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Forest stand age and the occurrence of chanterelle (*Cantharellus*) species in Oregon's central Cascade Mountains

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ABSTRACT

We describe watershed-scale habitat associations of three *Cantharellus* species with respect to stand age. During the 1998 autumn fruiting season we collected chanterelle sporocarps from 18 forest stands in and adjacent to the H.J. Andrews experimental forest in the central Cascade Mountains of Oregon. Sampled stands represented two age categories: old growth (~350+ y) and 40–60-y-old second growth naturally regenerated from clear-cut harvest. Old growth and second growth stands were spatially paired to reduce the chance of spurious habitat relationships caused by unmeasured correlated variables. We found stand age to be a good predictor of the distribution of *C. subalbidus* and *C. formosus*, but only marginally useful for predicting the occurrence of *C. cascadensis*. The odds that a randomly located chanterelle sporocarp will be *C. subalbidus*, compared to other chanterelles, are 3–23.5 times higher in old growth than in second growth. Alternatively, there is only a 4–38 % chance that a randomly located sporocarp will be *C. formosus* in old growth. *C. cascadensis* was found to be uncommon throughout the study area and showed no significant habitat associations. The abundance of *C. cascadensis* increased substantially with decreasing elevation indicating that landscape features other than stand age may be more useful in predicting its occurrence.

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Introduction

Ectomycorrhizal (EM) fungi play a prominent role in forest community dynamics because they form vital mutualisms with forest trees (Smith & Read 1997). Although we have gained important new knowledge on EM fungal communities from sporocarp and root tip studies (Horton & Bruns 2001), our knowledge of actual habitat requirements for individual fungal species remains incomplete (Molina *et al.* 2001; Dreisbach *et al.* 2002). This lack of information makes it difficult to include fungi in land management plans where habitat attributes are maintained to ensure species persistence (USDA & USDI 1994).

The intimate link between EM fungi and their host associates (Molina *et al.* 1992; Smith & Read 1997), makes plant community composition an important factor for predicting EM species occurrence at regional scales. Within individual watersheds, forest stand age and various disturbance regimes influence the composition of EM communities (Molina *et al.* 1992; O'Dell *et al.* 1992; Vogt *et al.* 1992; Waters *et al.* 1997; Baar *et al.* 1999; Colgan *et al.* 1999; Taylor & Bruns 1999; Kranabetter *et al.* 2005). For example, fire is a primary disturbance

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mechanism in Pacific Northwest (PNW) forests (Morrison & Swanson 1990; Agee 1993) and several studies demonstrate its impact on EM communities (Horton *et al.* 1998; Jonsson *et al.* 1999; Dahlberg 2002; Smith *et al.* 2005). Similarly, disturbance associated with forest harvest can affect the local persistence of EM species (Pilz & Perry 1984; Amaranthus & Perry 1987; Jones *et al.* 2003). In Sweden, where 95 % of forests are used for commercial purposes (Berg *et al.* 1994), negative impacts of forest management practices are implicated in the high proportion of threatened macrofungi in spruce forests (Rydin *et al.* 1997; Arnolds 2001).

In the PNW, timber harvest over the last 50 y has significantly reduced the area and fragmented the distribution of old growth forests (Spies & Franklin 1988). As a result, forests previously dominated by old growth Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) have been converted to a mosaic of mature and old growth remnants in a matrix of younger, managed forest (Franklin & Forman 1987; Morrison 1988). Several ecological characteristics that distinguish old growth (~200–1000 y of age) forests from young forests include high photosynthetic productivity that is largely invested in respiration and maintenance rather than new growth, and high nutrient retention. These distinctive functional characteristics are correlated with a complex set of structural characteristics (diverse tree age and size, multi-layered canopies, and abundant dead wood) that also differentiate old growth from young forests (Franklin & Spies 1991). As a result old growth forests support a taxonomically diverse set of organisms, including many fungi (Smith *et al.* 2002), that may be restricted to this increasingly rare habitat (Lehmkuhl & Ruggiero 1991; Thomas *et al.* 1993).

