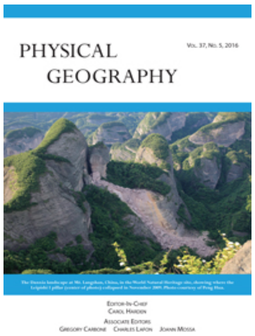

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The effect of sub-alpine landslides on headwater stream gradient and beaver habitat

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ABSTRACT
During previous work in the San Juan Mountains of Colorado, we observed that headwater (first-order) streams draining landslides were often characterized by the presence of beaver (*Castor canadensis*) dams whereas other headwater tributaries typically lacked evidence of beaver. Here, we hypothesize that hummocky landslide topography attracts beaver. To test the hypothesis, we examined 10 landslides and 11 adjacent headwater streams in the area, noting location, vegetation, elevation, and evidence of beaver activity, and then compared the landslide and non-landslide headwater streams using the *G*-test to determine whether or not variables were independent of one another. We reject the null hypothesis that beaver dam presence is unrelated to landslide deposits ($p = 0.003$). We further hypothesize that this relationship results from differences in stream gradient and concavity between landslide streams and other streams. We found streams on landslides to have a greater portion of their gradients below what geologic and ecologic literature suggests is a reasonable upper threshold (12%) for beaver dam maintenance. Additionally, streams on landslides are more concave. We conclude that the relationship between beaver presence and landslides results from a higher proportion of reaches below the 12% threshold and increased concavity of headwater streams on landslides.

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Beaver; landslides; stream gradient; mountain headwaters; habitat suitability

Introduction

Evidence of beaver (*Castor canadensis*) presence, including beaver dams, abandoned dams, and chewed logs, is common along second- and third-order streams in mountainous areas, but first-order streams are generally too steep to provide suitable habitat for beaver. However, complex post-glacial processes can lead to a variety of stream forms, including relatively low gradient streams, in otherwise high-relief areas (Brown, Hannah, & Milner, 2003). For instance, most models of postglacial sediment flux have an initial period of enhanced landslide activity (McColl, 2012), indicating that post-glacial hillslopes are more unstable immediately after deglaciation. Since slope is greatly altered by landslides (Retzer, 1956), and stream slope is one of the most important factors in the ability of beavers to inhabit an area (Gurnell, 1998), it is logical to think that landslides may create additional beaver habitat.

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In the southeastern San Juan Mountains, landscapes are characterized by an abundance of landslides (Howe, 1909; Lipman, 1974, 1975) as well as a variety of other post-glacial deposits (Johnson, Eppes, Diemer, Jiménez-Moreno, & Layzell, 2011; Johnson, Layzell, & Eppes, 2015; Layzell, Eppes, Johnson, & Diemer, 2012). Previous research suggests that terrain alterations resulting from slope failure create microtopography and depressions on the surface of the landslide that can provide beaver habitat (e.g. Geertsema & Pojar, 2007). This change in habitat is especially important in headwater (first-order) streams where pre-landslide stream gradients would have often been too steep for beaver. Though this trend has been noted previously (Geertsema & Pojar, 2007), no study we found tests the hypothesis that a relationship exists between evidence of beaver presence and landslides deposits. If a relationship does exist, it would further highlight the importance of geomorphic processes in creating or altering habitat. Specifically, it would highlight how landslides, through the action of beavers, may facilitate the creation of wetlands in mountainous areas.

This study examines the relationship between landslide deposits and beaver presence. Specifically, we examine landslide and non-landslide sites in the field to determine the distribution of evidence of beaver inhabitation. If there is a relationship between beaver presence and landslide deposits, then we will further hypothesize that (1) landslide streams have a higher percent of low-gradient stream reaches than non-landslide streams and (2) streams on landslides are more likely to be concave, which would provide more low-gradient habitat adjacent to trunk streams.

Field area

The southeastern San Juan Mountains are located in southern Colorado and northern New Mexico (Figure 1). The once-glaciated alpine and sub-alpine landscapes of the San Juan Mountains are now dominated by glacial and post-glacial landforms (Carver & Beeton, 2014; Johnson et al., 2011, 2015). Atwood and Mather (1932) mapped the last glacial maximum (LGM) glacial extent and various Quaternary landforms for the entire range. More recent research in the southeastern San Juan Mountains has focused on post-glacial landscape evolution and response to climate change. Specifically, Johnson et al. (2011) and Layzell et al. (2012) found significant periods of erosion and resultant sedimentation after the LGM, most often during periods of rapid climate change (Carver & Beeton, 2014; Johnson et al., 2011, 2015).

