be 50% of plant biomass, which is a common assumption [48].

We analyzed changes in aboveground tree C pools using two distinct metrics that each account for ecosystem C flux with different limitations. First, ABI measures aboveground tree biomass increment C and was estimated using repeat measures of biomass (2006, 2008) according to the equation:

$$ABI = (B_{t2} - B_{t1})/T \ (1)$$

where B_{t1} is the total aboveground tree biomass at time 1 (2006), B_{t2} is total aboveground tree biomass at time 2 (2008), and T refers to the number of years over which data were taken (2). This metric focuses on live trees, relies on estimation of foliar mass based on stem dimensions, and does not account for foliar loss due to abscission (*i.e.*, it only accounts for net changes in standing C without accounting for replacement of foliage produced and shed to the forest floor). This metric was available for most plots in our study because it relies on relatively simple field measurements.

Second, for the subset of 11 more intensively measured plots, we estimated $ANPP_{tree}$ by summing estimates of ABI with estimates of litterfall from litter traps. This metric provides a combined estimate of ANPP in trees through estimates of changes in aboveground tree woody increment, new foliar production, and foliar production that replaced foliage lost through litterfall. We collected litterfall using 50 cm diameter litter traps suspended 20 cm above the forest floor at plot center. Litterfall was collected monthly from November 2006 through November 2007. Following collection, litter was immediately dried at 70 °C for 72 h, sorted by species, and weighed to the nearest mg. While ABI was calculated as the average over two years (2006–2008), litterfall was estimated based on the 2006–2007 collection. Thus, $ANPP_{tree}$ estimates represent ABI averaged over two years and litterfall from the single year it was measured.

2.4. Coarse and Fine Woody Debris

Although not used for estimates of changes in C stocks over time, we measured CWD mass to estimate total plot aboveground C stocks (Table 1). A survey of coarse woody debris (CWD) was conducted in all plots between 2006–2008. We separate CWD into two categories, where all downed logs ≥10 cm in diameter are considered downed woody debris (DWD) and all standing dead tress

≥5 cm DBH are considered snags. All CWD falling into these two categories were tagged and measured in all plots [60] for estimation of total plot non-living C pool. Length (L) was measured on each piece of DWD and diameter was recorded at three points: base (A_b), middle (A_m) and top (A_t) of each piece of DWD. When DWD extended beyond the plot, end measurements were made at the plot boundary. Decay classes for each species were estimated using a five class decomposition scale [61]. Dimension measurements were used with Newton's formula to obtain volume for each piece of DWD [60]. We then used volumetric estimates combined with estimates of density and C content, based on decay stage, in order to provide estimates of DWD C. Density values were obtained from a table of mean density for decay classes of CWD in the Cascade-Temperate region [60] for the following species: *P. menziesii*, *T. plicata*, and *T. heterophylla*. Where a decay-class-sensitive density estimate could not be found for a species, a substitute density was used by selecting densities from decay classes of another species whose live tree bole densities closely matched published live tree bole density estimates for the species of concern.

Table 1. Stand characteristics and carbon (C) pools for measured plots *.

S	n	TPH	SPH	DWDPH	Tree C	Snag C	DWD C	Sap C	FWD C[1]	US C	Plot C
1	2	525.48	143.31	302.55	148.05	12.01	14.86	0.06	8.62 (2)	7.31	182.29
2	5	343.95	343.95	407.64	148.79	15.37	12.8	0.16	9.15 (1)	5.8	182.92
3	13	443.41	210.68	440.96	236.95	5.45	22.86	0.18	8.81 (4)	3.89	269.33
4	16	491.64	222.93	423.97	287.21	5.84	21.72	0.17	8.01 (4)	3.97	318.91
5	7	509.55	200.18	414.01	286.55	4.72	16.78	0.19	n/a	5.06	321.79[2]
6	1	668.79	127.39	95.54	154.35	13.2	1.25	0.32	n/a	5.08	182.69[2]
Weighted	Ave.	469.02	223.65	412.57	247.18	7.08	19.48	0.17	8.52	4.51	286.91

*Values represent averages within species richness (S) classes (1–6). Because number of plots (n) was variable among classes, averages are derived from among 1-16 individual plots. The average value (Ave.) for all plots measured is represented by the bottom row. TPH = trees per ha, SPH = snags per ha, DWDPH = downed woody debris (>10 cm diameter) per ha, Sap = sapling, FWD = fine woody debris (<10 cm diameter), US = understory. 1, FWD measured in a subset of 11 plots. Number of plots with richness is in parentheses. 2, Totals for plots with richness 5 and 6 given an assumed value of 8.52 Mg C ha^{-1} for estimations of FWD. Value derived from an average of the 11 plots where FWD C was collected.

Snags were measured for DBH and HT. A five class decomposition score (similar to the CWD scale) was also estimated for all snags measured, and used as above for DWD. The Huber formula was used for snag volume [60]. Biomass C of each snag was calculated using species- and decay-class-specific density values similar to those used for calculation of DWD.

An estimation of fine woody debris (FWD; any woody debris <10 cm in diameter) was produced from locations adjacent to each of a subset of 10 intensive plots in the fall of 2008. Four 0.25 m^2 sampling frames were placed just outside plot boundaries (to reduce plot disturbance) in four cardinal directions to determine C content of FWD of the forest floor. Woody debris <10 cm in diameter was collected, oven-dried at 70 °C for 72h, sorted, and weighed. As stated in Section 2.2, 50% of dry mass was assumed to be C. The four subplot values were averaged for an estimation of plot FWD C.

