



Increased streamflow in catchments affected by a forest disease epidemic

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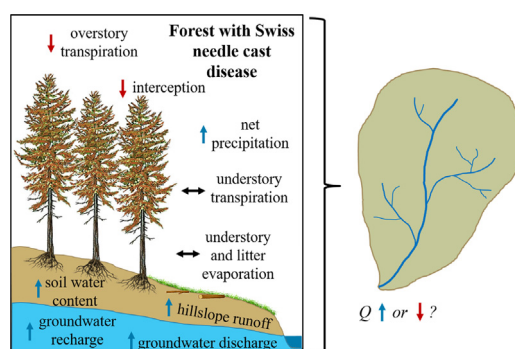
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HIGHLIGHTS

- The Swiss needle cast (SNC) epidemic in the Oregon Coast Range affects Douglas-fir.
- We quantified long-term effects (1990–2015) of SNC on catchment hydrology.
- Runoff ratios (RRs) increased in catchments with >10% area infected by SNC.
- No change in RRs in severely infected catchments related to compensatory transpiration or abiotic evaporation.
- This study is the first to link forest disease to long-term streamflow changes.

GRAPHICAL ABSTRACT



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Data used in this manuscript are all in the public domain. The data used in our analyses are available in the Supplementary material (Appendix 1). Analyses and figures referenced, but not included in the manuscript, can also be found in the Supplementary material.

ABSTRACT

Natural disturbances help maintain healthy forested and aquatic ecosystems. However, biotic and abiotic disturbance regimes are changing rapidly. For example, the Swiss needle cast (SNC) epidemic in the Coast Range of Oregon in the U.S. Pacific Northwest has increased in area from 53,050 to 238,705 ha over the 1996–2015 period. We investigated whether the hydrologic regime (i.e., annual streamflow, runoff ratio, and magnitude and timing of peak flows and low flows) was affected by SNC in 12 catchments in western Oregon. The catchments ranged in size from 183 to 1834 km² and area affected by SNC from 0 to 90.5%. To maximize the number of catchments included in the study, we analyzed 20 years of SNC aerial survey data and 15–26 years of stream discharge (Q) and PRISM precipitation (P) and air temperature (T_{air}) data to test for trends in hydrologic variables for each catchment. As expected, we found that runoff ratios (Q/P) increased in five catchments, all with an area impacted by SNC >10%. This was likely due to the effects of SNC on the hydraulic architecture (i.e., needle retention, sapwood area, sapwood permeability) of affected trees, leading to decreased canopy interception and transpiration losses. Interestingly, two catchments with the greatest area affected by SNC showed no changes in hydrologic regime. The lack of hydrologic response could either be due to compensatory transpiration by vegetation unaffected by the disease or sub-canopy abiotic evaporation, which counteracted reductions in transpiration. This study is the first to illustrate that chronic canopy disturbance from a foliage pathogen can influence catchment scale hydrology.

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1. Introduction

Natural disturbances are key for maintaining healthy forested ecosystems, but globally, disturbance regimes are changing rapidly (Allen et al., 2015; Raffa et al., 2008; Seidl et al., 2016; Sommerfeld et al., 2018; Turner, 2010). Recent evidence suggests increases in the occurrence, intensity, and severity of many of the major forest disturbance agents, including droughts (Allen et al., 2010; Dai, 2013), wildfire (Flannigan et al., 2009, 2013), insect outbreaks (Kurz et al., 2008; Logan et al., 2003), and disease (Mildrexler et al., 2019; Woods et al., 2016; Wyka et al., 2017). As such, rapid and widespread declines in tree growth rates and elevated tree mortality have emerged as phenomenon affecting forests in many parts of the world (Allen et al., 2015; Cohen et al., 2016; Seidl et al., 2017; Sommerfeld et al., 2018; van Mantgem et al., 2009). Intensification in disturbance regimes has raised concerns about maintenance of biological diversity and risks to ecosystem services from forests, including provision of natural storage, filtration, and supply of water (Allen et al., 2010; Bladon et al., 2014; Robinne et al., 2018; Thom and Seidl, 2016).

Disturbances affecting forest canopy composition and structure can have extensive impacts on forest hydrology (Adams et al., 2012; Hallema et al., 2017). A principle hydrologic response to a loss of forest canopy cover or leaf area is a decline in canopy interception storage capacity, resulting in more precipitation (i.e., throughfall) reaching the soil surface (Boon, 2012; Varhola et al., 2010). Disturbances that result in partial or complete removal of the forest canopy can also reduce catchment-scale transpiration (Bearup et al., 2014; Maxwell and Condon, 2016). These changes in hydrological processes can lead to increases in soil moisture (Mikkelsen et al., 2013) and groundwater recharge (Bent, 2001). Thus, close to a century of hydrology research has illustrated increases in net precipitation after forest disturbance, producing more annual streamflow, as well as elevated peak flows and summer low flows, in the first few years after the disturbance (Bates and Henry, 1928; Bethlahmy, 1974; Bosch and Hewlett, 1982; Brown et al., 2005; Hallema et al., 2018b; Stednick, 1996). Such shifts in annual water yields have important implications for source water quality from forests, increasing delivery of sediment, carbon, and nutrients to streams (Emelko et al., 2011, 2016). Moreover, disturbance effects on water yields can cause both immediate and longer-term effects on aquatic ecosystem health (Hicks et al., 1991; Silins et al., 2014).

Hydrologic responses to disturbances can be highly variable due to catchment differences in forest type, soils, geology, topography, climate, and hydrologic regime (e.g., rain-dominated versus snow-dominated) (Brown et al., 2005). In part, the hydrologic response will also depend on the type of disturbance and the nature of its damaging properties (e.g., frequency, magnitude, and severity) (Mirus et al., 2017; Poff, 1992). Temporally, disturbances may affect ecosystems in a pulse, press, or ramp manner, resulting in disparate effects on hydrologic processes and timescales of recovery (Lake, 2000). Pulse disturbances, which are abrupt or acute, such as a wildfire, landslide, earthquake, or forest harvest, tend to produce the most dramatic hydrologic responses, increasing annual water yields, peak flows, and low flows in the first few years after the disturbance (Ebel and Mirus, 2014; Hallema et al., 2018a; Mirus et al., 2017). Comparatively, press and ramp disturbances, which are stressors that are more gradual, often result in a progressive reduction in leaf area or forest canopy without an immediate soil disturbance (Biederman et al., 2014). The continual or persistent impacts on the forest canopy associated with these forest disturbances may have a less immediate impact on soil water content and result in a muted and difficult to detect streamflow signal (Adams et al., 2012; Mikkelsen et al., 2013). As a result, research on the hydrologic effects of press or ramp disturbances, such as bark beetle or forest pathogen outbreaks, have largely been ignored compared to the more dramatic pulse disturbances.

