1	Beaver dams mitigate the impacts of whiplash weather in a fragmented habitat: A Salinas River
2	case study
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## 12 Abstract

13 Beaver Castor canadensis create ecological refugia against drought, heat stress and fire, and policies to 14 support beaver conservation and recolonization in regions where they have been historically extirpated are 15 increasingly common. Between prolonged periods of drought, arid regions are increasingly challenged by 16 extreme precipitation events that promote flash floods, debris flows, and mudslides-a phenomenon known 17 as "whiplash weather". Understanding how beaver wetlands respond to whiplash weather will help inform 18 the development of restoration policies targeting the species as a natural climate solution. We used remotely 19 sensed normalized difference vegetation index data to characterize the influence of beaver complexes on 20 riparian greenness dynamics under whiplash weather by comparing three complexes and five nearby 21 reference areas along the Salinas River, California. Our study region is within a remanent patch of the 22 historic range of beaver and is highly impacted by agricultural and urban uses. Despite these limitations to 23 expansion and their low density due to historical extirpation, the Salinas River beaver complexes 24 demonstrated greater riparian greenness resistance to drought and resilience to flood disturbance than the 25 watershed reference areas. Thus, policies supporting beaver re-colonization-even within highly 26 fragmented and anthropogenically impacted habitats-may confer both riparian resistance and resilience to 27 increasingly erratic climatic conditions.

28

#### 29 Keywords

Beaver *Castor canadensis*; whiplash weather; wetlands; Arid West; restoration; normalized difference
vegetation index (NDVI); Salinas River; California

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# 45 Introduction

46

47 Like many areas globally, California is experiencing increasingly severe and prolonged drought periods 48 caused by anthropogenically driven climate change (Hayhoe et al. 2004; Gutzler and Robbins 2011; Mann 49 and Gleick 2015). Climate change accelerates the drying of plant biomass, extending fire season 50 vulnerability (Keeley and Syphard 2016; Williams et al. 2019; Higuera and Abatzoglou 2021; Swain 2021). 51 Between prolonged periods of drought and heightened wildfire risk, California and other regions of the arid 52 western US now face concerns of too much water—a phenomenon known as "whiplash weather," 53 characterized by extreme precipitation events following a dry spell that promote flash floods, debris flows, 54 and mudslides (Swain et al. 2018; He and Sheffield 2020; Francis et al. 2022). Given the myriad of socio-55 environmental consequences to extreme climatic variability, there is a growing need for mitigation and 56 adaptation. Beaver Castor canadensis is a keystone species that alters riparian corridors and lakes 57 throughout the boreal and temperate zones; these activies can increase local climate resiliency and 58 resistance to chronic disturbance through their dam building and wetland maintenance activities (Hood and 59 Bayley 2008; Dittbrenner et al. 2018; Brazier et al. 2021; Thompson et al. 2021; Nash et al. 2021). While 60 beaver wetland complexes can support ecological refugia to drought and fire (Hood and Bayley 2008; 61 Fairfax and Small 2018; Fairfax and Whittle 2020), how these wetlands affect ecosystem response to deluge 62 following drought is less well characterized. Documenting beaver wetland complex response to whiplash 63 weather is thus an important consideration in developing robust wetland restoration policies that target 64 beavers as a natural climate solution.

Wetland systems are sometimes characterized as the ecological equivalent of a "negative emission technology" due to their ability to store high carbon stocks (Griscom et al. 2017; Windham-Myers et al. 2018). Anerobic sediment supports methanogenesis while simultaneously slowing the rate of decomposition, allowing wetlands to store large pools of soil carbon while also supporting improved wildlife habitat quality and water filtration, among other ecosystem services (Page and Dalal 2011). The global extent of wetlands is estimated to be up to 21% of the total global land area although many wetlands have been degraded due to land use practices (Davidson et al. 2018). Some of the largest intact wetland areas occur in North America, primarily Canada and Alaska (Davidson et al. 2018; Tootchi et al. 2019). Historically perceived as undesirable systems (Vileisis 1997), 40-50% of wetlands in the conterminous US were destroyed due to agricultural drainage by the end of the 20<sup>th</sup> century (Kolka et al. 2021; Fluet-Chouinard et al. 2023). More recently, perception of wetlands has shifted from unwanted to intrinsically valuable due to their many ecosystem services, leading to the development of policies to conserve and restore these systems (Zedler 2000).