2.5. Saplings

A sapling survey was conducted in all plots to determine C storage of young trees and shrubs. Tree saplings <5 cm DBH and ≥1 m in HT were counted, while all shrubs <5 cm DBH and ≥2 m tall were counted. Trees and shrubs not meeting these minimum criteria were considered to be part of the understory community and were included in understory community sampling (see Section 2.6; *Understory Community*). Saplings were recorded for species and abundance. A random sampling of 40 saplings yielded a mean stem basal diameter at the litter surface (DBA) of approximately 2.5 cm. Based on this sampling each sapling was given a DBA of 2.5 cm for calculation of biomass using equations from the BIOPAK database [58]. While this assumption of similar biomass based on average sapling mass may be a source of error, sapling abundance contributed minimally to whole plot C estimates (<0.05%). Species that did not have an associated biomass equation were assigned a species closely related by genus, family, or morphology.

2.6. Understory Community

Understory vegetation (% cover) was measured in 2008 using 10 cm point-line intercepts along four 10 m transects from plot center to plot edge in cardinal directions. The mass of understory plants was determined using equations from the BIOPAK database [58]. Since understory community measurements were made only once during the study, measurements were used for estimates of plot C pools, but were not used for estimates of net changes in aboveground C pools.

2.7. Net Soil CO_2 Efflux Rate

We measured net soil CO_2 efflux in a subset of 11 intensively measured plots selected in 2008. Soil respiration was measured on the forest floor using a differential open system infrared gas analyzer with soil chamber attachment (ADC Bioscientific Ltd., Hertz, UK). In four evenly-stratified subplots per plot, 5-min measurements were taken monthly for a full year between January 2008 and January 2009. During spring and summer, 24-h measurements were conducted for assessment of diel patterns in soil CO_2 efflux. For each 24-hour measurement, two plots were sampled every three hours. These measurements suggested a mild diel pattern with peak soil CO_2 efflux from ~10:00–16:00, and all regular measurements were taken between these times for consistent measurement of soil CO_2 efflux within daily temperature and moisture regimes.

2.8. Overstory Richness and Diversity

We classified species richness within plots in two ways: (1) Using just the five most dominant overstory species (*P. menziesii, A. macrophyllum A. rubra, T. heterophylla, T. plicata*), referred to as 'Overstory Richness 5' in tables and figures. This was done to observe patterns associated with abundant species that have a significant physical presence in plots, and to avoid patterns in richness associated with small, rare individuals. The five most dominant overstory species comprise 95.5% of all tagged trees and account for 99% of total tree biomass. Thus, dominant species were assumed to drive a majority of the productivity-diversity relationship; (2) Using all 12 overstory species that occur within plots (also including *S. scouleriana, F. purshiana, I. aquifolium, Abies grandis*

[Douglas ex D. Don] Lindl., *C. cornuta*, *C. nuttallii*, and *Picea sitchensis* [Bong] Carrière], referred to as 'Overstory Richness All' in tables and figures. This was done to classify true plot tree richness so data could be analyzed with the influence of rare species. Any patterns related to richness or diversity in this study can be assumed to be based on random sampling, as this plot network is located throughout an even-aged forest using a stratified-random plot design. We included all 12 overstory species for both Shannon's (H') and Simpson's (D) diversity indices calculated using the program PC-Ord [62]. We also constructed an index of community similarity among plots based on non-metric multidimensional scaling (NMS) ordination of our tree data using a single axis solution of ordinated data and 500 max iterations [62]. The final stress of this ordination was 47.7, with instability of 0.0005. This single axis-ordination gives a score (hereafter NMS community similarity) where communities that are more similar exhibit a similar score.

2.9. Statistical Analysis

Our work analyzing tree diversity and C can be summarized by three sets of analyses: (1) We conducted linear regression analyses between species diversity indices and the variables ABI, $ANPP_{tree}$, and soil CO_2 efflux; (2) Because hyper-productive species (e.g., the N-fixing species *A. rubra*) could be responsible for productivity-diversity relationships, we also assessed individual co–variation with C flux by conducting separate linear regressions of C flux/pool measures and individual biomass-based stand dominance estimates for each tree species in each plot. Our regressions examined individual tree species stand dominance relationships with ABI, $ANPP_{tree}$, and soil CO_2 efflux; (3) Finally, in order to further clarify which factors were better predictors than others, we conducted model selection analysis to compare single-factor models using ranked model selection criteria [63]. For this analysis, we compared models where C flux was predicted from each diversity index, % biomass dominance of all species individually, a model that combined all species, NMS community similarity, inorganic N measures, or an intercept only (null model). Briefly, our approach used Akaike's Information Criterion, (adjusted for small sample size; AICc), model likelihood, computed weights of evidence (w_i), and an "evidence ratio" computed from these variables, to rank multiple models. Each measure provided an index of the best model given the data, and the "evidence ratio" gives a "gambler's odds" of the top model being the best model compared to other models. Models in the same set whose AICc differed by less than 2.0 where not considered statistically distinguishable, as is common [63]. This approach is considered less biased and less prone to error compared to other model ranking approaches like stepwise regression [63]. The approach favors more parsimonious models, and thus single factor models are generally selected over multivariate predictor models. Because we included soil N variables, this analysis was limited to only the plots in which soil N was measured (n = 8–11).

For exploratory examination of all other correlations among variables we used Pearson's product-moment correlation analysis. All data which did not meet normality assumptions were transformed using log transformations, or arcsine square-root transformations in the case of percentage data. All analyses were conducted in JMP 8.0 (SAS Institute Inc. Cary, NC). An $\alpha = 0.05$ was used to determine statistical significance.

3. Results

3.1. Species Diversity

We found significant positive relationships between aboveground biomass increment C flux (ABI) and overstory richness classified by the five most dominant overstory species (Figure 2) and all 12 tree species (Table 2). Similarly, in the 11 plots where tree aboveground net primary productivity C (ANPP$_{tree}$) was measured we found significant positive relationships between ANPP$_{tree}$ and tree species richness of the five most dominant species (Figure 2) and all 12 species (Table 2). The metrics ABI and ANPP$_{tree}$ also showed significant positive relationships with H' and D diversity indices (Table 2). In fact, in our model selection analyses (Table 3–5), H' and D diversity indices were the best models predicting ANPP$_{tree}$ and ABI respectively. However, these "best" predictive models were rarely statistically distinguishable from other diversity indices, and for ABI, diversity models were not statistically distinguishable from the intercept-only (null) model. Thus, while diversity indices significantly predicted one quarter to one third of ABI in regressions, with the more-limited subset of plots in the model selection analysis (constrained by soil N measures), we could not distinguish these models from each other.