Swiss needle cast (SNC) is a foliar disease specific to Douglas-fir (*Pseudotsuga menziesii*), which is caused by the fungus

Nothophaeocryptopus gaeumannii. It is the most damaging foliage disease of coastal Douglas-fir in the U.S. Pacific Northwest (Hansen et al., 2000; Shaw et al., 2011). Recent analysis of annual aerial detection surveys in coastal Oregon indicated a substantial increase in area affected—from 53,050 ha in 1996 to 238,705 ha in 2015 (Fig. 1) (Ritóková et al., 2016). SNC is an ideal example of a press disturbance—its impacts are gradual and can be sustained over decades (Hansen et al., 2000; Maguire et al., 2011; Shaw et al., 2011). Trees infected with the SNC pathogen, *N. gaeumannii*, suffer from chronic stomatal occlusion, leading to reduced needle retention, annual growth rates (i.e., less sapwood area), and sapwood permeability (i.e., increased proportion of latewood in functional sapwood) (Johnson et al., 2005; Manter et al., 2000; Manter and Kavanagh, 2003) (Fig. 2). In theory, these shifts in hydraulic architecture of trees affected by SNC should result in a reduction in forest stand transpiration, leading to increased soil moisture and catchment-scale runoff. However, a recent study following another press disturbance—mountain pine beetle—quantified increased abiotic evaporation, which surprisingly counteracted reductions in transpiration, resulting in no streamflow response (Biederman et al., 2014). Thus, the effects of SNC on streamflow response at the larger catchment scale relevant to water resources, remains uncertain.

The limited number of studies on the hydrologic effects of chronic disturbances, such as SNC disease, hinder predictions of streamflow responses. Moreover, the limited spatial scale (e.g., stand, hillslope) of many studies creates challenges for understanding the potential hydrologic response at the catchment scale, which is the primary decision-making unit of forest watershed managers. Here, we evaluated 20 years of SNC, precipitation, and streamflow data from 12 watersheds along the Oregon Coast Range to answer the question: *to what degree does the chronic press disturbance of SNC affect catchment hydrologic regime (i.e., annual streamflow, runoff ratio, and magnitude and timing of peak flows and low flows)?*

2. Materials and methods

2.1. Study area description

The study area consisted of 12 catchments located in the Coast Range ecoregion of western Oregon (Fig. 3). The catchments ranged in size from 183 to 1834 km² (Table 1). Across the study area the climate is maritime with mild winter temperatures and prolonged periods of clouds. The mean daily air temperature across the study catchments ranges between 3.3 and 6.1 °C in January and 16.9–19.1 °C in July. Diurnal temperature fluctuations are narrow, ranging from 6 to 10 °C in a day. Mean annual precipitation is mostly rain and ranges from

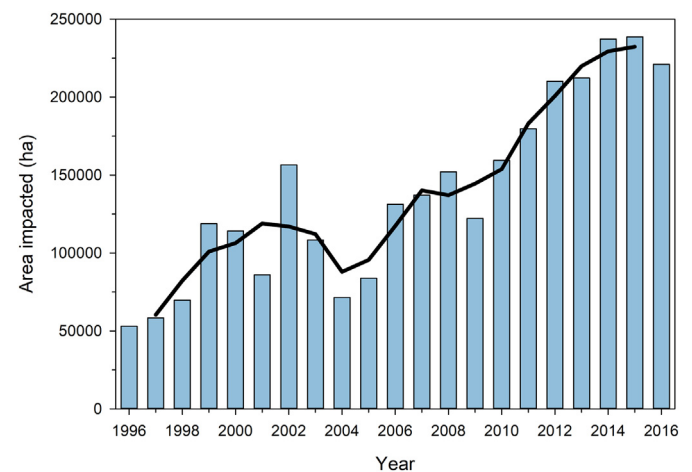


Fig. 1. Annual area (1996–2016) of Douglas-fir forests impacted by Swiss needle cast disease in the Oregon Coast Range as determined from aerial surveys. The solid line represents the rolling three-year average.

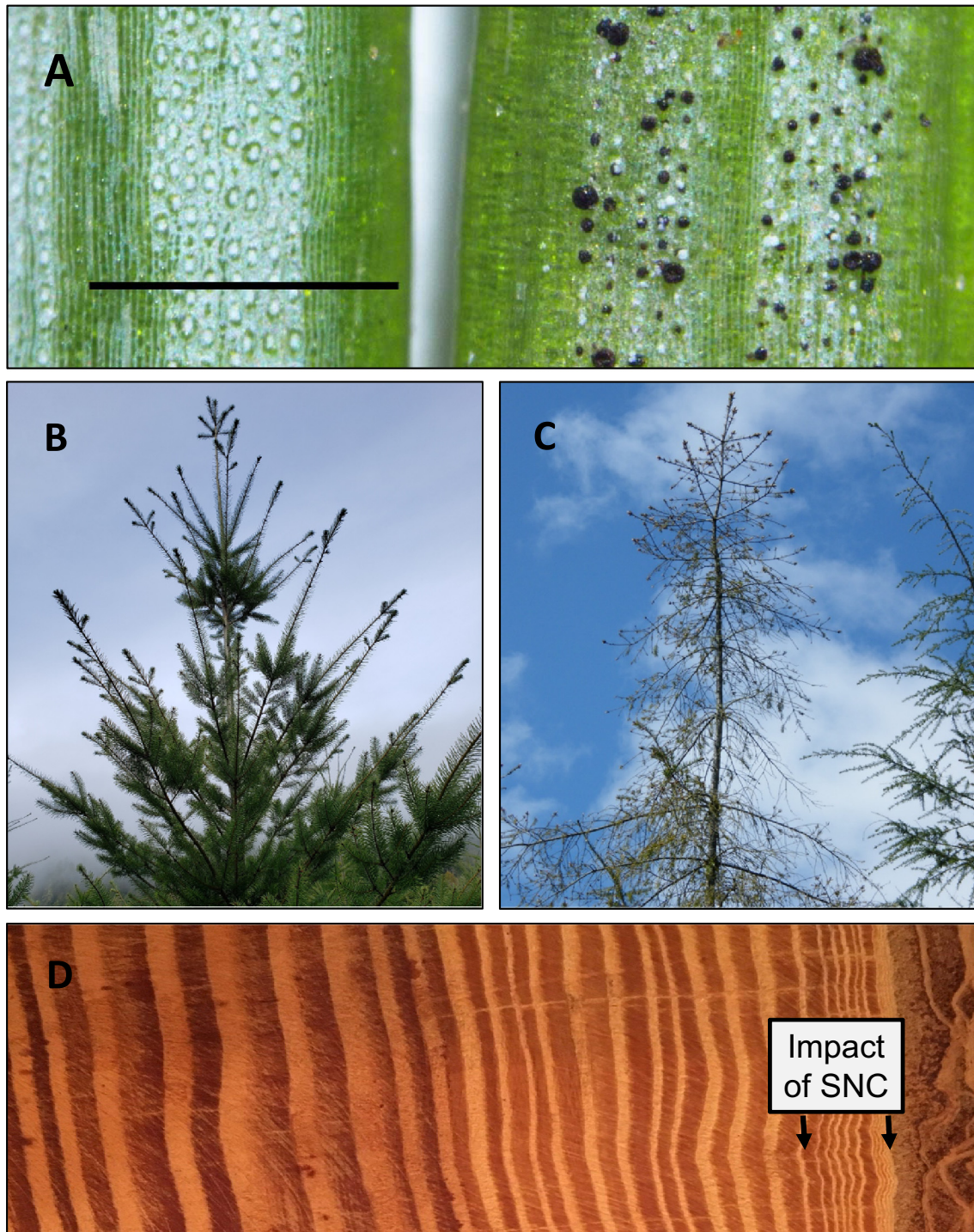


Fig. 2. Symptoms caused by the fungus *Nothophaeocryptopus gaeumannii*, the causal agent of Swiss needle cast. (A) The stomata of a healthy needle on the left and an infected needle on the right with stomatal occlusion due to the pseudothecia (scale bar 0.5 mm). (B) A healthy Douglas-fir will suffer from (C) reduced needle retention due to the occlusion of stomata. The reduced photosynthesis due to occlusion of stomata caused by the infection results in reduced radial growth, which can be observed as thinner annual growth rings. (D) Growth rings from an infected Douglas-fir, with normal growth before the infection and thinner radial growth rings after the infection (indicated with arrows).