78 Beaver create and restore wetlands at minimal cost and are increasingly recognized as an effective 79 natural climate solution (e.g., see California's 2024 'Beaver Bill" AB 2196; Griscom et al. 2017; Connolly 80 2024). Beavers use tree such as willow, aspen, and cottonwood to build their dams (Dittbrenner et al. 2018; 81 Puttock et al. 2021). Dam establishment slows water flow and creates ponds, increases channel complexity, 82 and facilitates floodplain creation, thus supporting sediment aggradation (Puttock et al. 2021; Grudzinski 83 et al. 2022). Higher surface and groundwater, greater channel complexity comprised of multiple small dams 84 and lateral river extensions, and larger floodplains created by beaver complexes also help to regulate flood 85 events by dampening, storing, and dissipating high flows (Westbrook et al. 2006, 2020; Feiner and Lowry 86 2015). Westbrook et.al (2020) noted that even failed beaver dams slowed downstream flood waves, 87 although beaver can have minimal impact on flood attenuation (Neumayer et al. 2020; Larsen et al. 2021).

88 Regions facing the dual threat of increasing drought and wildfire stress can benefit from beaver 89 recolonization and conservation due to the ecosystem services associated with their dam building activities 90 (Brazier et al. 2021; Thompson et al. 2021). Yet, the fluctuation between two extremes-drought and 91 flooding-may challenge beaver wetland ecosystem services provisioning and it remains uncertain if 92 beaver influenced hydrogeomorphology confers resiliency or resistance to whiplash weather. Resistance 93 is the ability of a system component to withstand change following a perturbation, while resilience is the 94 rate at which a component returns to its reference condition following a perturbation (Pimm 1984). 95 Therefore, systems exhibiting resistance or resilience in response to a perturbation are unlikely to exhibit 96 the other (i.e., a system will not be both resistant and resilient to drought but may be resistant to drought

and resilient to flood). Uncertainty in how beaver-influenced areas respond to more extreme weather has
raised the call for further investigation at different landscapes and scales (Wohl 2021; Graham et al. 2022).

99 To better understand how beaver activities influence riparian response to whiplash weather in the 100 Arid West, we assessed remotely sensed normalized difference vegetation index (NDVI) patterns in three 101 beaver complexes relative to five comparable areas that did not exhibit evidence of beaver damming activities in the Salinas River watershed in San Luis Obispo County, California (Figure 1). This area is 102 103 within the boundaries of the historic beaver range but in a remanent patch of its current extent that is highly 104 modified by farming, urbanization, and damming for agriculture (Baker and Hill 2003; Scamardo et al. 105 2022). Beginning in December 2022, an extraordinarily wet season followed a multi-year and increasingly 106 extreme drought period in San Luis Obispo County (National Integrated Drought Information System (U.S.) 107 2011). By characterizing NDVI response during a transition from an average precipitation period to extreme 108 drought conditions to flooding, we explored whether localized beaver impacts on a riparian corridor 109 influence plant community resistance to prolonged drought and heat stress, and whether this sustained 110 resistance correlates with resistance or resilience to a subsequent extraordinary flood event.

