1   **Headwaters fed by subterranean ice: potential climate refugia for mountain stream**

2   **communities?**

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23   **Running head:** Mountain stream climate refugia

24 **ABSTRACT**

25 Near-term extirpations of macroinvertebrates are predicted for mountain streams worldwide as a

26 warming climate drives the recession of high-elevation ice and snow. However, hydrological

27 sources likely vary in their resistance to climate change. Streams fed by more resistant sources

28 could persist as climate refugia for imperiled biota. In 2015-2016, we measured habitat

29 characteristics and quantified macroinvertebrate community structure along six alpine streams in

30 the Teton Range, Wyoming, USA. Strong differences in habitat characteristics (e.g., temperature,

31 bed stability, conductivity) confirmed three major alpine stream sources: surface glaciers,

32 perennial snowfields, and subterranean ice. Subterranean ice-fed streams – termed "icy seeps" –

33 are common but globally understudied. Macroinvertebrate communities in glacier- and

34 snowmelt-fed streams differed significantly in multivariate space, with icy-seep communities

35 intermediate, incorporating components of both glacier- and snowmelt-fed assemblages. Because

36 the thermal environment of subterranean ice, including rock glaciers, is decoupled from large-

37 scale climatic conditions, we predict that icy seeps may persist longer on the landscape than

38 streams fed by surface ice and snow sources. Our results suggest that icy seeps are suitable

39 habitat for many macroinvertebrates occupying streams fed by vulnerable hydrological sources.

40 Thus, icy seeps may act as key climate refugia for mountain stream biodiversity, an idea in need

41 of further investigation.

42 **INTRODUCTION**

43   The highest rates of climate change are occurring above the permanent treeline in alpine

44 and arctic ecosystems (Bradley et al. 2006). In the Rocky Mountains, warming is proceeding two

45 to three times more quickly than the global average (Hansen et al. 2005, Pederson et al. 2010),

46 resulting in extensive loss of glaciers and long-term snowpack (Hall & Fagre 2003). Streams fed

47 by permanent ice may exhibit short-term increases in flow as air temperature rises and source ice

48 melts more quickly, but eventually they will shift to reduced flow with the potential for

49 intermittency or drying permanently (Hotaling et al. 2017a). As climate change proceeds,

50 invertebrate diversity at the mountain range scale is predicted to decrease due to both overall loss

51 of habitat and summit traps, where the highest-altitude species and communities have nowhere

52 left to disperse as warmer conditions and lower elevation communities shift upward. Biodiversity

53 loss will be compounded by the loss of specific aquatic habitat types, particularly the unique

54 conditions associated with meltwater from once-permanent sources like glaciers, snowfields, or

55 subterranean ice (Brown et al. 2007, Milner et al. 2009, Jacobsen et al. 2012, Finn et al. 2013a.

56 2013b, Hotaling et al. 2017a). Given that many alpine stream communities appear adapted to

57 unique, meltwater-associated regimes, they are likely to be highly vulnerable to climate change

58 (Giersch et al. 2017, Lencioni 2018). However, because alpine streams are heterogeneous with

59 respect to hydrological source, the potential also exists to identify stream types that may be

60 locally buffered from broad-scale climate patterns and therefore represent potential climate

61 refugia for alpine stream biota (Morelli et al. 2016).

62   A major focus of alpine stream biology is understanding the links between hydrological

63 sources, the in-stream conditions they promote, and resident biotic communities (Ward 1994,

64 Hotaling et al. 2017a). Historically, according to primary hydrological source, three types of

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65   alpine streams have been recognized, following Ward (1994): surface glacier-fed, snowmelt-fed,

66   and groundwater-fed streams. A fourth, understudied stream type exists – icy seeps – which are

67   fed by subterranean ice (Hotaling et al. 2017a, Hotaling et al. 2019a). The most common form of

68   subterranean ice in alpine zones is rock glaciers, masses of debris-covered ice that act as

69   conveyor belts moving fallen rock and other debris slowly downhill (Anderson et al. 2018).

70   There may be more than 10,000 rock glaciers in the western United States (Johnson 2018) and

71   they also appear common in mountainous regions worldwide (e.g., Lilleøren et al. 2011, Scotti et

72   al. 2013, Charbonneau & Smith. 2018). In contrast, there are ~1,250 surface glaciers and ~3,750

73   perennial snowfields in the western United States (Fountain et al. 2017). Thermal conditions in

74   rock glaciers are decoupled from ambient climate due to insulating debris cover (Clark et al.

75   1994, Anderson et al. 2018, Knight et al. 2019) and local-scale air circulation patterns (Millar et

76   al. 2013). In a climate change context, an intriguing aspect of rock glaciers and other

77   subterranean ice is their potential to persist on the landscape longer than surface glaciers,

78   snowfields, and other more vulnerable sources of alpine streams. Icy seeps therefore may act as

79   climate refugia for cold-adapted stream organisms (Hotaling et al. 2019a).

80   Population genetic studies of alpine-endemic species of the Rocky Mountains have

81   revealed substantial genetic structure across relatively short geographic distances (Finn et al.

82   2006, Hotaling et al. 2018, 2019b), suggesting that mountaintop populations have evolved in

83   considerable isolation. This process contributes to the elevated *beta* (among-stream) diversity of

84   alpine streams (Brown et al. 2007, Jacobsen et al. 2012, Finn et al. 2013a), but genetic isolation

85   and small population sizes can lead to bottlenecking and/or inbreeding depression in alpine-

86   endemic species that are undergoing range contraction (e.g., Jordan et al. 2016). Like many

87   mountain ranges worldwide, virtually nothing is known of alpine stream ecology and

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88   biodiversity in the Teton Range, a granite-dominated, young subrange of the Rocky Mountains.

89   Previous studies of montane (but not alpine) streams revealed high diversity in streams in the

90   range, particularly when compared to nearby lentic habitats (Tronstad et al. 2016, Hotaling et al.