~1300–3100 mm across the region, with 75–85% falling between October 1 and March 31 (PRISM Climate Group, 2004).

Two forest types dominate the ecoregion. The Sitka spruce (*Picea sitchensis*) zone is immediately adjacent to the coast, but transitions into the western hemlock (*Tsuga heterophylla*) zone as the maritime influence decreases and elevation increases. In the *Picea sitchensis* zone, soils are typically deep, fine textured, and relatively rich. The major great soil group is Haplohumults (Soil Survey Staff, 2017). The surface soils are high in organic matter, typically acidic, high in total nitrogen,

and low in base saturation. In the western hemlock zone, soils are moderately deep with medium acidity. The soils surface horizons are well aggregated and porous with high organic matter content. The majority of the soils in this zone have a sandy loam to clay loam texture. There are a wider variety of great soils groups in this zone compared to the coastal areas, including Dystrochrepts, Haplumbrepts, and Haplohumults. Much of this zone has been logged or burned during the last 150 years and is now dominated by early- to mid-seral Douglas-fir forests, managed as short rotation timber farms.

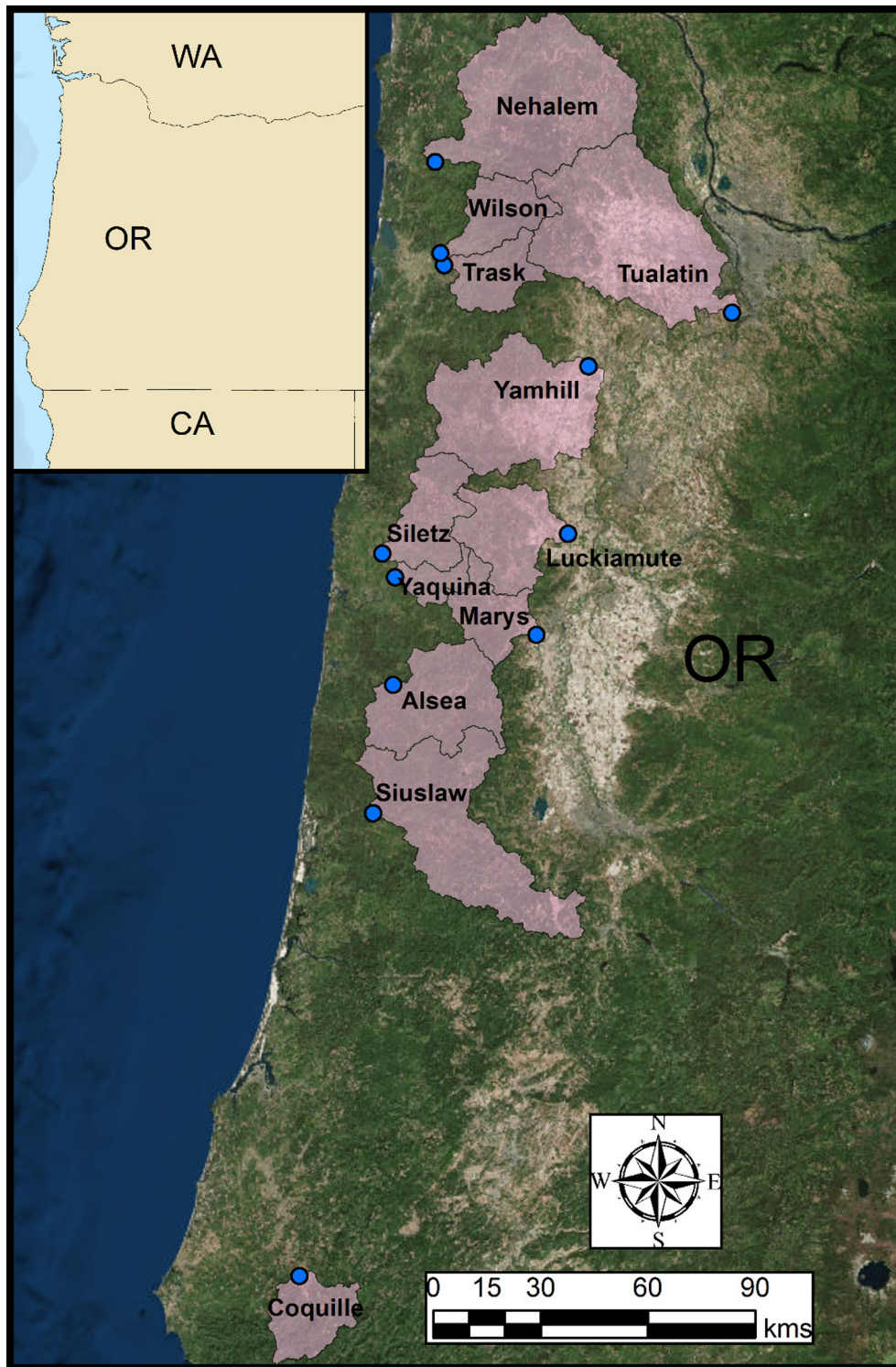


Fig. 3. Study catchments in western Oregon (outlined) impacted by Swiss needle cast with streamflow gauging sites (blue dots at gauges). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Swiss needle cast data

The Oregon Department of Forestry and the U.S. Forest Service have conducted annual aerial detection surveys for the presence of visible symptoms (chlorotic foliage) of SNC in the Oregon Coast Range from 1996 to present (USDA Forest Service, 2017). The surveyed area includes the Columbia River in northern Oregon south to the California border. It also extends east from the coastline until obvious symptoms

are no longer visible. The area included in the survey in western Oregon is approximately 1.5-million ha. The survey provides a conservative estimate of the impact of the disease, as only those stands with moderate and severe damage were identified. For the purposes of this study, SNC annual survey data from 1996 to 2015 (20 years) were classified in a binary manner—polygons were classified as either “SNC affected” or “SNC unaffected” (Oregon Department of Forestry, 2017). We calculated the percentage of catchment affected by SNC for each year of the study

Table 1
Catchment physiographic characteristics.

USGS site no.	Station name	# Years of data	% SNC ^b	Drainage Area ^c (km ²)	Relief ^c (m)	Mean Elevation ^c (m)	Mean Slope ^c (°)
14306030 ^a	Yaquina River near Chitwood	26	90.5	183	806	187	17
14305500	Siletz River at Siletz	26	58.4	526	1052	400	18
14302480	Trask R. above Cedar Ck, near Tillamook	19	43.1	374	1054	504	22
14301500	Wilson River near Tillamook	26	26.7	418	1103	509	59
14306500	Alsea River near Tidewater	26	16.5	857	1234	321	19
14301000	Nehalem River near Foss	26	14.5	1744	1111	359	14
14171000	Marys River near Philomath	15	10.8	393	1174	291	12
14194150	South Yamhill River at McMinnville	21	7.2	1358	1058	232	12
14190500	Luckiamute River near Suver	26	4.8	623	958	271	11
14307620	Siuslaw River near Mapleton	19	3.3	1529	1024	292	19
14325000	South Fork Coquille River at Powers	26	1.0	443	1179	653	19
14207500	Tualatin River at West Linn	26	0	1834	1041	195	8

^a Maintained by Oregon Water Resource Department.

