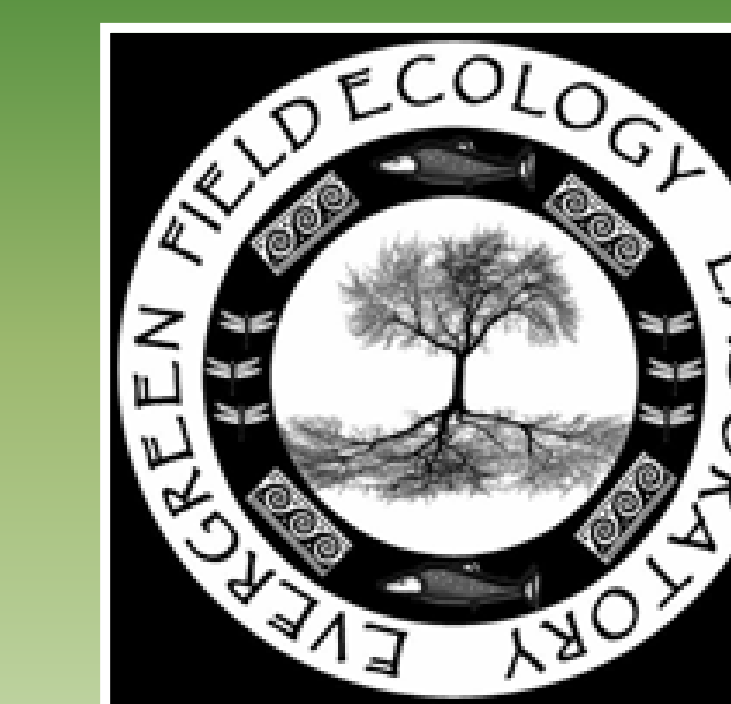


Pacific Northwest Second-Growth Forest Carbon Dynamics and Tree Diversity

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ABSTRACT

In order to determine patterns in carbon (C) storage and flux rates in a Pacific Northwest second-growth forest, we assess variability in tree above-ground net primary productivity (ANPP - litterfall=ANPP_{tree}), net soil CO₂ efflux (NCER) and understory community in relation to diversity of multiple coniferous, deciduous, and a nitrogen (N) fixing tree species (*Alnus rubra*). Four major findings arose from our study: 1) We find a positive linear relationship between ANPP_{tree} and tree species richness, where overstory richness explained 35% of ANPP_{tree} ($r^2=0.35$, $P=0.005$; **Figure 2**); 2) There was no significant difference in mean ANPP_{tree} among stands dominated by multiple evergreen, deciduous, and an N-fixing tree species ($P=0.18$). Generally, trends suggested decreases in ANPP_{tree} with biomass stand dominance for 4 of the 5 most abundant tree species (**Figure 3**). Presence of the soil modifying *A. rubra* had no significant effect on ANPP_{tree}, NCER, or above-ground C stocks ($P>0.05$; **Figure 4**); 3) We find a positive relationship between average growing-season NCER (April-October) and ANPP_{tree} ($r^2=0.75$, $P<0.05$). Additionally, stands with higher overstory richness typically had higher NCER ($r^2=0.71$, $P=0.0015$; **Figure 5**). Other indices of diversity were also predictive of NCER, where more diverse stands typically had higher NCER (**Figure 5**). 4) Variation in overstory stand dominance was not only mildly predictive of understory plant community composition ($r^2=0.1073$, $P<0.001$) (**Figure 6**). Understory plant diversity was unrelated to ANPP_{tree}, above-ground C stocks, and NCER using species richness ($P>0.05$), Shannon's ($P>0.05$) or Simpson's ($P>0.05$) diversity measures. These data highlight variability in second-growth forests that may have strong implications for net ecosystem productivity (NEP). We estimate ANPP_{tree} at 7.75 Mg C ha⁻¹ yr⁻¹. This and other plot level measurements imply NEP between ~ 5 and 2 Mg C ha⁻¹ yr⁻¹ at our lowland second growth forest site.

STUDY AREA AND METHODS

This study was conducted in the Lowland Puget Sound, Washington, USA; (**Figure 1A**). The ecosystem is a second-growth temperate rain forest receiving more than 1 meter of annual rainfall with an average annual temperature of ~10°C (TESC weather station; <http://rails.evergreen.edu/weather/>).

Data was collected from the Evergreen Ecological Observation Network (EEON; **Figure 1**), a long-term permanent plot network located throughout a 380 ha forest reserve owned and managed by the Evergreen State College.

The EEON is series of 44, 20 m diameter permanent forest monitoring plots located on a randomized grid approximately 250 meters apart (sample plot **Figure 1**)

44 plots were used to estimate above-ground C stocks and understory community composition. A subset of 21 plots were used to estimate ANPP_{tree}. Another subset of 11 plots were used to measure annual litterfall and NCER.

ANPP_{tree} was estimated using one year of tree height measurements (2007), and measurements tree diameter (1.4m ht; DBH) over two years (2006 & 2008). Tree biomass was estimated using independent allometric relationships based on DBH for all species (Means et al. 1994). Differences in tree biomass over time were summed for each plot. 50% of above-ground biomass was assumed to be C (*sensu* Harmon et al. 2005). Litterfall was included for estimates of ANPP.

NCER 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 subplots per plot, 5 minute measurements were taken monthly for a full year. Measurements were taken between 10:00-16:00 hrs for consistent measurement within daily temperature and moisture regimes.

Leaf litter was collected monthly using litter collection traps from 2006-2007. Leaf litter was used to better estimate ANPP (see **Figure 2**)

Understory vegetation was measured using a transect sampling method where 10 meter transects were run from plot center in 4 cardinal directions. All plant species <5cm in stem diameter were recorded every 10cm along transects using point line intercepts.