#### 111 Methods

112

## 113 Site Selection

114 Beavers exert a strong influence on riparian vegetation as a byproduct of their dam building and herbivory. 115 Cutting riparian trees can induce coppicing in some species, and the dam itself elevates water tables, 116 supporting greener vegetation which can be remotely measured using NDVI (Bento et al. 2018). We used 117 NDVI data derived from Landsat imagery that encompassed three known beaver complexes and nearby 118 reference areas along the Salinas River, CA from July 2017 through December 2023 to characterize the 119 effect of direct beaver activities on riparian resiliency after a high peak flow period due to extraordinary 120 rain conditions (December 2022 – March 2023) that followed sustained and increasingly extreme drought 121 conditions (January 2021-November 2022). Our study area is located in San Luis Obispo County, which 122 has a mean annual temperature of 15.4 °C and a mean annual precipitation of 45.6 cm that primarily falls 123 from December through March. The County received 75.3 cm of rain between December 2022 to March 124 2023 (NOAA 2025) causing all known beaver dams along the Salinas to breach with no re-built or newly 125 established beaver dams noted during field visits following the flooding through April 2023.

126 We identified beaver complex locations along the Salinas River in November and early December 127 2022 with field surveys that were supplemented by iNaturalist research-grade observations from 2015 -128 2022 (GBIF Occurrence Download 2025) and confirmation by local experts who had visited the sites. We 129 focused our study on three beaver complexes and five nearby reference areas; our site selection was limited 130 by public land access points interspersed with private land along a 40 km segment between Atascadero and 131 Paso Robles, CA within the 282 km span of the Salinas River. Although maintained by different beaver 132 families, we grouped some of the dams into complexes because they were directly adjacent to one another 133 in the stream network, making it difficult to distinguish at the aerial scale. We selected the focal sites 134 because they encapsulated riparian areas heavily influenced by beaver presence. Areas that were at least 135 100 meters upstream or downstream of the beaver complexes were haphazardly chosen as reference sites 136 (i.e., areas not directly influenced by beaver damming activities), since beavers generally do not stray more

than 50 meters from their complex as they are sluggish on land (Stoffyn-Egli and Willison 2011; SvanholmPejstrup et al. 2023).

139 The Salinas River is heavily impacted by agricultural water use and is characterized by dry riverbed 140 sections. While beaver influenced stream segments were braided and contained surface water year-round, 141 the reference sites did not have comparable channel complexity and lacked surface water year-round. 142 Cottonwood and willow trees were prominent in the beaver complex areas; reference sites had fewer trees 143 and sparse shrubs in the perimeter (Figure 2). Both beaver and reference sites were constrained by human 144 development along the Salinas River. There was no significant difference in the beaver complex and 145 reference site areas (beaver complex  $(56,4571.3 \pm 30,8095.7 \text{ m}^2)$  and non-beaver influenced  $(45,1562.0 \pm$ 146  $16,1301.7 \text{ m}^2; p = 0.6$ ).

147

# 148 Study area NDVI patterns

149 We used ArcGIS Pro to delineate beaver complex and reference sites, extracted Analysis Ready Landsat 8 150 and 9 Images with less than 10% cloud coverage from July 2017 to December 2023 that encompassed the 151 study area, and obtained Band 4 (Red) and Band 5 (near infrared, NIR) .tif files for each image (Data S1-152 Data S2). Landsat 8 and 9 satellites pass through the same area every 16 days with an 8-day offset. In 153 addition to the acquisition schedule, the constraints on cloud coverage yielded at most three usable images 154 produced per month for each site. We calculated NDVI in a Python notebook as (NIR - Red) / (NIR + Red) 155 for each pixel (Drisya et al. 2018). We placed a feature class of 100 random points within each site polygon 156 and calculated the daily NDVI for each point in ArcGIS Pro. We then filtered the NDVI raster set so that 157 any negative values (indicating standing water) were considered null values. For each site and time frame, 158 we used an average of 98.9 of the 100 points to derive the mean NDVI (i.e., non-negative NDVI values). 159 We calculated average daily NDVI within each site which we used to calculate the monthly means of the 160 study sites (n = 3 beaver complexes and n = 5 reference sites) across the six sub-datasets (Data S3).