91   2017b). Generally speaking, groundwater aquifers are rare in the Teton Range massif, and as

92   such, groundwater-fed streams are also virtually non-existent (L.M.T., personal observation).

93   Because groundwater-fed streams are traditionally considered to be the alpine stream type most

94   resistant to warming (e.g., Milner et al. 2009, Jacobsen et al. 2012), their rarity in the Teton

95   Range suggests alpine stream biodiversity in the region may be especially vulnerable to climate

96   change.

97   In this study, we addressed two major objectives. First, we sought to provide the first

98   assessment of alpine stream macroinvertebrate communities in the Teton Range. Second, we

99   explored associations between primary hydrological sources (surface glaciers, snowfields, and

100   subterranean ice) and community structure. Specifically, we asked if benthic communities

101   associated with icy seeps have substantial taxonomic overlap with the more vulnerable stream

102   types (glacier- and snowmelt-fed streams). Our study provides a preliminary look into whether

103   an underappreciated but globally common alpine stream type – icy seeps – may act as refugia for

104   ecological patterns and processes threatened by global change in mountain ecosystems.

105   Furthermore, our results provide new insight into the biodiversity in one of North America's

106   flagship protected areas, Grand Teton National Park, and neighboring wilderness areas.

107

108   **MATERIALS AND METHODS**

109   Study area

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110   During the summers of 2015 and 2016 (26 July-10 August), we sampled six streams in

111   the Teton Range of Grand Teton National Park and the adjacent Jedediah Smith Wilderness in

112   northwestern Wyoming, USA (Figure 1; Table 1). Study streams were selected to span the

113   breadth of alpine hydrological sources in the range and included two streams fed by surface

114   glaciers ('glacier-fed' hereafter), two fed by subterranean ice ('icy seep' hereafter) and two fed

115   by permanent snowpack ('snowmelt-fed'). In 2015, we sampled both upstream (near the source)

116   and downstream sites on each stream (Figure 1). On average, upper sites were 111 m higher in

117   elevation and 690 m stream distance from lower sites (Table 1). In 2016, we re-sampled the

118   upper sites with the same methods to assess inter-annual variability. We focused on upper sites

119   because they were as 'true' to primary hydrological source as possible while lower sites

120   inherently reflected various degrees of mixing among sources. In both years, snow depth in the

121   range was lower than average (152 cm in May, 1981-2010) with 2015 and 2016 at 63.3% and

122   80% of normal, respectively (Teton Pass, USDA SNOTEL).

123

124   Environmental data

125   At each site, we measured several environmental variables to characterize local habitat

126   and evaluate whether instream environmental conditions varied among stream types. We

127   measured water temperature for a full year (2015-2016) with *in situ* loggers (HOBO Pro v2,

128   Onset Computer Corporation) that recorded temperature hourly. We measured specific

129   conductivity (SPC), oxidation-reduction potential (ORP), pH, and dissolved oxygen (DO) with a

130   Yellow Springs Instrument (YSI) Professional Plus multiparameter sonde calibrated at the

131   trailhead (SPC, ORP, and pH) or at each site (DO). We estimated streambed stability with a

132   modified version of the Pfankuch Index (PI) following Peckarsky et al. (2014). Total suspended

133   sediments (TSS) were measured by filtering known volumes of streamwater through pre-

134   weighed filters (PALL Type A/E glass fiber filters) and measuring dry mass to the 10^{-5} grams.

135   Using the annual temperature data from each stream, we calculated mean temperature for

136   the entire year (T_{YEAR}), mean temperature between the summer solstice (21 June) and autumn

137   equinox (22 September; T_{SUMMER}), and maximum annual temperature range (T_{RANGE}). We also

138   estimated the date when seasonal snow covered (S_{ON}) and uncovered (S_{OFF}) each site by visually

139   inspecting thermographs to approximate the date when intraday variation ceased and in-stream

140   temperatures became constantly ~0°C (S_{ON}) or the opposite occurred (S_{OFF}). Using these values,

141   we calculated $S_{DURATION}$, the total days a site was snow covered between study years ($S_{DURATION}$

142   = S_{ON} - S_{OFF}). Finally, we used Principle Components Analysis (PCA; PC-ORD, McCune and

143   Mefford 2006) to characterize the upper sites on each stream according to four variables (SPC,

144   TSS, PI, T_{RANGE}) which comprise a modified 'glaciality index' (Ilg & Castella 2006). The

145   glaciality index has been useful in characterizing alpine stream hydrological sources globally

146   (e.g., Finn et al. 2013a, Cauvy-Fraunié et al. 2015).

147

148   Macroinvertebrate sampling

149   We quantitatively sampled benthic macroinvertebrates at each site using a Surber sampler

150   (Area: 0.09 m², Mesh size: 243 µm). At each location, a composite sample of 5-10 replicates was

151   collected depending on stream size, apparent biomass, and microhabitat diversity. Samples were

152   elutriated in the field to reduce the amount of inorganic substrate and stored in Whirl-Pak bags

153   with ~80% ethanol. In the laboratory, invertebrate samples were divided into large (>2 mm

154   mesh) and small (between 250 µm and 2 mm) fractions. For the large fraction, all invertebrates

155   were identified. The small fraction was subsampled using the record player method when smaller

156   invertebrates were numerous (Waters 1969). Invertebrates were sorted, identified to the lowest

157   taxonomic level possible and counted under a dissecting microscope using keys in Merritt et al.

158   (2008) and Thorp & Covich (2010). Insects were typically identified to genus when mature

159   specimens were present, except Chironomidae which were classified into two groups,

160   Tanypodinae or non-Tanypodinae. We estimated density by summing the total number of

161   individuals for a given site and dividing by the area of streambed sampled. We calculated

162   biomass by measuring the length of the first 20 individuals of each taxon and then using length-

163   mass regressions to estimate individual biomass (Benke et al. 1999). We multiplied the mean

164   individual biomass for each taxon by the total number collected to estimate total biomass.