Figure 2. Positive relationships between Aboveground Biomass Increment carbon (ABI), Aboveground Net Primary Productivity of trees (ANPP$_{tree}$), and Overstory Richness 5 which includes the five most dominant tree species; *P. menziesii, A. macrophyllum, A. rubra, T. heterophylla,* and *T. plicata.*
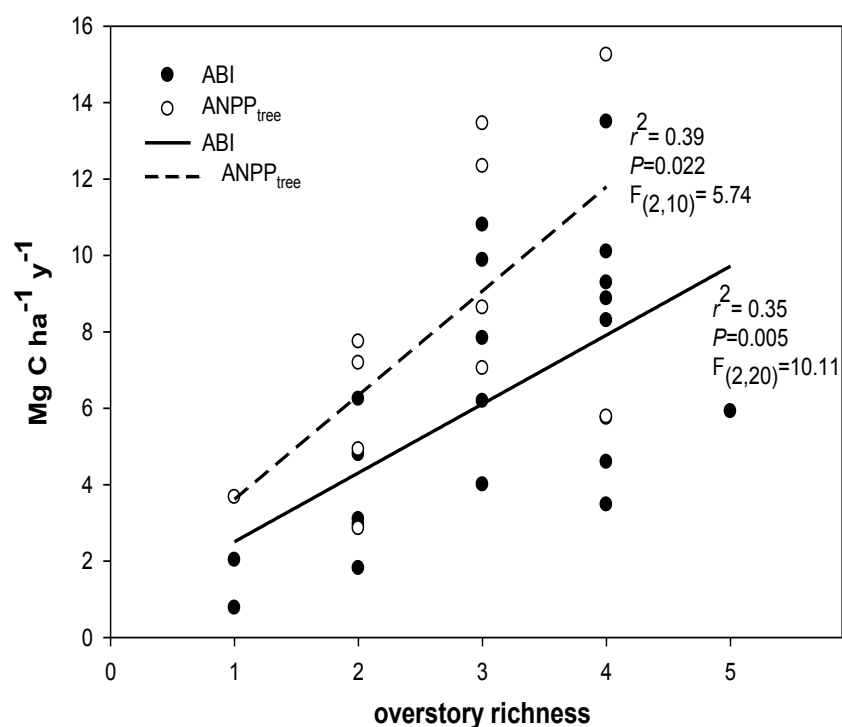
Table 2. Regression coefficient and significance results for regression analyses of plot carbon flux and pool estimates versus diversity metrics *.

	Tree C n = 44	Snag C n = 44	DWD C n = 44	Plot C n = 44	ABI n = 21	ANPP$_{tree}$ n = 11	Soil CO_2 efflux n = 11
Overstory Richness 5	**0.18, 0.004**	0.666	0.249	0.114	**0.35, 0.005**	**0.39, 0.022**	**0.71, 0.002**
Overstory Richness All	0.074	0.364	0.837	**0.175, 0.005**	**0.29, 0.013**	**0.52, 0.013**	**0.41, 0.034**
Simpson's D	0.131	0.071	0.622	0.177	**0.26, 0.017**	**0.40, 0.037**	**0.68, 0.002**
Shannon's H'	0.116	0.111	0.747	0.193	**0.30, 0.011**	**0.46, 0.022**	**0.69, 0.002**
P. menziesii % dom.	0.400	**0.183, 0.004**	0.737	0.326	0.093	0.404	0.123
A rubra % dom.	0.090	0.170	0.126	**0.09, 0.046**	0.174	0.591	**0.63, 0.004**
T. plicata % dom.	0.721	0.138	0.269	0.774	0.734	0.960	0.534
A. macrophyllum % dom.	0.448	0.540	0.327	0.408	0.548	0.553	0.775
T. heterophylla % dom.	0.752	0.240	0.740	0.799	0.438	0.658	0.659

*Values represent the r^2 value, and the *P*-value from regression analysis for significant analyses (**bold**). For non-significant findings, only the p-value is shown. Overstory Richness 5 includes the 5 most dominant species, while Overstory Richness All includes all 12 species occurring within plots. Tree C represents estimated aboveground tree C for 2008 using all 44 plots. Snag and DWD C represent C pools in 2008 for snags and downed woody debris respectively. Plot C represents aboveground plot C for all 44 plots measured in 2008 including trees, snags, DWD, saplings and understory C. Net change in aboveground tree C is represented by aboveground biomass increment (ABI). The metric ANPP$_{tree}$ (aboveground net primary production of trees) accounts for ABI (averaged over 2006-2008) + average annual litterfall for 2007/2008.

Table 3. Model selection ranking * for the best models predicting aboveground biomass increment (ABI) in plots where N data were also available.

	AICc		n	Lik-Model	wi (~probabilities)	Evid. Ratio
ABI						
Simpson's D	59.90	a	11	1.00	0.26	1.00
Shannon's H'	60.88	ab	11	0.61	0.16	1.64
Intercept Only	60.89	ab	11	0.61	0.16	1.65
Overstory Richness 5	61.25	b	11	0.51	0.13	1.97
Overstory Richness All	63.27	c	11	0.19	0.05	5.41
NH_4^+	63.33	c	11	0.18	0.05	5.56
NO_3^-	64.18	c	11	0.12	0.03	8.51
NMS Community Similarity	64.41	c	11	0.10	0.03	9.54
T. heterophylla % dom.	64.57	c	11	0.10	0.03	10.35
$NO_3^- + NH_4^+$	64.60	c	11	0.10	0.02	10.49
P. menziesii % dom.	64.68	c	11	0.09	0.02	10.94
A. macrophyllum % dom.	64.76	c	11	0.09	0.02	11.38
T. plicata % dom.	64.78	c	11	0.09	0.02	11.50
A rubra % dom.	64.82	c	11	0.09	0.02	11.74
All Species	106.01	d	11	0.00	0.00	1.03E + 10

Table 4. Model selection ranking * for the best models predicting aboveground net primary productivity of trees (ANPP$_{tree}$) in plots where N data were also available.