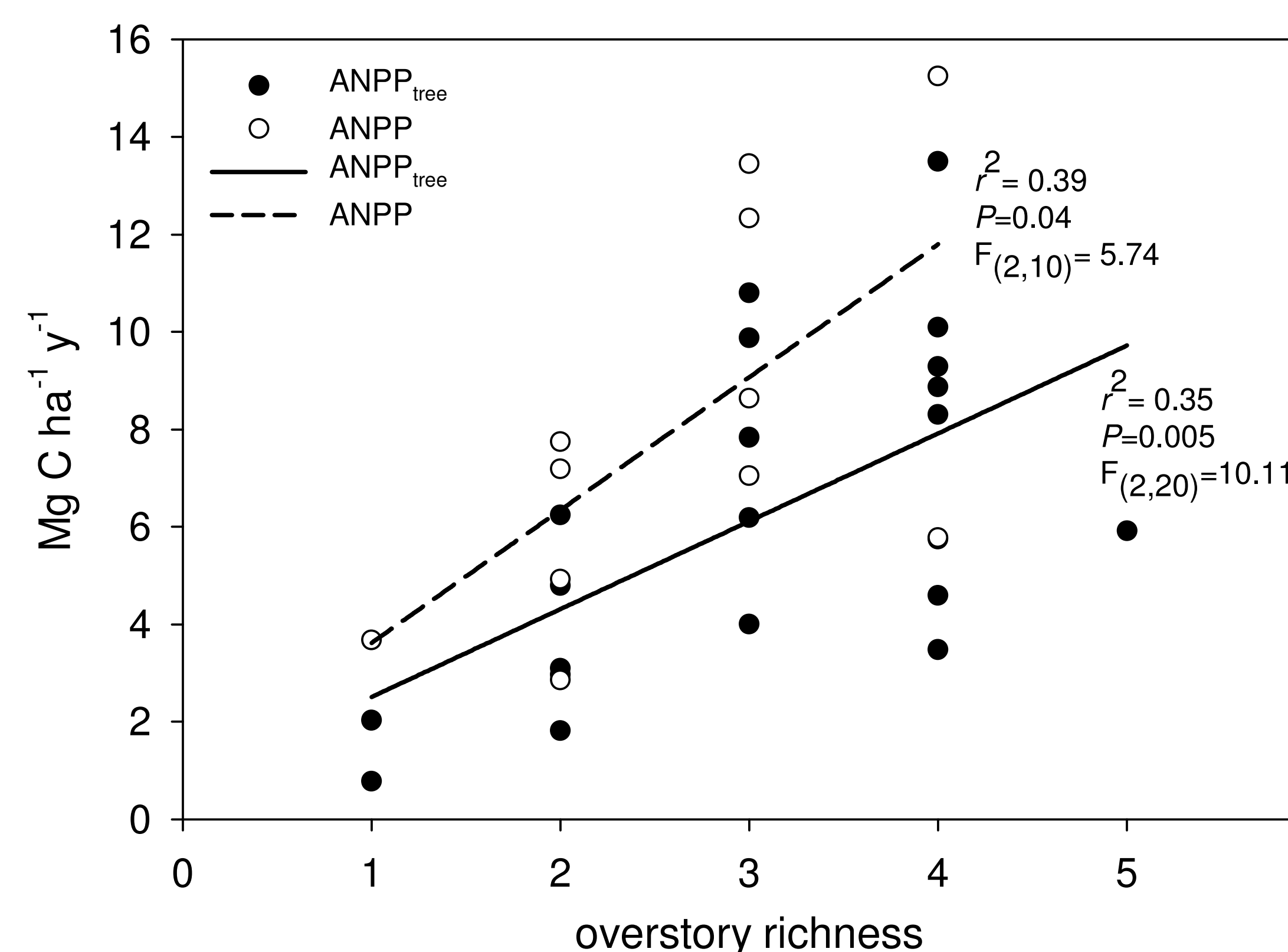


Figure 2. Positive relationships between overstory richness and estimated ANPP and ANPP_{tree}. ANPP_{tree} represents the net change in standing tree biomass C averaged between 2006 and 2008. Aboveground Net Primary Productivity estimates are better represented by ANPP, which also includes annual litterfall C from 0.5 m diameter litter buckets placed at the center of a subset of 11 plots. Richness is for the 5 most dominant species sampled; *Pseudotsuga menziesii*, *Acer macrophyllum*, *Alnus rubra*, *Tsuga heterophylla*, and *Thuja plicata*. These 5 species are also represented in **Figure 3**.

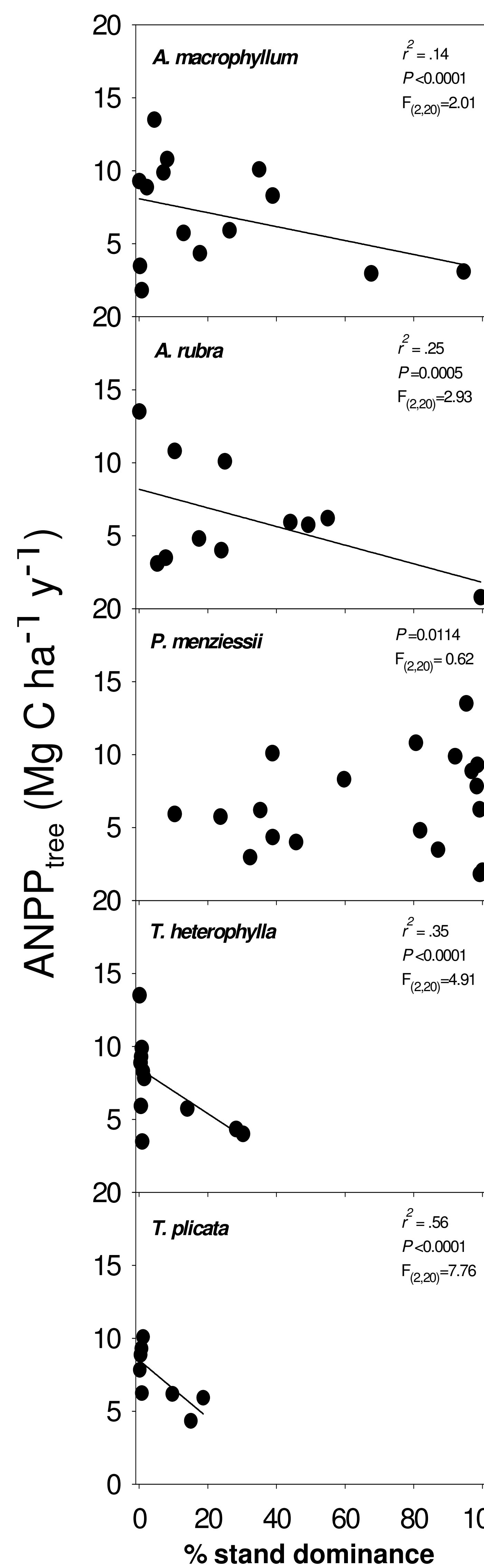


Figure 3. Influence of tree species biomass stand dominance on tree productivity (ANPP_{tree}; ANPP excluding litterfall). The 5 most abundant tree species are represented. Data is only included for plots where each species was present.



Site Photos. Permanent plot photos (2006) demonstrating variability in stand conditions. Photos from left to right show a typical deciduous-dominated stand with *Acer macrophyllum* and *Alnus rubra*, a typical *Pseudotsuga menziesii* dominated stand, and a mixed stand with very productive *P. menziesii* in the foreground. Mixed stands have a tendency to be more productive at our study site.