Post-glacial landslides have also played a large role in the evolution of the San Juan Mountains (e.g. Howe, 1909; Lipman, 1974, 1975). In fact, glacial erosion and subsequent glacial retreat throughout the San Juan Mountains resulted in hillsides that are over-steepened and pre-conditioned for failure (Atwood & Mather, 1932; Johnson, Smith, & Diemer, in review). Some landslides in the area seem to be paraglacial in nature, while others occurred in the mid to late-Holocene (Johnson et al., in review). The underlying cause of the landslides was likely weakness of the local volcanic bedrock. Specifically, volcaniclastic rocks and vent facies are extremely heterogeneous, are often poorly cemented, and vary significantly laterally even within individual units (Lipman, 1974, 1975). Triggering events for the landslides are not known but are likely to have been related to weather events, as the area is tectonically inactive. As a result, landslides of a variety of sizes are common in this area. None of the landslides examined appear to be active and all of the landslides are deep-seated with headwalls greater than 150 m and a median size of 4.5 km^2.

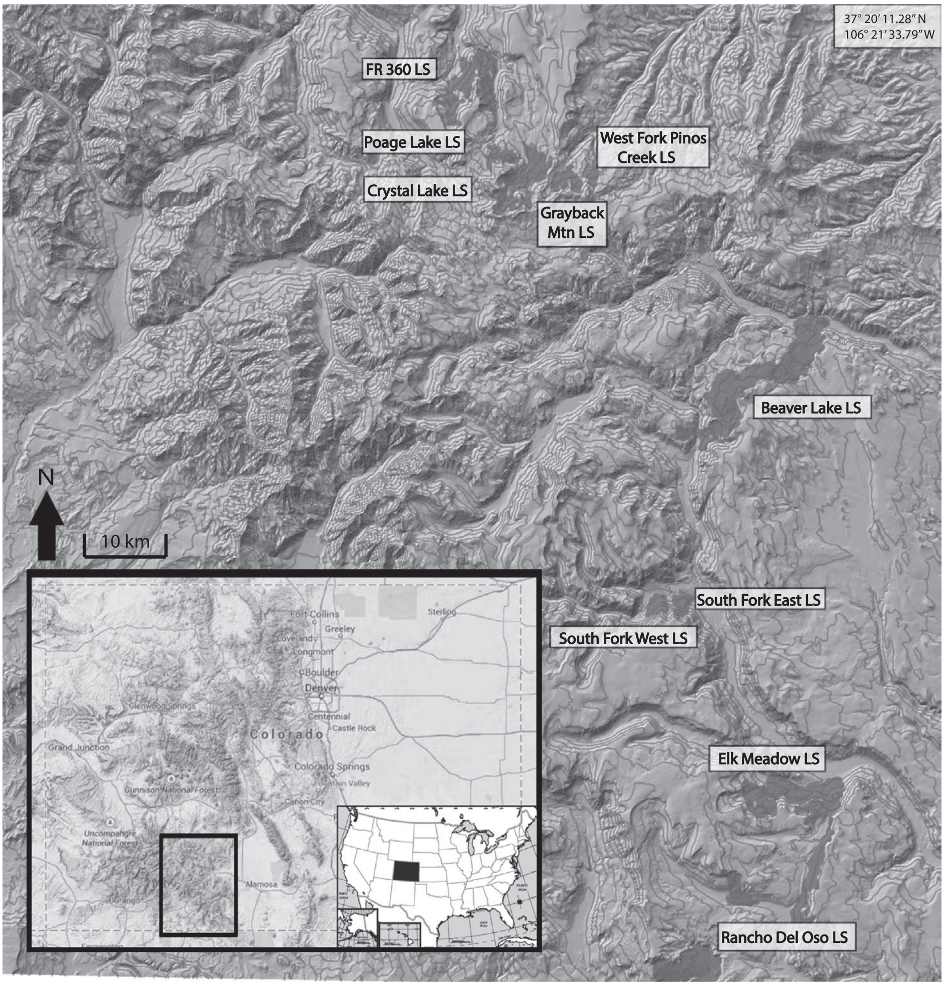

Figure 1. The location of the field area and the individual landslides examined.
Note: The inset map shows the location within the borders of Colorado, USA.

Landslides as habitat

Landslides affect environmental conditions such as topography, hydrology of the watershed (rivers, streams, and groundwater flow), forests, and habitats of wildlife (Geertsema & Pojar, 2007). The erosional and subsequent depositional processes influence the terrain and change surface morphology. The resulting range of microtopography includes both positive (hummocks and ridges that rise up from the main ground) and negative topographic areas (sag ponds). In other regions, the complex microtopography has been shown to create variations in substrate, soil, nutrients, moisture regime, and vegetation (Geertsema & Pojar, 2007). This increase in biophysical diversity leads to a variety of habitat options for different species (Butler & Malanson, 2005; Geertsema & Pojar, 2007; Gurnell, 1998).