	AICc		n	Lik-Model	wi (~probabilities)	Evid. Ratio
ANPPtree						
Shannon's H'	47.46	a	8	1.00	0.27	1.00
Simpson's D	48.01	ab	8	0.76	0.20	1.32
Overstory Richness All	48.07	ab	8	0.74	0.20	1.36
Overstory Richness 5	48.19	ab	8	0.69	0.19	1.44
Intercept Only	49.56	b	8	0.35	0.09	2.87
NH_4^+	54.05	c	8	0.04	0.01	27.00
NMS Community Similarity	54.73	c	8	0.03	0.01	38.02
A. macrophyllum % dom.	54.88	c	8	0.02	0.01	40.83
P. menziesii % dom.	54.99	c	8	0.02	0.01	43.19
A rubra % dom.	55.04	c	8	0.02	0.01	44.31
T. plicata % dom.	55.05	c	8	0.02	0.01	44.59
T. heterophylla % dom.	55.16	c	8	0.02	0.01	46.98
NO_3^-	55.16	c	8	0.02	0.01	47.14
$NO_3^- + NH_4^+$	63.15	d	8	0.00	0.00	2554.15
All Species	133.75	e	8	0.00	0.00	5.46E + 18

* Models are ranked from the best (top) to worst (bottom) model based on low AICc values. Letter superscripts (a-c) are shared by models that are statistically indistinguishable from each other based on similar ΔAIC_c values [63]. All models used the variable listed in the row to predict the C flux indicated in bold along with an intercept value. An "Intercept" only model was also evaluated. The likelihood value predicts a likelihood of the best model given the factors evaluated, the weight of evidence indicates the amount of weight a given factor had in explaining variance compared to other models in the candidate set, and the evidence ratio gives a gambler's odds or model comparison with the top model.

Table 5. Model selection ranking * for the best models predicting net soil CO_2 efflux in plots where N data were also available.

	AICc		n	Lik-Model	wi (~probabilities)	Evid. Ratio
Net Soil CO_2 Efflux						
Simpson's D	42.18	a	10	1.00	0.50	1.00
Shannon's H'	44.36	b	10	0.34	0.17	2.97
Overstory Richness 5	44.66	b	10	0.29	0.14	3.45
A rubra % dom.	45.33	b	10	0.21	0.10	4.82
Overstory Richness All	46.23	b	10	0.13	0.07	7.56
Intercept Only	50.49	c	10	0.02	0.01	63.74
P. menziesii % dom.	50.71	c	10	0.01	0.01	71.11
NMS Community						
Similarity	53.12	d	10	0.00	0.00	237.68
T. plicata % dom.	54.16	d	10	0.00	0.00	398.23
T. heterophylla % dom.	54.42	d	10	0.00	0.00	454.17
NH4+	54.50	d	10	0.00	0.00	472.71
NO3-	54.68	d	10	0.00	0.00	516.76
A. macrophyllum % dom.	54.78	d	10	0.00	0.00	542.62
NO3- + NH4+	60.09	e	10	0.00	0.00	7719.19
All Species	101.49	f	10	0.00	0.00	7.56E + 12

* Models are ranked from the best (top) to worst (bottom) model based on low AICc values. Letter superscripts (a-c) are shared by models that are statistically indistinguishable from each other based on similar ΔAIC_c values [63]. All models used the variable listed in the row to predict the C flux indicated in bold along with an intercept value. An "Intercept" only model was also evaluated. The likelihood value predicts a likelihood of the best model given the factors evaluated, the weight of evidence indicates the amount of weight a given factor had in explaining variance compared to other models in the candidate set, and the evidence ratio gives a gambler's odds or model comparison with the top model.

3.2. Biomass-Based Stand Dominance

Because it has been hypothesized that biodiversity-ecosystem function relationships may be driven by single species (see Loreau *et al*. [21]), the five most biomass-dominant overstory species were selected for analysis of effects of individual tree species dominance on ABI, ANPP$_{tree}$, overstory biomass C, and net soil CO_2 efflux. We found that total biomass of the five dominant tree species within plots initially was not predictive of ABI or ANPP$_{tree}$ ($P > 0.05$; Table 2). However, when we re-analyzed these data for each species, discounting plots where each given species was absent (zero data not included), we found significant relationships for *T. plicata, T. heterophylla* and *A. rubra* and found a weak significant relationship for *A. macrophyllum*, where individual species biomass dominance in a stand (% dominance) provided predictions of ABI. Contrary to the expectations of hyper-productive species driving positive productivity-diversity relationships, the slopes of our stand dominance by ABI relationships were generally negative (Figure 3), suggesting that most plots were actually less productive when dominated by any single species. Only *P. menziesii* demonstrated a lack of a significant negative relationship between dominance and ABI when analyzed this way ($P > 0.05$; Figure 3).