165

166   Biological data analysis

167   We used analysis of variance (ANOVA) statistical tests and the R package 'plyr' (R Core

168   Development Team 2017; Wickham 2011) to characterize differences in invertebrate density,

169   biomass and richness among stream types. When stream type was significant ($\alpha = 0.05$), we used

170   Tukey's HSD to distinguish which stream types differed from one another ($P \leq 0.05$). Our use of

171   Tukey's HSD tests was highly conservative, given the small sample size of streams in this

172   preliminary study. To assess the relationship between taxonomic richness or biomass with stream

173   characteristics of interest ($S_{DURATION}$, T_{SUMMER}, Pfankuch Index), we performed both Pearson and

174   Spearman's rank-order correlations using the R package 'Hmisc' (Harrell Jr. 2013). For

175   correlation analyses, taxonomic richness and biomass were averaged for 2015 and 2016 for each

176   upper site.

177   We evaluated differences in community structure across streams, sites, and years using

178   non-metric multidimensional scaling (NMS) with PC-ORD (McCune & Mefford 2006). We

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179    $\log_{10} (n + 1)$ transformed density data for all taxa, removed rare taxa (either those private to a

180   single site in the matrix and/or representing < 1% of the total abundance), and used Sørensen's

181   dissimilarities to create distance matrices. We ran NMS analyses independently on two data

182   matrices: one including each of the upper and lower sites collected in 2015 only (N = 12 sites)

183   and the other including only the upper sites (sampled in both 2015 and 2016; N = 12 sites).

184   Dimensionality of the final solutions was chosen as the number of axes that produced the lowest

185   stress following 200 iterations. Following NMS we applied multi-response permutation

186   procedures (MRPP) in PC-ORD to assess whether there were differences in either community

187   structure and/or mean community distance within the following groups: upstream compared to

188   downstream sites in 2015 and among the three stream types for the upper sites only (2015 +

189   2016).

190

191   **RESULTS**

192   Environmental variation

193   The upper sites of our study streams clearly separated into three groups according to the

194   glaciality index: glacier-fed streams, snowmelt-fed streams, and icy seeps (Figure 2; Table 2).

195   Streambed stability, measured by the Pfankuch Index (Peckarsky et al. 2014), was highest in

196   snowmelt-fed streams and lowest in glacier-fed streams (Table 2). Annual temperature range

197   (T_{RANGE}) was highest in snowmelt-fed streams and lowest in icy seeps. Specific conductivity was

198   highest in icy seeps (SPC >100 μS cm^{-1} at upper sites) and minimal in the other two stream types

199   (Table 2). Total suspended solids (TSS) was highest in glacier-fed streams (mean TSS, glacier-

200   fed = 0.157 g/L, Table 2), indicating active glacier beds were present upstream. Summer

201   temperature (T_{SUMMER}) was low in glacier-fed streams (mean = 1.6 °C) and icy seeps (mean =

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202   2.2 °C), and higher in snowmelt-fed streams (mean = 6.9 °C; Table 2). T_{SUMMER} was correlated

203   with T_{RANGE} and therefore excluded from the PCA. Upper sites were on average 1.2°C colder in

204   the summer and had less stable stream beds than lower sites (mean PI, upper = 27; mean PI,

205   lower = 20.33; Table 1). Other environmental metrics (i.e., DO, pH, ORP, days under snow) did

206   not vary consistently among stream types or between upper and lower sites (Table 2).

207

208   Biological variation

209   We collected a total of 35 invertebrate taxa of which 28 were insects (Supplementary

210   Appendix 1). Insects composed 95% of the total mean densities and 92% of the total biomass.

211   The highest densities, biomass, and richness of invertebrate communities were collected in

212   snowmelt-fed streams. Total macroinvertebrate density did not differ among stream types (F =

213   1.3, df = 2, $P = 0.31$; Figure 3A), but biomass was ~7x higher in snowmelt-fed streams compared

214   to glacier-fed streams and icy seeps (F = 7.1, df = 2, $P < 0.009$; Tukey's HSD, $P \leq 0.02$; Figure

215   3B). Additionally, invertebrate richness was ~2x higher in snowmelt-fed streams than glacier-fed

216   streams and icy seeps (F = 10.4, df = 2, $P < 0.002$, Tukey's HSD, $P < 0.008$; Figure 3C). We

217   observed generally higher and more variable densities (F = 2.7, df = 1, $P = 0.13$; Figure 3D) and

218   higher biomass (F = 2.6, df = 1, $P = 0.13$; Figure 3E) at the lower sites. We also observed ~50%

219   more taxa at lower versus upper sites (F = 8.5, df = 1, $P = 0.012$; Figure 3F). Pearson

220   correlations between richness or biomass and $S_{DURATION}$, $T_{SUMMER,}$ or streambed stability

221   indicated that only T_{SUMMER} was significantly correlated with the biological responses (Richness:

222   Pearson $r = 0.81$, $P = 0.002$; Biomass: Pearson $r = 0.63$, $P = 0.038$; Figure 4). Spearman's rank-

223   order correlations of the same relationships exhibited similar patterns, again with only T_{SUMMER}

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224   exhibiting significant correlations with richness (Spearman's $r = 0.89$, $P = 0.003$) and biomass

225   (Spearman's $r = 0.67$, $P = 0.023$).

226   The most stable NMS solution for comparing community structure between upper and

227   lower sites in 2015 was three-dimensional (stress = 9.6). The first two axes explained 88% of the

228   total variation. Communities from the six lower sites overlapped substantially in ordination space

229   with communities from the six upper sites (MRPP $A = 0.013$; $P = 0.27$). However, the mean

230   pairwise community distance was greater among the upper sites than the lower (0.58 vs. 0.47), a

231   trend that is apparent in the NMS bi-plot (Figure 5A) as a constriction of the total ordination

232   space occupied by lower sites compared to the increased space occupied by the upper sites.