Beaver habitat suitability

Microtopography, such as that created by landslides, has been observed to promote inhabitation by beaver (Geertsema & Pojar, 2007). Surface water features with constant water levels, including large rivers, impoundments, and lakes, are often colonized by beaver. Although beaver can occupy large portions of a forested stream network, they prefer unconfined, low-gradient alluvial channels, without steep, rocky, or bedrock bottoms, and below a stream-power threshold (Gurnell, 1998; McComb, Sedell, & Buchholz, 1990; Persico & Meyer, 2009; Pollock, Beechie, & Jordan, 2007). A suitable beaver habitat must provide a stable aquatic habitat with steady water levels, sufficient amounts of quality food species (Aspen, *Populus tremuloides*, are preferable in mountainous areas (Gurnell, 1998)), and channel gradients below a reasonable threshold for maintaining dams. Specifically, a gradient less than 12–15% is realistic for dam maintenance (McComb et al., 1990; Naiman, Johnston, & Kelley, 1988; Persico & Meyer, 2009; Polvi & Wohl, 2012).

In the Rocky Mountains, beaver populations have rebounded from historic lows that occurred during the late 1800s, but are still at a fraction of their peak population (Boyle & Owens, 2007). Each state manages its beaver population independently, so region-wide population trends are difficult to assess. Colorado specifically has outlawed trapping, leading to beaver populations that are likely either stable or growing (Boyle & Owens, 2007).

Exploiting headwaters

Previous research has found that first-order streams are rarely used as beaver habitat (Gurnell, 1998). There are likely a number of different reasons why first-order alpine and sub-alpine streams do not make good beaver habitat. First, mountain headwater/first-order streams are typically characterized by high channel gradients and narrow stream geometry (Gurnell, 1998; Wright, Jones, & Flecker, 2002), which prevent dam construction. Further, these high gradients cause erosion along (Polvi & Wohl, 2012), and upslope of (Johnson et al., 2011) headwater streams, resulting in high rates of sediment transport, which would rapidly fill or damage a beaver-dammed reservoir. However, the hummocky surfaces of landslides lead to lower gradient streams, thereby lowering sediment load (Geertsema, Highland, & Vaugeouis, 2009). Thus, we hypothesize that the change in topography created by landslides can offer suitable habitat for beaver in headwater streams.

Methodology

Overview

In order to answer the questions posed above, it was necessary to locate landslides, identify evidence of beaver, and compare sites draining landslides to those that clearly do not drain landslide deposits (referred to here as 'non-landslide' sites). To do so, we located landslides using Colorado Geologic Survey data and examined each landslide using aerial photographs. We narrowed the number of landslides by identifying large, accessible landslides. We then selected streams that drained large landslides and paired them with adjacent streams draining colluvium. For each of these pairs, we walked the length of the stream noting any evidence of current or past beaver inhabitation. Further, we characterized each site in terms of geomorphology and vegetation. We then used a *G*-test to determine if the presence of beaver sites was independent of landslide presence. Lastly, we compared the gradient and concavity of streams draining landslides to those draining adjacent slopes.

Landslide identification and examination

The Colorado Geologic Survey has digitized landslide locations from a number of different field and bedrock maps at differing scales. We imported their data into GIS and overlaid the data on a digital elevation model (DEM; sourced from the National Elevation Data-set) and aerial imagery (DigitalGlobe data accessed through both Google Earth and the ArcGIS Imagery Basemap; <1 m pixels). We used aerial imagery to examine all of the landslides in the southeastern San Juan Mountains (southeast of the South Fork of the Rio Grande and south of the main Rio Grande River). From this subset, we chose landslides to study that were (1) large enough to support surface water drainage (>~1.5 km^2), (2) accessible, and (3) adjacent to non-landslide headwater streams with similar drainage areas. During the narrowing process, we omitted sites that (1) appeared to be talus deposits and not landslides, (2) had low-relief headwalls (small, or low-relief landslides could be caused by ponding water, creating a chicken-and-egg problem), or (3) were actively on fire or had recently burned. Lastly, some private landowners prohibit access to landslides. In all, 10 landslides remained after the criteria were set.

After landslides were selected, we examined the headwater stream draining each of the 10 landslides and a paired non-landslide, headwater stream located directly adjacent to or across the valley floor from each landslide. One landslide site (Trujillo Meadows) was omitted because of human activity in the area (Trujillo Meadows Reservoir uses the toe of the landslide as a natural dam), but the corresponding non-landslide stream was kept in the analysis because the area was free of human activity. We followed every headwater stream on foot to its origin and noted any evidence of beaver activity. Additionally, we looked for topography suitable for beaver inhabitation, including small basins and ponds/reservoir sites away from the stream, and examined those for activity. Along all stream reaches visited, we photographed any evidence of beaver activity, including downed trees, beaver dams, impounded ponds, or tooth marks on trees. Reaches where no evidence of beaver inhabitation was found were noted. The age of beaver dams was not assessed, as we assume previous beaver suitability would not differ from active beaver suitability. Variables characterizing each site were then recorded, including latitude, longitude, elevation, estimated size of pond/reservoir site, and vegetation type. Examining the influence of vegetation on beaver distribution is more difficult because of positive feedbacks such as geomorphic controls on vegetation patterns in alpine areas (e.g. Butler, Malanson, Walsh, & Fagre, 2007; Resler, 2006) and vegetation alteration after beaver dams are built (e.g. Neff, 1957; Terwilliger & Pastor, 1999). Thus, landslide presence, along with gradient and concavity, become the primary variables in our study.

