The Role of Natural Vegetative Disturbance in Determining Stream Reach Characteristics in Central Idaho and Western Montana

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Abstract

We evaluated the relationship between natural vegetative disturbance and changes in stream habitat and macroinvertebrate metrics within 33 randomly selected minimally managed watersheds in central Idaho and western Montana. Changes in stream reach conditions were related to vegetative disturbance for the time periods from 1985 to 1993 and 1993 to 2000, respectively, at the following three spatial scales; within the stream buffer and less than 1 km from the evaluated reach, within the watershed and within 1 km of the stream reach, and within the watershed. Data for stream reaches were based on field surveys and vegetative disturbance was generated for the watershed above the sampled reach using remotely sensed data and geographical information systems. Large scale (>100 ha) vegetative disturbance was common within the study area. Even though natural vegetative disturbance rates were high, we found that few of the measured attributes were related to the magnitude of vegetative disturbance. The three physical habitat attributes that changed significantly were sinuosity, median particle size, and percentage of undercut bank; each was related to the disturbance in the earlier (1985-1993) time frame. There was a significant relationship between changes in two macroinvertebrate metrics, abundance and percent collectors/filterers, and the magnitude of disturbance during the more recent time period (1993-2000). We did not find a consistent relationship between the location of the disturbance within the watershed and changes in stream conditions. Our findings suggest that natural vegetative disturbance within the northern Rocky Mountains is complex but likely does not result in substantial short-term changes in the characteristics of most stream reaches.

Introduction

Current and historic geoclimatic conditions govern stream morphology (Montgomery and Buffington 1997, Ebersole et al. 1997). Physical components and processes within this setting, such as water and sediment movement through a watershed, form the basis for understanding how stream channels develop and are maintained (for reviews see Leopold et al. 1964 or Knighton 1998). These physical processes, however; are mediated by vegetation. The presence of vegetation can reduce peak stream flows (Hicks et al. 1991), decrease overland flow, and trap sediment (Gregory et al. 1991, Belt and O'Laughlin 1994), while the loss of vegetation can have the opposite effects (Minshall et al. 1989, Gresswell 1999, Benda et al. 2003). Since changes in vegetation alter physical processes, changes in vegetation can ultimately change channel form (Benda et al. 2003) as well as the composition of aquatic biota dependent upon that channel form (Rieman and Clayton 1997, Minshall et al. 2001, Dunham et al. 2003).

Natural disturbance processes such as fire, wind throw, and insect activity alter vegetative structure and function (Agee 1993, Frelich 2002). Changes in vegetation that result from these natural processes vary in intensity (the amount of energy released), severity (vegetative mortality), and magnitude (spatial scale) (Frelich 2002). While each of these processes can lead to altered aquatic conditions, vegetative disturbances that are intense, severe, and proximate to streams have the greatest likelihood of causing changes in aquatic systems (Gresswell 1999).

While there have been a number of studies evaluating the relationship between natural vegetative disturbance and stream channel conditions, much of the sampling effort has been opportunistic focusing in areas of high public interest (e.g., the

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Greater Yellowstone fires; Minshall et al. 1989) or where the disturbance created a large and visible effect on a stream channel (Benda et al. 2003). In these studies, sampling effort has generally focused on areas where the vegetative disturbance was intense, severe, and proximate to a stream and disturbances were found to have an immediate and measurable impact on stream attributes (Potyondy and Hardy 1994, Benda et al. 2003).

Opportunistic sampling is not based on a probabilistic sample design, and as such it is difficult to ascertain whether results from these studies are representative of how vegetative disturbance affects stream attributes in general. So while past studies have greatly improved our understanding of the relationship between vegetative disturbance and streams, we still have much to learn about the more general relationship between how natural vegetative disturbance, the distance of this disturbance from evaluated stream reaches, and/or the time since the disturbance are related to stream characteristics. To better understand the role vegetative disturbance plays in determining stream channel characteristics, it is necessary to have a sample design that includes numerous watersheds subject to a range of vegetative disturbance events.

Understanding how natural vegetative disturbance shapes stream characteristics is important because federal land management agencies are trying to design timber management strategies that mimic these disturbances (Office of the White House 2002). Describing how the location, extent, and timing of natural vegetative disturbance is related to changes in stream conditions should therefore facilitate quantifying allowable levels of change in stream conditions following human-caused vegetative disturbance.

The objective of this paper is to determine how stream characteristics are altered by the magnitude and proximity of vegetative disturbance and whether there is a time lag between disturbances and changes in stream characteristics. We will do this by using a probabilistic sample of watersheds to: 1) describe the spatial extent and temporal variability of vegetative disturbance within and among watersheds: 2) estimate how often vegetative disturbance occurs proximate to any given stream reach: and 3) relate how the location, timing, and magnitude of these vegetative disturbances affect physical and biological stream characteristics.

Study Site and Methods

We evaluated vegetative disturbance and stream conditions within 33 sub-watersheds (Figure 1). These sub-watersheds were within Frank Church/River of No Return Wilderness, Selway Bitteroot Wilderness, and on nearby federally managed watersheds that have seen minimal land management activities (minimally managed in these cases was defined as less than 0.5 km km^{-2} road density, <5% of the watershed subject to timber harvest, and no grazing in the last 30 years). Watershed areas ranged from 450 to 9000 hectares (Table 1), were primarily underlain by granitic geologies, and managed (>99%) by the U.S. Forest Service and Bureau of Land Management. We evaluated these sites because the direct impact of human disturbance on both stream and vegetative conditions was low.