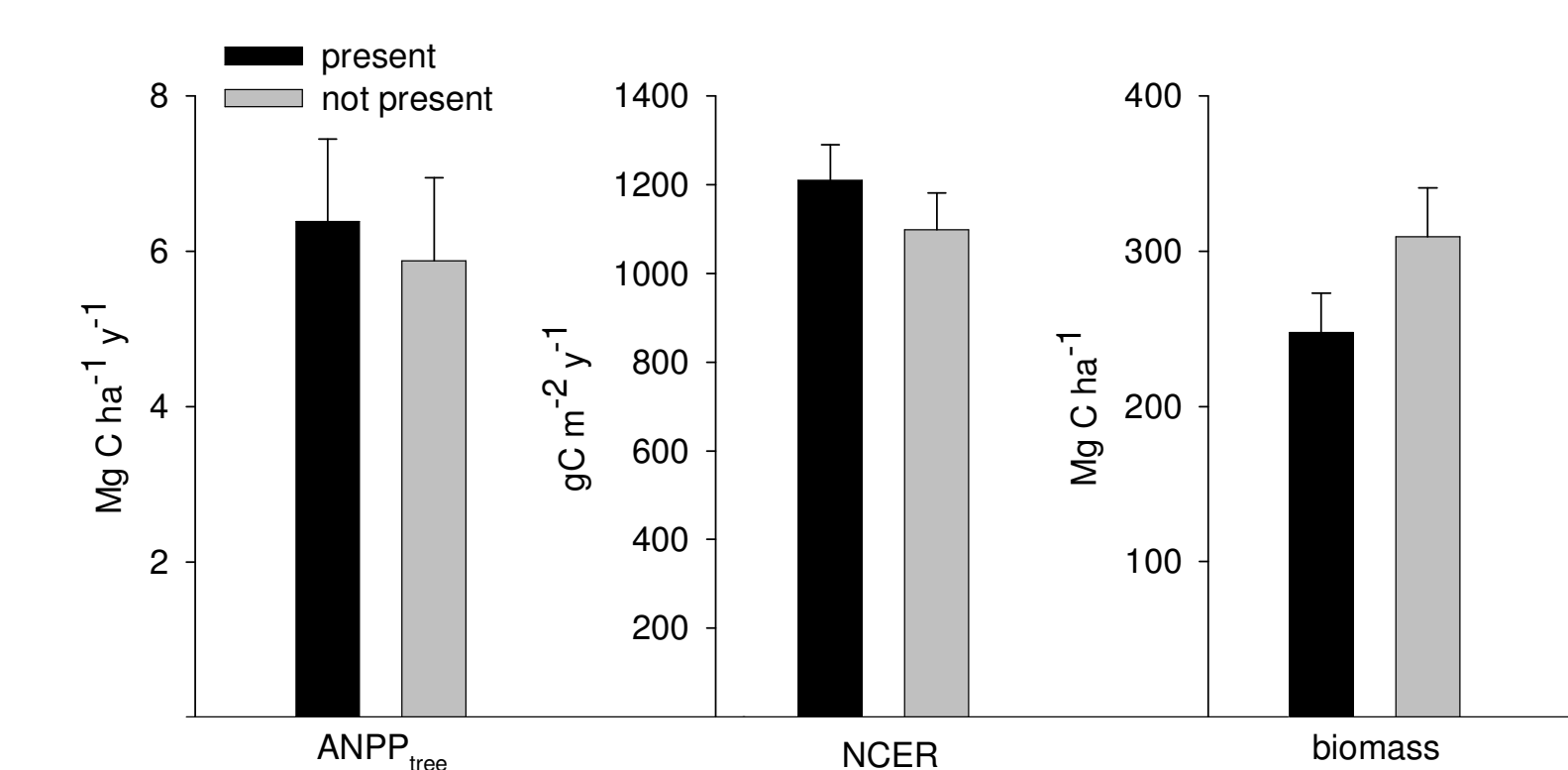


Figure 4. Carbon flux and pools between stands with the N-fixing tree *Alnus rubra* (light grey bars) and without (black bars). We found no significant differences between stands with and without *A. rubra* in estimated aboveground net primary productivity (ANPP_{tree}), Net soil CO₂ efflux (NCER) or changes in above-ground C stocks.

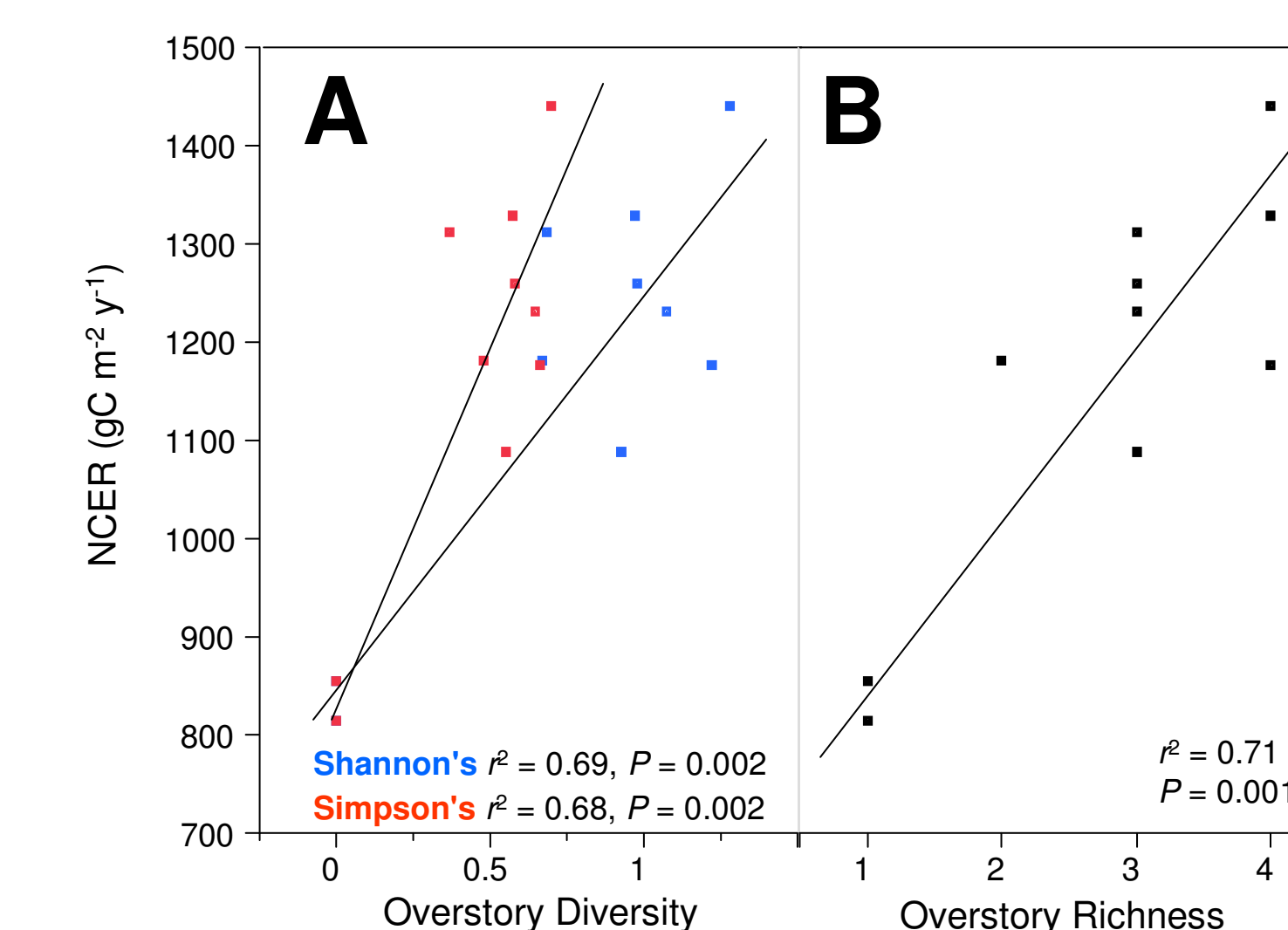


Figure 5. Positive relationships between NCER and overstory diversity represented by Shannon's and Simpson's diversity indices (A), and overstory richness (B). Here the 5 most abundant tree species are represented.