Among species with suspected affinities to old growth habitats are some chanterelles in the genus *Cantharellus*, which are popular edible EM fungi both commercially and recreationally harvested from wild populations in the western USA (Danell 1999; Pilz *et al.* 2003; Pilz *et al.* 2006). Timber harvests have been reduced on Federal lands over the last decade and concurrently the demand for non-timber forest products has increased. As a result, chanterelles (primarily *C. formosus*; Redhead *et al.* 1997) have become one of the most widely collected edible mushrooms taken from PNW forests (Pilz & Molina 2002). Because chanterelle species are both economically and ecologically important in the PNW region, forest managers desire information about habitat preferences of each species.

During the autumn of 1997, we conducted genetic studies to determine the size of chanterelle genets (individual mycelial networks) and to assess whether variation in genet size is related to forest disturbance (Dunham *et al.* 2003a). The species under study were not evenly distributed across the sampled disturbance treatments. A recently described species, *C. cascadensis* (Dunham *et al.* 2003b), along with *C. subalbidus* primarily occurred on old growth (OG) plots, whereas *C. formosus* dominated second growth (SG) plots. In this study we expanded sampling of OG and SG stands to the watershed scale to characterize the relative abundances and habitat associations of the Pacific golden chanterelle (*C. formosus*), white chanterelle (*C. subalbidus*), and a recently described species (*C. cascadensis*), in old growth and second growth forests.

Methods

Study areas

The H. J. Andrews Experimental Forest (HJA; lat. 44°15′N, long. 122°10′W) is a 6400 ha watershed that has been administered as a long-term ecological research site on the Willamette National Forest since 1948 (Franklin *et al.* 1990). Elevations within the HJA range from 420–1630 m and the area is typical of the central portion of the western Cascade range in Oregon (Franklin *et al.* 1990). About 90 % of the annual precipitation falls from October to April with the wettest period in December and driest conditions occurring in July.

Within the HJA, seven OG stands (350+ y old) with no history of recent fire and seven SG stands naturally regenerated from clear cuts (1950–1960) were selected based on their accessibility and spatial arrangement. Two additional pairs of OG and SG stands were selected in the Mill Creek area that lies along the southeast boundary of the HJA. To reduce the chance of spurious habitat associations caused by unmeasured habitat variables (slope, aspect, elevation, etc.) each OG stand was spatially paired with a nearby SG stand. Stands selected for this study ranged from 420–1100 m in elevation, had north, south, southwest, or southeast aspects, and ranged from 20–35 % in average slope. To avoid the confounding affects of additional EM host species (e.g., Pacific silver fir, *Abies amabilis*), we selected only stands dominated by Douglas fir and western hemlock. All stands fall within the western hemlock community type patterns of Franklin (1979) with understory vascular plants including *Polystichum munitum*/*Oxalis oregana* in wet sites, *Berberis nervosa*/*Rhododendron macrophyllum* in mesic sites, *Berberis nervosa*/*Gautheria shallon* in drier sites, and *Linnaea borealis* in cooler, drier sites. The post cutting history of Mill Creek SG stands are not well documented, but the forest zone (Franklin & Dyrness 1973) and habitat associations (Franklin 1979) are similar to the HJA.

Field sampling methods

Collecting began two weeks after the first substantial autumn rain in October of 1998 and ended when the first winter snows covered the area in December. Two individuals searched in each stand for a total of 1.5 h once in October and once in November and data from these two time periods were pooled for analysis. Within each stand, random sampling was initiated by walking to a tree for which the ground at the base was not visible from the road used to access the site. Randomly compass bearings selected at this initial point and at each chanterelle sporocarp collection location were used to direct a continuous series of 150–200 m transects. If a random compass bearing directed a collector out of the stand either the reverse azimuth was followed or a completely new random bearing was selected. Second growth stands ranged from 10–20 ha in total area and the area searched within larger old growth stands roughly approximated this range. When chanterelle sporocarps were located within visual range, a minimum of 5 m (approximate genet size, Dunham *et al.* 2003a) was kept between any two collections to avoid re-sampling genets. Each collection location was flagged to avoid re-sampling genets encountered by the two collectors at different times within a sampling effort or during the November collection period. Genetic samples were taken from each sporocarp collected and the species identification confirmed using molecular genetic techniques and vouchers collected during previous studies (Dunham *et al.* 2003a, b).

Molecular methods

DNA extraction and PCR amplifications of the ITS region were carried out using standard methods described in Dunham *et al.* (2003a, b). According to the manufacturer's recommendations (GIBCO BRL, Grand Island, NY), unpurified PCR products amplified with ITS1-F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990) were digested separately with two restriction enzymes (*Hinf*I and *Hae*III) known to differentiate the three species of interest (Dunham *et al.* 2003b).