^b Percent area of SNC calculated in ArcMap 10.2.2 as the total footprint of area affected 1996–2016 from Oregon Department of Forestry Forest Health Aerial Surveys (Oregon Department of Forestry, 2017).

^c Watershed attributes from StreamStats.

after union of SNC polygons and watershed polygons using the *union* function from the 'raster' package (Hijmans et al., 2016) in R 3.4.0 (R Core Team, 2016). All shapefiles were read into R with the *readOGR* function of the 'rgdal' package (Bivand et al., 2017).

2.3. Hydrometric data

We analyzed streamflow data from 11 U.S. Geological Survey (USGS) and one Oregon Water Resources Department (12 total) gauging sites draining catchments in the Oregon Coast Range (Table 1). Sites were selected based on their record length (minimum 15 yrs. of discharge data), catchment size (>100 km²), and area of the catchment affected by SNC (>1%). For catchments with the minimum 15 years of discharge data, we included as many preceding years as possible (back to 1990) to strengthen time trend analysis, while maximizing the number of catchments to include in the analysis. This resulted in the inclusion of catchments with discharge data spanning 15–26 years. One catchment (Tualatin River, USGS No. 14207500), adjacent to the SNC-affected catchments, was included as an undisturbed reference. We analyzed all hydrometric data according to the water year (October–September). Annual discharge was calculated for each catchment from the mean daily streamflow values, which were imported into R with the 'dataRetrieval' package (Hirsch and De Cicco, 2015). We normalized the volumetric discharge data by drainage area from each catchment. Drainage area and other geospatial attributes (e.g., geology, soils, topography) of catchments were obtained from Gages-II: Geospatial Attributes of Gages for Evaluating Streamflow (Falcone, 2011).

We used the spatial climate dataset from the PRISM Climate Group to determine the annual precipitation (*P*) and annual air temperature (*T_{air}*) for each catchment (PRISM Climate Group, 2004). As the PRISM climate data were more complete and longer than the discharge records, we used the most comprehensive data range possible for our

study catchments, which included 1990–2015. Annual *P* and *T_{air}* were calculated from extracted (Hijmans et al., 2016) raster values obtained from the *get_prism_monthlys* function of the 'prism' package (Hart et al., 2015). Mean monthly air temperatures were calculated as the mean of monthly minimum and maximum air temperatures estimated for each catchment. We calculated mean annual temperatures as the average of the mean monthly air temperatures.

We estimated annual potential evapotranspiration (PET) using the Thornthwaite equation, with monthly air temperature and the catchment location (i.e., latitude) (Black, 2007). Location (latitude and longitude) was determined with the *calcCentroid* function of 'PBSmapping' package (Schnute et al., 2017). We then calculated the annual runoff ratio for each catchment as the ratio between annual discharge (*Q*) and annual precipitation (*P*).

2.4. Data analysis

We tested for trends over time using the available data record (15–26 years) in each catchment for the following variables: annual discharge, annual minimum discharge, annual maximum discharge, two metrics of flow timing (timing of minimum flow and timing of maximum flow), annual precipitation, annual runoff ratio (*Q/P*), annual ET (mass balance), annual air temperature (*T_{air}*), and annual PET (Thornthwaite). Because of autocorrelation, which creates inaccurate assessments of the significance of a trend, we used the Yue-Pilon method to remove serial correlation from time series by pre-whitening (Yue et al., 2002). Trends were detected with the *zyp.trend* function of library 'zyp', which computes Sen's slope and performs the rank-based, non-parametric Mann-Kendall (MK) statistical test for significance (Bronaugh and Werner, 2013).

As a more in-depth analysis of factors contributing to detected changes in runoff ratio, we conducted a separate analysis predicting

Table 2
Mean annual precipitation, streamflow, runoff ratio, January air temperature, and July air temperature by catchment for study period.

USGS site no.	Station name	Mean annual <i>P</i> (mm)	Mean annual <i>Q</i> (mm)	Mean runoff Ratio (<i>Q/P</i>)	Jan. <i>T_{air}</i> (°C)	Jul. <i>T_{air}</i> (°C)
14306030	Yaquina River near Chitwood	1735	1192	0.68	5.6	17.2
14305500	Siletz River at Siletz	2802	2467	0.88	4.6	16.8
14302480	Trask River above Cedar Creek, near Tillamook	2960	2173	0.73	3.3	17.0
14301500	Wilson River near Tillamook	3153	2542	0.81	3.1	16.8
14306500	Alsea River near Tidewater	2063	1415	0.68	5.0	18.2
14301000	Nehalem River near Foss	2325	1360	0.58	3.3	16.7
14171000	Marys River near Philomath	1741	828	0.47	4.3	18.1
14194150	South Yamhill River at McMinnville	1721	1134	0.64	4.5	18.5
14190500	Luckiamute River near Suver	1871	1174	0.62	4.2	18.3
14307620	Siuslaw River near Mapleton	1606	1049	0.65	5.2	18.9
14325000	South Fork Coquille River at Powers	2012	1504	0.73	6.0	18.2
14207500	Tualatin River at West Linn	1287	736	0.55	4.2	18.8

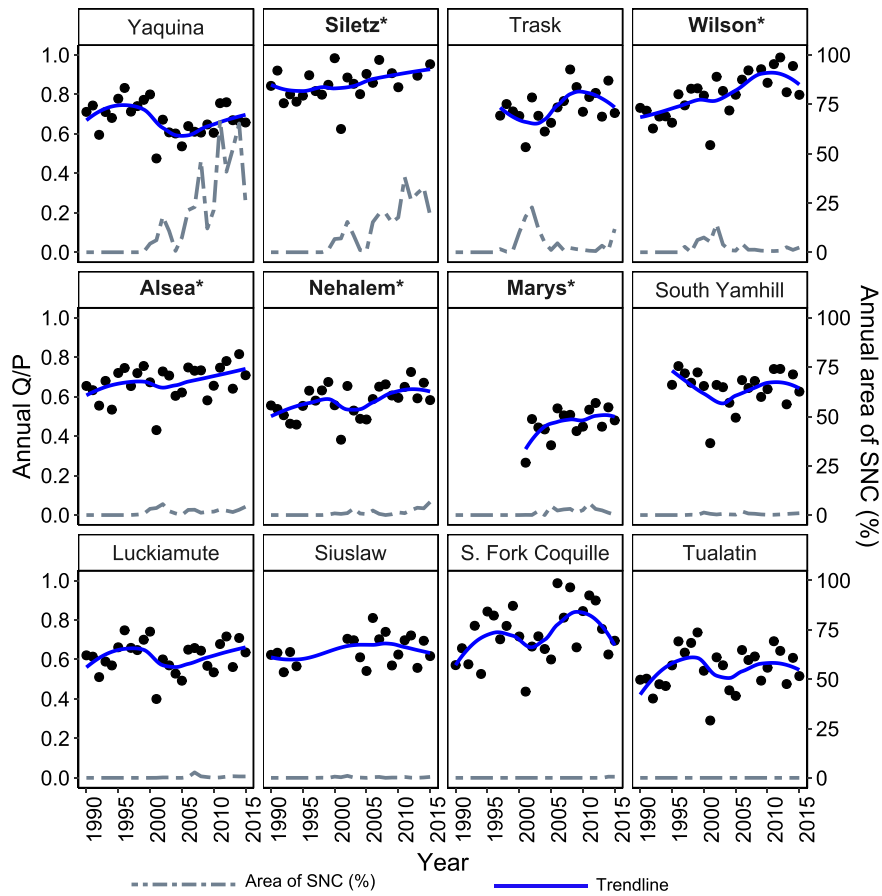


Fig. 4. Annual runoff ratios (Q/P) (dots), smoothed trend (blue line), and SNC coverage (%) (grey dashed line) from 1990 to 2015 for the 12 study catchments. If no SNC polygons were mapped, 0% SNC was assumed. * = Significant changes in Q/P . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