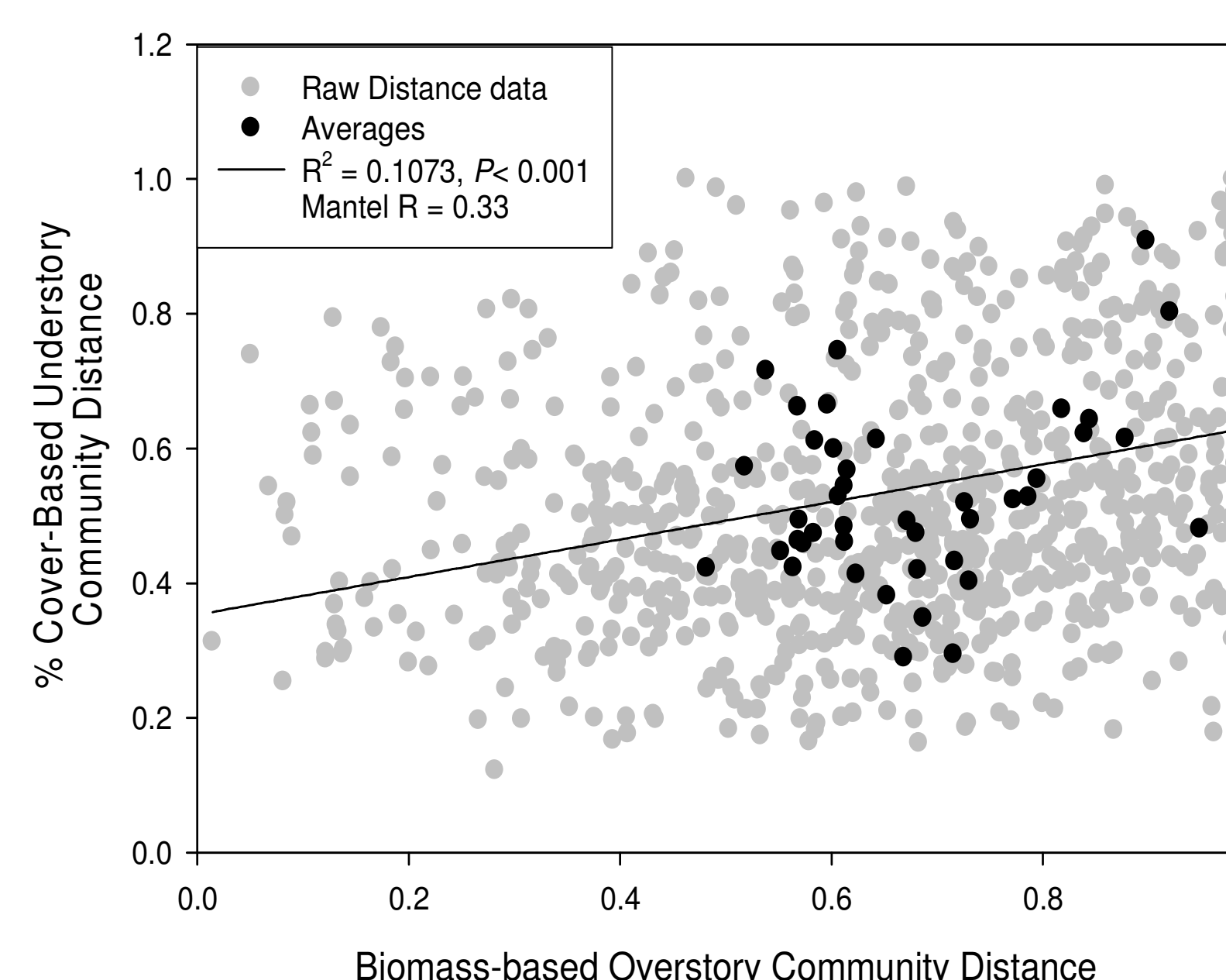


Figure 6. Mantel analysis of understory and overstory community relatedness. Gray points represent all pair wise comparisons, and the line is fit to the mean distances (black points) for ease of presentation. A mild relationship is shown between overstory biomass and understory community matrices. The x-axis is community distance of biomass-based overstory species data for all plots, while the y-axis is community distance in % cover of all understory species in all plots.

KEY FINDINGS

Overstory richness ANPP_{tree} and ANPP were positively related (**Figure 2**), suggesting more diverse forests may take up more carbon

Biomass-based stand dominance was negatively related to ANPP_{tree} in four of the five major overstory species (**Figure 3**), which suggests increases in ANPP_{tree} may not be driven by key hyper-abundant tree species.

ANPP_{tree}, NCER, and above-ground C stocks were not significantly different among stands dominated by N-fixing species, i.e. *A. rubra* (**Figure 4**), suggesting N fixation alone is not enough to describe significant variability in ANPP_{tree}

Both overstory diversity and richness were strongly predictive of NCER (**Figure 5**)

Understory diversity was not predictive of any measure of carbon flux or pool included in this study ($P > 0.05$).

Biomass-based overstory community profiles were unrelated to understory community profiles (**Figure 6**)

Conifer and hardwood dominated plots were not significantly different in terms of estimated ANPP_{tree} ($P=0.08$), NCER ($P>0.05$), or total above-ground C stocks ($P>0.05$). However, conifer dominated plots tended to be higher in estimated ANPP_{tree}, NCER, and above-ground C stocks.

We estimate over-all average ANPP_{tree} of 7.75 Tons C ha⁻¹ yr⁻¹ from 2006-08, and estimate C storage of ~354 tons ha⁻¹

IMPLICATIONS AND FUTURE RESEARCH

More diverse forests may also be more productive, and sequester more carbon.

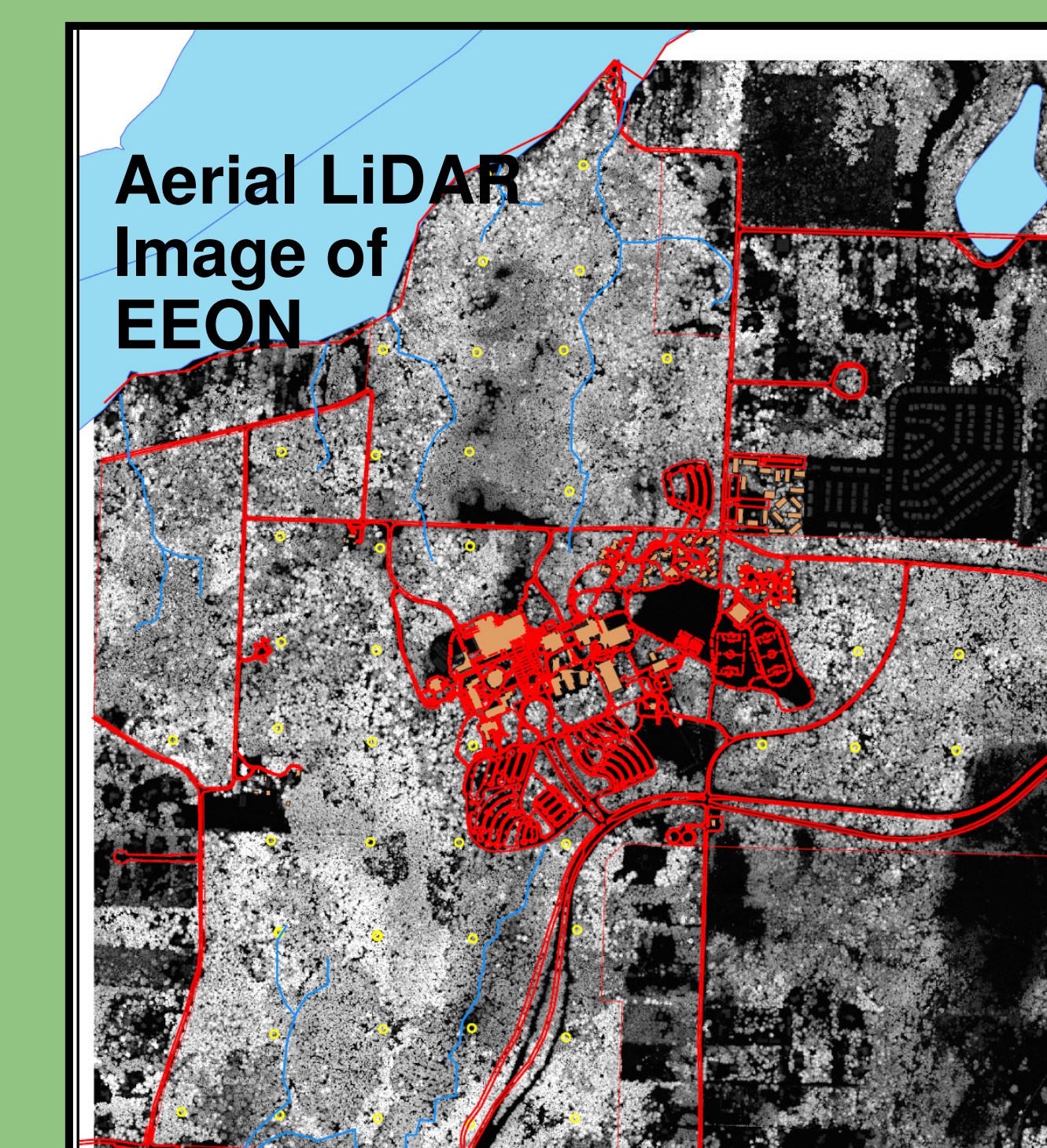
Significant variation in ANPP exists within this second-growth forest, suggesting minor changes in forest composition, environmental variables, and topography can have big implications for forest carbon uptake