Statistical analysis

Two-dimensional Chi-square analysis was used to determine if the frequency of chanterelle occurrence in the two stand age categories (i.e., OG & SG) was dependent on species identity. The habitat responses of individual species were determined using paired *t*-test analysis of abundance data with individual stands as replicates. To better characterize the strength of chanterelle habitat association, binomial logistic regression (Allison 1999) was used to test if, relative to two other species, the odds of occurrence for each species is equal in OG and SG. The LOGISTIC procedure available in SAS v.9.1 (SAS Institute Inc.; Allison 1999) was used to estimate intercept and slope parameters for three binary logit models with each equation corresponding to a comparison between the species of interest and all other collections. For example, we used a single binary analysis that included *Cantharellus subalbidus versus C. formosus* and *C. cascadensis* combined as alternate response levels to model the relative odds of randomly encountering each species in OG habitat. Drop-in deviance *F*-tests were used to test the significance of regression slopes that were used to calculate the relative odds of the three chanterelle species occurring in OG stands. Stand location was included as an additional categorical predictive variable in initial regression models to test whether model predictions were equal across the study area.

Results

Distribution and abundance of chanterelle species

A total of 596 chanterelle sporocarps were collected across the 18 OG and SG stands during the autumn fruiting seasons of 1998 (Table 1). Using RFLP analysis we detected only the three genotypes expected from the three species of interest, *Cantharellus formosus*, *C. subalbidus*, and *C. cascadensis*. The overall Chi-square analysis showed that stand age was strongly associated with the identity of species found in stands ($\chi^2 = 144.85$, $df = 2$, $P < 0.0001$). *C. formosus* and *C. subalbidus* occurred in stands across the entire study area with *C. formosus* significantly associated with SG stands ($t = -2.82$, $df = 8$, $P = 0.023$; Table 1) and infrequent or not detected in OG stands. The reverse was true for *C. subalbidus,* which was significantly associated with OG stands ($t = 4.35$, $df = 8$, $P = 0.003$; Table 1) and infrequent or not detected in SG stands. The total number of *C. cascadensis* collections was lower compared with *C. formosus* and *C. subalbidus* but still adequate for analyses. The distribution of *C. cascadensis* collections was patchy across the study area and its occurrence within stands not associated with stand age ($t = -0.05$, $df = 8$, $P = 0.96$; Table 1).

Stand location had no significant influence in the binary logit models. In other words, the location of paired OG and SG stands did not affect the response (species). However, *C. cascadensis* was not found in four SG and two OG stands and 26 of 34 *C. cascadensis* SG collections were taken from a single SG stand in the Mill Creek area (Table 1). This stand has the lowest elevation (426 m) of all the stands sampled. An OG stand, also in the Mill Creek area, with the second lowest elevation (490 m) had the second highest abundance of *C. cascadensis* with 12 collections. All other stands sampled were 600 m or higher in elevation and contained eight or fewer *C. cascadensis* collections (Table 1, Fig 1). It appears that elevation may be associated with the distribution of *C. cascadensis*, but because elevation was not a factor of interest in the design of this study, it was not sampled well enough to include it as an explanatory variable in logistic regression analyses. To better understand the distribution of this species in stands above 600 m, and independently to examine the influence of stands located below 600 m, we repeated all analyses both with and without stands with mean elevations below 600 m. This did not change the overall results of the Chi-square and paired *t*-test analyses, but it did dramatically decrease the *P*-value associated with the *C. cascadensis* comparison ($t = 1.99$, $df = 6$, $P = 0.09$; Table 1) indicating that stand age may weakly influence the distribution of this species at higher elevations.

Strength of habitat associations

Intercept and slope parameters for the logistic regression analyses were estimated for both the data sets including all stands and excluding stands below 600 m (Table 2). When all the observations are considered, *Cantharellus subalbidus* was more likely to occur in OG stands relative to *C. formosus* and *C. cascadensis* ($P = 0.0006$). Conversely, *C. formosus* was more likely to occur in SG relative to *C. subalbidus* and *C. cascadensis* ($P = 0.002$). The likelihood that a randomly located sporocarp will be *C. subalbidus* (*versus C. cascadensis* or *C. formosus*) is 3–23.5 (95 % CI, $P = 0.0006$) times higher when that sporocarp is found in OG than in SG (Table 2).

