Species Structure, Diversity, and Tree Regeneration on Stumps in Second-Growth Temperate Rainforests of British Columbia, Canada

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Research

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Abstract

Background: The significance of stumps and other coarse woody debris (CWD) in maintaining biodiversity has been widely recognized. However, there is a paucity of research on the role of stumps in tree regeneration. We studied vascular plant structure, diversity, and tree regeneration on stumps in temperate rainforests across three sites in British Columbia, Canada (Malcom Knapp Research Forest, MKRF; Pacific Spirit Regional Park, PSRP; and Stanley Park, SP).

Results: 1) There were 19 vascular plant species found on stumps, including eight tree species, 2) Overall seedling abundance was higher on stumps than the nearby ground, 3) The number of established plants showed a positive linear (MKRF, SP) or Gaussian (PSRP) relationship with stump basal diameter, 4) Vegetation abundance varied with site (MKRF > SP > PSRP), 5) The overall species established on stumps were positively associated in MKRF (Variance ratio = 2.74) and SP (Variance ratio = 1.37), but negatively associated in PSRP (Variance ratio = 0.57), and 6) Tree species appeared to compete with each other on stumps and were likely to co-occur with understorey species.

Conclusion: Our results highlight community and species associations on stumps. We found that stump diameter is a major factor affecting tree regeneration in these second-growth temperate rainforests. To aid future research on stump-vegetation relationships, we synthesize our results in a schematic of vascular plant biodiversity and tree regeneration on stumps. Our work and this schematic can be used to stimulate ideas for new hypothesis generation and for studies relevant for conservation, management and basic science research.

Background

Rainforests are important for carbon and nitrogen cycling (Hamaoui et al. 2016; Mackey et al. 2017), timber production, biodiversity, ecosystem services (Catterrall et al. 2005; Nahuelhual et al. 2007), and even beauty, mystery and spirituality (DellaSala 2011). While the majority of rainforests occur within the tropics, temperate rainforests are roughly 0.2% of the earth's land area, with a significant portion occurring in British Columbia, Canada (Farr 2003; Mackey et al. 2017). British Columbia's temperate rainforests are composed mainly of coniferous trees, with Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) as the dominant species (Jenkins 2004). The number of species able to grow within these coastal forests is limited by dense overstorey canopy (Kimmins 2004), low temperature and limited winter daylight. These conditions also cause slow vegetation succession processes (Super et al. 2013; Defrenne et al. 2016).

The important role of coarse woody debris (CWD) in maintaining biodiversity has been widely recognized (Hörnberg et al. 1995, 1997), and has been the subject of intensive research (Chmura et al. 2016; Staniaszek-Kik et al. 2016; Unar et al. 2017; Kumar et al. 2018; Stroheker et al. 2018). Stumps are initially created by disturbance events such as wind, lightning, harvesting or fire (Oliver and Larson 1996). They are the largest coarse woody debris (CWD) component in second-growth forests (Hörnberg et al. 1995; Nordén et al. 2004; Rackham 2008; Wirth et al. 2009), and play an important role in nutrient cycling (Kubin 1977; Finér et al. 2003). Generally, nutrient availability increases on stumps after moss mortality (During 1979) and is further enhanced by fungal activity (Johansson et al., 2002). However, stump decomposition can be slow, e.g., one study indicated that a net release of nitrogen from pine stumps may take as long as 40 years (Palviainen et al. 2010). Tree seedlings tend to establish in higher concentrations on CWD than the nearby ground (Kumar et al. 2018). While stumps have limited surface area, they are a particularly important component of CWD for tree and understory species establishment (Hörnberg et al. 1995, 1997). Despite this, management considerations for tree stumps have often focused their provisions of nests for animals or habitat for bryophytes and fungi (Lindelöw et al. 1993; Hörnberg et al. 1997; Waldien et al. 2000; Prescott 2002; Konuk et al. 2007; Laitila et al. 2015) 1979). Surprisingly, we find very few or no studies aimed at estimating vascular plant species associations during tree regeneration and species establishment on stumps, despite the abundance of stumps.

Tree regeneration on stumps can be classified into two types: sprouting (regeneration re-sprouting, or new growth originating from the stump) and new establishment seedlings (not from sprouting, different origin, e.g., regeneration from seed rain of a nearby tree) (Oliver and Larson 1996). Tree seedlings established on stumps can be affected by stump structures (e.g., basal diameter and height), which may, in turn, relate to nitrogen and water content availability (Vonhof and Barclay 1996), and influence the survival and fitness of vascular plants species. Only limited research related to tree regeneration on stumps has been reported. A study on Norway spruce (*Picea abies*) regeneration in Italy found stump diameter to be the most important factor maximizing the regeneration potential of tree species (Motta et al. 2006). Similarly, such a trend was found with re-sprouting of stumps (sprouting as mentioned above) discovered in India (Khan and Tripathi 1986). However, these studies exclusively dealt with the understorey species or tree species on stumps, and thus present an incomplete assessment (e.g., species diversity) as both understorey plants and tree species should be concurrently considered to represent the entire community.