runoff ratio by potential predictors with autoregressive moving average (ARIMA) models. We constructed candidate models predicting runoff ratio (Q/P) by PET, % SNC, or both PET and % SNC and a null model for each site with the exception of the Tualatin River catchment (USGS 14207500), which was not impacted by SNC and served as a reference. For the Tualatin River catchment, we considered a null model and one including PET. Models were developed using the *auto.arima* function of the ‘forecast’ package, which constructs ARIMA models (Hyndman and Khandakar, 2008). Akaike Information Criterion was used to compare models, where the lowest AIC model, and reduction of AIC of less than four ($\Delta AIC < 4$) is preferred (Akaike, 1974; Burnham and Anderson, 2002; Mazerolle, 2017).

2.5. Gradient nearest neighbor vegetation data

To determine potential vegetation structure and composition changes coincident with SNC disturbance, we used annual Gradient Nearest Neighbor (GNN) spatial biomass estimates provided by Landscape Ecology, Modeling, Mapping, & Analysis (LEMMA; USDOJ, USGS, 2019). The digital GNN product provides an estimate of vegetation cover and species by combining field data, statistical modeling, remotely-sensed time-series imagery, and small-footprint LiDAR data at 30-m resolution (LEMMA; USDOJ and USGS, 2019). Within the model, we used the vegetation class change variable, where classifications were categorical and based on dominant species composition

Table 3
Statistical results from the trend analysis of runoff ratios (Q/P). Catchments with $p < .05$ are bolded.

USGS site no	Station name	Intercept of Sen's slope	Sen's slope (Q/P per year)	lbound	ubound	Kendall's tau	Kendall's p-value	Least squares trend	% SNC	Years data
14306030	Yaquina River near Chitwood	0.718	-0.0027	-0.0073	0.0025	-0.1467	0.315	-0.0030	90.5	26
14305500	Siletz River at Siletz	0.761	0.0079	0.0038	0.0126	0.5333	<0.001	0.0080	58.4	26
14302480	Trask R. above Cedar Ck, near Tillamook	0.680	0.0071	-0.0012	0.0129	0.2549	0.150	0.0066	43.1	19
14301500	Wilson River near Tillamook	0.676	0.0107	0.0064	0.0151	0.5400	<0.001	0.0103	26.7	26
14306500	Alesa River near Tidewater	0.651	0.0040	-0.0006	0.0076	0.2933	0.042	0.0037	16.5	26
14301000	Nehalem River near Foss	0.521	0.0045	0.0011	0.0086	0.3000	0.038	0.0049	14.5	26
14171000	Marys River near Philomath	0.422	0.0072	-0.0005	0.0167	0.4286	0.037	0.0096	10.8	15
14194150	S. Yamhill River at McMinnville	0.667	-0.0018	-0.0073	0.0036	-0.1368	0.417	-0.0005	7.2	21
14190500	Luckiamute River near Suver	0.616	0.0010	-0.0037	0.0054	0.0467	0.761	0.0008	4.8	26
14307620	Siuslaw River near Mapleton	0.630	0.0020	-0.0045	0.0099	0.1373	0.449	0.0026	3.3	19
14325000	S. Fork Coquille River at Powers	0.654	0.0050	-0.0034	0.0137	0.1267	0.388	0.0060	1	26
14207500	Tualatin River at West Linn	0.520	0.0029	-0.0045	0.0089	0.0733	0.624	0.0024	0	26

Table 4
Comparison of ARIMA models^a predicting runoff ratio (Q/P) (Table 3). Models with moderate to strong evidence ($p < .05$) of a probable trend are bolded.

USGS Site No	Station Name	AIC Model 1	AIC Model 2	AIC Model 3	AIC Model 4	% SNC	Best Model
14306030	Yaquina R. near Chitwood	−51.70	−51.70	−49.81	−48.32	90.5	1
14305500	Siletz R. at Siletz	−40.88	−40.88	−53.42	−51.56	58.4	3
14302480	Trask R., near Tillamook	−34.20	−34.20	−34.94	−32.00	43.1	3
14301500	Wilson R. near Tillamook	−39.54	−39.54	−35.13	−37.47	26.7	1
14306500	Alsea R. near Tidewater	−51.04	−51.04	−49.86	−49.81	16.5	1
14301000	Nehalem R. near Foss	−45.40	−45.40	−53.02	−53.72	14.5	4
14171000	Marys R. near Philomath	−22.98	−22.98	−29.77	−29.37	10.8	3
14194150	South Yamhill R. at McMinnville	−37.90	−37.90	−36.19	−34.36	7.2	1
14190500	Luckiamute R. near Suver	−53.06	−53.06	−52.00	−50.58	4.8	1
14307620	Siuslaw R. near Mapleton	−41.34	−41.34	−43.34	−46.78	3.3	4
14325000	South Fork Coquille R. at Powers	−26.06	−26.06	−24.71	−29.03	1	4
14207500	Tualatin R. at West Linn	−40.07	−40.07	NA	NA	0	1

^a Model 1 = $Q/P - 1$, Model 2 = $Q/P - PET$, Model 3 = $Q/P - \% SNC$, Model 4 = $Q/P - PET + \% SNC$.

(e.g., broadleaf, conifer, mixed), canopy cover, quadratic mean diameter of all dominant and codominant trees, and basal area of live trees and Douglas-fir. The dominant class was determined for each watershed polygon per year using zonal statistics in ArcMap 10.5. As a more detailed investigation, we considered separately the spatial average of canopy cover of live trees by watershed polygon per year. Because GNN vegetation structure (class) data are considered more reliable than composition (species) data, we used this analysis to provide insights into potential vegetation changes. Additional research is required to determine vegetation structure and composition changes with the spread of SNC disease.

3. Results

Over the 20-years (1996–2015) of available aerial surveys in the Coast Range of Oregon, Swiss needle cast (SNC) disease increased by approximately 4.2-times (Fig. 1) (Ritókóvá et al., 2016). However, this response was spatially heterogeneous across the region. We captured that variability in our study catchments, with the area impacted by SNC ranging from 1.0 to 90.5% (Table 2; Fig. 4). The hydrologic variables were also highly variable across study catchments. Mean annual precipitation ranged from 1300 mm (Tualatin River) to 3100 mm (Wilson River; Table 2). Mean annual discharge was generally correlated with precipitation trends (Fig. S1), with the lowest discharge (0.7 m) for Tualatin and highest for Wilson (2.5 m). The mean annual runoff ratios (Q/P) ranged from 0.48 to 0.88 (Table 2).