Elevations within the study area ranged from 600 m to over 3000 m. The dominant vegetation at lower elevation was sagebrush (*Artemisia tridentata*), mountain mahogany (*Cercocarpus ledifolius)*, and ponderosa pine (*Pinus ponderosa)* on the south aspect slopes and Douglas-fir (*Pseudotsuga menziesii*) on north aspects. Vegetation on mid-elevation slopes was primarily lodgepole pine *(Pinus contorta* var. *latifolia),* while at higher elevations there were Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*). Most vegetation types within this area evolved with fire as a component of natural processes (Forest Service 2003). For many of these vegetation types, insect infestations often expand the extent of mortality in areas subject to fire (Agee 1993).

We determined the watersheds to be evaluated probabilistically using the approach described in Kershner et al. (2004a). This approach identified larger scale watersheds (≈ 5th Hydrologic Unit Code (HUC) scale) containing approximately 25 sub-watersheds (≈ 6th HUC scale). The larger scale watersheds were randomly sampled in a manner that ensured that samples were spread across the Interior Columbia River Basin (Stevens and Olsen 1999), and then the sub-watersheds within the larger watershed were selected at random.

We determined stream characteristics by evaluating the lowermost low gradient stream reach (<3%) within each of the selected watersheds. Low gradient reaches were evaluated because they are most likely to be sensitive to changes caused by

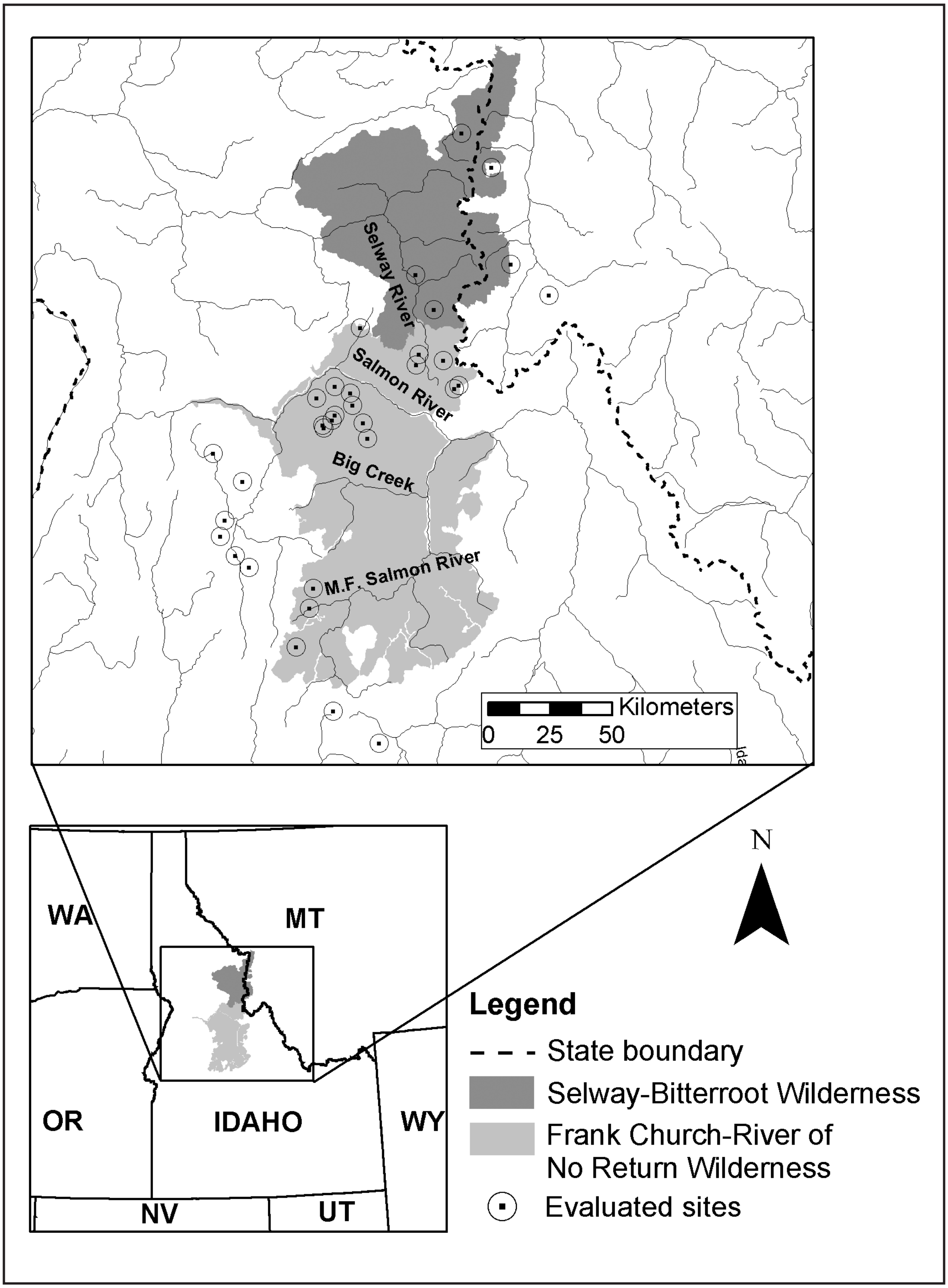

Figure 1. Locations of sites evaluated for this study.

TABLE 1. General description of each of the evaluated watersheds. NF stands for North Fork. WF Chamber is the West Fork Chamberlain.