To date, the effect of intraspecific tree species competition and the competition with other vascular plants on stumps remain unclear. Furthermore, spatial relationships of vegetation growth on stumps seem unexplored. Therefore, the objectives of our study were to: 1) quantify temperate rainforest vascular plant diversity on stumps; 2) assess vegetation associations and competition related to tree regeneration on stumps; and 3) synthesize ideas into a schematic illustrating the conceptual process of tree regeneration on stumps useful for future research on stump-vegetation relationships.

Materials And Methods

Study Sites

Three study sites were selected in southwestern British Columbia, Canada. These were Malcolm Knapp Research Forest, Pacific Spirit Regional Park, and Stanley Park (Fig. 1). Subplots were situated at these main study sites.

Malcolm Knapp Research Forest (MKRF), which is owned and operated by The University of British Columbia (UBC), is 5,157 hectares and located in Maple Ridge, British Columbia (Farahbakhchian 2017). MKRF has coastal forest stands characteristic of the Pacific Northwest with naturally regenerated and plantation forests, including variable retention, as well as other forms of management for research and education purposes. Portions of MKRF experienced logging between 1920 and 1931. The second-growth areas surveyed in this study were approximately 80-year-old forest stands that were naturally regenerated (personal communication Ionut Aron, MKRF, 2019) and composed mostly of western hemlock and western redcedar, with a smaller amount of Douglas fir. The site history is evident, including massive cedar stumps.

Pacific Spirit Regional Park (PSRP) is an urban greenbelt valued for recreation, education, and biodiversity. The park is located in UBC Endowment Lands, Point Grey to the west of Vancouver, British Columbia, and is bordered by the UBC campus (Artibise and Meligrana 2005; Super et al. 2013). PSRP has a maritime climate with warm, dry summers and mild, wet winters (Meidinger and Pojar 1991). PSRP is within the Coastal Western Hemlock zone of the provincial Biogeoclimatic Ecosystem Classification (Krajina and Brooke 1965), and has typical temperate rainforest tree species such as western hemlock and western redcedar (Goward 1994). Vegetation throughout PSRP has been impacted by past anthropogenic disturbances, and has secondary growth regeneration in many places (Super et al. 2013). Our study plots were located in an area that was clear-cut and burned in the year 1910.

Stanley Park (SP) is approximately 400 hectares and located in the Coastal Western Hemlock zone in the city-centre of Vancouver, one of the largest city-centre parks in North America (McDonald 1984). It is regarded as an "invaluable commercial and advertising asset" for nature, recreation, education and history for local people and many tourists (Kheraj 2007) and has impacted people-wildlife relationships in Canada (Kheraj 2012). The most abundant species include western hemlock, western redcedar, Douglas-fir, bigleaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*), wild cherry (*Prunus avium*), red alder (*Alnus rubra*), Pacific yew (*Taxus brevifolia*), Cascara (*Rhamnus purshiana*), and Pacific dogwood (*Cornus nuttallii*). Thousands of trees were uprooted and blown over in several extreme weather events, especially wind storms in 1934–1960, and 2006 (Kheraj 2007). Our study plots in SP were located near Beaver Lake.

Data collection

Permits were secured from UBC to survey MKRF and PSRP as well as from SP management. For each site, 10–11, 30 × 30 m plots were delineated. To minimize disturbance effects from trail-use, all plots were established at least 5 m into the forest from the trail edge. For each plot, all the species on the ground and overall canopy coverage were recorded. For each stump in each plot, its maximum height, basal diameter, decay stage, and the height of trees growing on it (height: 5 to 200 cm) were measured. In addition, species names and the number of individuals of all plants (tree and understory species) growing on stumps were recorded.

Data analysis

To identify factors affecting vegetation growth on stumps, we used linear regression to analyze the association between the number of individuals on stumps and other possible variables, such as stump basal area, stump height, and canopy coverage. We did not find a clear pattern for stump height, and canopy coverage contributed to species abundance on stumps. A regression analysis was also used to test Individual Species Area Relationship (ISAR) respect to relationship between the number of species on stumps and the stump basal area. All analyses were conducted in R 3.3.1 (R Development Core Team 2014). To further evaluate the species relationship on stumps, we used the variance ratio (VR) (Vroh et al. 2016), which indicates that the total species relationship and total species association will be positively and negatively associated when VR > 1 and VR < 1, respectively. We measured the strength of the linear association between species pairs growing on stumps by using the Pearson product-moment correlation coefficient (Sedgwick 2012). Species relationships on the same stump species were further analyzed using the R "spaa" package (Zhang and Zhang 2013; Griffith et al. 2016).