161 We subset the NDVI data to account for seasonality (plant community green up versus dry down 162 senescence) and the conditions during the water year as reported by the National Integrated Drought 163 Information System and County of San Luis Obispo Water Resources Advisory Committee Rain and 164 Reservoir Reports (National Integrated Drought Information System (U.S.) 2011; Rain and Reservoir 165 Reports, County of San Luis Obispo 2024). We filtered the data based on local drought status and monthly 166 precipitation records: normal (July 2017 – December 2020, which encompassed periods where some of the 167 region experienced abnormal to moderate drought interspersed with drought-free periods), abnormally dry 168 to extreme drought (January 2021 – November 2022, where 100% of the region was in extreme drought or 169 higher from June 2021 – December 27, 2021), and flood to wet (January 2022 – December 2023). We 170 further filtered the data by site type (i.e., beaver complex normal conditions, beaver complex dry conditions, 171 beaver complex wet conditions, reference site normal conditions, reference site dry conditions, and 172 reference site wet conditions).

173

# 174 Data analysis

175 We calculated: (1) the annual peak, minimum, and range of NDVI in the complex and reference sites and 176 (2) rates of change in NDVI for each site type the shared months of green-up and dry down to explore how 177 beaver complexes influence riparian greenness in response to whiplash weather. We tested the influence of 178 beaver complexes on the average NDVI and annual NDVI range, peak, and minimum within a given 179 precipitation period using a repeated measures mixed effect model with complex status (beaver-influenced 180 or reference) and year treated as fixed factors and site as a random effect. We tested how peak and minimum 181 NDVI change across the transition from normal to dry to wet conditions by subsetting the data by site status 182 (complex and reference), treating climate period as a fixed factor and unique site ID (3 beaver complexes, 183 5 references) as a random effect, and using estimated marginal means and a Tukey HSD correction to 184 control for multiple comparisons across the three climate periods.

185 We distinguished green-up months as the periods between the minimum mean NDVI value and the186 peak, whereas dry-down months were between the peak and the minimum. We assessed the influence of

beaver complexes on the rate of riparian green-up and dry-down during an average precipitation period followed by whiplash drought to flood conditions using a repeated measures mixed effect model to test the effects of complex status (beaver-influenced or reference) and time (number of days elapsed from the earliest date within a given year), with site treated as a random effect. Year was included as a fixed factor only for the normal and drought periods, which encompass multiple years (whereas the flooding and postflood span included the end of December 2022 and was otherwise entirely the year 2023).

We completed all statistical modeling in R Studio v 2023.3.0.386 using R v 4.2.3 using the packages: ggplot2 (3.5.0), dplyr (1.1.3), tidyverse (2.0.0), lubridate (1.9.3), lme4 (1.1-35.1), and lmerTest (0.9-40) (Grolemund and Wickham 2011; Bates et al. 2015; Wickham 2016; Kuznetsova et al. 2017; Wickham et al. 2019, 2023), with coding assistance from ChatGPT (Data S4). We reported all results as mean value  $\pm$  standard error and designated statistical significance at  $\alpha < 0.05$ . 198 Results