Statistical methods and stream profile assessment

Data collected in the field were then evaluated by analyzing the relationship between two variables: (1) the presence of a landslide and (2) evidence of beaver presence. To do so, we employed the *G*-test, a version of the chi-square test of independence derived from the likelihood-ratio test methodology. Given the null hypothesis that beaver presence and landslide presence are independent of each other, we used the test to assess the relative frequencies of the different combinations of the two variables (McDonald, 2014, pp. 53–58). We rejected the null hypothesis if $p < 0.05$.

If a relationship between beaver presence and streams on landslides exists, we wanted to quantify slope differences between landslide and non-landslide streams. To do so, we created longitudinal profiles of each headwater stream by hand using 7.5-min topographic quadrangles (40 ft (12.2 m) contour intervals, average segment length ~65 m, where each segment equals one contour interval of drop) because the pixels in 10- and 30-m digital elevation models are too large to examine small streams and the results often show streams flowing uphill. The resultant data-set was imported into Excel and used to create digital profiles for each headwater stream.

The resulting stream profiles were then organized by landslide and non-landslide headwaters. For each stream, we were able to see changes in the slope throughout the profile and highlight the exact locale within each profile that supported dam creation. Because a stream may have a single low-gradient reach despite a steep overall morphology, we determined what percentage of each stream length had a gradient <12% (threshold for beaver dam maintenance). In using this proxy, we were able to identify how much of the stream provided potential beaver habitat, assuming that low-gradient reaches would be more likely to fit other requirements of the beavers.

Other beaver habitat classification studies strongly stress the importance of stream gradient (e.g. Allen, 1982; Howard & Larson, 1985; Slough & Sadleir, 1977; Smith, 1950). More specifically, Retzer's (1956) work in Colorado divided beaver locations as occupied or abandoned and showed that streams with lower gradients contained a higher percentage of the beaver population. Moreover, 96% of occupied reaches had gradients <13 and 95% of abandoned sites had gradients <13%, with only 1% of beaver in streams with gradients >15%. Similarly, Williams (1965) indicated that suitable habitat for beaver requires a channel gradient of <15%. Thus, it would seem that the absolute stream gradient threshold for beaver dam construction in mountainous areas is somewhere between 15 and 18% (Retzer, 1956) even if most beavers prefer even lower gradient streams (67% are between 1 and 6% slope). However, the vast majority (95% based on our definition of beaver activity; Retzer, 1956) of dam locations lie in streams with gradients of 12% or lower, suggesting that beaver inhabiting streams with gradients >12% may be outliers. Thus, we use 12% (less than or equal to) as the threshold in this study. Gurnell (1998) suggested that dams were 'very unlikely' to be constructed above 4% gradient, but Retzer's (1956) large data-set ($n = 365$) makes it clear that at least some dams are built in higher gradient reaches.

To compare the concavity of landslide streams to that of non-landslide streams, we employed a version of the Stream Concavity Index (SCI; Zaprowski, Pazzaglia, & Evenson, 2005) to calculate the concavity or convexity of each stream profile. It is logical to assume that more concave streams would be easier for beaver to inhabit since most low-gradient reaches would be near the confluence with the trunk stream. Alternatively, convex streams would place the majority of low-gradient reaches both away from trunk stream habitat and at higher elevations where the climate is much harsher. By using an area-normalized SCI, we found the integral area between the channel profile and a line connecting the channel end points. The resultant SCI values correlate to stream shape, such that an SCI value of zero represents a straight profile, an SCI value less than zero is convex, and a positive SCI value is concave. The SCI examines the overall shape of the profile, and any stream may contain individual reaches that are either concave or convex.

Results

Field observations

The majority of beaver dams found appeared to be unmaintained and the associated ponds abandoned, although some ponds (<5) were likely inhabited. Dams varied in size of structure (1–3 m tall; 5–30 m wide) and size of resultant wetted area (~5000 m^2 to 0.1 km^2). The raw data (Table 1) show location information (latitude, longitude, elevation, landslide presence) along with information regarding the type of beaver activity observed. We observed that beaver tended to build with (and likely eat) aspen (*Populus tremuloides*) at lower elevations and alders (*Alnus incana)* at higher elevations. We also observed that all sites, both off and on landslides, examined had suitable vegetation for beaver.