Results

Vascular plant distribution, abundance, and community composition

A total of 23 vascular species (9 tree and 14 understorey species), belonging to 15 plant families, were found in the three study sites (Table 1), with 19 species (8 tree and 11 understorey species) found on both stumps and the ground. Species abundance was highest in Malcolm Knapp Research Forest (MKRF), followed by Stanley Park (SP) and then Pacific Spirit Regional Park (PSRP). In the MKRF site, the major stump species were western redcedar and western hemlock. A total of 2,381 individuals belonging to 17 vascular plant species (of 13 families) grew on 93 (76.23%) out of the 122 sampled stumps; on stumps, the most abundant tree species was western hemlock, while the most abundant understorey species was red huckleberry (*Vaccinium parvifolium*) (Table 2, Fig. 2). MKRF and SP sites had similar species. In the PSRP site, the major stump species were western redcedar, western hemlock, and Douglas-fir. A total of 155 individuals belonging to nine vascular plant species (of seven families) grew on 38 (35.19%) out of the 108 sampled stumps. The most abundant tree species was western hemlock, and the most abundant understorey species was salal (*Gaultheria shallon*) growing on stumps (Table 2, Fig. 2). In the SP site, the major stump species were western redcedar and western hemlock. A total of 842 individuals belonging to 14 vascular plant species (of 13 families) grew on 92 (81.41%) out of the 113 sampled stumps; on stumps, the most abundant tree species was western hemlock, while the most abundant understorey species was red huckleberry (Table 2, Fig. 2).

Table 1
Vascular plant species found in the study three sites (Malcom Knapp Research Forest, MKRF; Pacific Spirit Regional Park, PSRP; Stanley Park, SP).

No.[1]	English name	Scientific name	Family	Code	MKRF	PSRP	SP
1	Western redcedar	*Thuja plicata*	Cupressaceae	THPL	√	√	√
2	Douglas-fir	*Pseudotsuga menziesii*	Pinaceae	PSME	√	√	
3	Western hemlock	*Tsuga heterophylla*	Pinaceae	TSHE	√	√	√
4	Red alder	*Alnus rubra*	Betulaceae	ALRU	√	√	√
5	Bigleaf maple	*Acer macrophyllum*	Sapindaceae	ACMA	√		√
6	Vine maple	*Acer circinatum*	Sapindaceae	ACCI	√	√	√
7	Mountain ash	*Sorbus aucuparia*	Rosaceae	SOAU	√	√	√
8	English holly	*Ilex aquifolium*	Aquifoliaceae	ILAQ	√	√	√
9	English oak	*Quercus robur*	Fagaceae	QURO	√		√
10	Salal	*Gaultheria shallon*	Ericaceae	GASH	√	√	√
11	Red huckleberry	*Vaccinium parvifolium*	Ericaceae	VAPA	√	√	√
12	Salmonberry	*Rubus spectabilis*	Rosaceae	RUSP	√	√	√
13	Black raspberry	*Rubus leucodermis*	Rosaceae	RULE	√	√	√
14	Dull Oregon-grape	*Mahonia nervosa*	Berberidaceae	MANE	√	√	√
15	Sword fern	*Polystichum munitum*	Dryopteridaceae	POMU	√	√	√
16	Bracken fern	*Pteridium aquilinum*	Denstaedtiaceae	PTAQ	√	√	√
17	Spiny wood fern	*Dryopteris expansa*	Dryopteridaceae	DREX	√	√	√
18	Deer fern	*Blechnum spicant*	Blechnaceae	BLSP	√	√	√
19	Trailing blackberry	*Rubus ursinus*	Rosaceae	RUUR	√	√	√
20	English ivy	*Hedera helix*	Araliaceae	HEHE			√
21	Foamflower	*Tiarella wherryi*	Saxifragaceae	TIWH	√		√
22	False azalea	*Menziesia ferruginea*	Ericaceae	MEFE	√		√
23	Canadian bunchberry	*Cornus canadensis*	Cornaceae	COCA	√		√

[1]No.1–9 are tree species; 10–23 are understorey species.

Table 2
Basic information of the three study sites (Malcom Knapp Research Forest, MKRF; Pacific Spirit Regional Park, PSRP; Stanley Park, SP).

Attributes	MKRF	PSRP	SP
Average Canopy coverage	65.50%	59.50%	53.50%
Number of stumps	122	108	113
Major stump species	Western redcedar, western hemlock	Western redcedar, western hemlock, Douglas-fir	Western redcedar, western hemlock
Average stump basal diameter/cm	89.783	42.769	74.904
No. of stumps with species occurrence	93	38	92

Species abundance-stump basal diameter relationship

The average basal diameters of stumps were 89.78, 42.77 and 74.90 cm for MKRF, PSRP, and SP, respectively (Table 2). Regression analysis showed that basal diameter was significantly correlated with the species abundance on stumps (MKRF: $P < 0.05$; PSRP: $P < 0.001$; and SP: $P < 0.001$) (Fig. 2). In MKRF and SP the number of individuals increased with increasing basal diameter of stumps. Whereas in PSRP, there was a Gaussian distribution of plant abundance with the basal diameter of stumps; stumps with medium basal diameter had more individuals (Fig. 2).

Vegetation association on stumps

Vascular plant species had significant co-occurrence patterns on stumps. The overall species established on stumps were positively associated in MKRF (variance ratio = 2.74) and SP (variance ratio = 1.37), but negatively associated in PSRP (variance ratio = 0.57). In MKRF, there were two highly significant (P< 0.01) and eight significant (P< 0.05) positive associations, and four highly significant (P< 0.01) and 50 significant (P< 0.05) negative associations between species pairs were observed (Table 3a). In PSRP, no positive association between species pairs but five negative associations pairs (P< 0.05) were observed (Table 3b). In the SP site, four highly significant (P< 0.01) and two significant (P< 0.05) positive associations, and one highly significant (P< 0.01) and 49 significant (P< 0.05) negative associations between species pairs were observed (Table 3c).