These estimates of ANPP provide a baseline for estimation of carbon sequestration in local PNW forests

- Future work will incorporate:
 - > Belowground NPP (fine root productivity)
 - > Evaluating differences in N availability
 - > Measurement of leaf litter layer, FWD, soil, and humus layer C stocks

We are currently working with high resolution imagery, Aerial LiDAR, and ground-based LiDAR to integrate our C measurements with remotely sensed data.

We are experimenting with litter addition to base of trees to test influence litter on C flux



Acknowledgements

This work was made possible by the Evergreen Field Ecology Lab Group, the academic programs IES - 2005/6, IES 2006/7, Field Ecology, and Temperate Rainforests 2007. For field and lab support we also thank Alison Styring, Paul Przybylowicz, Carri LeRoy, Rob Cole, Jora Rehm-Lorber, Kyle Galloway, Pat Babbitt, Josh Brann, Jordan Erickson, Don Loft, Margaret Pryor, Casey Broderick, and Lindsey Wright. Financial support has been provided by the Evergreen State College Foundation, Evergreen Sponsored Research, The Evergreen Fund for Innovation, and Microsoft Corporation.

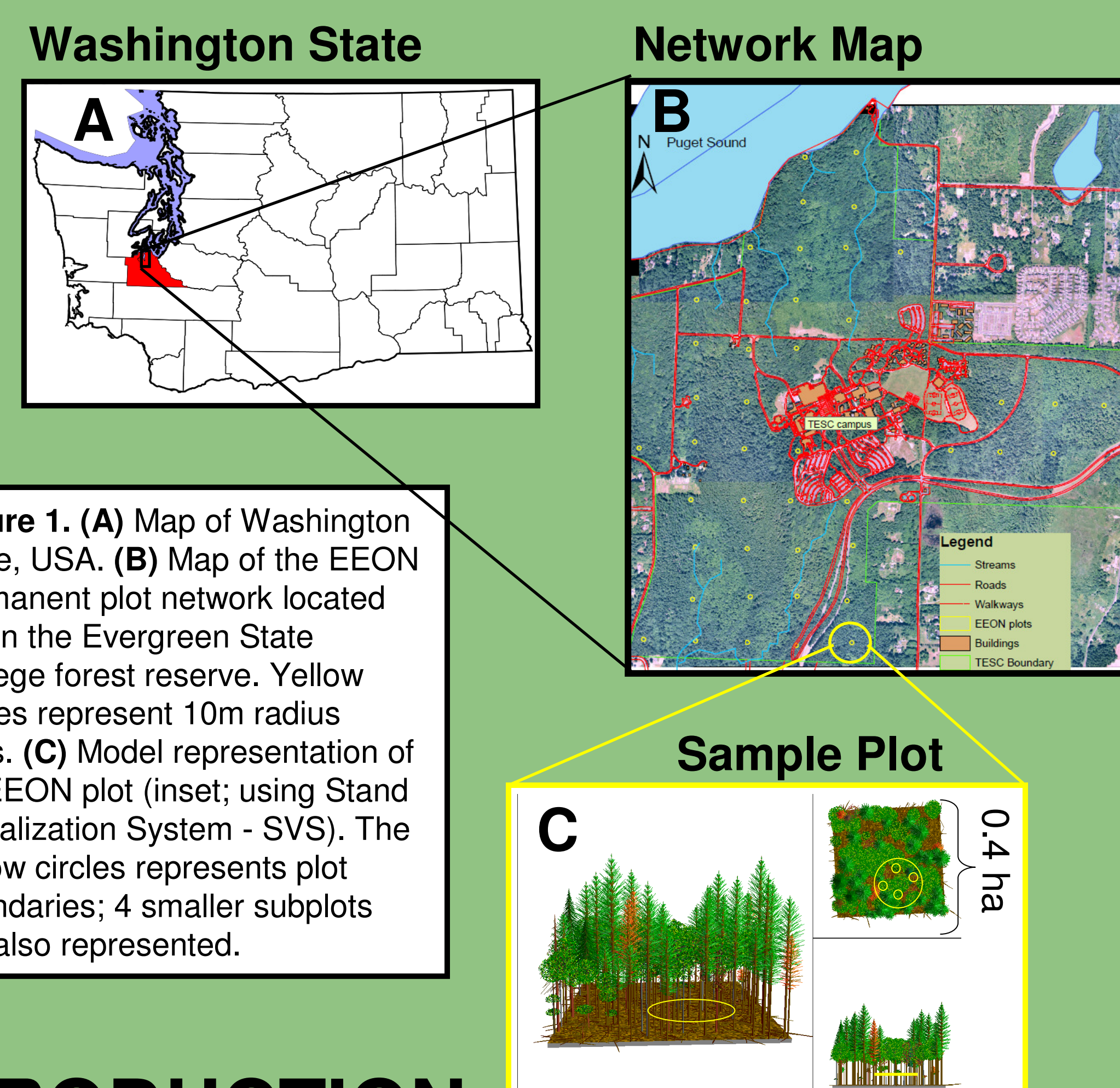


Figure 1. (A) Map of Washington State, USA. (B) Map of the EEON permanent plot network located within the Evergreen State College forest reserve. Yellow circles represent 10m radius plots. (C) Model representation of an EEON plot (inset; using Stand Visualization System - SVS). The yellow circles represent plot boundaries; 4 smaller subplots are also represented.