Beaver distribution

Presence or absence of beaver in headwater streams appears closely tied to the presence of landslides. Specifically, evidence of beaver inhabitation was observed in seven out of the 10 landslides that we visited. Beaver were only found at one of the 11 non-landslide headwaters (Table 2). The null hypothesis that beaver presence is independent of landslide presence was rejected (p = 0.003) suggesting that beaver presence in headwater streams is a function of landslide presence.

Stream gradient and concavity

Differences in gradient are noticeable in the profiles of landslide streams and non-landslide streams (Figure 2(A) and (B)). Average gradient is generally lower and less variable on landslide streams, while non-landslide streams show more variability and higher gradients in places (Figure 3). Due to high variability in stream gradient throughout individual profiles, minimum, maximum, and average slopes are not useful in differentiating between alpine streams of varying morphologies because individual stream segments are not a good indicator of morphology for the rest of the stream. For instance, beaver sites exist throughout the range of average stream gradients we measured (Figure 3). Since average stream gradient does not account for the percentage of each stream that might be inhabitable, we additionally examined the portion of each stream that lies below the 12% threshold. A larger percentage of longitudinal profiles on headwater streams affected by landslides have gradients below the 12% gradient threshold (mean = 53%, median = 60%; Table 1) compared to longitudinal profiles of headwaters not affected by landslides (mean = 26%, median 21%; Figure 4(B)). We also found that beaver sites tended to exist in streams with higher portions of low-gradient reaches (Figure 4(B)).

Lower gradient along landslide streams is partially related to longer overall length. Stream length for landslide streams varied from 619 to 2704 m before their first confluence, with an average of 1540 m length. Non-landslide headwater streams varied from 726 to 1462 m, with an average of 1042 m, indicating a generally shorter length among non-landslide

Table 1. Summary of beaver evidence for landslide and non-landslide sites.

Landslides										Non-landslides								
Name	SCI	% < 12%	Avg. slope (%)	Length (m)	Latitude	Longitude	Elev. (m)	Beaver (Y/N)	Beaver Sites	Name	SCI	% < 12%	Avg. slope (%)	Length (m)	Latitude	Longitude	Elev. (m)	Beaver (Y/N)	Beaver sites
Beaver Lake LS	0.28	51.2%	15	1551	37°19′22″	106°28′06″	3013	Y	2	Bear Lake headwater	−0.09	19.3%	26	1113	37°17′41″	106°28′16″	3516	N	0
Crystal Lake LS	−0.14	65.1%	11	1597	37°28′34″	106°35′24″	3476	Y	1	Gunsight Pass headwater	−0.04	23.1%	19	1462	37°15′43″	106°40′43″	3537	N	0
Elk Meadows LS	0.36	59.4%	15	1693	37°06′28″	106°25′42″	3071	Y	1	Lake Ann headwater	0.04	11.0%	24	946	37°16′24″	106°41′15″	3637	N	0
FR 360 LS	0.01	25.6%	17	899	37°29′23″	106°37′44″	3353	N	0	N. Fork L. Fork headwater	0.00	21.2%	18	1087	37°17′30″	106°39′55″	3391	N	0
Grayback Mtn LS	0.13	18.4%	20	1497	37°28′29″	106°33′07″	3458	N	0	N. Fork R. Fork headwater	0.00	11.6%	19	1058	37°17′54″	106°39′51″	3472	N	0
Poage Lake LS	0.23	84.0%	9	2399	37°30′01″	106°38′44″	3376	N	0	Adams Fork headwater	−0.07	30.4%	30	726	37°19′59″	106°41′42″	3531	N	0
Rancho Del Oso LS	−0.21	34.6%	20	1281	37°00′27″	106°28′44″	3014	Y	1	Haskell Rincon headwater	0.08	34.2%	15	1388	37°19′09″	106°39′15″	3423	N	0
South Fork East LS	0.28	61.7%	14	619	37°13′55″	106°28′46″	2797	Y	1	TM headwater	0.10	82.9%	10	849	37°02′57″	106°26′47″	3048	N	0
South Fork West LS	0.52	60.7%	14	1155	37°12′53″	106°30′56″	2820	Y	1	South Fork North headwater	0.33	51.5%	16	1039	37°13′46″	106°29′49″	2802	Y	1

(*Continued*)

Table 1. (*Continued*)