Table 3:
Vascular plant species associations on stumps based on Pearson product-moment correlation coefficients. a) MKRF, b) PSRP and c) SP. Negative and pc
associations are assumed to suggest species competition during seed germination and before seedling establishment respectively (see Table 1, for species
Significance level: ^{ns} not significant, * P<0.05, ** P<0.01.

	ACCI	ACMA	ALRU	BLSP	COCA	DREX	GASH	MEFE	POMU	PSME	PTAQ	RUUR	THPL	T
ACMA	0.489^{ns}													
ALRU	0.170^{ns}	-0.011*												
BLSP	0.089^{ns}	-0.031*	0.554^{ns}											
COCA	0.265^{ns}	0.096^{ns}	-0.045*	-0.032*										
DREX	0.003**	-0.021*	-0.021*	0.20 ^{ns}	0.325^{ns}									
GASH	0.335^{ns}	0.113^{ns}	-0.076^{ns}	0.006**	0.918^{ns}	0.310^{ns}								
MEFE	0.201^{ns}	-0.024*	-0.024*	-0.066^{ns}	0.427^{ns}	-0.044*	0.401^{ns}							
POMU	0.336^{ns}	-0.031*	0.523^{ns}	0.655^{ns}	0.088^{ns}	0.165^{ns}	0.102^{ns}	-0.066^{ns}						
PSME	-0.042*	-0.011*	-0.011*	-0.031*	-0.045*	-0.021*	-0.076^{ns}	-0.024*	-0.031*					
PTAQ	0.060^{ns}	-0.021*	0.462^{ns}	0.612^{ns}	0.083^{ns}	-0.039*	0.053^{ns}	-0.046*	0.351^{ns}	-0.021*				
RUUR	0.117^{ns}	-0.011*	-0.011*	-0.031*	0.238^{ns}	0.485^{ns}	0.258^{ns}	-0.024*	0.025*	-0.011*	-0.021*			
THPL	-0.004**	-0.023*	-0.023*	0.086^{ns}	0.388^{ns}	0.729^{ns}	0.368^{ns}	-0.049*	0.106^{ns}	0.492^{ns}	-0.044*	0.492^{ns}		
TIWH	-0.042*	-0.011*	-0.011*	-0.031*	-0.045*	-0.021*	-0.076^{ns}	-0.024*	-0.031*	-0.011*	-0.021*	-0.011*	-0.023*	
TSHE	0.237^{ns}	0.007**	0.569^{ns}	0.336^{ns}	0.296^{ns}	0.064^{ns}	0.300^{ns}	-0.040*	0.383^{ns}	-0.048*	0.277^{ns}	-0.015*	0.009**	-(
VAPA	0.082^{ns}	-0.044*	-0.011*	0.185^{ns}	0.110^{ns}	-0.066^{ns}	0.122^{ns}	0.155^{ns}	0.162^{ns}	0.375^{ns}	0.066^{ns}	0.033*	0.112^{ns}	-(

Significance level: ^{ns} not significant, ** P<0.05, *** P<0.01.

(a)

	ACCI	DREX	GASH	ILAQ	PSME	PTAQ	THPL	TSHE
DREX	-0.055^{ns}							
GASH	0.165^{ns}	0.520^{ns}						
ILAQ	-0.038*	-0.089 ^{ns}	-0.091^{ns}					
PSME	-0.049^{ns}	-0.114^{ns}	0.099^{ns}	-0.034*				
PTAQ	0.473^{ns}	-0.184^{ns}	-0.105^{ns}	-0.056^{ns}	-0.071^{ns}			
THPL	-0.080^{ns}	-0.186^{ns}	-0.150^{ns}	-0.056^{ns}	-0.072^{ns}	0.105^{ns}		
TSHE	-0.019*	-0.078^{ns}	-0.028*	-0.039*	-0.050^{ns}	-0.081^{ns}	-0.082^{ns}	
VAPA	-0.104^{ns}	-0.200^{ns}	-0.197^{ns}	-0.074^{ns}	-0.094^{ns}	0.065^{ns}	-0.154^{ns}	0.288^{ns}

Significance level: ^{ns} not significant, ** P<0.05, *** P<0.01.