INTRODUCTION

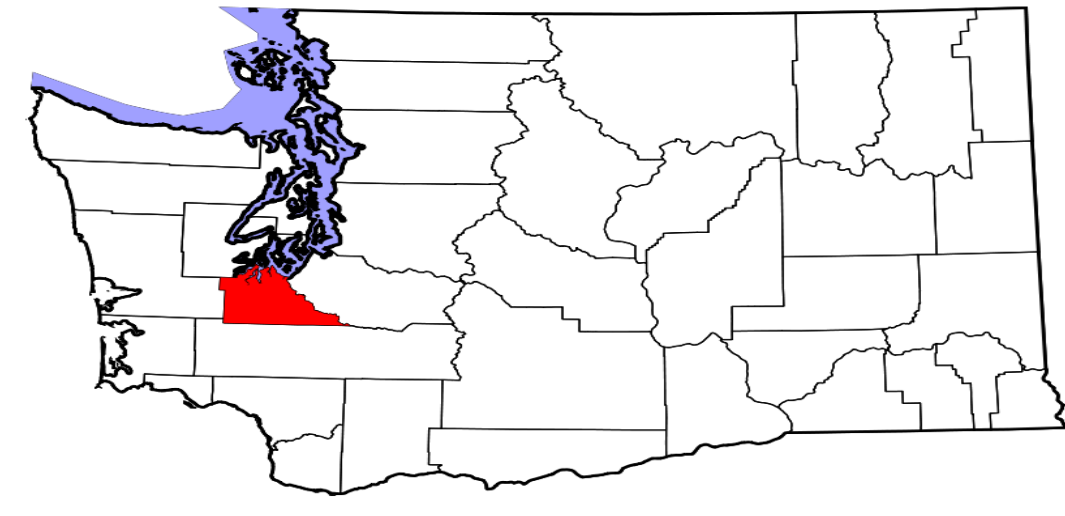
Terrestrial forest ecosystems can represent a major carbon sink and may even account for missing C in global budgeting (Keeling et al. 1996, Fan et al. 1998, Carey et al. 2001, Giardina et al. 2005).

Studying productivity and carbon cycling in previously disturbed and second-growth habitats has become particularly important as fewer terrestrial ecosystems remain undisturbed.

Other experiments (esp. in grassland and marine systems) suggest a positive relationship between ecosystem productivity and species diversity (Naeem et al. 1994, Tilman et al. 1996, 2001, Hector et al. 1999)

Finally, key dominant plant species can play a major role in determining the productivity of ecosystems (Ellison et al. 2005). Species differences in functional traits can be important as drivers of ecosystem productivity and are well recognized as important controls on processes (Scott and Binkley 1997, Binkley and Menyailo 2005).

Our primary goal was to identify biological determinants of variation in productivity and C uptake in a second-growth forest ecosystem.



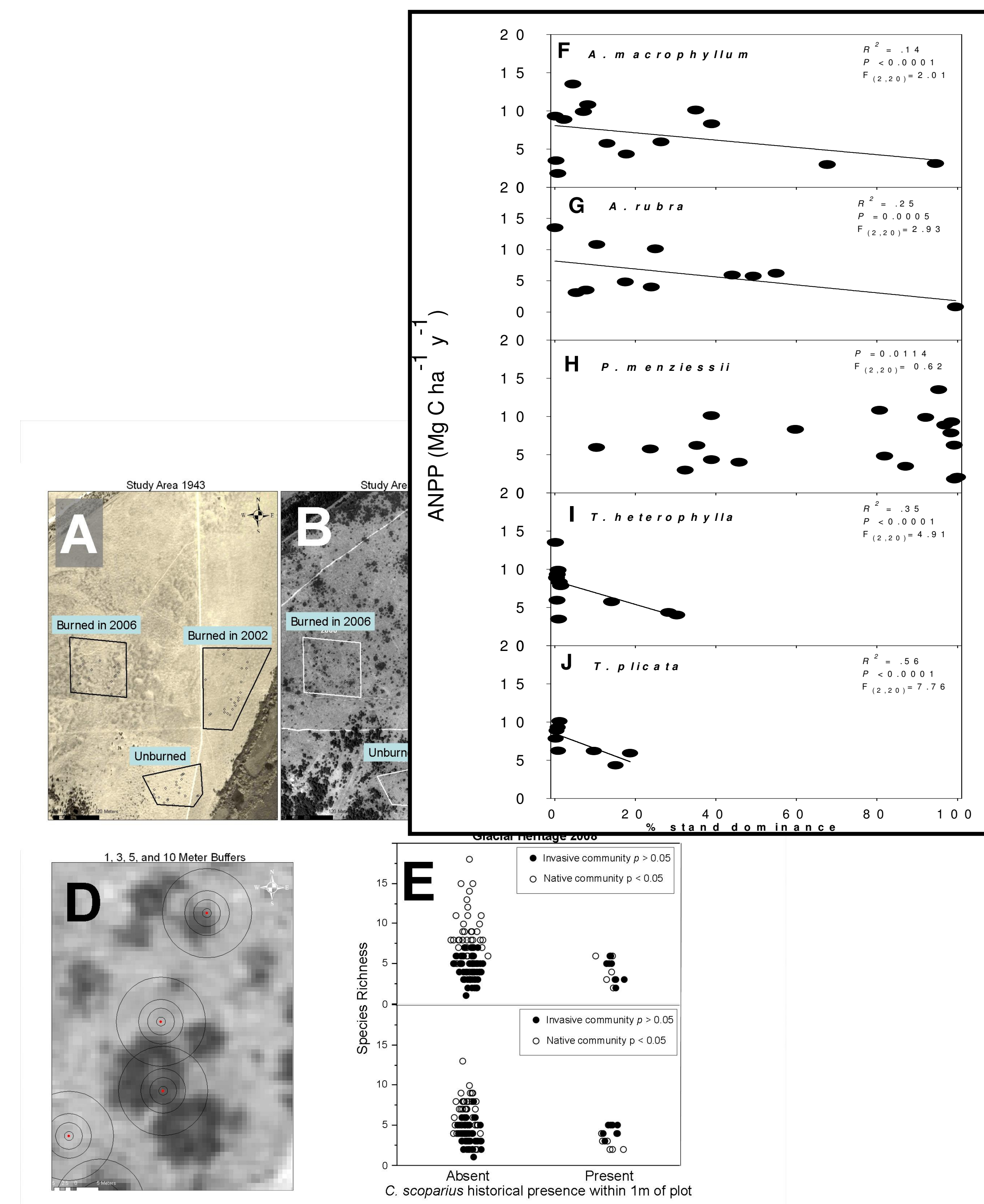


Figure 4. Aerial photography of glacial outwash study area showing early prairie conditions (A; 1943), invasion by *C. scoparius* (B; 1996; dark grey vegetation), and post restoration of vegetation physiognomy (C, 2006). Polygons show study areas with burn treatments in different years and vegetation plots (circles). Panel D shows individual plots (center of circles) with buffers to demonstrate analysis of historical proximity to *C. scoparius* (dark gray) at multiple spatial scales. Finally, panel E shows analysis of native and invasive plant species richness within 1 m of historic *C. scoparius*, compared to plots where the shrub was not present. *Cytisus scoparius* occupation has a legacy effect on plant communities that suppresses the native community. We hypothesize that this effect is due to changes in soil N associated with N-fixation by *C. scoparius*. All data and maps are from curriculum-integrated undergraduate student research.