Landslides										Non-landslides									
Name	SCI	% < 12%	Avg. slope (%)	Length (m)	Latitude	Longitude	Elev. (m)	Beaver (Y/N)	Beaver Sites	Name	SCI	% < 12%	Avg. slope (%)	Length (m)	Latitude	Longitude	Elev. (m)	Beaver (Y/N)	Beaver sites
West Fork Pinos Creek LS	0.14	70.1%	10	2704	37°28′18″	106°34′49″	3449	Y	1	Lake Fork head-water	0.08	0.0%	28	824	37°18′43″	106°28′20″	2987	N	0
										Beaver Lake head-water	−0.04	0.0%	28	971	37°19′56″	106°28′07″	3036	N	0
Median	0.185	60%	15	1524						Median	0.00	21%	19	1039					
Mean	0.16	53.1%	35	1540			*Total*	7/10		Average	0.04	25.9%	21	1042			*Total*	1/11	
Stdev	0.22	20.7%								Stdev	0.12	24.2%							
25th per-centile	−0.03	32.4%								25th per-centile	−0.04	11.0%							
75th per-centile	0.3	66.4%								75th per-centile	0.09	34.2%							

Table 2. *G*-test distribution box, comparing landslide presence to evidence of beaver.

	Landslide presence?		
Evidence of beaver?	Yes	No	Sum
Yes	7	1	8
No	3	10	13
Sum	10	11	$n = 21$

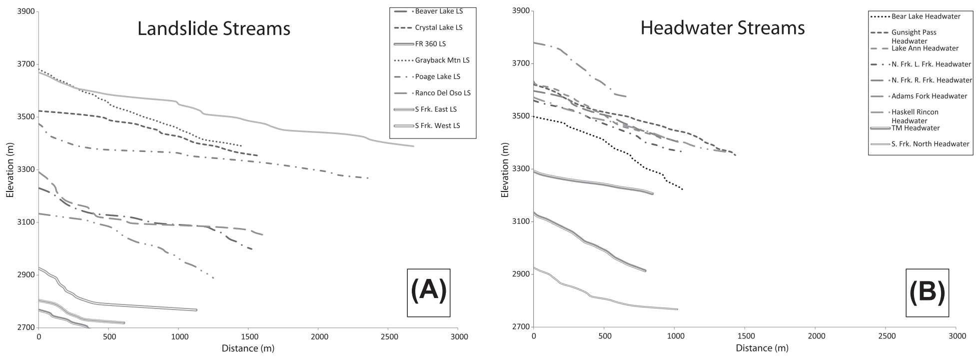

Figure 2. (A) Stream profiles for each of the first-order streams that drain landslide deposits. (B) Stream profiles for each of the first-order streams that drains an adjacent, non-landslide hillslope. For (A) and (B), vertical exaggeration is the same (1.9×).

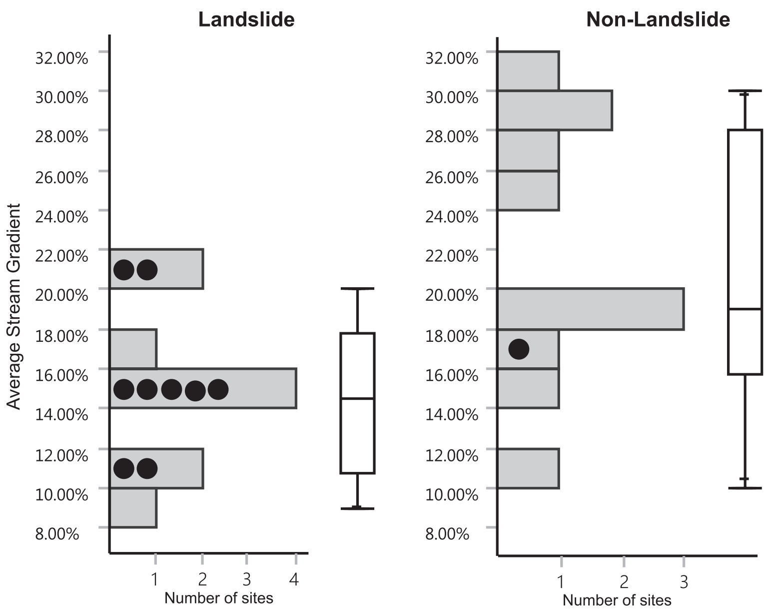

Figure 3. A comparison of average stream gradient on landslide streams and non-landslide streams.
Notes: Box-and-whisker plots show range, quartiles, and median. Black dots show which streams contained evidence of beaver presence.