(b)

	BLSP	ACCI	ACMA	ALRU	COCA	DREX	GASH	HEHE	ILAQ	MEFE	PTAQ	QURO	RUSP	RUUR
ACCI	0.003**													
ACMA	-0.021*	-0.026*												
ALRU	-0.021*	-0.026*	-0.013*											
COCA	-0.021*	0.045*	-0.013*	-0.013*										
DREX	-0.003*	0.195 ns	-0.056 ns	0.188 ns	0.188 ns									
GASH	-0.010*	0.178 ns	-0.041*	-0.041*	0.069 ns	0.022*								
HEHE	-0.076 ns	0.327 ns	0.046*	0.160 ns	0.103 ns	0.237 ns	0.462 ns							
ILAQ	-0.021*	-0.026*	-0.013*	-0.013*	-0.013*	-0.056 ns	-0.041*							
MEFE	-0.025*	-0.030*	0.980 ns	-0.016*	-0.016*	-0.066 ns	-0.049*	0.031*	-0.016*					
PTAQ	0.066 ns	0.006**	0.144 ns	-0.046*	-0.046*	0.363 ns	0.132 ns	0.044*	-0.046*	0.132 ns				
QURO	-0.021*	-0.026*	-0.013*	-0.013*	-0.013*	-0.056 ns	-0.041*	-0.069 ns	-0.013*	-0.016*	-0.046*			
RUSP	-0.041*	-0.028*	-0.025*	-0.025*	-0.025*	0.262 ns	0.171 ns	0.507 ns	-0.025*	-0.030*	-0.040*	-0.025*		
RUUR	-0.021*	-0.026*	-0.013*	-0.013*	-0.013*	0.188 ns	0.069 ns	-0.069 ns	-0.013*	-0.016*	-0.046*	-0.013*	0.050*	
THPL	-0.030*	-0.036*	-0.019*	0.702 ns	-0.019*	0.094 ns	0.204 ns	0.147 ns	-0.019*	-0.022*	-0.032*	-0.019*	-0.036*	-0.019*
TIWH	-0.030*	-0.036*	-0.019*	-0.019*	-0.019*	-0.080 ns	0.519 ns	0.106 ns	-0.019*	-0.022*	-0.066 ns	-0.019*	-0.036*	-0.019*
TSHE	-0.061 ns	-0.125 ns	0.156 ns	-0.025*	-0.045*	-0.098 ns	-0.002**	-0.013*	-0.065 ns	0.156 ns	0.094 ns	0.015*	0.158 ns	-0.065 ns
VAPA	0.020*	-0.013*	0.294 ns	-0.089*	-0.089 ns	0.114 ns	0.034*	-0.062 ns	-0.046*	0.280 ns	0.224 ns	-0.004**	-0.033*	-0.004**

Significance level: ^{ns} not significant, ** P<0.05, *** P<0.01.

(c)

Discussion

Vascular plants kingdom on stumps

Previous studies related to tree regeneration on stumps in temperate forests have been restricted to only a few tree and stump species such as *Picea abies* (Hörnberg et al. 1997), *Abies alba*, and *Fagus sylvatica* (Szewczyk and Szwagrzyk 1996). Thus, we have expanded the current level of knowledge through reporting for the first time on the growth of different herbaceous, tree and shrub species on conifer stumps. We have examined the composition of tree species on stumps in diverse understorey plant communities. Of the total 23 vascular plant species that we identified in the three sites, 19 were found growing on stumps. It is likely that these stumps created a suitable habitat for the establishment of these plant species by providing additional moisture through the water-holding mosses that regularly colonize coarse woody debris (During 1979). As stumps are elevated from the ground, they provide vascular plants with growing conditions that receive more sunlight and have higher temperatures than the forest floor, which may help to promote additional plant growth (Nelson 1951). In addition to this, animals have been shown to select the best seeds of vascular plants to store in stumps (Breen-Needham 1994). These factors may help tree and understorey regeneration on stumps within second-growth temperate rainforests in spite of the thick overstorey canopy and cool temperatures (Wirth et al. 2009). Stumps have been researched for their importance for animal biodiversity conservation and management (Lindelöw et al. 1993; Hörnberg et al. 1997; Waldien et al. 2000; Prescott 2002; Konuk et al. 2007; Laitila et al. 2015), while the focus of our assessment adds new information regarding vascular plants and tree regeneration on stumps.

Vegetation-stump basal area relationship

The relationship between vegetation-stump basal area has not been fully studied and it was among the goals of the present study. Re-sprouting on stumps research has shown that the age class of a stump is one of the major factors affecting tree regeneration. A study on the relationship between vegetation-stump basal area conducted in India has indicated that the median basal diameter may have maximized the regeneration of tree species (Khan and Tripathi 1986). This pattern was detected in one out of the three study sites, PSRP, suggesting that stumps of median basal area had maximized established vascular plant quantities. In other words, for PSRP we did not find an explicit "individual species-area relationship", i.e., the number of individuals increase with increasing habitat area as reported by "Individual Species Area Relationship (ISAR)" by Tsai et al. (2015). The Gaussian distribution of vascular plant species with basal stump area may be due to the understorey species mortality caused by competition with the canopy of tree species on larger stumps, as the mean basal diameter of stumps in PSRP (42.77 cm) is much smaller than that in MKRF (89.78 cm) and SP (74.90 cm) (Table 2). In contrast, for MKRF and SP, there was a clear ISAR, with increasing numbers of individuals as basal area increases. To our knowledge, this is the first time that a study has examined the ISAR concept in a small area (74.90-89.78 cm in diameter). Stumps are ubiquitous in many forests, but still under researched, especially with respect to vascular plants and tree regeneration; thus, we suggest additional research efforts be dedicated to epixylic communities on stumps. Interestingly, our data did not show a correlation between vegetation diversity and stump height. However, this may be due to our exclusion of stumps greater than 200 cm, which we described as snags. Further research is also needed to illustrate the role of high stumps on the various steps and processes in vascular plant establishment.