Stream	Area (ha)	Elevation (m)	Precipitation (m)	Basin Slope Tree	Cover (%)
Bad Luck	3060	982	0.87	54	48
Bargamin	8985	1470	1.05	29	97
Bear	882	1976	1.06	33	69
Bench	1163	2122	1.10	35	81
Blodgett	4175	1646	1.15	54	55
Cayuse	3058	1634	0.89	35	94
Chamberlain	6972	1805	1.00	27	89
Cougar	3945	1207	1.00	51	80
Dillinger	625	1971	1.04	17	98
Flossie	1484	1723	0.85	22	97
Fourmile	1984	1727	1.27	50	85
Goat	1288	1625	1.06	42	92
Hotspring	454	2082	0.76	14	99
Indian	8261	1409	1.05	45	93
Little Pistol	4370	1825	1.32	45	70
McCalla	7446	1497	0.82	26	86
Meadow	1076	1951	0.69	45	93
Moose	3569	1848	0.96	22	85
NF Buckhorn	1212	1823	0.96	49	67
NF Fitsum	3505	1329	1.02	47	71
NF Trapper	1967	1664	1.04	66	48
Piah	973	1757	1.03	30	83
Pistol	5799	1841	1.31	39	79
Queen	823	1942	0.81	17	99
Reynolds	4360	1707	0.99	35	90
Storm	4380	1659	0.97	43	92
Sulpher	6214	1816	1.27	29	72
Swet	2745	1784	1.04	44	92
Trout	2102	1915	0.99	22	96
Warm Spring	8865	1494	0.86	43	89
WF Chamber	5234	1695	0.97	22	82
Whimstick	6515	1709	0.72	30	89
White Sands	4809	1482	1.45	45	75

disturbance (Montgomery and MacDonald 2002). The lowest response reach was selected because this reach is thought to integrate the cumulative disturbances within the watershed (Kershner et al. 2004a).

The surveyed stream reaches were 20 times the bankfull width in length, but had a minimum length of 80 m and a maximum length of 500 m. Field survey crews evaluated a number of physical characteristics within each reach that will be described later. These crews also collected benthic macroinvertebrate samples from several riffles within each reach. Macroinvertebrates were sorted and identified using criteria developed at the National Aquatic Monitoring Center (2005). Reach locations were identified using global positioning systems. Field surveys were conducted during the summers of 2001-2003.

We used geographical information systems (GIS; Environmental Systems Research Institute (ESRI) ArcGIS Version 8.3) to consistently determine the watershed size and the locations of streams within each of the 33 evaluated watersheds. We used the downstream location of the evaluated stream reach and 10-m Digital Elevation Models (DEMs) to automatically delineate the catchment above the sampled reach and the stream network (Tarboton et al. 1991, Maidment and Djokic 2000). To assess the accuracy of this process, we compared GIS-delineated basins and streams with hand-delineated basins and stream layers from 1:24000 cartographic feature files (CFF). Because of the large amount of relief in this area we found little difference in watershed area (the overall average difference was 2%), and minor differences in the exact locations of the GIS-delineated higher-order streams (≥ second order based on CFF). We also found that our GIS-delineated streams expanded the extent of first-order streams by approximately 10% (for a review of possible hydrologic errors when using GIS see Maidment and Djokic 2000 and Baker et al. 2006).

The extent and location of vegetative disturbances within the evaluated catchments were determined using 30-m resolution satellite-derived Normalized Difference Vegetation Index (NDVI) from Landsat images. The NDVI is a measure of greenness, or photosynthetic activity (Jensen 1996) and is increasingly used as a tool for remotely assessing environmental change (Petorelli et al. 2005), including mapping of fires (Goetz et al. 2006, Hamill and Brodstock 2006). Vegetative disturbance through time was estimated by: 1) acquiring cloud-free satellite images for three time periods (late August 1985, mid September 1993, and early October 2000); 2) co-registering these images to one another; and 3) calculating the changes in NDVI for the two time periods (1985-1993 [8 years] and 1993-2000 [7 years]). We used a high NDVI change threshold to ensure differences between the two time periods were due to changes in vegetation rather than to intra-annual changes in vegetation phenology (Zhang et al. 2003).

To ensure changes in NDVI were accurately capturing true changes in vegetation, we visually compared the area mapped with NDVI as undergoing vegetative disturbance to recent (2004-2006) high resolution (1 m) imagery. The large NDVI polygons (> 100 ha) found in 24 of the watersheds overlapped with areas where the imagery indicated a stand-replacing fire had occurred. The NDVI polygons often included areas adjacent to these stand-replacing fires. These areas were likely either affected by mixed-severity fires or insect activity that followed the fire. Causes for the vegetative disturbance in the remaining watersheds included avalanche chutes (the disturbance was primarily near or in these chutes in four cases) and changing water levels in meadows (observed in two cases and possibly associated with beaver activity); in three cases there was no obvious cause. In these three cases, the disturbance was likely a result of insect activity or windthrow because mapped disturbances were small and associated with conifer stands.

We calculated disturbance at three scales within each watershed. First the watershed was divided into areas defined as proximate (≤ 1 km map distance) and distant (>1 km map distance) from the evaluated reach. The proximate area was further divided into two subcategories: ≤ 90 m of a delineated stream (within stream buffer) and > 90 m of a delineated stream (outside of stream buffer). A GIS approach was used to combine the NDVI change and the watershed data so that we could calculate the percent of area with vegetative disturbance at each of three scales: 1) within the stream buffer and ≤ 1 km from the evaluated reach; 2) within the watershed and within 1 km of the stream reach; and 3) within the watershed. This was repeated for two time periods (1985-1993 and 1993-2000).