In our model selection approach, diversity models were consistently more predictive than models based on dominance of individual species, models based on presence of all species, or a model based on community similarity among plots (Table 3–5). Where single-species biomass values were included as predictor variables for ABI and ANPP$_{tree}$ (Tables 3–5), biomass dominance was consistently among the lower ranked predictive models. For example, the evidence ratio (Table 3–5) indicated that relative biomass of *A. rubra* (the N-fixing deciduous tree species) had between a 1:12 and a 1:44 odds of producing a better predictive model than the top ranked diversity indices, and the variable only accounted for between 1 and 3% of the explanatory weight (weights of evidence; w_i) of all the variables we analyzed. Similarly, the models including all species biomass values or community similarity were generally low-ranked models. In combination, these results suggest that single productive species or predictable groupings of only a few species were unlikely to be driving diversity and aboveground C flux relationships in our study.
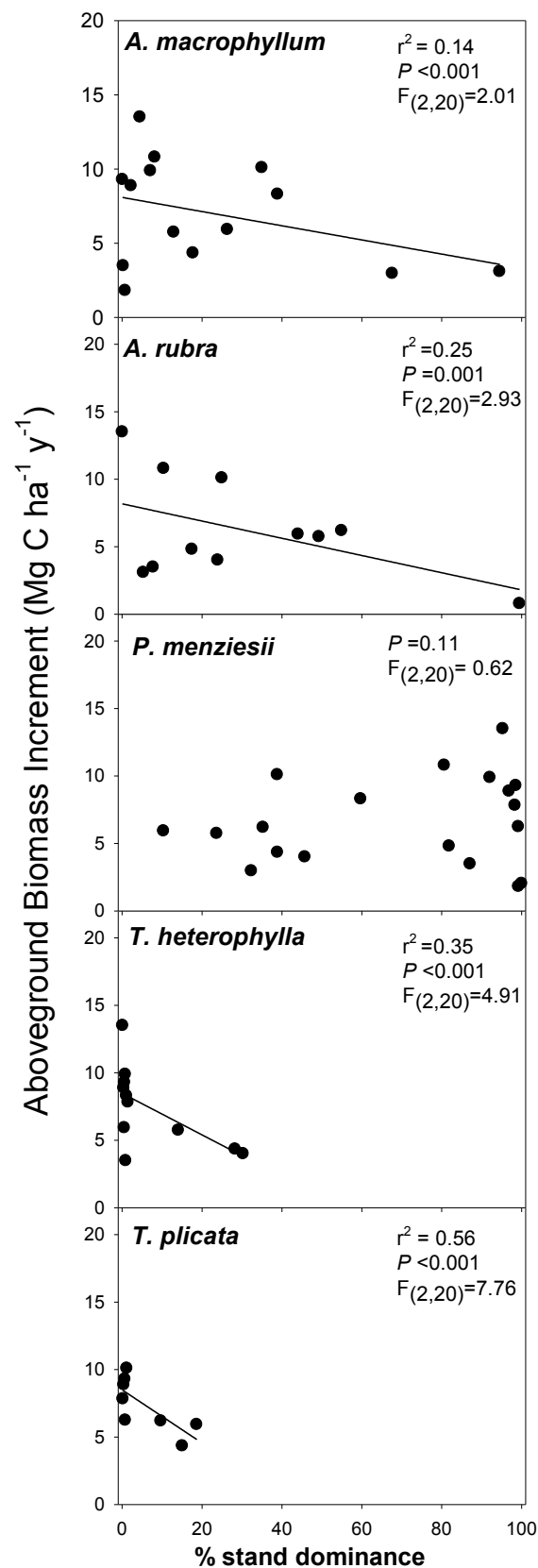
3.3. Net Soil CO2 Efflux

In accordance with our predictions of high C flux with increasing plot diversity, soil CO_2 efflux demonstrated patterns similar to ABI and ANPP$_{tree}$. Total growing season soil CO_2 efflux demonstrated positive relationships with richness of both the five most dominant species, and all 12 tree species (Table 2). Positive relationships were also found for soil CO_2 efflux predicted by H' and D diversity indices (Figure 4; Table 2). When examining single species relationships, only % stand dominance of *A. rubra* demonstrated a significant relationship with soil CO_2 efflux. This was a relatively strong negative relationship ($r^2 = 0.63$; $P < 0.004$), where soil CO_2 efflux declined as *A. rubra* presence increased in plots (Table 2). All other relationships between single species dominance and soil CO_2 efflux were non-significant ($P > 0.05$; Table 2). In our model selection approach, the Simpson's D diversity index was the best ranked model, and this variable had odds of 5:1 of being a better explanatory variable compared to *A. rubra* presence. Similar to results above, other single species, all-species combinations, or measures of community similarity were not strong predictors of this variable (Tables 3–5).

3.4. Soil Nutrients

In our model selection approach we directly ranked models predicting C flux which contained inorganic N pools (Table 3–5). We consistently found that the inorganic N pools, NO_3^- and NH_4^+, and a combination model which included both, provided poorly ranked models in our candidate set, and they were always distinguishable from the better ranked models (Table 3–5). We also did not find any significant correlations among soil CO_2 efflux values and measured soil nutrients (PO_4^{3-}, K^+, Ca^{2+}, NO_3^-, NH_4^+; All $P > 0.05$; Table 6). Interestingly, we also did not find any correlations among NO_3^- or NH_4^+ and % dominance by *A. rubra* ($P = 0.66$ and 0.81 respectively; data not shown).

Figure 3. Influence of overstory stand dominance on overstory Aboveground Biomass Increment carbon (ABI). The five most dominant overstory species are represented (*P. menziesii, A. macrophyllum, A. rubra, T. heterophylla,* and *T. plicata*). Data is only shown for plots where each species is present (zero data excluded).