Species competition patterns on stumps

Species interactions on stumps can be influenced by factors related to natural enemy, density-dependence, inter and intra-specific competition, and species coexistence (Chesson 2013). Competition is one of the most fundamental interactions of ecological organization (Solé et al. 1992; Chesson 2013). Species competition patterns on stumps may help unveil tree regeneration processes on stumps. In the present study we focused on interspecific competition and species coexistence. As previously mentioned, the overall species associations on stumps were positive in MKRF and SP but negative in PSRP which could be caused by factors related to the smaller average basal diameter in PSRP. Within all the studied sites, tree species seemed to significantly compete with each other, such as ACCI vs. ILAQ (species abbreviations in Table 1), ACCI vs. TSHE, ILAQ vs. TSHE, ILAQ vs. PSME, ACCI vs. PSME, and THPL vs. ACCI (Table 3). Tree species also compete with other highly occurring species such as GASH and VAPA. However, in SP, two positive pairs of tree species are ACMA and TSHE, THPL and TSHE; this may due to the large occurrence of TSHE. It should to be noted that ILAQ, an invasive species, successfully colonized stumps; mitigating invasive species is under management consideration in Vancouver (Mosquin 1997).

Tree regeneration process

Tree regeneration and vascular plant biodiversity on stumps have intricate processes and patterns. Our literature searching uncovered that little is known about stump-vegetation relationships other than non-vascular plants, and linking processes to patterns is relatively rare. Our research suggests that stumps can play an important role in tree regeneration in Pacific Northwest temperate rainforests, and a conceptual model for future stump-vegetation research would be useful. To fill this gap, we have included a schematic depicting the regeneration process (Fig. 3), which can be described as:

1. *Disturbance*: Stumps are initially created by abiotic disturbances (e.g., wind, lightning, harvesting, or fire) synergistically with biotic disturbance (e.g., a weakened tree by disease could be more likely to be broken by wind). Canopy gaps resulted from the disturbances start allowing for shifts in succession on stumps.
2. *Stump decay*: Stumps begin the decay process, which is enhanced by the activity of agents such as insects, fungi, bacteria, etc. (Palviainen et al. 2010). At this stage, the chemistry of the stump and nutrient cycling and accumulation matter especially. After consistent rainfall, bryophytes and lichens appear on stumps, and then, the habitat on the stump becomes suitable for the establishment of tree species and vascular plant biodiversity.
3. *Seed or propagule dispersal*: Tree seeds are dispersed on to stumps passively (e.g., falling from nearby trees, wind), or actively by animals (e.g., squirrels, birds, including hiding by animals). Seed survival can be affected by multiple processes, e.g., pathogens, seed predation, facilitation, mutualism, etc. The seeds that move into germination and subsequently other stages will be impacted by stochastic and deterministic processes.
4. *Germination*: Tree seeds and other propagules germinate. As water, light, nutrition and other factors support favorable growth, seedlings and other vascular plants can grow. Seedlings compete with bryophytes and lichens, as well as other vascular plants for growing space and vying for light, so they can move into emergent seedling stage.
5. *Seedling stage*: Tree seedlings continue in growth (seedlings greater than one year in age but less than 1.3 meter in height) as well as vascular plants. Bryophytes and lichens at this stage likely have reduced effects on tree seedlings but if present, other vascular plants continue to compete and have other species interactions in relation to resources and space. The previous steps may still be relevant at this stage, as the plant starts influencing the stump as well as other organisms that break down the stump (potentially releasing nutrients, depleting nutrients, etc.). As the seedlings grow bigger, they move into the establishment stage.
6. *Tree establishment stage*: At this stage, trees are bigger than 1.3 m. Inter and/or intra-specific competition is likely to occur among seedlings growing on a single stump. Years after establishment, one or more trees may eventually grow tall enough to be a canopy tree.

Within our study, we observed a higher density of tree seedling individuals growing on stumps than on the nearby ground, which suggests the stumps in stages one and two underwent processes that provided suitable habitat stages three to six (Fig. 3). The presence of more regeneration on stumps is supported by a study conducted in old-growth boreal swamp forests in Sweden where *Picea abies* seedlings were more concentrated in elevated micro-relief features (logs, roots, or stumps) than the forest floor (Hörnberg et al. 1995, 1997). For a re-sprouting study, stages four to six are more relevant for the seedling stages as they arise directly from stumps. We can only infer what happened in stages one to four for our study sites because we did not do a long-term study or manipulative experiment. We focused mainly on plant species patterns relevant to stages five and six; whereby we found ISAR with respect to individual plants and stump basal area for two study sites (MKRF and SP) and a Gaussian distribution instead ISAR for PSRP. To our knowledge, our study is the first to evaluate the ISAR with stumps with to plants and any organism on stumps. Another pattern across these stages was species associations on stumps, which suggested species interactions such as competition.