We used these data to determine the proximity of the vegetative disturbance to the evaluated reaches and whether the rates of disturbance were similar for each of the three distances or the two time frames. The null hypotheses were that the disturbance at each of the three spatial scales and the two time periods did not differ significantly (or since the first time period was slightly longer (8 years vs. 7), that the disturbance rate in this time frame was slightly greater). We used a paired t-test (Dowdy and Wearden 1983) to test for differences in disturbance rates in the two time periods.

Because stream reaches just downstream of vegetative disturbance are more likely to be directly or indirectly affected by vegetative disturbance (Gresswell 1999, Benda et al. 2003), we evaluated how many watersheds had extensive vegetative disturbance within 1 km of the measured reach. The probabilistic nature of our samples allowed us to infer the proportion of stream reaches within the sample population that likely had undergone a similar level of vegetative disturbance. We considered proximate areas with vegetative disturbance >15% to have been subjected to considerable disturbance: this value is often used to represent the amount of human-induced vegetative disturbance that results in unwanted changes in hydrologic conditions (Ager and Clifton 2005). Confidence intervals (90%) for these estimates were derived directly from the binomial distribution.

We then evaluated how the magnitude, timing and location of vegetative disturbance within a watershed (the independent variables) were related to 11 physical stream reach characteristics: sinuosity, width-to-depth ratio, median stream particle size, percent fines (< 4 mm), bank stability, bank angle, percentage of undercut banks, undercut depth, percent pool, residual pool depth, and large woody debris count (3 m long × 0.1 m diameter; see Kershner et al. 2004a for protocols). We also evaluated the effects these independent variables had on 14 macroinvertebrate metrics, four of which are thought to be specifically affected by a natural vegetative disturbance (Minshall et al. 1989) and 10 of which are thought to be related to human-induced disturbances (Karr and Chu 1999; pages 76 and 134).

Before determining the relationship between natural disturbance and stream conditions, we wanted to account for variability due to the inherent differences among the sampled streams and watersheds. An example of this concern is that the expected median stream substrate particle within a reach is dependent on the stream size and gradient (Olsen et al. 1997, Yang 2003). These types of relationships are important to account for in order to ensure that significant relationships between stream conditions and natural disturbances are not driven by landscape or stream characteristics. We identified seven landscape and stream characteristics not generally thought to be directly related to vegetative disturbance that could explain natural variation in the response variables (Kershner et al. 2004b). The possible covariates were basin area, bankfull width, average basin slope, gradient, average precipitation, elevation, and percentage of the basin covered by trees. Catchment areas were calculated as described above. The average basin slope was determined for each delineated basin using the 10-m DEM's and the spatial analyst component of ArcGIS. Average precipitation was derived using data from the Interior Columbia Ecosystem Basin Ecosystem Project data layers (1997). Tree cover was determined using the National Land Cover Data (United States Geological Survey 1992). Stream reach elevation was derived from the DEM located at the lower most point of the reach. Stream reach gradient and bankfull width were determined by field measurements (except for three gradient values that, because of broken hand levels, came from DEMs).

We used stepwise regression to determine which set of covariates should be used. Statistical significance was defined as $P < 0.10$ in order for an attribute to enter into or stay in the model. To ensure multiple highly correlated covariates were not incorporated into these models, we used a variance inflation factor (VIF) > 10 to preclude inclusion of correlated attributes into the model. When attributes had a VIF > 10, the attribute with the lower significance value was removed.

Following the incorporation of significant covariates into our models, we explored the relationships between location and magnitude of vegetative disturbance and each of the stream characteristics. Data from both time periods (1985-1993 and 1993-2000) were included. The objective of this step was to determine if one or more of the six different vegetative disturbance indices (three areas × two time periods) explained observed variation in the measured stream attributes. We again used stepwise regression to determine which of these indices of vegetative disturbance were related to the dependent variables. Significance was defined as being $P < 0.10$ to enter into or stay in the model. We used a VIF > 10 to preclude inclusion of correlated attributes into the model. When attributes had a VIF > 10, the attribute with the lower significance value was removed.

Results

We saw three basic patterns of vegetative disturbance within the 33 watersheds (Table 2; Figure 2): 1) essentially no disturbance (< 5 hectare change in vegetation within a time period); 2) small-scale patchy vegetative disturbances that were likely a combination of insect mortality, avalanches, beaver activity, small fires, or the watershed being on the perimeter of a larger fire located outside the evaluated watershed (operationally identified as no single delimited disturbance polygon within a watershed > 100 hectares in size); and 3) large-scale disturbances that were primarily large fires (operationally identified as at least one delimited disturbance polygon within a watershed that was > 100 hectares in size). The magnitude of vegetative disturbance differed greatly between the two time periods. The number of watersheds experiencing large fires was three times greater in the 1993-2000 timeframe than in the 1985-1993 timeframe (19 with large fires vs. 6), and the average percent of the watershed that underwent change in vegetation increased from 5.1% in the 1985-1993 time period to 25.6% in the 1993-2000 time period (even though the second timeframe was a year shorter; Table 3). A paired t-test indicated that the percent of the watersheds showing changes in vegetation differed significantly between these two time periods ($P < 0.10$).

TABLE 2. Watershed area and area within the watershed in which vegetation was disturbed in each of the two time periods. Vegetative change is expressed as the number of hectares and the percent of watershed disturbed during the time period Vegetative change categories are: N = none (< 5 ha), S = small-scale vegetative disturbance (>5 ha but no single disturbance polygon >100 ha, and L = large-scale disturbance (a disturbance polygon > 100 ha). NF is the North Fork, while WF Chamber is the West Fork Chamberlain.