Figure 4. Positive relationships between soil CO_2 efflux and overstory diversity represented by Shannon's and Simpson's diversity indices (which includes all 12 overstory species **(A)**), and Overstory Richness 5 which includes the five most dominate tree species; *P. menziesii, A. macrophyllum, A. rubra, T. heterophylla,* and *T. plicata* **(B)**; note that even though five species are represented, maximum species richness in the intensively measured plots was four.
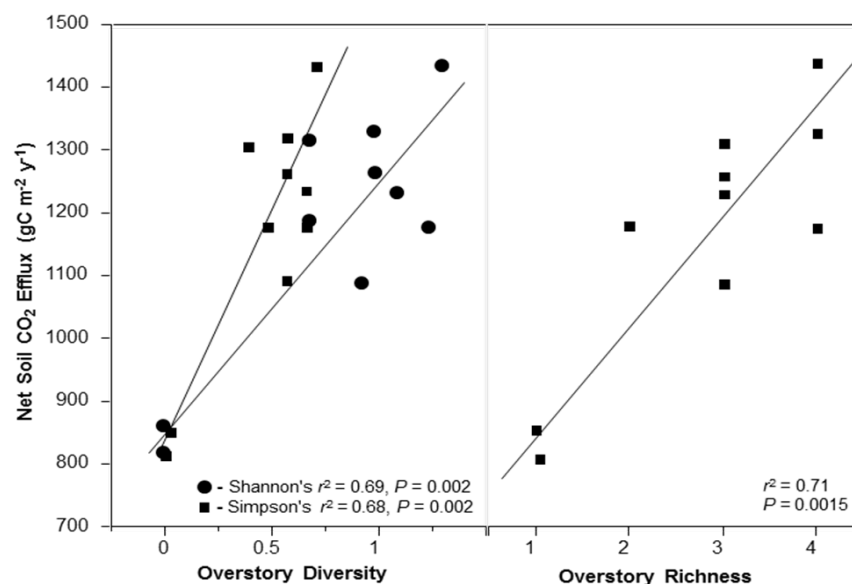
Figure 5. Percent dominance by biomass of individual species by species richness. Most species were represented evenly across richness categories.
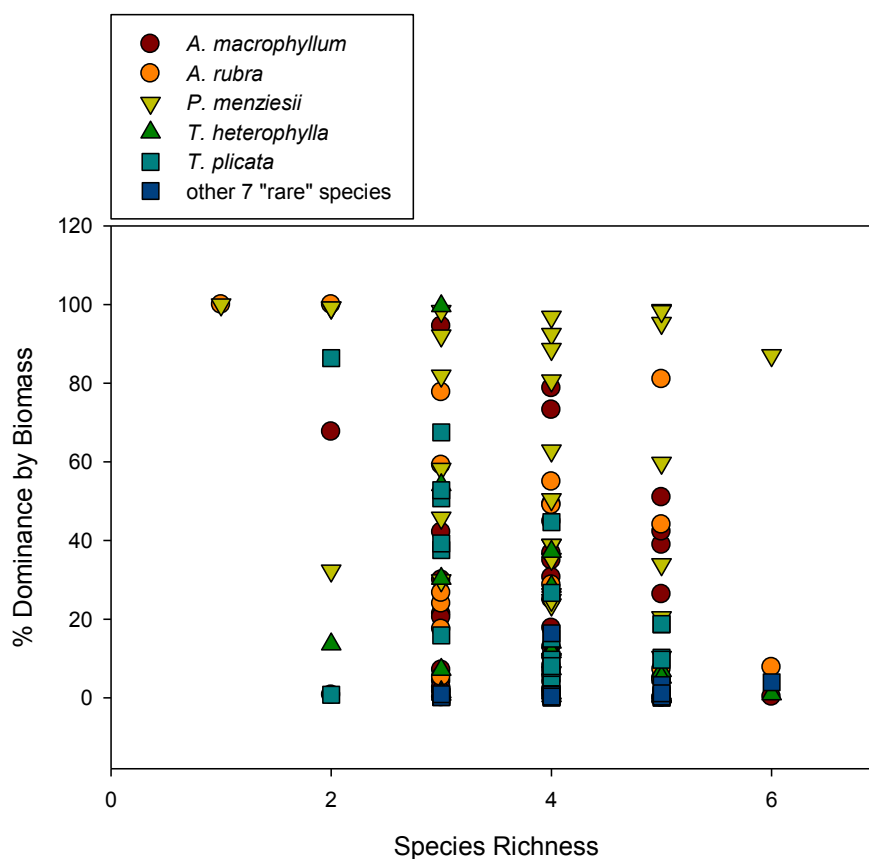
Table 6. Pearson Product Moment Correlation values and significance for C flux * *versus* mineral soil chemistry measures.

C flux/pool	Mineral Soil Chemistry Pool	Pearson Correlation Coefficient	*P-value*
ABI	PO_4^{3-}	−0.04	0.93
ABI	K^+	−0.48	0.33
ABI	Ca^{2+}	−0.06	0.91
ABI	% C	0.09	0.87
ABI	NO_3^-	0.37	0.33
ABI	NH_4^+	0.13	0.73
ABI	% Moisture	0.16	0.68
$ANPP_{tree}$	PO_4^{3-}	0.03	0.95
$ANPP_{tree}$	K^+	-0.47	0.35
$ANPP_{tree}$	Ca^{2+}	-0.06	0.91
$ANPP_{tree}$	% C	0.04	0.94
$ANPP_{tree}$	NO_3^-	0.52	0.19
$ANPP_{tree}$	NH_4^+	0.20	0.64
$ANPP_{tree}$	% Moisture	0.54	0.17
Net Soil CO_2 Efflux	PO_4^{3-}	0.35	0.32
Net Soil CO_2 Efflux	K^+	−0.03	0.92
Net Soil CO_2 Efflux	Ca^{2+}	0.29	0.41
Net Soil CO_2 Efflux	% C	0.23	0.53
Net Soil CO_2 Efflux	NO_3^-	0.40	0.25
Net Soil CO_2 Efflux	NH_4^+	0.23	0.51

*ABI represents change in aboveground live carbon in trees, $ANPP_{tree}$ represents aboveground net primary productivity C in trees, and % moisture refers to gravimetric soil moisture.