Stump history from stage one to stage three may play a crucial role in setting up the habitat conditions needed to create the association patterns that we found in this study. Further experiments could do manipulative transplant and growth experiments to study this further and look at other patterns such as plant fitness (or survival ratio) and species cover (how much of stump surface area covered by vegetation). These appear to not yet be measured by any researchers to our knowledge. Furthermore, studies could compare how different stump species at different sizes impact regeneration processes. The patterns and processes mentioned with our schematic are not simple and could potentially have downstream effects, with not all stages being mutually exclusive and may happen together. For example, some seeds may land when other seedlings are already established. Very early processes such as insects could affect the entire trajectory; for example, mountain pine beetle attack could modify the nutrition of tree which affect it as a stump relative to non-beetle kill stumps, which potentially affect all the other processes. The nutrition processes of stumps could be further studied with isotope methods that tease apart the different substrate (e.g., redcedar stump vs. other species, etc.) and chemistries. The habitat matrix around stumps potentially has a significant impact on seedling regeneration and vascular plant biodiversity on stumps. Many factors could impact the start of a stump's trajectory for tree seedling regeneration and vascular plant biodiversity.

Conclusion

This study elucidated vascular plant biodiversity on stumps in Pacific Northwest temperate rainforest sites, including the individual species-area relationship (ISAR), and inferred species interactions (e.g., competition) on stumps. Furthermore, we generated a schematic that integrates our findings; this synthesis can help with further research related to understanding the role of tree regeneration on stumps beyond the present study. Vascular plant diversity and tree regeneration arise due to complex processes. To test and explore the implications of our schematic, one could explore tree regeneration and vegetation succession on stumps in second-growth forests across various climatic zones in British Columbia, or elsewhere. Such research could lead to novel discoveries relevant to management, conservation, and to an overall better understanding of tree regeneration processes.

Declarations

Authors' contributions

Experimental design (QW, VS, YAE), fieldwork (QW, VS, LS), data analyses (QW, TW), manuscript writing and editing (QW, VS, LS, TW, YAE), and project coordination (YAE).

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Availability of data and materials

The datasets used during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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Figures

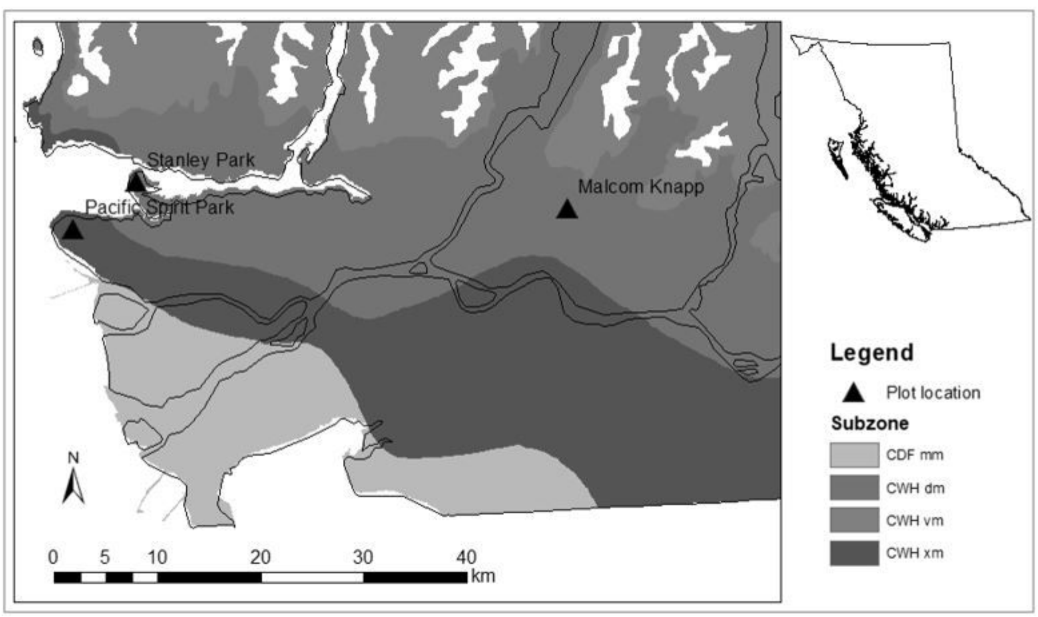

Figure 1

Locations of the three study sites (Malcom Knapp Research Forest, Pacific Spirit Regional Park, and Stanley SP). Key: CDF - Coastal Douglas-fir, CWH – Coastal Western Hemlock, dm - Dry Maritime, mm - Moist Maritime, xm - Very Dry Maritime, and vm - Very Wet Maritime.