# 199 Impacts of beaver influence on annual NDVI patterns across a whiplash weather period

200 Beaver complex sites maintained a higher mean monthly NDVI relative to non-beaver influenced sites 201 across the study period (Figure 3). In the normal precipitation period (July 2017 – December 2020), beaver 202 complexes had a greater range between annual peak and minimum NDVI relative to reference sites (0.115  $\pm 0.006$  vs  $0.055 \pm 0.004$ , F = 53.6, p = 0.0003). This effect was driven by the beaver complexes maintaining 203 204 a higher maximum NDVI than the reference areas  $(0.238 \pm 0.006 \text{ vs } 0.149 \pm 0.004, \text{ F} = 701.1, p = 0.0002)$ , 205 while also maintaining a greater average minimum NDVI ( $0.123 \pm 0.003$  vs  $0.094 \pm 0.002$ , F = 81.4, p = 206 0.0001). Beaver influenced areas maintained a greater range between annual peak and minimum NDVI 207 relative to the reference during drought (January 2021 - November 2022;  $0.148 \pm 0.008$  vs  $0.05 \pm 0.006$ , 208 F=86.8, p <0.0001), with the beaver complex areas attaining a higher maximum NDVI than the reference 209 areas  $(0.25 \pm 0.008 \text{ vs } 0.13 \pm 0.003, F = 115.8, p < 0.0001)$ , while complex and reference area minimum 210 NDVI was comparable  $(0.103 \pm 0.01 \text{ vs } 0.086 \pm 0.005, \text{ F} = 3.1, p = 0.13)$ . Following the December 2022 – 211 March 2023 flood events, beaver influenced areas no longer significantly differed in their annual NDVI 212 range relative to the non-beaver reference sites  $(0.075 \pm 0.03 \text{ vs} 0.05 \pm 0.02, \text{ F} = 0.46, p = 0.5, \text{ F}$ = 0.5). This shift in the extent of green up between complex and reference areas reflected that the peak 213 214 NDVI of the beaver complex areas  $(0.163 \pm 0.03)$  was comparable to the reference peak  $(0.124 \pm 0.02)$ , 215 despite the complex NDVI minimum (0.088  $\pm$  0.003) being higher than the reference (0.073  $\pm$  0.002, F = 216 14.9, *p* < 0.002).

Peak NDVI in the reference areas was lower during drought (0.134  $\pm$  0.006) and higher following flood (0.172  $\pm$  0.008) than the normal conditions (0.149  $\pm$  0.005, F=9.4, p = 0.0007). In contrast, the complex peak NDVI did not significantly differ between drought (0.251  $\pm$  0.02) and normal conditions (0.234  $\pm$  0.01), while post-flood peak NDVI was reduced relative to the baseline (0.163  $\pm$  0.02, F = 9.2, *p* = 0.002). Minimum NDVI in the reference areas was reduced both under drought conditions (0.0856  $\pm$ 0.003) and following flood (0.0731  $\pm$  0.003) relative to the baseline precipitation conditions (0.0942  $\pm$ 0.002, F = 16.2, *p* < 0.0001). This effect was paralleled by the complex NDVI, which also had significantly reduced minimum annual NDVI during the drought period (0.1029  $\pm$  0.006) and following flood (0.0876  $\pm$  0.002) than under normal precipitation conditions (0.1226  $\pm$  0.005, F = 11.7, p = 0.0005).

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# 227 Seasonal patterns in the rate of green-up and dry down in relation to drought status

228 Beaver complex riparian areas greened-up for a longer duration and senesced later in the summer (and for 229 a shorter duration) than non-beaver sites in both the normal and dry periods (July 2017 - November 2022; 230 Figure 4). From July 2017 – December 2020, average NDVI in the beaver complex-influenced riparian 231 areas increased twice as rapidly than the reference sites during the shared green up months (monthly average NDVI increase of  $1.29 \times 10^{-3}$  (beaver complex) vs.  $6.72 \times 10^{-4}$  (reference; F = 39.2, p = 0.0007). However, 232 233 the beaver complex NDVI declined more rapidly than the reference NDVI during the overlapping dry-down phase (monthly average NDVI decline of  $-5.42 \times 10^{-4}$  (beaver complex) vs.  $-2.33 \times 10^{-4}$  (reference); F = 234 235 68.5, *p* = 0.0002).