Trend analysis of the primary climatic variables across the period of record available for each (15–26 years) of the study catchments indicated relatively stable trends. Specifically, there was no evidence for trends in annual precipitation ($p = .11-.98$; Table S1), air temperature ($p = .16-.90$; Table S2), or potential evapotranspiration ($p = .21-.98$; Table S3). Despite no evidence for trends in climatic variables, there was strong evidence ($p < .01$) for decreasing trends in actual ET in six of the study catchments (Table S4). Interestingly, there was also suggestive evidence ($p = .10$) for an increasing trend in ET in the Yaquina River catchment, which was the most severely affected by SNC (Table S4).

Table 5
ARIMA model results for five sites with significant Q/P trends ($P < .05$), showing coefficients for modeling including % SNC as well as % SNC + PET.

USGS site no	Station name	Arima	% SNC	Coefficients PET+% SNC	
				PET	% SNC
14305500	Siletz River at Siletz	(0,0,0)	0.006	−2.00E−04	0.0059
14301500	Wilson River near Tillamook	(0,1,0)	0.013	−8.00E−04	0.0089
14306500	Alsea River near Tidewater	(0,0,0)	0.010	−9.00E−04	0.0086
14301000	Nehalem River near Foss	(0,0,0)	0.010	−0.0012	0.017
14171000	Marys River near Philomath	(0,0,0)	0.013	6.00E−04	0.0153

Time trend analysis also provided moderate to strong evidence that the increase in area disturbed by SNC contributed to increases in runoff ratios (Q/P) in many of the Coast Range catchments in our study. Specifically, there was moderate evidence ($.01 \leq p < .05$) for increases in three of the 12 study catchments with percent area impacted by SNC rising to 10.8 to 16.5% of the catchment by the end of the analysis period (Table 3). The runoff ratios in these catchments increased ~10% in Alsea, 13% in Nehalem, 14% in Marys over the analysis period. Comparatively, there was strong evidence ($p < .001$) that Q/P increased over the period of study in the Wilson River (26.7% SNC) and Siletz River (58.4%) catchments. The increases in Q/P in these more severely affected catchments increased by ~21% in Siletz and 27% in Wilson (Fig. 4).

The five catchments with increased Q/P were some of the more heavily impacted areas, with SNC disturbance covering >10% of the catchment area. All sites with a detectible trend in runoff ratio ($p < .05$) had preferred ARIMA models (lowest AIC) that included percent SNC, or had preferred models indistinguishable ($\Delta AIC < 4$) from ones including percent SNC (Table 4). The ARIMA models suggest positive coefficients for percent SNC, ranging from 0.006 to 0.017 $Q/P y^{-1}$ (Table 5). These models predict an increase in runoff ratio of ~6–17% for a 10% area impacted by SNC. When included, PET had a small, usually negative coefficient, indicating more water loss with increasing PET. Comparatively, in five of the study catchments where there was no evidence for change in Q/P , the area of SNC disturbance was <10% (Tables 2 and 3).

However, increases in runoff ratios with increasing SNC disturbance were not observed in all catchments. Interestingly, there was no evidence for Q/P increases in two of the most heavily impacted catchments—the Yaquina River (91% SNC) or Trask River (43% SNC). For the Yaquina River catchment, in particular, there was suggestive evidence for an increase in ET over the analysis period ($p < .10$), despite presumably lower transpiration for SNC-impacted Douglas-fir in this watershed. General nearest neighbor (GNN) vegetation data suggest a structural or composition change in the forest type for Yaquina during 1990–2001, whereby composition changed from conifer-dominated to broadleaf-dominated, then back to conifer after 2001 (Fig. 5). The forest composition change back to conifer coincided with the first severe peak in SNC incidence in 2001–2002 (Fig. 3). After 2001–2002, and the peaks in the SNC epidemic in 2007–2008 and 2010–2014, GNN data for Yaquina indicated a gradual increase in total basal area of live trees along with decreasing basal area of Douglas-fir (Fig. 6). However, due to problems related to distinguishing Douglas-fir and other conifers based on aerial images, the changes in the basal area of Douglas-fir are speculative. The Luckiamute catchment had a similar trend in vegetation composition, changing from small/medium conifer to open, but then returned to small/medium conifer by the end of the study period (Fig. 5), accompanied by an increase in total basal area of live trees (Fig. 6). In contrast to Yaquina, this catchment had a low SNC footprint (5%) and no detectible changes in hydrologic variables (Tables 2 and 3).

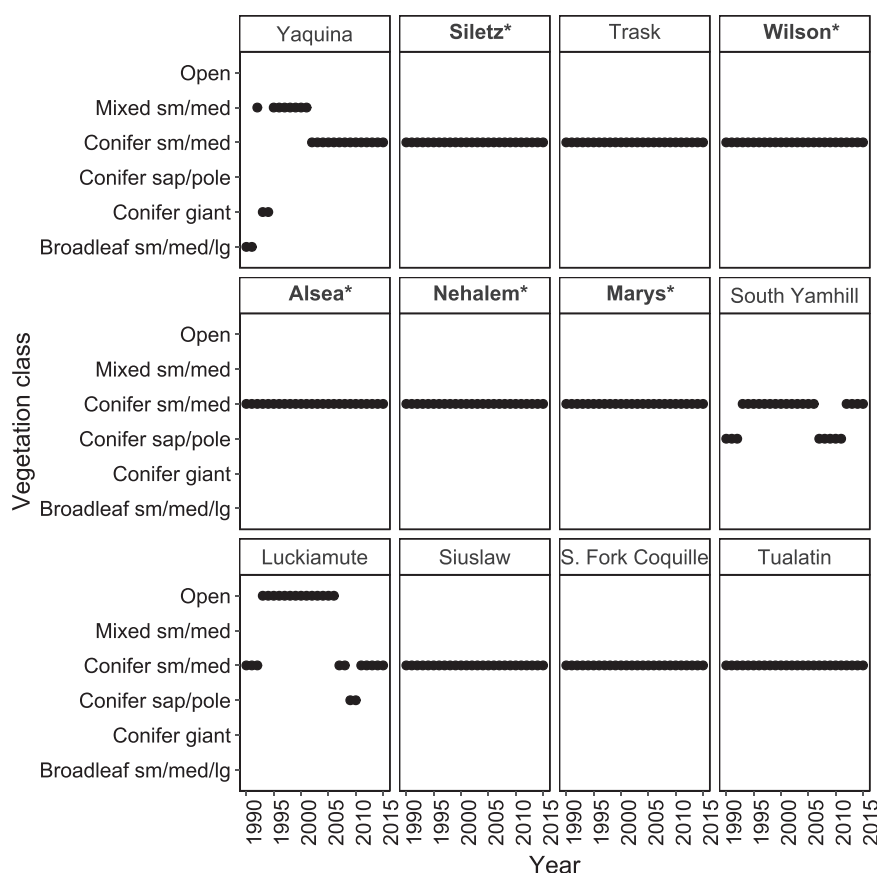


Fig. 5. Gradient Nearest Neighbor (GNN) estimates of vegetation class from 1990 to 2015 based on composition and structure for each study catchment. The Yaquina River catchment, which had the greatest area affected by Swiss needle cast had a change in vegetation class in 2001 to small (sm)/medium (med) conifers. * = Significant changes in Q/P.