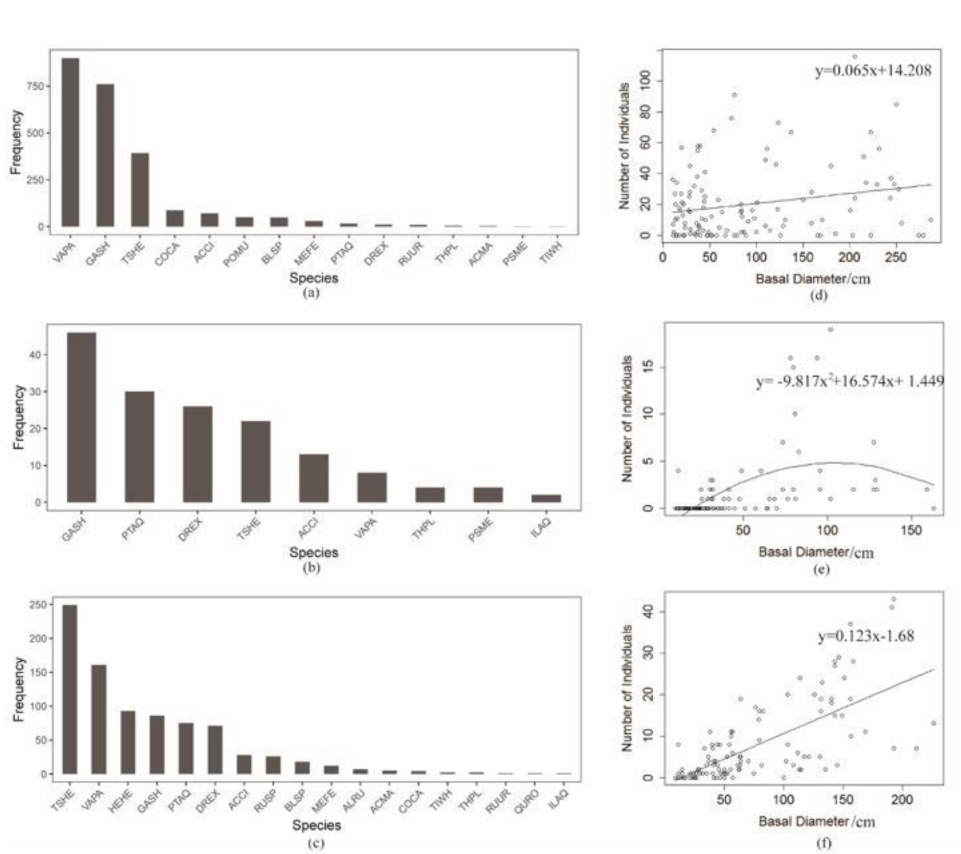

Figure 2

Frequency distribution of vascular plant species occurrence on stumps: a) MKRF, b) PSRP, and c) SP (see Table 1, for abbreviations). Regressions are between stump basal area and the number of individuals on each stump: d) MKRF (n = 122, P = 0.01832), e) PSRP (n = 108, P< 0.0001), and f) SP (n = 113, P< 0.0001).

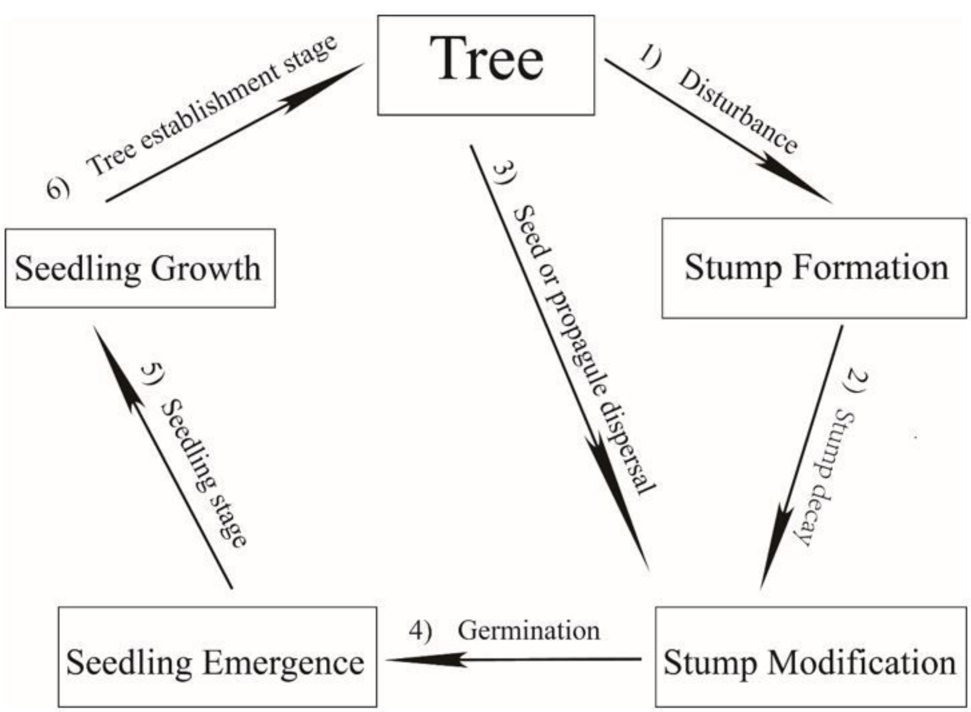

Figure 3

Schematic of the tree regeneration on stumps. This schematic illustrates concepts explored in this study illustrating the processes of tree regeneration on stumps in second-growth temperate rainforests. An emergent seedling refers to a seedling less than one-year-old, and an established seedling is greater than one-year-old and up to 1.3 m in height (Hornberg et al., 1997).