236 During the drought period (Figure 4), beaver complexes maintained a 3.8-fold higher NDVI green-237 up relative to the reference sites (daily average NDVI increase of  $1.08 \times 10^{-3}$  (beaver complex) vs. 2.81 × 238  $10^{-4}$  (reference; F = 63.8, p = 0.0002). Comparable to drought-free conditions, beaver complex NDVI 239 declined more rapidly during senescence yet still maintained a higher mean NDVI value overall (daily NDVI decline of  $-6.47 \times 10^{-4}$  (beaver complex) vs.  $-1.46 \times 10^{-4}$  (reference; F = 112.6, p < 0.0001). High 240 241 peak flow disturbance began December 2022 and persisted until March of 2023. The post-flood green-up 242 phase began later than in pre-flood years (starting in April vs. January) and the subsequent dry-down phase 243 was shortened (likely due to increased water availability during the drier summer months). Beaver complex 244 monthly average NDVI increased twice as fast as the reference sites average NDVI during the overlapping 245 post-flood green up months (April – July,  $1.07 \times 10^{-3}$  (beaver complex) vs.  $5.61 \times 10^{-4}$  (reference); F = 51.2, 246 p < 0.0001). Across the entire shared green up period (January – July) the beaver complexes still maintained a faster green-up rate relative to the reference sites  $(8.98 \times 10^{-4} \text{ vs. } 4.90 \times 10^{-4}, \text{ F} = 43.5, p < 0.0001)$ . In the 247 248 post-flood 2023 dry season, beaver complexes monthly mean NDVI declined more rapidly than the reference sites  $(-2.50 \times 10^{-4} \text{ vs.} -1.48 \times 10^{-4}, \text{ F} = 202.5, p = 0.004)$ . 249

#### 250 Discussion

251 The Arid West is experiencing increasing risk of both high heat and drought stress events as well 252 as more extensive flooding this century (Keeley and Syphard 2016; Swain et al. 2018; Higuera and 253 Abatzoglou 2021; Swain 2021). Beaver can buffer undesirable consequences of wetland loss and help to 254 increase the formation of multichannel drainages under increasing climate warming stressors (Beechie et 255 al. 2010; Pilliod et al. 2018; Wohl 2021). A Beaver Restoration Program established by the California 256 Department of Fish and Wildlife in 2023 exemplifies a shift in perception of the species as a problematic 257 and harvested resource to a keystone species for supporting critical wetland systems. This plan was 258 propelled by the evidence that beavers serve as climate change mitigators due to their ability to increase the 259 resiliency of wetland and riparian ecosystems to drought and wildfire (Hood and Bayley 2008; Fairfax and 260 Small 2018; Fesenmyer et al. 2018; Fairfax and Whittle 2020). However, observations of beaver activity 261 and impacts within the Mediterranean California ecoregion and in other areas of their fragmented 262 southwestern US range remains limited (Grudzinski et al. 2022), challenging the ability to develop sound 263 protocols for beaver reintroduction and restoration. We found that the Salinas River beaver complexes 264 demonstrated greater riparian greenness resistance to drought and resilience to flood disturbance than 265 nearby reference areas through a whiplash weather period, even in highly anthropogenically disturbed 266 riparian areas with sustained periods of extremely low waterflow.

267 Despite promising evidence that beaver activities and the complexes they form support the 268 development of ecological refugia from climate stressors and increase local water tables (Hood and Bayley 269 2008; Fairfax and Small 2018; Karran et al. 2018), there is ongoing debate on whether the resiliency beavers 270 provide to riparian areas under drought and wildfire extends to whiplash weather periods (Wohl 2021; 271 Larsen et al. 2021; Graham et al. 2022). We assessed how remotely derived NDVI in beaver complex 272 relative to non-complex areas responded to a high intensity pulse disturbance (extreme flood event) 273 following a chronic pressure (prolonged drought and heat stress) and as compared to a more average 274 precipitation period preceding the whiplash weather event. While a resilient system may undergo some 275 state change following a disturbance, it will be more readily able to rebound to its previous ecological state as compared to a resistant system, which tends to be less responsive to a disturbance but also slower to recover to the previous state (or may not recover) if change does occur (Lake 2013; Van Meerbeek et al. 2021). Beaver complexes demonstrated greater resistance to drought (by maintaining a comparable peak NDVI to the normal climate period) and resilience to flood (greening twice as fast as the reference area, although achieving a lower peak NDVI than during the normal climate period) relative to nearby reference areas of the watershed. These patterns highlight the ability of these ecosystem engineers to confer multiple ecological benefits under increasingly variable climate conditions.