For the Trask River catchment, which also had one of the highest areas disturbed by SNC, there was also no discernible trend in the runoff ratio. However, unlike the Yaquina catchment there was not any evidence from the GNN data of a structural change in the forest type. These negative results could be due to a number of factors, including (a) a muted response to the SNC press disturbance, (b) other activities or disturbances in the catchment, or (c) the coarse resolution of the GNN data, which may not have captured a compensatory vegetation response in this catchment.

Statistically, there was no evidence for trends in the timing of annual minimum (Table S6) or maximum (Table S7) streamflow in any of the 12 study catchments. Similarly, there was no evidence for trends in annual minimum (Table S8) or maximum (Table S9) discharge in 11 of the 12 study catchments. The lack of effects of SNC on streamflow timing and peak flows were not surprising in this wet, Mediterranean region where the majority of precipitation falls as rain during the winter, which is out of phase with the period of peak transpiration in this region. However, the lack of effect of SNC on low flows was surprising as the timing of these flows is coincident with the period of peak transpiration and likely peak effects of SNC on affected Douglas-fir. We postulate that the lack of observable effect on low flows is likely due to the coarseness of the available streamflow data, but this requires further investigation to provide more robust evidence to support or refute.

4. Discussion

This study was the first to document a catchment scale hydrologic response to a forest pathogen, *Nothophaeocryptopus gaeumannii*, which causes Swiss needle cast (SNC), the most damaging foliage disease of coastal Douglas-fir in the U.S. Pacific Northwest. Our analysis demonstrates an increase in runoff ratio proportional to the area of

the catchment affected by SNC. In general, we identified a threshold of ~10% SNC beyond which streamflow increased in a manner proportional to the area affected by the disease. The increased streamflow in catchments impacted by SNC is likely a result of the chronic effects of the disease on the hydraulic architecture (i.e., reduced needle retention, sapwood area, and sapwood permeability) of the affected trees (Manter et al., 2000; Manter and Kavanagh, 2003; Shaw et al., 2011). At a catchment scale, these effects would decrease interception and transpiration losses, potentially leading to increased soil water storage, groundwater recharge, and runoff (Fig. 7A) (Nijzink et al., 2016; Phillips et al., 2016). Although, increased streamflow after vegetation removal by a pulse disturbance (e.g., wildfire, forest harvest) has been well established (Bates and Henry, 1928; Bethlahmy, 1974; Bosch and Hewlett, 1982; Brown et al., 2005; Stednick, 1996), this is the first evidence of a similar but more nuanced trend in streamflow caused by a more gradual disturbance—a forest disease.

A second pattern we revealed with our analysis was a lack of streamflow response in the catchments most severely affected by SNC. For instance, the Yaquina River catchment had the greatest area affected by SNC (90.5%), yet we did not observe any changes in runoff ratios. This nuance illustrates the difficulty in predicting the response of streamflow to forest cover change, in part, due to high variability in subsurface storage and differential forest access to available water (McDonnell et al., 2018).

While observations of hydrologic processes were beyond the scope of this project, we posit a couple explanations for the lack of streamflow response, which could be studied further. It is plausible that compensatory transpiration by understory or co-dominant vegetation that wasn't affected by the SNC pathogen may have contributed to the lack of change in streamflow in the heavily impacted catchments (Fig. 7B) (Biederman et al., 2015; Bladon et al., 2006; Reed et al., 2014). In

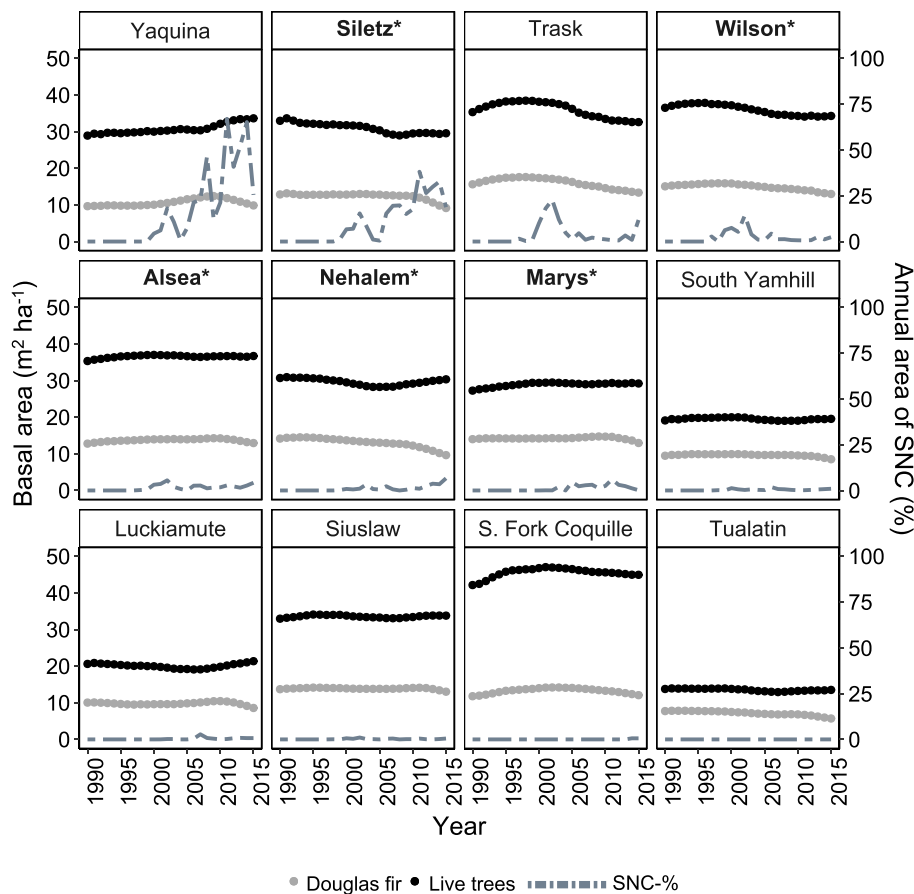


Fig. 6. Annual total basal areas ($\text{m}^2 \text{ha}^{-1}$) for live trees (black dots) and Douglas-fir (grey dots), and SNC coverage (%) (grey dashed line) from 1990 to 2015 for the 12 study catchments. If no SNC polygons were mapped, 0% SNC was assumed. * = Significant changes in Q/P.

catchments severely affected by SNC, like the Yaquina, understory trees (e.g., western hemlock, hardwood species) may increase their transpiration rates and outcompete the weakened Douglas-fir causing increased mortality (Maguire et al., 2011). We also observed evidence for compensatory transpiration and increased growth rates in the spatial biomass data (GNN), where total basal area increased in the Yaquina catchment, despite the high SNC footprint (Fig. 5; Fig. 6). This potential explanation for the lack of streamflow response is also consistent with previous observations that younger trees (unaffected understory trees) tend to have higher rates of evapotranspiration due to several physiological differences from older, overstory trees (e.g., higher sapwood area, higher sapflow per unit sapwood area, higher concentration of leaf area in the upper canopy, less ability to limit transpiration) (Moore et al., 2004; Perry and Jones, 2017).