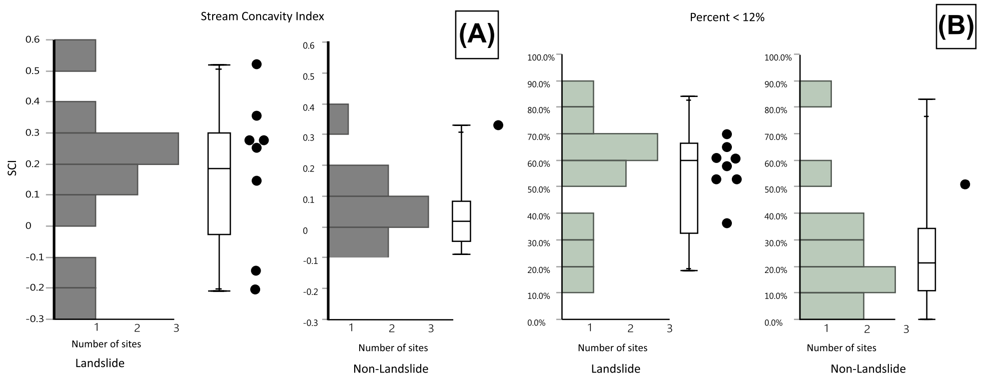

Figure 4. (A) Stream concavity index (SCI) for landslide and non-landslide streams. (B) Percent of total stream length < 12% for landslide and non-landslide streams.
Notes: Box-and-whisker plots show range, quartiles and median. Black dots show which streams contained evidence of beaver presence.

streams (Table 1). Each landslide was generally only drained by a single stream although some landslides have additional, internally drained areas.

Streams affected by landslides also tend to be more concave, indicated by a higher, positive SCI value (mean of 0.16 vs. 0.04; Figure 4(A)). Both of the datasets contain outliers, but it is nonetheless clear that concavities of the middle 25% of the sites differ distinctly. Specifically, the landslide SCI ranges from −0.03 at first quartile to 0.3 at the third quartile, while the non-landslide SCI ranges from −0.04 at the first quartile to 0.09 at the third quartile. Similarly, the percent of stream reaches with gradients below12% on landslides ranges from 32% at the first quartile to 66% at the third quartile, compared to the range from 11% at the first quartile to 34% at the third quartile for non-landslide streams. The broad range of SCI values on landslides highlights the topographic variability of landslide surfaces compared to surfaces in headwater streams without landslides. Beaver sites occurred throughout the entire range of SCI values (Figure 4(A)). Overall, stream profiles vary greatly between those on and off landslides: profiles of streams affected by landslides had more frequent low-gradient reaches and natural dips in topography.

Discussion

Headwater streams in the San Juan Mountains drain steep, high-relief topography. In many places, headwater streams are little more than waterfalls or cascades (Figure 5). However, first-order streams draining landslides are different. These streams are often longer (Table 1 and Figure 2) as they cross a more complicated, hummocky topography. The hummocky surfaces of landslide deposits also include sag ponds and basins with no outflow that are not part of this analysis. Overall, the simple statistical relationship between beaver presence and landslide deposits highlights an expanded range for beaver in areas with landslides, as beaver are clearly more likely to inhabit first-order streams on landslides than those on adjacent streams. The preference of beavers for first-order streams on landslides is logical given the significant morphologic differences between streams draining landslides and other (non-landslide) headwater streams.

Figure 5. Photograph of a typical reach of a landslide stream (A), compared with a typical reach on a non-landslide stream (B). Note that even without the presence of beaver debris, the gradient would still be lower on the landslide stream.

Stream gradient

While we found an overall difference in average stream gradient between landslide and non-landslide sites (Figure 2(A) and (B), Figure 3), average gradient is too simple a metric of this difference because it does not account for the variability of the stream. Instead, percent of the stream (percent of stream segments covering one 12.2-m (40-ft-) contour) below 12% gradient is more informative about the likely existence of beaver sites. Specifically, an increase in the number of low-gradient stream segments results in an increase in the number of reaches of the stream that may fit other beaver habitat criteria, including valley width (e.g. Levine & Meyer, 2014). Valley width, which is easy to consider for larger streams, is particularly difficult to quantify on small streams because of the lack of high-resolution mapping in mountainous areas. Specifically, a headwater stream (1–3 m in width) is too small to compare with valley width since elevation data are typically presented in 10- or 30-m grids.

Evidence of depressions within the profiles illustrates the generally heterogeneous character of headwaters on landslides (Figure 2(A) and (B)). On the contrary, headwaters not on landslides often maintain a more homogeneous flow route, and natural ponds that could potentially attract beaver are rare. In the mountainous terrain that characterizes our field area, headwater streams are typically short and steep (Table 1).

The impact of landsliding on stream concavity is visible in the difference between the distribution of SCI values from landslides and non-landslide streams (Figure 4(A)). As one might expect, concave streams are more common in streams draining landslides (Hovius, Stark, Tutton, & Abbott, 1998) due to the transformation of a valley wall into a more hummocky topography. Concavity also ensures that low-gradient sections of the stream are at lower elevations, adjacent to larger trunk streams. We also see more convex streams on landslides, which highlights the variability in the morphology of landslide deposits. In contrast, the vast majority of non-landslide streams in the southeastern San Juan Mountains have nearly neutral SCI, showing almost no convexity or concavity.