283 For example, the ability of beavers to trap water supports greater net primary productivity (NPP) 284 and therefore carbon sequestration potential within beaver-influenced riparian areas. While NDVI is not a 285 surrogate for NPP estimation, multiple ecosystems demonstrate a positive correlation between NDVI and 286 NPP (Rafique et al. 2016). Higher mean NDVI values observed in the beaver influenced riparian zones will 287 likely have higher NPP-and thus increased carbon sequestration and storage potential following whiplash 288 weather events—relative to river areas that do not support a beaver population. Without beavers 289 maintaining high water levels, the capacity of a landscape to sequester and store carbon declines over time 290 (Laurel and Wohl 2019; Wohl 2021). Thus, sustained carbon sequestration following whiplash weather that 291 causes the complete loss of beaver dams is likely dependent upon local beaver reestablishment.

292 Paralleling other studies (Hood and Bayley 2008; Fairfax and Small 2018; Fesenmyer et al. 2018), 293 we found that immediate proximity to beaver wetlands promoted vegetation resistance to extreme drought, 294 with complexes supporting a 66% greater monthly average NDVI and a greater annual NDVI range than 295 neighboring reference areas during a prolonged, extreme drought period. Beaver complex riparian areas 296 also greened-up for a longer duration and dried-down later in the summer (but for a shorter duration) than 297 non-complex influenced areas under drought stress. Greater NDVI within the complex areas likely reflects 298 increased dam-driven soil water storage and distribution in the riparian corridor (Larsen et al. 2021). Beaver 299 dam complex areas also demonstrated vegetation growth resilience (but not resistance) as the system rapidly 300 transitioned out of drought, maintaining a higher green up rate that was comparable to the normal and dry 301 periods and higher minimum NDVI during the flood and post-flood period than the reference areas. This 302 pattern was maintained even when complexes were washed out during the flood and the river-scoured 303 structures were no longer visible post-flood, as reflected by a lower minimum NDVI for both complex and 304 reference sites than under normal and drought conditions. This resilience was likely driven by greater river 305 channel complexity and sediment build up along the beaver dammed areas. Beaver areas maintained a 306 greater minimum NDVI and more rapid green-up rate relative to the reference areas but reached a 307 comparable peak NDVI due to the greater green-up of the reference following the flood period.

308 North American beavers were historically abundant across the continent's waterways, with an 309 estimated population of upwards of 400 million individuals prior to European settlement (Boyle and Owens 310 2007). By the 1850s, beavers were nearly extirpated throughout their historic range due to extraordinary 311 hunting pressure for pelts. The beaver population has rebounded to 9-12 million individuals (Scamardo et 312 al., 2022); however, beavers often remain classified as a problematic species by natural resource governance 313 guidelines (often due to human-wildlife conflicts including undesirable flooding and tree loss) and subject 314 to management strategies including extermination (Miller and Yarrow 2015). As climate change intensifies, 315 beaver presence is increasingly positively perceived by natural resource managers due to the plethora of 316 ecosystem services they can provide through wetland creation (Brazier et al. 2021; Thompson et al. 2021). 317 The ability of beaver complexes to dampen riparian disturbance following whiplash weather events further 318 supports this paradigm shift from beavers as a pest to a 'natural climate solution.'