However, it is also plausible that increased abiotic evaporation may have offset the overall reductions in transpiration by affected Douglas-fir, constraining the expected streamflow increases (Fig. 7B) (Biederman et al., 2014, 2015). Specifically, reduced canopy shading in catchments most severely impacted by SNC could lead to increased incident shortwave radiation, wind speed, and vapor pressure deficit, resulting in increased evaporation and limited water availability (Grant et al., 2013; Kaiser et al., 2013). For forest and water resource managers to make informed decisions in response to SNC, future research should quantify the relative role of vegetation feedbacks or subcanopy vapor loss effects on runoff ratios in catchments chronically impacted by SNC.

The final pattern we observed was no observable changes in ET or runoff in the absence of SNC or under low SNC occurrence (<10% of catchment area) (Fig. 4). Moreover, we did not observe any detectable

trends in precipitation or potential evapotranspiration over the period of study. These were important contextual observations for the first two major findings from this research, suggesting that the changes in runoff ratio we observed were predominantly a result of the SNC epidemic in the Oregon Coast Range and not due to climatic factors. However, it is important to note that there may be slight changes in catchment storage and runoff in catchments with low SNC occurrence, which are difficult to quantify, but could persist for long periods. As such combining observations from long-term gages with robust hydrologic models could provide valuable additional hydrologic forecasting (Penn et al., 2016).

Given that forest diseases, such as SNC, are likely to continue to increase globally (Seidl et al., 2017), the effects on water supply may become more pronounced with impacts to water quantity and aquatic ecosystem health. For example, pulse disturbances, such as timber harvest and wildfire, have been associated with changes in streamflow and suspended sediment (Bywater-Reyes et al., 2018; Wondzell and King, 2003), nutrient concentrations and yields (Rust et al., 2018; Vitousek and Melillo, 1979), with cascading impacts on fish populations (Silins et al., 2014). Similarly, chronic defoliation due to SNC could influence riparian shade, increasing stream temperature and overall aquatic ecosystem health (Kaylor and Warren, 2017; McCullough et al., 2009; Wondzell et al., 2019). In addition to stream impacts, press disturbances like SNC can affect soil moisture, soil temperature, and below-ground carbon allocation (Allen and Kitajima, 2013; Shi et al., 2019). As pressures on water supply and forest health continue to grow (Cohen et al., 2016; Vörösmarty et al., 2010), the corollary effects of foliar diseases in forests on merit further study.

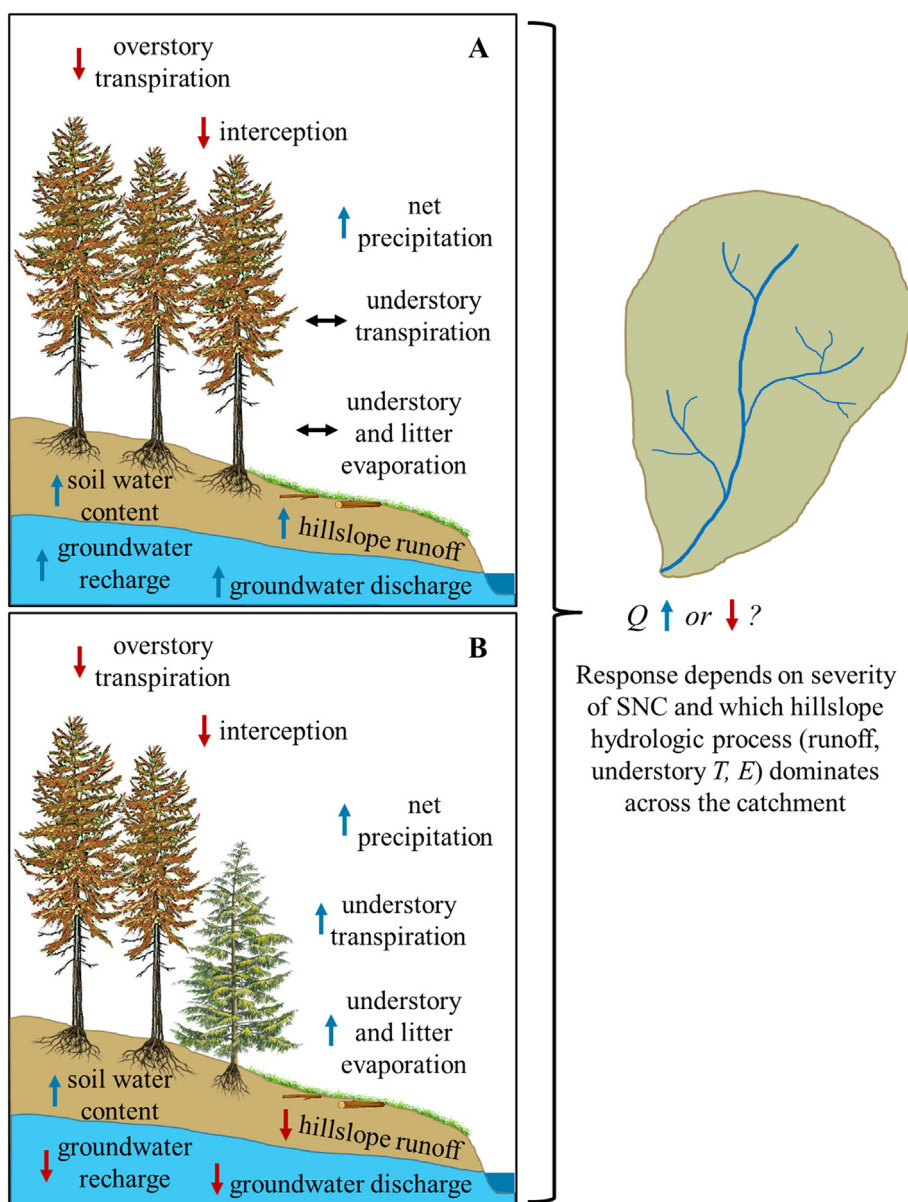


Fig. 7. Conceptual models of the effects of Swiss needle cast disease on hillslope hydrologic processes, resulting in differential streamflow responses at the catchment-scale. (A) Douglas-fir dominated stands affected by a moderate severity Swiss needle cast outbreak may experience increased hillslope runoff and groundwater discharge to streams, resulting in increased runoff ratios. (B) Mixed conifer-Douglas-fir stands severely impacted by Swiss needle cast disease may experience a compensatory growth response and elevated transpiration from understory tree species (e.g., hemlock) and/or elevated evaporation rates from the understory and litter layer, resulting in decreased runoff ratios.

5. Conclusions

We combined 20 years of SNC severity data and streamflow records from 12 catchments to demonstrate that a chronic, press disturbance can affect runoff ratios. In general, streamflow increased as the proportion of the catchment affected by SNC increased. The results also suggested that mixed species stands may be buffered against both the impact of the SNC disease and the changes in streamflow that it can cause. Faced with the increasing occurrence of forest disturbance and extreme weather phenomena driven by global climate change (Allen et al., 2010, 2015; Seidl et al., 2017), it may become increasingly important to switch the emphasis of forest management towards maximizing ecosystem resilience. Thus, forest management should favor genetically diverse mixed species stands, since they appear to be more resilient to SNC and other forest pathogens (Ennos, 2015; Mildrexler et al., 2019). Additionally, given the observed effect of SNC on runoff ratios, there may be associated effects on water quality (sediment, turbidity,

temperature, nutrients) with important implications for aquatic ecosystem health and downstream community drinking water supply that should be investigated in future research.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.07.127>.

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