3.5. Carbon Pools

Whole plot C pool estimates, measured in all 44 plots (Table 1), demonstrated a single weak but significant positive relationship with species richness for the five most dominant species, but interestingly total C pool values were not significantly related to H' or D diversity indices (Table 2). When C pools in trees, DWD, and snags were examined independently (Table 1), only tree C was found to have a positive relationship (albeit a weak relationship; $r^2 = 0.18$; $P = 0.004$) with richness of the five most dominant species (Table 2). All other relationships among these C pools and richness, H' and D were non-significant ($P > 0.05$; Table 2). In all but two cases, relationships between tree, DWD, snag and plot C pools and % stand dominance by any single species were also not significant (Table 2). Snag C pools were significantly (albeit weakly) positively related to % dominance by *P. menziesii*, and total plot C was negatively (and very weakly) related to % dominance by *A. rubra* indicating the slight trend for *A. rubra*-dominated plots to have lower biomass C.

4. Discussion

4.1. Carbon Flux and Diversity

Our data suggest mild positive relationships among both C uptake (measured in aboveground biomass increment (ABI), and tree aboveground net primary productivity ($ANPP_{tree}$)) and C release from soils with multiple indices of naturally occurring forest diversity. These findings are important for several reasons: (1) These data suggest positive relationships between productivity and diversity in a relatively homogeneous natural system [4,26,33]; (2) natural forest ecosystems may exhibit patterns in productivity-diversity relationships similar to previous grassland studies (e.g., [26]) even when far fewer species are dominant (5 in the current study *vs.* 16+ in experimental grassland studies); (3) these findings support a productivity-diversity relationship suggested by a recent analysis at the regional scale [4], and may potentially suggest that other regional analyses between productivity and diversity (e.g., [16]) may reflect diversity influences on productivity in addition to site productivity influences on tree diversity; and (4) that more productive forests may also release more C from soils. This last finding is especially important since it demonstrates another side of biodiversity-ecosystem function relationships, where more diverse systems may also release more C back into the atmosphere via belowground autotrophic respiration and decomposition processes (see Litton *et al.* [17] and Johnson *et al.* [49]).

4.2. Productivity-Diversity Relationships

Our results generally suggest increased productivity was associated with increases in overstory diversity. Both measures of aboveground productivity (ABI and $ANPP_{tree}$) generally increased with increases in richness and diversity. While the highest regression coefficients came from relationships with richness and C flux (Figure 2), our model selection analysis indicated that this result may be indistinguishable from relationships with diversity indices such as Shannon's H' and Simpson's D (Table 3–5). These findings show concordance among results related to species richness and indices where both species richness and evenness are taken into account (H' and D). Though regression coefficients were generally not strong, any factor in a complex forest system that accounts for between one third to half of ecosystem carbon flux should be acknowledged.

Other studies in forested and non-forested ecosystems have suggested positive relationships between ecosystem productivity and richness of primary producers at the site level, and a curvilinear relationship when measurements are compared across sites of variable quality [16, 25-28]. However, recent analyses of data spanning forests of the PNW, USA suggest that despite major differences in site characteristics, there is a general increase in productivity along species diversity gradients [4]. Earlier studies have also found correlations across continental scales between forest productivity and diversity [29]. Our data suggest that when larger regional variation in site quality is absent (*i.e.*, with similar climate, relief, topography, parent material, soils, and time since disturbance in our ~400 ha site), productivity-diversity relationships are still apparent. Such findings are important because they demonstrate that patterns from more experimental systems (e.g., experimental grassland systems) may have relevance for natural forested ecosystems.

Additionally, our data suggest that it is possible to detect productivity-diversity relationships on a scale with relatively few species. While a six-species plot is locally diverse in a region characterized by forests dominated by single species (e.g. *P. menziesii*), this value for species richness is much lower than the 16 species mixtures common to previous grassland studies (e.g., reviewed in Loreau *et al.* [21]), and forests where previous forest diversity research has been conducted [16,30]. However, even in a gradient that ranges from one to six species, mild positive relationships between productivity and diversity were apparent in our study.

4.3. Possible Mechanisms Explaining Productivity-Diversity Relationships

It has been hypothesized that ecological niche complementarity (where intra-specific differences allow for complementary use of resources, [26]) provides one mechanism where higher productivity at higher diversity levels may occur due to an over-yielding effect [28]. An alternative mechanism suggests higher productivity in higher diversity plots could be explained by "sampling effect" [32], where there is a greater chance of a highly productive species being present in plots with greater species richness. Our data provide observational evidence that complementarity is more likely than sampling effects in our system. We were able to detect weak significant relationships between most species and the productivity index ABI. However, all significant relationships were negative, suggesting that as plots become dominated by a single species they generally became less productive. Thus, contrary to the expectations of sampling phenomena leading to a higher probability of including a hyper-productive species at high diversity levels, we found that plots were less productive as single-species dominance increased, even when observed through the lens of single potentially productive species.

Such a finding is highlighted by our results for *A. rubra.* Because of its N-fixing association with *Frankia* sp., *A. rubra* could drive productivity by increasing N availability. Nevertheless, we found no relationship between *A. rubra* and plot productivity ($P > 0.05$; Table 2). *A. rubra* was also not found to be our most productive species despite N-fixing traits (data not shown), and *A. rubra* presence consistently produced poorly-ranked predictive models compared to diversity metrics. Although our results in this respect are somewhat surprising, previous studies have found that *A. rubra* presence only leads to increased productivity in N-limited systems (e.g., [44]). Interestingly, measures of inorganic N pools were similarly non-effective in predicting C flux variation. It is possible that measures of N-mineralization may be more predictive of productivity than inorganic N pools. We also did not find any correlation between *A. rubra* presence and soil NO_3^- or NH_4^+. *A. rubra* may not have been a vital species determining C flux if N is not limiting. It is important to note that our one-time measures of NO_3^- and NH_4^+ do not necessarily reflect N-availability, since N-availability is best measured as N-mineralization over time rather than a one-time pool. Mechanistically, despite high volumetric presence in stands they dominate, declines in plot C in *A. rubra*-dominated stands (Table 2) might be due to its species-specific density, which is one of the lowest among five dominant tree species. The high N content of *A. rubra* might also encourage rapid vegetative decomposition and C release. We did not find any correlations, however, between inorganic soil N pools and soil CO_2 efflux. If high vegetative N is driving patterns in decomposition and soil CO_2 efflux, it does not necessarily result in high inorganic N soils.