		Vegetative Change (ha[%])		Vegetative change category	
Stream	Area (ha)	1985-1993	1993-2000	1985-1993	1993-2000
Bad Luck	3060	130 (4)	17 (<1)	S	S
Bargamin	8985	41 (<1)	93 (1)	S	S
Bear	882	46 (5)	60 (6)	S	S
Bench	1163	16 (1)	16 (1)	S	S
Blodgett	4175	244 (6)	170 (4)	S	S
Cayuse	3058	3 (<1)	754 (24)	N	L
Chamberlain	6972	569 (8)	3553 (51)	L	L
Cougar	3945	224 (6)	121 (3)	S	S
Dillinger	625	0 (<1)	10 (2)	N	S
Flossie	1484	191 (13)	1247 (84)	L	L
Fourmile	1984	66 (3)	1140 (58)	S	L
Goat	1288	18 (1)	743 (58)	S	L
Hotspring	454	0 (<1)	357 (79)	N	L
Indian	8261	63 (1)	1032 (13)	S	L
Little Pistol	4370	45 (1)	246 (6)	S	L
McCalla	7446	650 (9)	2486 (33)	L	L
Meadow	1076	4 (<1)	60 (6)	N	S
Moose	3569	1187 (33)	629 (18)	L	L
NF Buckhorn	1212	71 (6)	347 (29)	S	L
NF Fitsum	3505	306 (9)	222 (6)	L	S
NF Trapper	1967	114 (6)	94 (5)	S	S
Piah	973	3 (<1)	382 (39)	N	L
Pistol	5799	155 (3)	145 (3)	S	S
Queen	823	0 (<1)	596 (72)	N	L
Reynolds	4360	1 (<1)	95 (2)	N	S
Storm	4380	3 (<1)	2886 (66)	N	L
Sulpher	6214	284 (5)	168 (3)	S	S
Swet	2745	15 (<1)	1045 (38)	S	L
Trout	2102	24 (1)	1143 (54)	S	L
Warm Spring	8865	16 (<1)	1356 (15)	S	L
WF Chamber	5234	17 (<1)	2612 (50)	S	L
Whimstick	6515	2921 (45)	81 (1)	L	S
White Sands	4809	71 (2)	789 (16)	S	L

While there were significant differences in the rates of vegetative disturbance between the two time periods, the distributions of these differences were not normally distributed. This non-normal distribution likely has little bearing on the conclusion since most statistical models are robust to departures from normality (Zar 1996), and using raw data results in conservative (larger) estimates of variance. These data were not normally distributed because more watersheds than expected had little disturbance in either period; 14 of the 33 (42%) had less than 10% of the vegetation disturbed in either time frame (Table 2). So while the mean disturbance rate for the second time period was high, the plurality of watersheds still saw little or no natural vegetative disturbance in the 15 year analysis time frame. Many watersheds did not have large-scale disturbance so the median disturbance value was less than the mean disturbance value (Table 3).

All three scales of evaluation—the whole watershed, within 1 km of the reach and within