When stands with mean elevations below 600 m are deleted from the analysis the strong habitat associations of *C. subalbidus* (OG) and *C. formosus* (SG) remain statistically significant with only minor shifts in the 95 % confidence intervals for the odds ratios (Table 2). The comparisons between *C. cascadensis* and the other two species are similar to the *t*-test results with non-significant results in the overall analysis that move toward a marginal OG association when only stands above 600 m are analysed ($P = 0.98$ and 0.18, respectively).

Table 1 – Abundances (sporocarp number) of the three chanterelle species pooled across 18 stands

Age	*Cantharellus cascadensis* (*n*=67; 16)	Mean Difference[a] (95 % CI)	*Cantharellus formosus* (*n*=281; 227)	Mean Difference[a] (95 % CI)	*Cantharellus subalbidus* (*n*=248; 217)	Mean Difference[a] (95 % CI)
Old growth (all data)	33 (11.3 %)	−0.1	68 (23.4 %)	−15.0	190 (65.3 %)	14.7
Second growth (all data)	34 (11.1 %)	(−5.6, 5.4)	213 (69.8 %)	(−27.3, −2.7)	58 (19.1 %)	(6.9, 22.5)
Old growth (600 m+)	13 (5.4 %)	1.4	62 (26.0 %)	−13.3	164 (68.6 %)	15.9
Second growth (600 m+)	3 (1.0 %)	(−0.3, 3.2)	165 (75.0 %)	(−26.1, −0.5)	53 (24 %)	(5.5, 26.2)

In the three abundance columns, the values represent the abundance for that species followed by the percentage of the total sporocarps found at that age class and elevation (shown in parentheses). The first two rows show results for the entire data set and the second two rows (600 m+) show data from stands above 600 m in elevation.

[a] The mean of the differences in abundance (OG−SG) across all stand pairs and the associated 95 % confidence interval around this mean difference.

Discussion

Long-term species persistence is dependent on both the size and geographic distributions of populations (Rabinowitz 1981; Rey Benayas *et al.* 1999). For EM fungi, these population characteristics are dependent on the status of small and large-scale landscape habitat characteristics. Here we describe the habitat associations of three chanterelle species with respect to stand age. At the watershed scale where stands of 10–20 ha are the sampling units, stand age is a good predictor of the distribution of *Cantharellus subalbidus* and *C. formosus*, but is only marginally important for *C. cascadensis*. Other patterns not captured by this study may explain the distribution of *C. cascadensis* better. Our sampling scale was too coarse to tease out the biological processes that control the presence of species within stands, but clearly stand age and possibly elevation are correlated with the spatial arrangement of finer scale habitat variables important to chanterelle species. A logical extension of this work would be to study the fine scale soil and host tree characteristics that control the distribution of each species within stands (e.g., Bergemann & Largent 2000; Trappe 2004).

The SG stands that we selected are the youngest where abundant chanterelle fruiting is common (S. Dunham, pers. obs.) and the OG stands are some of the oldest and least disturbed sites on the HJA. PNW forest ecosystems are complex and the treatment categories used here (OG and SG) encompass multiple ecological characteristics. We can speculate on potential causal factors, but more research is needed to characterize species distributions in the broad range of intermediate age classes.

Cantharellus subalbidus

Our results demonstrate that the probability of locating *Cantharellus subalbidus* fruit bodies increases significantly in OG habitats. On the HJA, OG surrounds all sampled SG stands creating a habitat mosaic that would maximize the chances of *C. subalbidus* colonizing SG stands as they matured. The reduced odds of finding *C. subalbidus* in SG indicate that they did not persist following logging and that biological, physical or chemical characteristics of the soil or competition from other newly establishing species are limiting its re-establishment in young stands. Alternatively, *C. subalbidus* may be able to establish mycelia in young stands, but subsequently experience suppressed fruiting until OG characteristics begin to develop. Characteristic features of OG forests include the abundance of coarse woody debris in all stages of decay, uneven aged trees, gaps and uneven soil surface caused by large uprooted trees (Spies *et al.* 1988; Spies & Franklin 1989; 1991).