233   The NMS analysis that included upper sites only (2015 and 2016) converged on a two-

234   dimensional solution as the most stable result (stress = 8.9). The two axes explained 86% of the

235   total variation, with axis-1 alone explaining 70% of the variation. In general, communities

236   occupying glacier-fed streams had the lowest axis-1 values, communities in snowmelt-fed

237   streams had the highest axis-1 values and icy seep communities had intermediate axis-1 values

238   (Figure 5B). MRPP results suggested that communities occupying these three stream types were

239   significantly different from one another ($A = 0.19$; $P = 0.006$). Pairwise differences were strong

240   between glacier-fed and snowmelt-fed communities ($A = 0.21$; $P = 0.005$) and were weaker but

241   significant for the two pairs that included icy seep communities (icy seep vs. glacier-fed: $A =$

242   0.11; $P = 0.05$; icy seep vs. snowmelt: $A = 0.12$; $P = 0.03$).

243

244   **DISCUSSION**

245   As climate change proceeds and mountain glaciers recede, there is a need to develop a

246   clearer understanding of how patterns of extant biodiversity and habitat heterogeneity are linked

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247   in high-elevation ecosystems. In this study, we provide the first description of macroinvertebrate

248   diversity in the high Teton Range, Wyoming, where three primary stream types exist: glacier-fed

249   streams, snowmelt-fed streams, and icy seeps. To the best of our knowledge, no streams fed by

250   groundwater aquifers have been documented in the alpine zone of the granitic Teton Range.

251   From a global perspective, icy seeps, which are fed by subterranean ice (primarily by rock

252   glaciers), rather than aquifers of liquid water, are of particular interest as they are likely to persist

253   on the landscape longer than surface ice features (Hotaling et al. 2019a). For the Teton Range, a

254   scarcity of groundwater-fed streams suggests that biodiversity in the region may be even more

255   reliant on meltwater than other high-alpine regions (e.g., European ranges, Brown et al. 2007;

256   tropical Andes, Finn et al. 2016; Glacier National Park, Giersch et al. 2017), and thus may be

257   especially reliant on icy seep-associated climate refugia in the decades to come. In the streams

258   sampled for this study, glacier- and snowmelt-fed streams exhibited significantly different

259   invertebrate communities; however, icy seeps were intermediate between the two in terms of

260   community structure and invertebrate density, biomass, and richness. These results suggest that

261   icy seep communities share some characteristics with both glacier- and snowmelt-fed streams

262   and might have the potential to act as climate refugia for at least a subset of the unique

263   communities present in each of the other more vulnerable stream types. Thus, the potential for

264   icy seeps and ice-influenced terrestrial refugia (Millar et al. 2015) to buffer climate-induced

265   biodiversity loss has profound, global implications.

266   The recession of meltwater sources is predicted to strongly affect downstream

267   invertebrate communities (Jacobsen et al. 2012). In the near term, rising in-stream temperatures

268   are expected as ice melt comprises ever smaller proportions of stream flow. In alpine streams

269   worldwide, warmer conditions have been correlated with increased species richness for microbial

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270   diversity (e.g., Wilhelm et al. 2013, Hotaling et al. 2019a), diatoms (Fell et al. 2018) and

271   macroinvertebrates (Finn & Poff 2005, Jacobsen et al. 2012). Our study adds another line of

272   evidence to this global pattern as we detected a positive correlation between species richness and

273   mean summer temperature (T_{SUMMER}) for macroinvertebrate communities of the Teton Range.

274   We also observed greater richness at lower (mean = 15 taxa) versus upper (mean = 10 taxa) sites.

275   This finding also aligned with, and extended, the conclusions of Tronstad et al. (2016), the only

276   other study to investigate longitudinal patterns of macroinvertebrate richness in montane streams

277   of the Teton Range. We observed far fewer taxa at our highest elevation sites (10 taxa; ~3,150

278   m) versus the highest elevation sites included in Tronstad et al. (2016): 26 taxa at ~2,700 m.

279   Although local (alpha) diversity is expected to increase with warming water

280   temperatures, among-stream (beta) diversity may decrease as more diverse communities shift

281   upstream, effectively homogenizing biological diversity at the regional scale (Jacobsen et al.

282   2012, Wilhelm et al. 2013, Hotaling et al. 2017a). In the Teton Range, we observed greater beta

283   diversity among our upper sample sites than our lower sites, even with wide variation in

284   landscape features (e.g., a lake separating stream reaches at one of our sites) and variable

285   distances between upper and lower sites among our six focal streams. This spatial pattern

286   suggests that in the Teton Range, like elsewhere in the world, heterogeneous hydrological

287   sources bolster regional-scale alpine stream biodiversity.

288   Ultimately, the degree to which alpine streams will be affected by climate change in

289   terms of flow magnitude and persistence remains largely unknown. While many studies of alpine

290   streams operate under the assumption that perennial flow will continue for many streams in the

291   decades to come (e.g., Jacobsen et al. 2012), this may not be the case (e.g., Haldorsen & Heim

292   1999). Thus, the biological ramifications of declining meltwater sources in places like the Teton

293 Range, where groundwater aquifer-fed springs are scarce, may be even more profound than in

294 ranges with a greater diversity of alpine stream sources (e.g., Glacier National Park, Giersch et

295 al. 2017). Indeed, if alpine streams supported by surface glaciers and permanent snowfields

296 transition to intermittency or dry completely, the future of biodiversity in these ecosystems may

297 depend almost exclusively on icy seeps. Our study paired with the broader glaciological

298 literature, however, suggests that there is room for optimism in this regard. Indeed, icy seeps

299 have the potential to span a wide beta diversity profile, perhaps bridging the taxonomic gap

300 between glacier- and snowmelt-fed communities (e.g., Hotaling et al. 2019a). Moreover, rock

301 glaciers and other subterranean ice forms are common in alpine regions worldwide and likely the

302 most resistant ice form to future warming. Clearly, research focused on subterranean ice sources

303 and associated icy seeps, and the biological communities they support, represents a pressing need

304 in alpine stream biology. We suggest that future studies incorporate temporal monitoring of

305 alpine stream types, including icy seeps, to explicitly test how biodiversity and habitat

306 characteristics may be altered across alpine stream types as climate change proceeds.