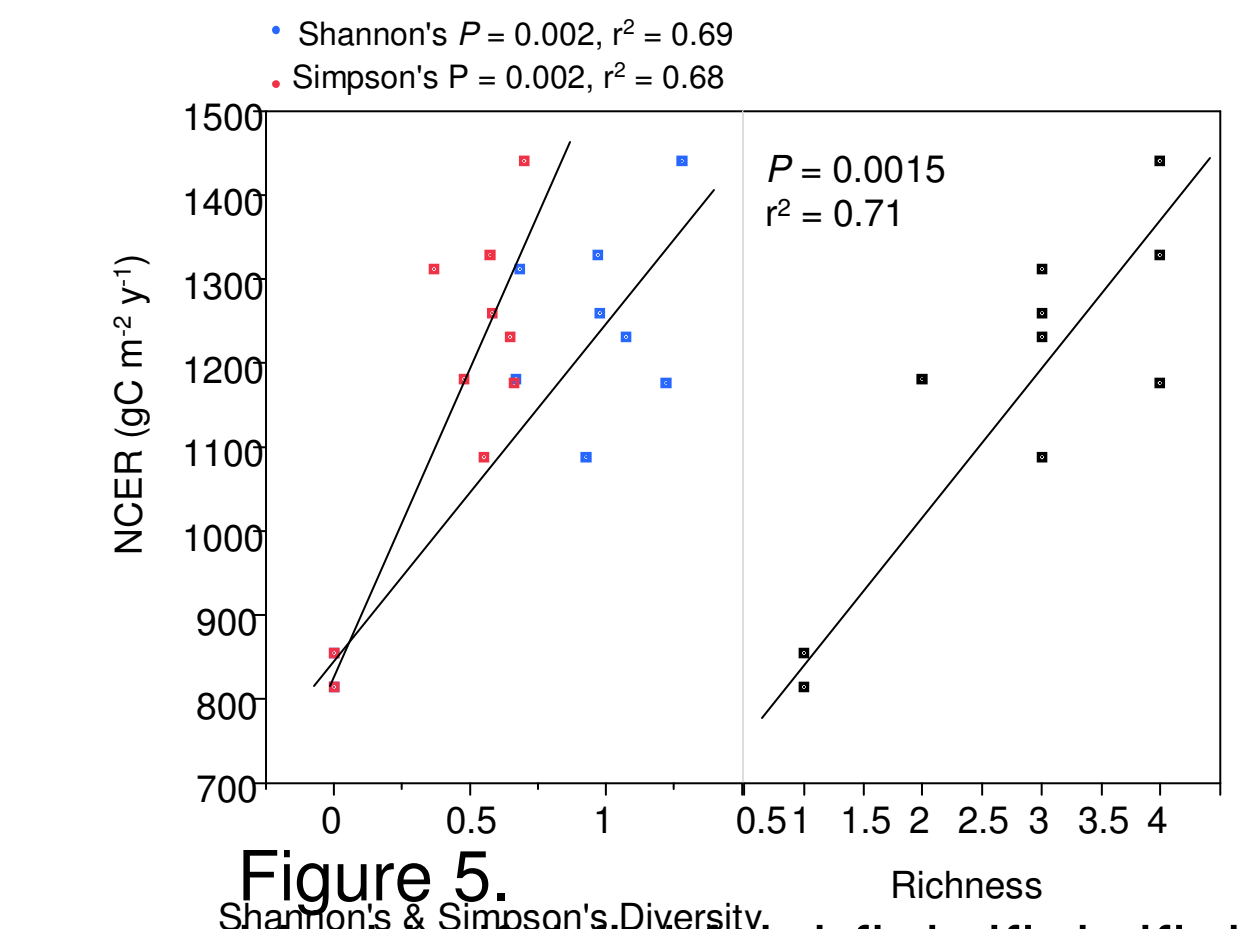
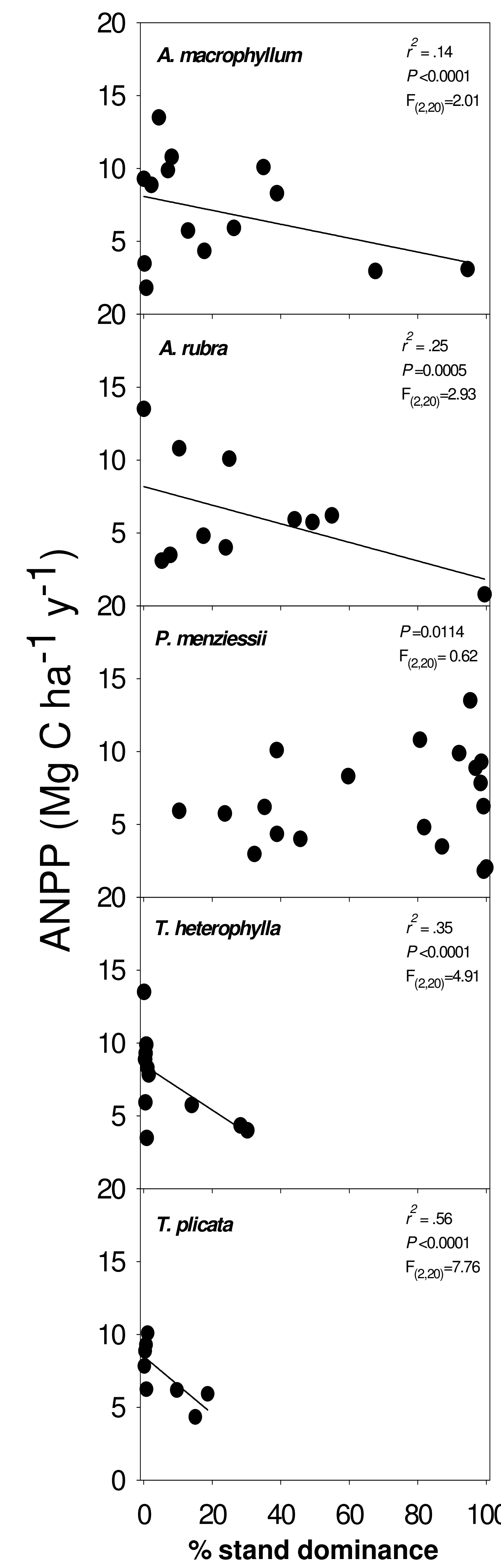
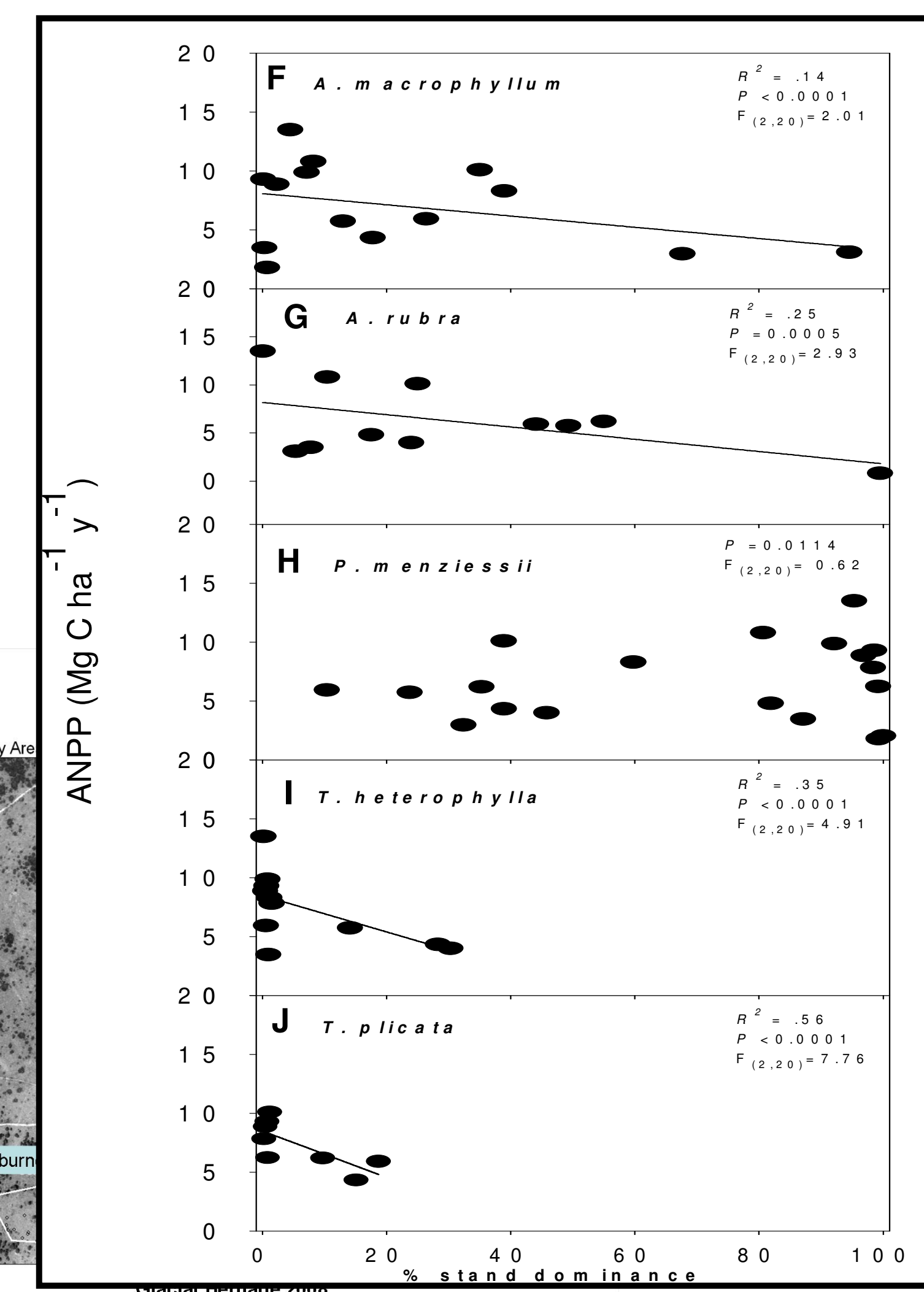