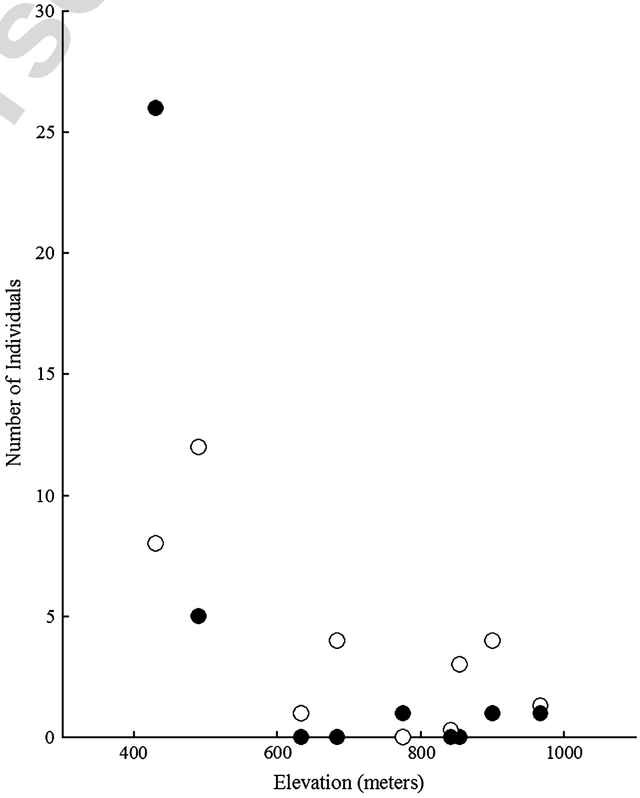

Fig 1 – Number of *Cantharellus cascadensis* collections plotted against the mean elevation of the paired old growth and second growth stands where collections were made. Open circles represent old growth collections and closed circles represent second growth collections. At two elevations equal abundances are represented by overlapping filled and open circles.

Table 2 – Parameter estimates for the relationship between species type (response) and stand age using three binary logit models

Estimate	*Cantharellus cascadensis* All data; above 600 m	*Cantharellus subalbidus* All data; above 600 m	*Cantharellus formosus* All data; above 600 m
Intercept	−2.06; −3.51	−1.45; −1.32	0.84; 1.15
Standard error	0.62; 0.69	0.40; 0.41	0.38; 0.37
95 % CI[a]	−3.53, −1.01; −5.24, −2.38	−2.31, −0.72; −2.19, −0.58	0.13, 1.63; 0.46, 1.93
Stand age	0.019; 1.09	2.08; 2.01	−2.03; −2.24
Standard error	0.88; 0.82	0.52; 0.54	0.57; 0.52
95 % CI	−1.80, 1.82; −0.42, 2.97	1.10, 3.16; 0.98, 3.13	−3.19, −0.96; −3.32, −1.25
P-value[b]	$F_{1,16}=0.00$; $F_{1,14}=1.97$ $p = 0.98$; $p = 0.18$	$F_{1,16}=18.26$; $F_{1,14}=15.49$ $p = 0.0006$; $p = 0.002$	$F_{1,16}=14.59$; $F_{1,14}=21.10$ $p = 0.002$; $p = 0.0004$
Odds ratio	1.02; 2.97	8.00; 7.46	0.13; 0.11
95 % CI	0.17, 6.17; 0.66, 19.49	3.00, 23.57; 2.66, 22.87	0.04, 0.38; 0.04, 0.29

In each column the second set of values are parameter estimates from analyses where stands below 600 m in elevation were not included.

a Maximum likelihood ratio estimates.

b From drop in deviance likelihood ratio tests.

The importance of coarse woody debris in predicting the occurrence of threatened macrofungi in late successional conifer forests in Europe has been demonstrated (Berg *et al.* 1994; Rydin *et al.* 1997). Wide confidence intervals for the odds ratio characterizing the association between *C. subalbidus* and OG may result from the retention of coarse woody debris in SG stands allowing for patchy development of pre-harvest soil conditions required by this species.