307

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446   **TABLES**

447   Table 1. Key characteristics of the study streams and sites in the Teton Range, Wyoming, USA.

448   Distances to source (D) are cumulative. Both elevation and D are in meters.

| Stream	Code	Site	Type	Lat., Long.	Elev.	D
Petersen Glacier	PG	Upper	Glacier-fed	43.782, -110.846	2,922	51
		Lower	Glacier-fed	43.785, -110.841	2,900	673
Middle Teton	MT	Upper	Glacier-fed	43.728, -110.795	2,955	178
		Lower	Glacier-fed	43.725, -110.790	2,802	780
South Cascade Creek	SCC	Upper	Icy seep	43.722, -110.838	3,152	165
		Lower	Icy seep	43.729, -110.837	2,943	1,051
Wind Cave	WC	Upper	Icy seep	43.666, -110.961	2,692	29
		Lower	Icy seep	43.667, -110.955	2,564	144
S. Fork Teton Creek	SFT	Upper	Snowmelt	43.691, -110.843	2,987	1,227
		Lower	Snowmelt	43.693, -110.859	2,881	2,757
N. Fork Teton Creek	NFT	Upper	Snowmelt	43.777, -110.860	2,955	9
		Lower	Snowmelt	43.775, -110.861	2,910	393

449

21

450   Table 2. Environmental characteristics of the streams and sites included in this study. T_{YEAR}:

451   mean temperature for a calendar year. T_{SUM}: mean temperature between the summer solstice (21

452   June) and autumn equinox (22 September). T_{RANGE}: the difference between the maximum and

453   minimum temperatures recorded in the stream during the calendar year. S_{ON} and S_{OFF} indicate

454   the day of the year when a site was covered (S_{ON}) or uncovered (S_{OFF}) by snow according to

455   thermographs. $S_{DURATION}$ (S_{DUR} below) is the approximate total number of days each site spent

456   under snow in 2015-2016. Abbreviations and units: temperature (T; °C), dissolved oxygen (DO,

457   percent saturation), specific conductivity (SPC; μS cm^{-1}), oxidation-reduction potential (ORP,

458   mV), total suspended solids (TSS; g/L; upper sites only) and the Pfankuch Index (PI; higher

459   values correspond to a less stable streambed). All data (except for S_{ON}, S_{OFF}, and S_{DUR}) are for

460   2015 only. Stream codes are provided in Table 1.

| Stream	Site	T_{YEAR}	T_{SUM}	T_{RANGE}	S_{ON}	S_{OFF}	S_{DUR}	DO	SPC	pH	ORP	TSS	PI
PG	Upper	0.6	1.4	13.7	306	195	254	118	3.7	7.9	128.4	0.21	42
	Lower	1.9	6.0	16.2	303	128	190	103	9.9	8.6	24.8	--	23
MT	Upper	0.7	1.7	10.3	300	128	193	101	4.8	8.4	41.2	0.105	42
	Lower	1.5	4.1	13.6	296	150	219	100	5.7	8.9	62.9	--	30
SCC	Upper	0.5	1.5	10.0	298	204	271	104	113.2	8.5	-4.6	0.033	21
	Lower	1.5	4.6	13.0	297	155	223	104	110.3	8.4	58.4	--	16
WC	Upper	1.7	2.9	4.4	No cover			102	176.8	8.6	47	0.023	18
	Lower	1.9	4.2	7.3	309	98	154	99	175.2	8.4	77.2	--	18
SFT	Upper	1.9	7.1	17.7	300	174	239	101	74.3	8.6	-0.2	0.013	24
	Lower	Logger failed						101	114.7	8.5	23	--	17
NFT	Upper	2.5	6.6	15.2	300	125	190	101	11.1	8.5	64.9	0.024	15
	Lower	2.5	6.0	10.7	328	133	170	96	11.8	7.8	89.6	--	18