Beaver behavior

Beaver in the San Juan Mountains are mostly established in valley bottom streams (second and third order). During periods of colony expansion, dispersal occurs (e.g. Svendsen, 1980), and ideal valley bottom sites are inhabited. If further expansion and dispersal occurs, beaver move upstream towards headwater sites, which are typically less desirable because the slope of headwater streams makes dam construction difficult and limits the potential size of beaver ponds. However, our results suggest that there are a limited number of headwater stream areas suitable for beaver and that these streams are mainly on landslides because landslides reduce reach gradients and because a higher percentage of low-gradient reaches makes it more likely that a reach would be suitable for dam construction. Further, the concavity of some landslide streams ensures that potential dam locations are adjacent to the trunk streams, which serve as the source for dispersing beaver. It is worth noting that these sites may only be utilized during periods when beaver populations are at their largest, and more desirable sites on second- and third-order streams (lower gradient, larger pond sites, consistent water flow) have already been occupied. This provides a possible explanation for why the majority of landslide dams are currently abandoned and only the most desirable dam sites on landslides are currently inhabited, although human action (Butler & Schipke, 1992; Neff, 1957) and natural changes to the population size are also possibilities.

Consequences of beaver inhabitation

In considering the significance of the relationship between beaver and landslide terrain, it is important to recognize the potential consequences of beaver inhabitation on a landscape. Studies across a range of forested, temperate environments like that of the San Juan Mountains have documented the ecological importance of beaver (Naiman et al., 1988; Polvi & Wohl, 2012; Wright et al., 2002). Beaver are unique because they are capable of altering geomorphology (Burchsted & Daniels, 2010; Butler & Malanson, 2005; Naiman et al., 1988; Persico & Meyer, 2009, 2013; Polvi & Wohl, 2012; Ruedemann & Schoonmaker, 1938), engineering ecosystems, (Gurnell, 1998; Levine & Meyer, 2014; McComb et al., 1990; Rosell, Bozser, Collen, & Parker, 2005; Smith & Mather, 2013; Wilkinson, 2003; Williams, 1965; Wright et al., 2002) and are a keystone species. The concept of keystone species, introduced by Paine (1969), refers to species that have a disproportionately large effect on their environment. These species maintain the structure of an ecological community and largely determine the types and numbers of species in a specific environment. In our area, we found that beaver at higher elevations tended to utilize willows growing along the stream, and that damming the stream tended to produce additional willow habitat. Thus, vegetation can be a result of beaver distribution and not a limiting factor in their site location.

In the case of beaver in headwater streams, dams prevent sediment transport by reducing the amount of energy available for moving large material (sand and cobbles) and by impounding fine sediment (silt and clay). Because mountainous environments provide extensive sediment (e.g. Butler & Malanson, 1995), sedimentation rates on headwater streams are likely to be even higher than those measured in trunk streams. In this way, it is likely that beaver habitats in first-order streams have a limited window for occupation, as ponds shallow into bogs and eventually meadows (Terwilliger & Pastor, 1999). This may be another reason that some of the dams we examined appeared to be currently unoccupied. In fact, the handful of studies that have examined the ecological impacts of abandoned beaver dams have done so without discussing a behavioral reason for site abandonment (Aznar & Desrochers, 2008; Terwilliger & Pastor, 1999). One explanation may be that beaver ponds are abandoned as they evolve into meadows.

Landslides in headwater mountain valleys may be viewed as suitable beaver habitat in areas where beaver population restoration or reintroduction is ongoing. The presence of landslide deposits may also increase resiliency among the beaver population and allow population establishment more quickly after wildfires and floods by increasing the diversity of habitats in the landscape. Furthermore, areas where landslide deposits are common can be viewed as potentially having higher biodiversity when compared with similar terrain with more stable hillslopes. The impact of landslides on biodiversity is an important one because beaver, in turn, further increase biodiversity as ecosystem engineers. In this way, a landslide may start a system of positive feedbacks that increase habitat diversity, biodiversity, and wetland resources.

Conclusions

There is a statistically significant relationship between beaver dam sites and landslide deposits on first-order streams in the San Juan Mountains. First-order streams in mountainous areas are commonly too steep for beaver dam construction, yet the hummocky topography produced by landslides provides inhabitable stream reaches. Our results suggest that the percentage of stream segments with gradients <12% is significantly higher on landslides than on adjacent headwater streams. Not surprisingly, beaver tend to inhabit streams with a high portion of reaches with low gradients. Further, first-order streams on landslide terrain show more concavity, which would indicate that their lower gradient sections are generally adjacent to second- and third- order streams that beaver more typically inhabit. Understanding that landslides provide additional habitat for beaver, beyond the more typical trunk stream sites, may have important implications for beaver conservation and sub-alpine biodiversity.

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