Figure 5. Shannon's P = 0.002, r² = 0.69
Simpson's P = 0.002, r² = 0.68
P = 0.0015
r² = 0.71

ABSTRACT

In order to determine patterns in carbon (C) storage and flux rates in a Pacific Northwest second-growth forest, we assess variability in 1)



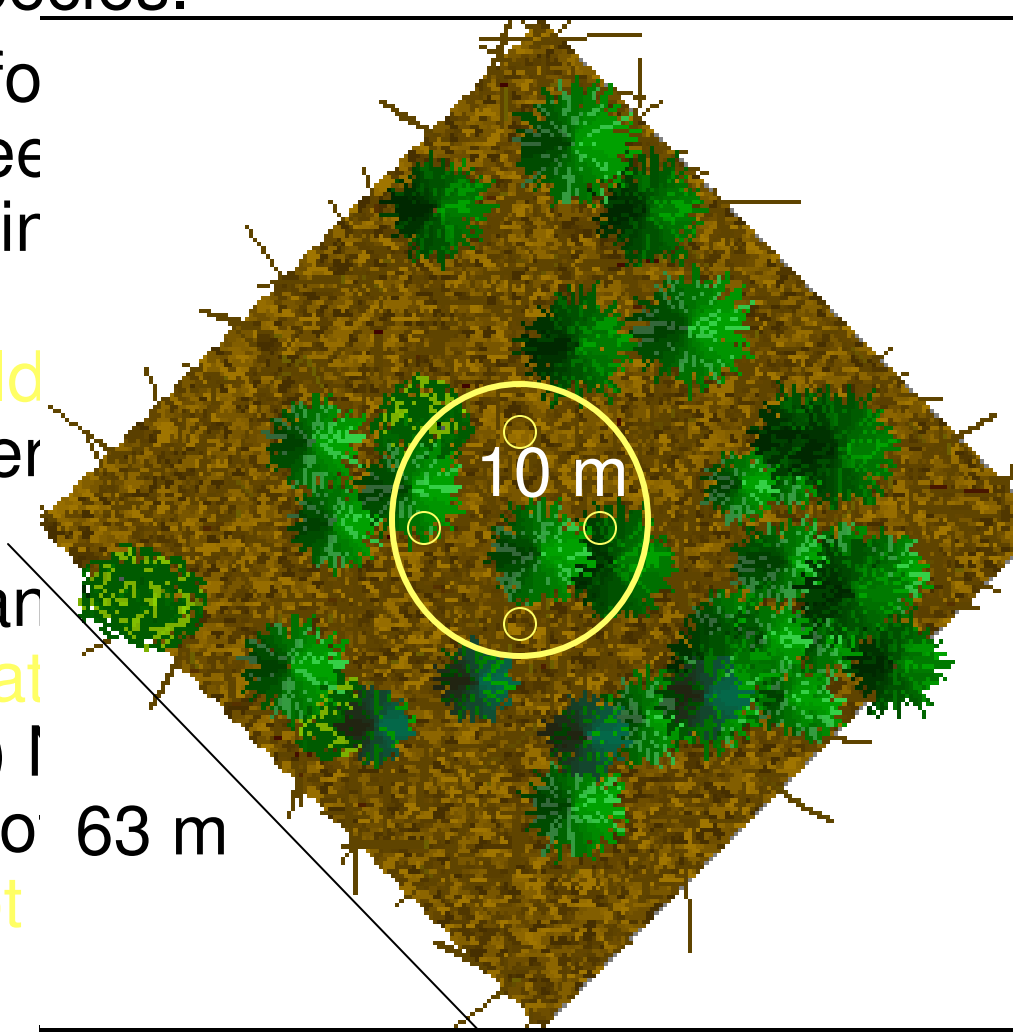
ABSTRACT

In order to determine patterns in carbon (C) storage and flux rates in a Pacific Northwest second-growth forest, we assess variability in 1) Above-ground net primary productivity (ANPP); 2) Net soil CO₂ efflux (NCER) in relation to presence of coniferous, deciduous, and nitrogen (N) fixing tree species and understory species.

Four major findings arose from our study: 1) We found a positive linear relationship between ANPP and tree species richness, where overstory richness explained 35% of NPP ($r^2=0.35$, $P<0.05$; **Figure 2**). 2)

MULTIPANEL. Mean ANPP was **ANOVA only mildly different** among stands dominated by multiple evergreen, deciduous, and an N-fixing tree species. Trends suggested decreases in ANPP with stand dominance by any single species. 3) We also find a **positive relationship between average growing-season (April-October) 1 and productivity ($r^2=0.75$, $P<0.05$)**, additionally plots with more tree species generally had higher NCER got ($r^2=0.30$, $P<0.05$); 4) Variation in overstory stand dominance was strongly predictive of understory plant community composition (**MRPP $P<0.05$**). Relationships between understory plant diversity and NCER were not significant for species richness ($P>0.05$), Shannon's ($P>0.05$) and Simpson's ($P>0.05$) diversity indices.

However, ANPP, net changes in C stocks, and understory plant communities were unrelated ($P>0.05$). These data highlight variability in second-growth forests that may have strong implications for net ecosystem productivity (NEP). We estimate NPP at 7.75 Mg C ha⁻¹ yr⁻¹, and suggest that this and other plot level measurements imply an upper bounds on NEP of ~3.7 Mg C ha⁻¹ yr⁻¹, and a lower bounds of ~2.7 Mg C ha⁻¹ yr⁻¹.



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