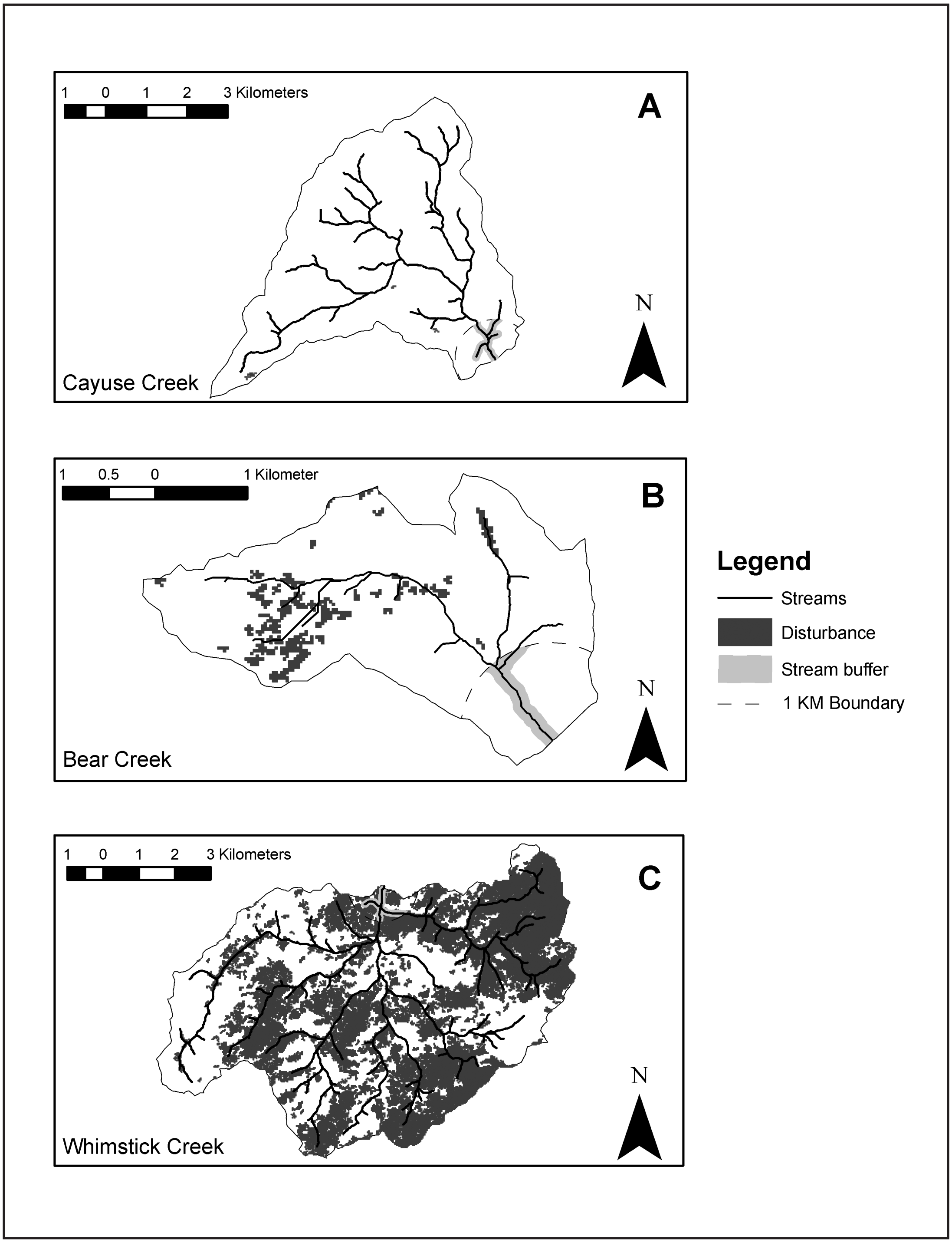

Figure 2. Examples of the ranges of natural vegetative disturbance in three sampled watersheds. A is an example of no disturbance, B is an example of small-scale disturbance, and C is an example of large-scale vegetative disturbance. All data are from the 1985 to 1993 time frame.

TABLE 3. Percent of the area within each of the three distance categories determined to have undergone vegetative disturbance within the time frame. *Watershed* is the percent of the entire catchment with signs of vegetative disturbance. *Near* was the area within the watershed and 1 km of the downstream point of the evaluated reach. *Near, within buffer* was the area within the watershed that within 1 km of the downstream point of the evaluated reach, and within 90 m of a stream.

	1985-1993			1993-2000		
	Watershed	Near	Near, Within Buffer	Watershed	Near	Near, Within Buffer
Average	5.1	3.4	4.5	25.6	27.9	26.0
Median	1.4	1.0	0.7	15.3	16.7	10.4
Minimum	0.0	0.0	0.0	0.6	0.0	0.0
Maximum	44.8	39.5	59.1	84.0	61.3	98.8

90 m of a stream within 1 km of the reach—had similar levels of disturbance within a time period (Table 3). This was not surprising given the high correlation of disturbance magnitudes between each of the three spatial scales within a time period ($P < 0.10$, all correlations within each time period > 0.7). Because disturbance magnitudes were similar and highly correlated, little evidence exists to support the conclusion, at least in this region, that areas near streams (≤ 90 m) were less prone to vegetative disturbance than areas further away from streams.

Depending on the time period analyzed, extensive natural vegetative disturbance within a kilometer of the evaluated reach was rare or common. In the earlier time period we found that approximately 0 to 14% (90% C.I.) of the reaches within the study area with characteristics similar to those sampled would likely have had at least 15% of the proximate watershed area affected by vegetative disturbance. This compares with an estimate of 40 to 64% of these reaches having this level of disturbance in the second time frame. Given the large variability in disturbance rates through time it is likely that the role disturbance has in shaping stream conditions also varies through time.

Even with the high average vegetative disturbance rates in the second time period, only three of the physical stream attributes—sinuosity, median particle size, and percent undercut—were significantly related to one of the indices of vegetative disturbances (Table 4). These three attributes were related to disturbance rates in the earlier (1985 to 1993) rather than latter (1993 to 2000) time frame. All physical habitat attributes, whether significantly related to disturbance or not, were related to at least one landscape attribute that measured either stream size (bankfull width, basin area), gradient (average basin slope, stream gradient), or precipitation (Kershner et al. 2004b).

Two of the 14 macroinvertebrate attributes we evaluated—abundance and percent of collectors/filterers—were significantly related to one of the indices of vegetative disturbance (Table 4). In contrast to the habitat attributes, changes in these two metrics were related to recent disturbances (1993 to 2000) rather than disturbance in the earlier timeframe (1985 to 1993). None of the commonly used metrics for human disturbance (Karr and Chu 1999) were significant and there was no consistent inclusion of landscape attributes within the macroinvertebrate models.

Discussion

Vegetative disturbance measured at watershed and smaller spatial scales explained variation in some stream characteristics measured at the reach scale. A clear pattern existed for temporal relationships: past disturbance magnitude (1985-1993) explained variation in the physical stream attributes while recent disturbance magnitude (1993-2000) explained variation in macroinvertebrate metrics. We found no consistent pattern relating the location of the disturbance within the watershed and changes measured at the scale of the stream reach. The absence of a location effect was likely due to the lack of independence of disturbance rates among the three scales of evaluation, resulting in similar level of disturbance at each of the three scales.