461 **FIGURES**
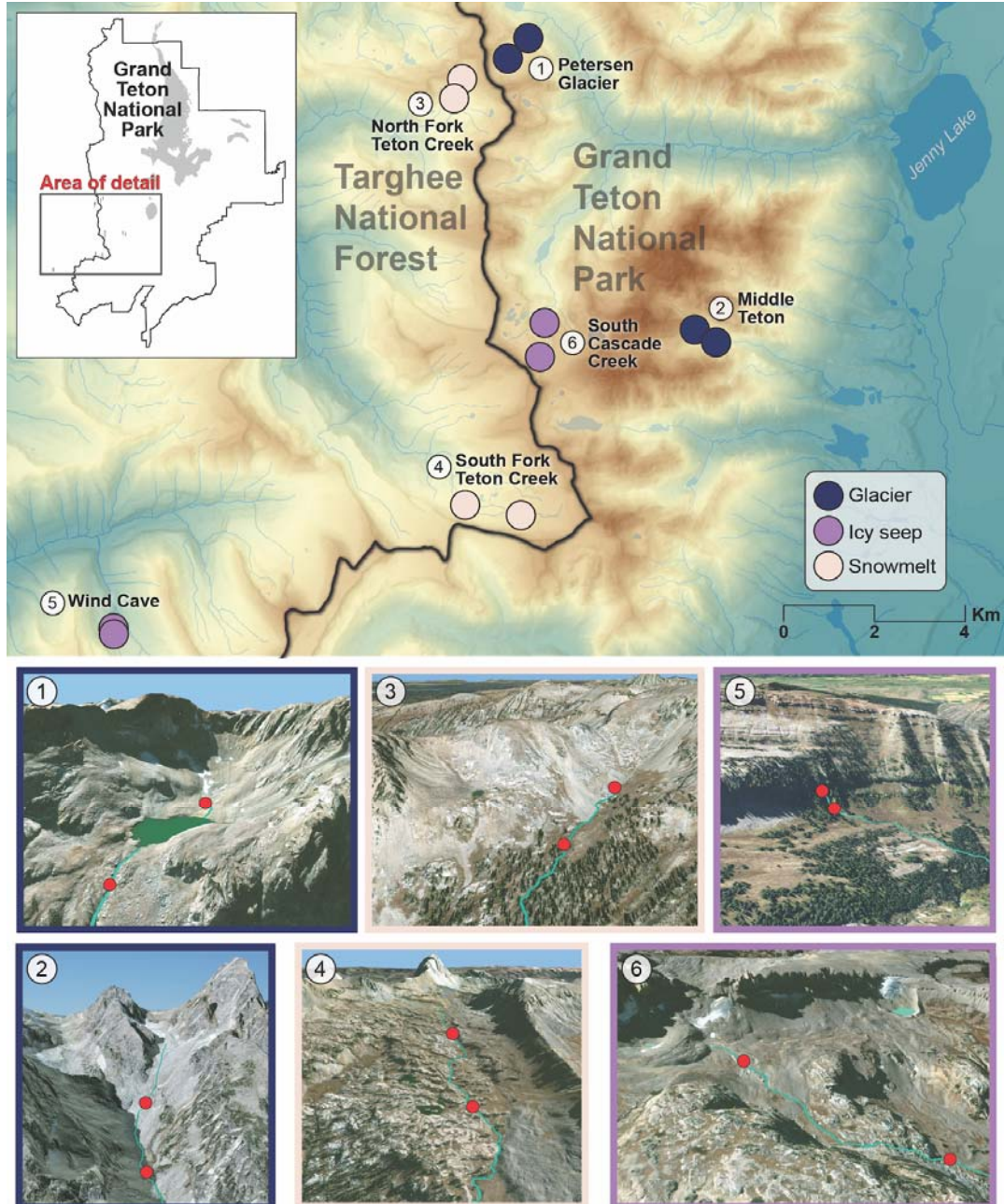
462

463   Figure 1. All streams and sites in the Teton Range, Wyoming, USA, included in this study.

464   Upper sites were selected to be as close to the primary hydrological source as possible. Numbers

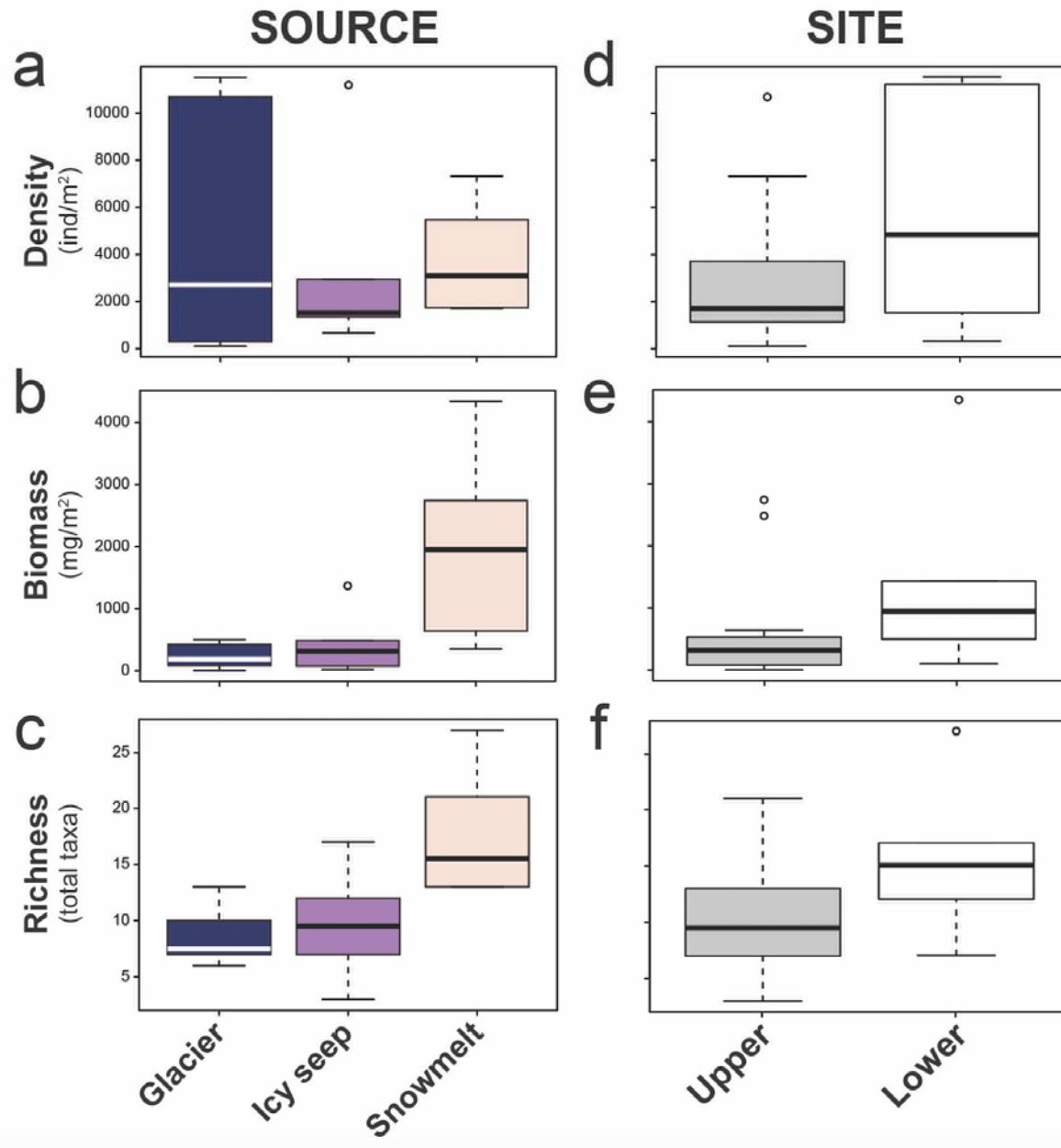465   in the top panel correspond to satellite imagery (DigitalGlobe, 15 October 2015, bottom panel)

466   with stream channel (light blue) and sample sites (red dots) marked.