319 While we observed both NDVI resistance and resilience in response to whiplash weather patterns, 320 the extent of these responses was limited to within an approximately 200-meter lateral distance from beaver 321 dams in our study system, which is highly modified by agricultural and urban development that include 322 damming, water diversion, and off-road vehicle uses in the riparian corridor. Given these structural 323 limitations to their expansion and low density due to historic extirpation (Baker and Hill 2003; Carrillo et 324 al. 2009; White et al. 2015), the Salinas River beaver complexes still exhibited resistance to drought and 325 resilience to high peak flow events with regards to plant community greenness. Our research reinforces the 326 concept that policies promoting beaver re-colonization into fragmented habitats can help to confer both 327 riparian stability in the face of increasingly erratic climatic conditions. By supporting nearly year-round

328 green riparian areas adjacent to their dam complexes and increasing *both* riparian corridor vegetation 329 resistance to extreme, chronic drought and resiliency to extraordinary flood events, these findings showcase 330 the ability of beavers to serve as a natural climate change mitigators and lends support to policies that 331 encourage beaver relocation and restoration within the edges and fragmented patches of their historic 332 habitat ranges.

# 333 Supplemental material

335	Data S1. A python script for calculating normalized difference vegetation index (NDVI) in the study focal
336	areas from the USGS EarthExplorer website. In brief, 30-m resolution Landsat 8 and 9 Imagery (10% or
337	less cloud cover) was collected using United States Geographical Survey's webtool Earth Explorer from
338	2017-07-01 to 2023-12-31 using Landsat C2 U.S. Analysis Ready Data. Band 4 (red) and Band 5 (near
339	infrared) .tif files were downloaded to calculate NDVI.
340	
341	Data S2. A python notebook for deriving a zonal statistics table for normalized difference vegetation index
342	data in the Salinas River, California study region encompassing beaver complex and reference areas.
343	
344	Data S3. Comma separated value file of remotely sensed mean normalized difference vegetation index data
345	for 3 beaver complexes and 5 non-beaver reference areas along the Salinas River, California from July 2017
346	until December 2023 derived from Landsat C2 U.S. Analysis Ready Data on the USGS EarthExplorer
347	website and Data S1 and Data S2 scripts.
348	
349	Data S4. Statistical models used to analyze how normalized difference vegetation index in beaver-complex
350	and nearby reference areas of the Salinas River, CA respond to whiplash weather (July 2017 through
351	December 2023) using an RMD file to process the associated 'Data S3.csv' file.
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#### 644 Figure Legends

Figure 1. A map of beaver *Castor canadensis* complex and reference (non-beaver complex) sites along the Salinas River in San Luis Obispo County, California where change in remotely sensed normalized difference vegetation index (NDVI) from July 2017 – December 2023 was used to assess the relative resistance and resilience of beaver complex riparian systems to whiplash weather. The "BW" sites represent three beaver wetlands whereas the "C" sites represent five reference sites. The NDVI value for May 22, 2022 is presented and the inset shows where the study region is located within California.

651

Figure 2. Images taken from Fall 2022 site visits sites along the Salinas River in San Luis Obispo County,

653 California showing three beaver Castor canadensis complex influenced riparian areas (a-c) and three

654 nearby reference areas outside of the direct influence of the beaver complexes (d–f).

655

Figure 3. Monthly average normalized difference vegetation index (NDVI) distinguished by site type (beaver *Castor canadensis* complex or wetland) and period (normal, drought, flood, wet) from July 2017 – December 2023 along the Salinas River in San Luis Obispo County, California. The center line denotes the median value, while the box contains the 25<sup>th</sup> to 75<sup>th</sup> percentiles, and whiskers mark the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Significant differences in average NDVI between the beaver complex and reference area for each period are denoted (\*\*\* p < 0.001, \*\* p < 0.01, \* p < 0.05).

662

Figure 4. Monthly average normalized difference vegetation index (NDVI) in beaver *Castor canadensis* complex and reference (non-beaver complex) sites along the Salinas River in San Luis Obispo County, California over a whiplash weather period (July 2017 – December 2023). The vertical bars represent the standard deviation over the monthly sample periods and the shaded areas surrounding the lines highlight the months in which sites experience a green-up (i.e., an increase in mean NDVI relative to the minimum in a given year). Beaver complex green up and senescence rates were significantly greater than reference areas in all the weather periods (p < 0.005 in all cases).