The delay we found between the onset of vegetative disturbance and the ability to detect in-channel physical habitat changes is consistent with results reported elsewhere (Gresswell 1999, Minshall et al. 2001). The delay in measuring change has been attributed to the time it takes

TABLE 4. Summary of attributes evaluated to determine if they were related to vegetative disturbance. The different attributes are the response variables. Landscape attribute are those significantly related (covariate) to the response variable (P<0.1). Variability between the landscape attribute and the response variable was accounted for in the model. The sign is the direction of the relationship between the landscape attribute and the response variable. Vegetative disturbance is the time and location of the disturbance rate that is significantly related to the response variable (P<0.1). Significance is the p-value of significant relationships between the attribute and the vegetative disturbance. Intolerant species are defined at the family level with a Hilsenhoff Biotic Index score of 0-2; Tolerant taxa are Hilsenhoff Biotic Score of 8-10 (see Hilsenhoff 1987). The macroinvertebrate metrics denoted with a [1] come from Karr and Chu (1999, pages 76 and 134) and have been used as indicators of human disturbance rather than disturbance in general.

Attribute	Landscape Attributes(sign)	Vegetative Disturbance (sign)	Significance
Sinuosity	Gradient (-)	1993 Basin (+)	0.01
	Average basin slope (-)		
	Percent tree (-)		
Median particle size	Area (+)	1993 Near (-)	0.09
Percent Fines (<4 mm)	Area (-)	None	NS
Width to depth ratio	Bankfull width (+)	None	NS
Bank stability	Bankfull width (-)	None	NS
	Average precipitation (+)		
	Average basin slope (-)		
Bank angle	Gradient (+)	None	NS
	Average precipitation (-)		
	Area (+)		
	Percent trees (-)		
Percent undercut	Average precipitation (+)	1993 near buffer (-)	0.03
	Area (-)		
	Gradient (-)		
Undercut depth	Gradient (-)	None	NS
	Average precipitation (+)		
Percent pool	Gradient (-)	None	NS
	Average precipitation (+)		
Residual pool depth	Gradient (-)	None	NS
	Area (-)		
	Bankfull width (+)		
Large Wood (.1x 3m)	Average basin slope (+)	None	NS
	Elevation (+)		
Abundance	None	2000 near buffer (+)	0.04
Collector/filter (%)	Gradient (+)	2000 Basin (+)	0.01
Shredder (%)	Percent trees (+)	None	NS
Scrapers (%)	Average slope (+)	None	NS
Richness[1]	Percent Trees (-)	None	NS
Ephemeroptera taxa[1]	Average slope (+)	None	NS
Plecoptera taxa[1]	None	None	NS
Trichoptera taxa[1]	Elevation (-)	None	NS
Long-lived taxa[1]	Gradient	None	NS
Intolerant taxa[1]	None	None	NS
Tolerant taxa(%)[1]	Gradient (+)	None	NS
Percent predators[1]	Percent tree (+)	None	NS
Clinger taxa[1]	Elevation (-)	None	NS
Dominant 3 taxa (%)[1]	Percent tree (+)	None	NS

sediment waves related to disturbance to propagate from where they enter the stream to downstream reaches (Benda 1994, Sutherland et al. 2002). All significant changes in stream habitat characteristics indicated increasing inputs of water and/or sediment. Sinuosity increased while substrate size decreased, a pattern indicative of a channel seeking to equilibrate its slope given increased sediment transport (Knighton 1998). The decrease in the percentage of the evaluated reach with undercut banks could have resulted from either channel-changing effects of increased flows and/or the stream channel altering its path due to increased sediment.

Although three of the physical attributes were significantly related to vegetative disturbance rates within the watershed, it is important to recognize that eight attributes were not. The failure to find significant relationships between natural vegetative disturbance and stream conditions was likely due to the low magnitude (mean ≈ 5%) and high variability (0-44.8%) of vegetative disturbance in the early time period. These conditions did not produce a signal sufficient to detect changes in stream conditions given the inherent variability among watersheds (Kershner et al. 2004b) or within stream assessment methods (Roper et al. 2002, Olsen et al. 2005). Although we cannot directly address this issue at present, we plan to re-evaluate these stream reaches between 2006 and 2008 when the more recent, higher disturbance rates will have had more time to reorganize the evaluated stream reaches. Revisiting sites should increase the environmental signal and increase our sample size so that the statistical power of detecting differences increases (Larsen et al. 2001, Roper et al. 2002, Roper et al. 2003). We predict that many more of the physical variables will be significantly related to vegetative disturbance at that time.

Even though we did not find many significant relationships between disturbance rates and physical stream characteristics, each of the stream characteristics was related to at least one landscape or stream scale covariate. The strong linkage between stream reach and geophysical characteristics belies the importance of incorporating these relationships (Benda et al. 2004) into models prior to evaluating the effect of vegetative disturbance on stream conditions (Kershner et al. 2004b). Failure to account for these geophysical attributes can either increase the amount of unexplained variation in the model or, if the vegetative disturbance within a watershed is correlated with a covariate, can result in a spurious effect attributed to vegetative disturbance.

In contrast to the relationship between natural vegetative disturbance and physical habitat attributes, macroinvertebrate attributes were significantly related to recent (1993-2000) disturbance rates. Both significant metrics, macroinvertebrate abundance and the percent of the macroinvertebrate community that are collectors/filterers, have been shown to increase following natural disturbance. Vegetative disturbance increases inputs of allochthonous material and often increases solar inputs so that autochthonous production is fostered (Minshall et al. 1989, Jones et al. 1993 as cited by Gresswell 1999).