The PNW region has been an important supplier to the world timber market (Waddell *et al.* 1989). Clear-cut harvesting and subsequent even-aged forest management has been practised on private lands for well over a century (Robbins 1988) and on federal lands since the 1940s (Harris 1984). During the past few decades, rotation lengths on public lands have generally been in the range of 80–100 y, while private landowners generally cut on rotation lengths of 50 y (Spies *et al.* 1994). This intense forest harvest activity has resulted in profound alterations in the age structure of the forest environment since extensive logging began (Wallin *et al.* 1996). Estimates of the percentage of old growth forests >200 y old remaining from pre-logging time periods range from 13.1 % (Spies & Franklin 1988; Booth 1991) to 17.5 % (Haynes 1986). Depending on the minimum stand age at which the OG characteristics necessary for the establishment and fruiting of *C. subalbidus* develop, the conversion of PNW forests from OG to SG may have significantly reduced the distribution of *C. subalbidus* in the western Cascades.

This assertion depends on how representative the HJA is of the western Cascades as a whole. The HJA is representative of the winter climate of the northern Cascades and of the PNW in general (Greenland 1994) and has been included in an enormous amount of basic and applied research used in the development of forest management plans for the region (Cissel *et al.* 1999). If these results can be extended to other areas, *C. subalbidus* has likely been largely excluded from private lands with short cutting rotations and possibly also from large portions of public lands if 80–100 y rotation cycles are not long enough for it to establish and maintain viable populations. *C. subalbidus* was also listed under the survey and manage guidelines of the Northwest Forest Plan (USDA & USDI 1994) that were intended to protect rare, little-known species associated with late-successional (OG) forests. Our results confirm the strong association of *C. subalbidus* with late-successional forests, thus verifying original assumptions made by experts who developed the plan. Future research on this species should be directed towards identifying factors that limit its distribution and determining if appropriate conditions for its establishment and persistence develop as SG stands continue to mature beyond 50 y.

Cantharellus formosus

Analyses presented here indicate that *Cantharellus formosus* is strongly associated with 40–60-y-old SG habitats so the large-scale harvesting disturbance that has taken place throughout the PNW probably has increased the distribution of this species. Given the proximity of our sampled SG stands to OG, it is likely that *C. formosus* is adapted to soils altered by disturbance or to physiological differences associated with younger host trees. Buried coarse woody debris has been identified as a factor important to the ecology of *C. formosus* (Largent & Sime 1994; Norvell *et al.* 1996) but in our OG soils this was not a limiting resource. Conversely, quantitative work completed by Bergemann & Largent (2000) demonstrated that above-ground coarse woody debris is not a significant predictor of *C. formosus* occurrence. Instead, the percent cover of bare humus unoccupied by moss, moderate duff depth, and low exchangeable acidity, were found to be useful variables for predicting *C. formosus* fruiting (Bergemann & Largent 2000) on small study plots.

Disturbances associated with forest harvest usually result in a loss of soil spatial heterogeneity (Miller & Lodge 1997) that can alter many soil characteristics important to EM fungi (Harvey *et al.* 1980a, b; Pilz & Perry 1984; Amaranthus & Perry 1987). After such a major disturbance, stress tolerance can allow some fungal species to replace others that are less tolerant (Lodge & Cantrell 1995). Fungi that are favoured by disturbance generally exhibit effective dispersal, rapid nutrient uptake, and rapid mycelial extension for capturing nutrients and water (Pugh & Boddy 1988). The age at which stands regenerating from clear-cut harvest are colonized by *C. formosus* is unclear because the fungus may establish the EM symbiosis with young trees early on but delay fruiting until the stand is somewhat recovered from the initial disturbance. Future research on this species should be directed at exploring conditions favourable to both host tree colonization and the onset of fruiting to determine if there is a significant time lag between the two events.

Cantharellus cascadensis

Uneven abundances and the patchy distribution of *Cantharellus cascadensis* across the study area make characterization of its habitat associations difficult given our study design. However, the spatial pairing of stands has allowed us to detect a confounding variable possibly associated with the distribution of *C. cascadensis*. It is possible that environmental variables correlated with stand age have some weak control over the distribution of *C. cascadensis* but this relationship is not constant over the range of elevation we sampled as the size of *C. cascadensis* populations increased substantially at elevations below 600 m. It was clear from this sampling that *C. cascadensis* is uncommon in the study area relative to other chanterelles and much survey work still is required to fully understand its distribution in Oregon. This analysis indicates that future survey work should focus on lower elevation habitats.

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