23
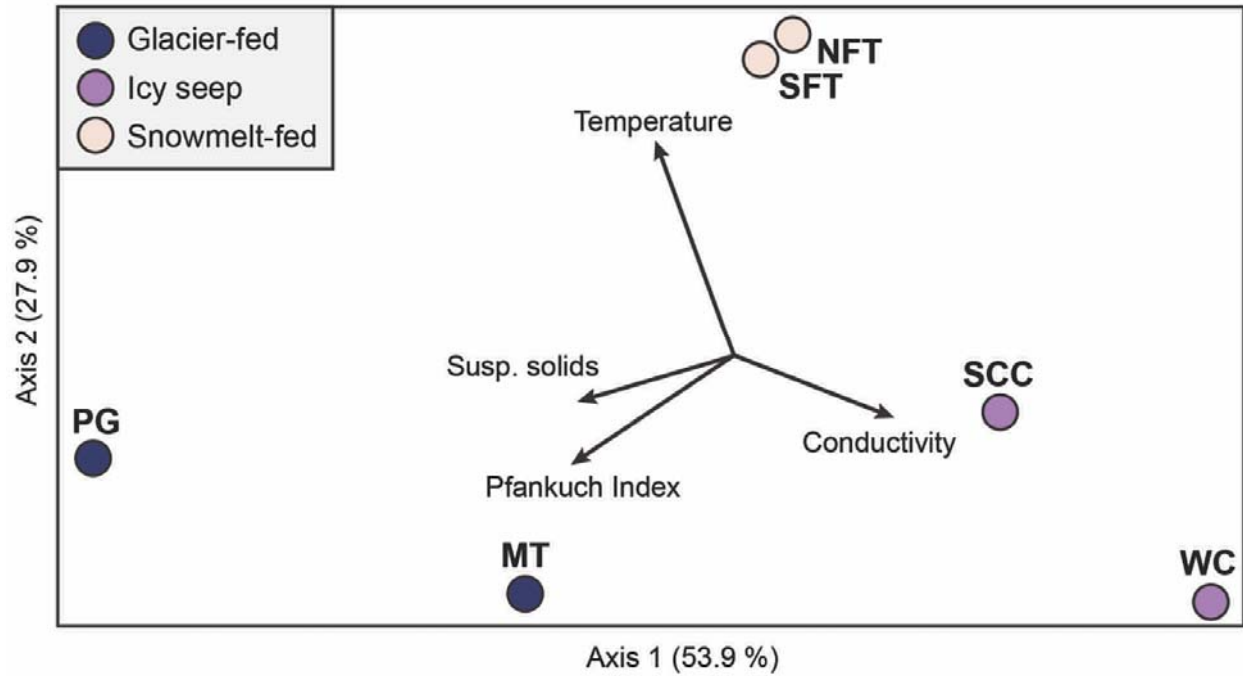
467

468   Figure 2. Principal components analysis (PCA) results showing environmental variation among

469   the upper sites according to the four variables of the glaciality index.

470

471   Figure 3. Macroinvertebrate density, biomass and richness among sites categorized by

472   hydrologic source (a-c) or site (d-f). Bold lines are median values, lower and upper box limits

473   indicate the 25th and 75th percentiles, respectively, and whiskers represent the lower and upper

474   limits of the data (excluding outliers which are shown as circles).

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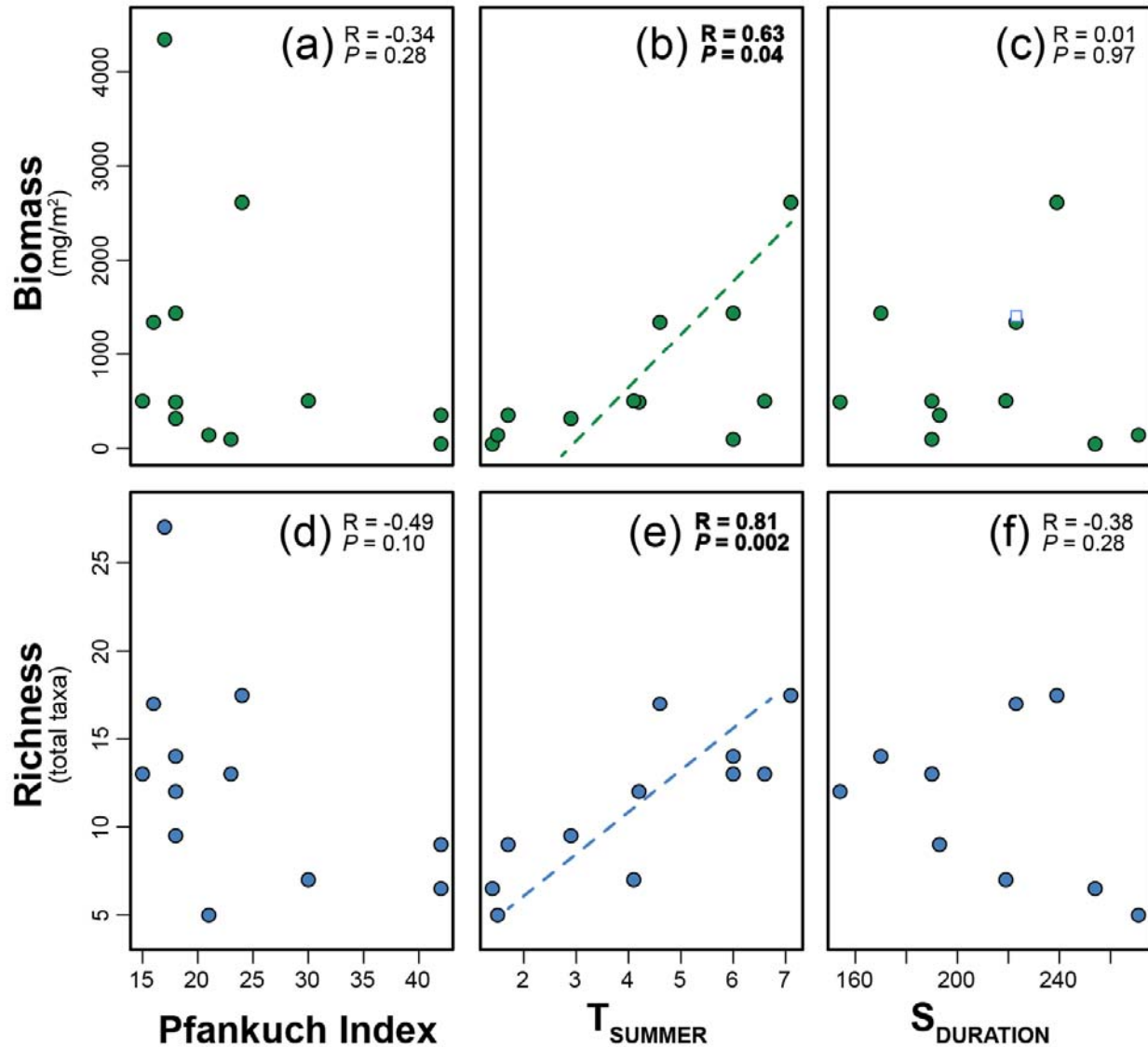
Figure 4. Bivariate plots of biomass (a-c) and richness (d-f) versus the Pfankuch Index, a measure of stream bed stability (higher = less stable), $S_{DURATION}$ (the approximate number of days each stream was snow-covered in 2015-2016), and T_{SUMMER} (mean stream temperature between the summer and autumn solstices). Significant Pearson correlations ($P < 0.05$) are in bold with trendlines shown. The number of data points varies across plots due to a lack of snow cover at upper Wind Cave during the study period and a failed temperature logger at lower South Fork Teton Creek (see Table 2).