The changes we observed in stream attributes and macroinvertbrate metrics following natural vegetative disturbance were less than those commonly associated with human disturbance of vegetation. Kershner et al. (2004b) evaluated the effects of human vegetative disturbance on 9 of the 11 attributes we included in our analysis (their study did not include sinuosity or large wood) and found that seven differed significantly between low gradient stream reaches in managed and minimally managed watersheds. Wood-Smith and Buffington (1996) found that differences in the percent of the stream area in pool habitat, median particle size, and residual pool depth were sufficient to discriminate between logged and unlogged streams in southeast Alaska. Logging was also shown to alter pool area and residual pool depth in western Washington (Ralph et al. 1994). Similarly, Fore et al. (1996) and Karr and Chu (1999) found that many macroinvertebrate metrics we evaluated are significantly related to levels of human-induces vegetative disturbance within a watershed.

A greater change in stream conditions following a human vegetative disturbance than following a natural disturbance suggests an underlying difference in the two types of disturbance. One difference could have been the level of disturbance within these minimally managed watersheds, but this is unlikely since nearly 50% of the watersheds in this study experienced a natural disturbance event in the last 15 years which covered at least a third of the watershed area. A more likely explanation for the difference is the additive effects of activities that complement human manipulation of vegetation such a road building (Furniss et al. 1991, Dose and Roper 1994, Lee et al. 1997) and harvesting methods (Chamberlin et al. 1991).

A second important difference is the pattern of natural and human-induced vegetative disturbance within and among watersheds. While 50% of the watersheds saw extensive disturbance, almost half (42%) of the evaluated watersheds saw little vegetative disturbance (< 10%) in either of the two evaluated time periods. Because many watersheds in minimally managed areas are allowed to recover between disturbance events, they show a pulse rather than a press disturbance. Pulse disturbances are defined by the rapid alteration of a system, but because of the time between events, the system is allowed to recover to its preexisting state. Press disturbances are sustained so that they eventually lead to changes in the system (Yount and Niemi 1990). The asynchronous and pulsed nature of natural disturbance events among these watershed result a mosaic of stream habitats conditions that support biological diversity (Rieman et al. 1993, Reeves et al. 1995). This situation contrasts with the ubiquitous simplified habitat often found in watersheds that face press disturbances associated with road-building, grazing, and timber harvest (Hicks et al. 1991). Since variability makes identifying significant differences difficult, it will generally be easier to detect changes in stream conditions in managed watersheds where there are systematic, consistent, and continual disturbances than in minimally managed watersheds where the disturbance is highly variable, inconsistent, and punctuated.

Overall we found that natural vegetative disturbance, even when it was caused by spatially extensive events such as fires, affected stream characteristics and biota, but that these changes were not as large as might have been expected. This may have been because most of our expectations for change have been shaped by evaluating the effects of human-caused vegetative disturbance (Meehan 1991, Karr and Chu 1999, Kershner et al. 2004b) or areas where fires had an obvious effect on stream channels (Benda et al. 2003). In one of the few papers that related natural disturbance to stream conditions, Reeves et al. (1995) found that natural disturbance alone played a major role in shaping stream conditions. Because these authors found substantial change in stream habitat attributes related to vegetative disturbance, they suggested that natural disturbance processes must be incorporated into any plan attempting to maintain or restore aquatic habitats. While we concur with this study's conclusion, it is important to note that natural disturbance processes differ depending on the geoclimatic setting (Brown et al. 2004).

The Oregon Coast Range where Reeves et al. (1995) conducted their study has large stand-replacing fires (high intensity) with a return interval of 400 to 600 years (Agee 1993), high annual precipitation rates (≈ 2 m annually), and frequent widespread intense winter rainstorms. This disturbance pattern often results in large-scale episodic delivery of sediment to stream channels following vegetative disturbance (Miller et al. 2003). This results in stream reaches having high gravel and wood loading following a major disturbance, then in the centuries between disturbance events, changing to bedrock channels as these materials are transported out of the watershed (Benda 1994, Reeves et al. 1995).

In contrast, our study area has a less intense, shorter natural fire return interval of approximately 100 years (Rollins et al. 2000) and less precipitation (≈ 1 m annually) that primarily comes as snow during winter months or as infrequent localized summer thunderstorms (Benda et al. 2003). Our analysis of vegetative disturbance found that 20 of the 33 watersheds (70%) had at least one large spatial scale (> 100 hectares) natural disturbance, and that 3 of the 33 watersheds (9%) had at least at least one large natural disturbance in both of the analyzed time periods. This high disturbance rate would likely result in nearly constant input of sediment and large woody material from somewhere within a watershed. Because precipitation within our study area was less than in the coastal Oregon, in most situations, there would be a slower average movement of material from terrestrial to aquatic systems and then through the stream network. Continuous inputs coupled with a reduced capacity to mobilize the material once it enters the stream should result in most stream reaches constantly adjusting to natural vegetative disturbance that occurred at some time in the past within the watershed.

Our ability to evaluate the relationship between vegetative disturbance and stream conditions will depend on our ability to monitor landscapes and streams (Dale et al. 2001). We found that remotely sensed data analyzed with GIS provided a rapid and consistent method of assessing natural vegetative disturbance and landscape conditions in an area where little other consistent data exist (Cohen et al. 2000). Relating vegetative conditions to stream conditions in areas where humans have had minimal impacts provides better templates of acceptable environmental change than those derived from managed landscapes (Reynoldson et al. 1997, Kershner et al. 2004a). While the exact relationship we found between natural vegetative disturbance and stream conditions will differ in other geoclimatic settings (see Reeves et al. 1995), it is important to recognize that changes in vegetation and stream characteristics are a result of natural processes. Ensuring that the natural vegetative disturbance regimes within a region are maintained or mimicked by human disturbance plays an important role in maintaining the long-term complexity (Buffington and Montgomery 1999) and productivity (Reeves et al. 1995) of aquatic systems.

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