Hyper-productive species combinations and consistent changes in plot composition could also be responsible for apparent relationships between productivity and diversity. For example, if a predictable combination of productive species dominate at high species richness values, a change in species composition, not diversity, might drive productivity. In our study, however, species were relatively haphazardly distributed among plots in richness categories (Figure 5). For example, *P. menziesii*, a dominant conifer, was represented by plots with high *P. menziesii* biomass across all richness categories (Figure 5). This species was especially prominent in our highest tree richness (6 species) plot, and interestingly this plot also had lower plot C than many of the 5-species plots with more even representation of species (Table 1). Similarly, a model containing biomass distribution of all species individually and a model based on community similarity, were both far less predictive than diversity models in our model selection analysis (Table 3–5). Thus, it seems unlikely that a few species or a predictable species combination drives our patterns.

4.4. Net Soil CO2 Efflux and Stand Diversity

Soil CO_2 efflux is an important ecosystem process governing the return transfer to the atmosphere of roughly half of all C taken up by plants, and thus variation in this process due to tree diversity has widespread local and global implications. Our data suggest the potential that, in addition to higher C uptake, more diverse forests may also have higher rates of C release from soils. Soil CO_2 efflux was significantly related to all indices of overstory diversity, and was not driven by the inclusion of any single overstory species, community similarity, or soil nutrient pools. Since more than half of soil CO_2 efflux can be attributable to tree root respiration [64,65], these data suggest that a combination of heterotrophic and autotrophic responses in more diverse stands could lead to higher soil CO_2 release. While our sample size was small and our regression coefficients were not always strong, our data compare favorably to measured rates of soil CO_2 efflux from soils in other systems [66], and our data may show reduced variation since each plot was sub-sampled in four locations and averaged for every plot measurement.

Recent experimental work with grasslands species has shown that soil CO_2 efflux was driven by plant community composition rather than diversity [49]. Other research has only rarely addressed soil CO_2 efflux responses to plant species richness, and both positive [67,68] and non-significant effects [69] have been found. Nevertheless, in forested systems, responses of soil CO_2 efflux to overstory diversity are not well-understood. Our data suggest that in PNW forests, significant relationships between soil CO_2 efflux and diversity may exist and are worthy of further investigation. Further, lack of a relationship between dominance of any single species or community composition and soil CO_2 efflux may be suggestive of complementarity effects [26]. From a phenological perspective this makes sense because soil CO_2 efflux can be driven by autotrophic respiration [70], and tree species have long been understood to have variable and complimentary phenologies of root production [71]. Thus, for measures such as soil CO_2 efflux that require continuous measurement throughout growing and non-growing seasons, complementarity in phenology may ensure continuity of tree root respiration and inputs to the soil microbial community realized as higher annual respiration. We did find interesting declines in soil CO_2 efflux associated with *A. rubra* dominance, and this could be indicative of reduced C allocation belowground in an N-rich species. Our work

documents patterns in naturally occurring systems which is a rare but important approach in biodiversity-ecosystem function research [33].

4.5. Carbon Pools

While our sites represented a large range in C pool values for trees, snags, and DWD (Table 1), we found few interesting relationships between forest tree diversity and total accumulated aboveground C pools (Table 2). These results could suggest that although aboveground C flux inputs can be generally higher in more diverse forests, C efflux out of the system, for example soil CO_2 efflux, may counter higher C inputs resulting in relatively similar C pools. More productive species and species combinations may decay faster, and result in reduced C pools. Since our study did not holistically address the causes of the lack of relationship between diversity and C storage, these data highlight the need for future C flux research across diversity gradients which integrates C flux into and out of ecosystems above- and belowground.

4.6. Assumptions and Error

We made several assumptions in our methods which could be sources of error in our data, but are likely to wield a small effect on the magnitude of our measurements. For example, biomass estimates based on small diameter plots are likely to produce large variance due to the impact of rare large diameter trees, especially in mixed-age stands. This phenomenon might explain why we do not find any relationships between diversity and total C stock in our plots. Nevertheless, this may be less-problematic in our study as the forest is even aged. Additionally, while the assumption that all saplings had a DBA of 2.5 cm may be a source of error in calculation of plot C pool estimates, sapling abundance contributed minimally to whole plot C estimates (<0.05%). The biomass equation for *A. rubra* was substituted for the species *S. scouleriana*, *F. purshiana* C. *cornuta, C. nuttalli,* and *I. aquifolium* as these species did not have an available biomass equation on the BIOPAK database. While these substitutions may be also be source of error in our study, these trees consist of less than 4% of the total number of tagged trees and contributed less than 0.12% of total tree biomass, so their contribution to plot C pools and fluxes are minimal. Finally, it should be noted that our study design generated results that are correlative only, and so should be interpreted with caution.

5. Conclusion

Overall, our data demonstrate the significant potential for future studies testing predictable biodiversity-ecosystem function relationships in second-growth temperate forests. These data suggest: (1) more diverse overstories could also be more productive; (2) such relationships might not be predicable based on the dominance of any single species; and (3) biodiversity-ecosystem function relationships may also extend to soil CO_2 efflux, where we found higher CO_2 release with a more diverse overstory. Thus 70 years following a clear-cut, more diverse overstories were mildly more productive, but also released more C back to the atmosphere, potentially helping explain the lack of correlation between tree diversity and C pools.

Acknowledgements

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