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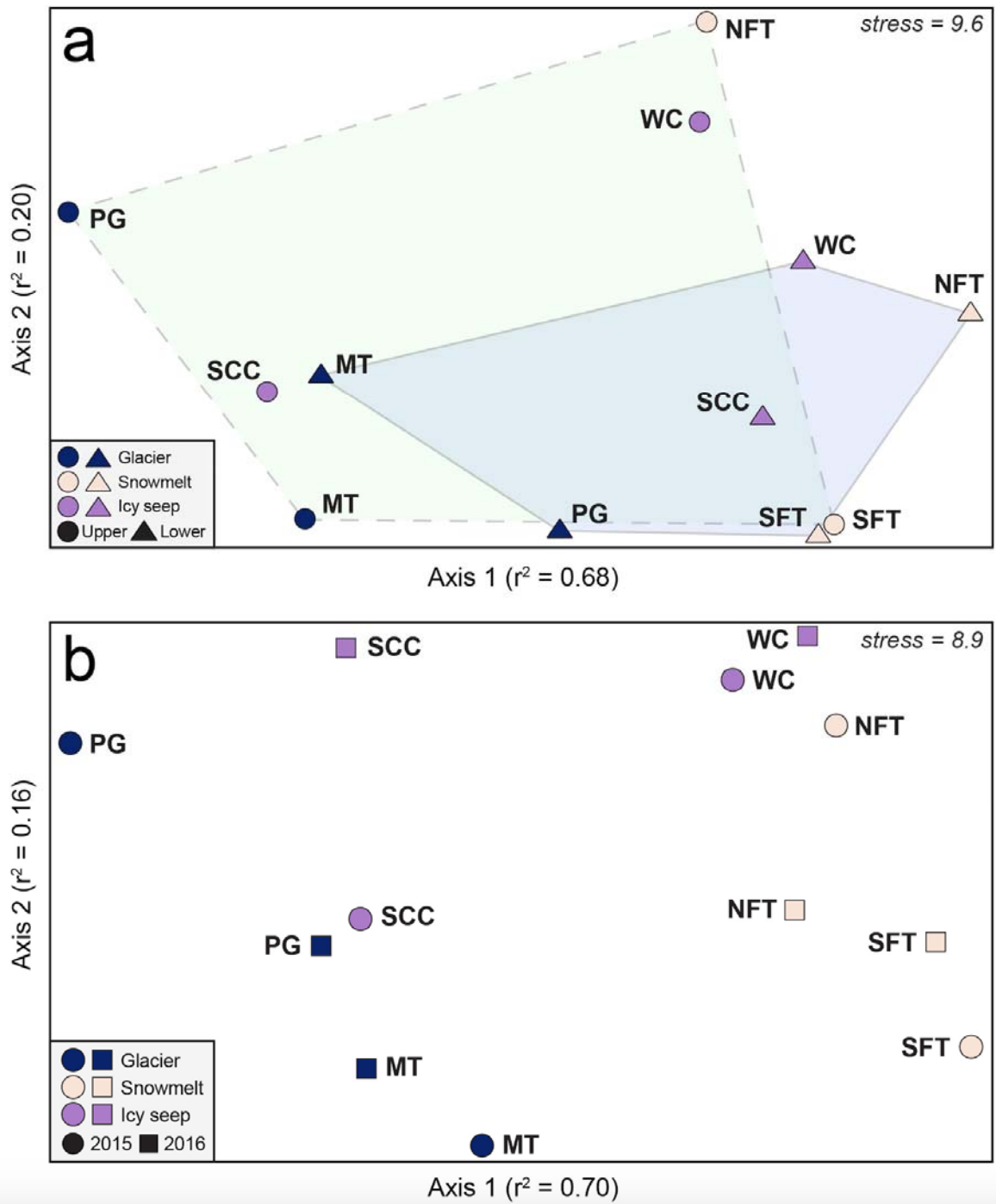
Figure 5. Non-metric multidimensional scaling (NMS) plots of macroinvertebrate communities comparing (a) upper (circles) versus lower (triangles) sites in 2015 only and (b) upper sites only between 2015 (circles) and 2016 (squares). Colored polygons in (a) reflect the breadth of NMS space occupied by upper (dashed lines, green fill) and lower (solid lines, blue fill) sites.