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2 **Mapping hotspots of potential ecosystem fragility using commonly available spatial data.**

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1 Abstract

2 Effective conservation requires prioritizing areas that are vulnerable to large, irreversible changes.
3 Unfortunately, rigorously documenting these changes with experiments and long-term monitoring is not
4 only costly, but may provide evidence that is too late to facilitate proactive decisions.

5 We use a simple model to illustrate that commonly available short-term spatial, “snapshot”, data from a
6 given ecosystem along an environmental gradient can be used to identify environmental conditions under
7 which different ecosystem states (e.g. different species compositions) co-occur in space. These
8 environmental conditions are those under which future perturbations have the potential for discontinuous
9 large, sometimes irreversible, effects; and can be mapped in space to *predict* potential spatial hotspots of
10 ecosystem fragility.

11 We apply these insights to ecologically important high-elevation subalpine meadows of the Sierra Nevada
12 (California). Our analysis reveals specific areas within meadows that may be more vulnerable than others
13 because their plant communities have the potential to shift to a different state. These shifts can be
14 mechanistically explained by interactions between the vegetation and the local water regimes and/or the
15 upper soil conditions.

16 Our study provides a simple workflow using commonly available data to help prioritize conservation areas
17 based on their potential sensitivity to upcoming perturbations. Such an approach could be very valuable to
18 make most efficient use of conservation and management resources in the context of ongoing global
19 changes.

20

21 Keywords

22 global changes; management; subalpine ecosystems; alternative states; perturbations; spatial data

23

25 Introduction

26 While many ecosystems respond gradually to environmental changes, others can exhibit ecological shifts,
27 where disproportional changes in an ecosystem state occur following gradual changes in environmental
28 conditions (Scheffer et al. 2001, Suding et al. 2004). This represents a global conservation concern, as a
29 wide array of terrestrial and marine ecosystems have shown such large degradation events, including coral
30 reefs (Hughes 1994), fish stocks (Sguotti et al. 2019), arid ecosystems (Kéfi et al. 2007), shallow lakes
31 (Scheffer et al. 1993) and kelp forests (Steneck et al. 2013). In general, because these systems have
32 attracted a large research effort, the ecological mechanisms underpinning these shifts have been identified.
33 Yet, this knowledge does not always translate into actionable conservation directives because local factors
34 can alter ecological dynamics in seemingly idiosyncratic ways (Suding and Hobbs 2009). For example, in
35 rangelands, erosion and fire regimes can tip ecosystems between grass and shrub-dominated states
36 (Suding et al. 2004). Yet, because such dynamics are altered by local factors (such as topography or
37 grazing pressure), it remains difficult to pinpoint the ecological conditions at which a state shift will occur
38 for a given piece of land (Bestelmeyer 2006). Such uncertainty can severely hinder effective conservation
39 efforts, because the potential of some areas to undergo large changes and become degraded can be left
40 overlooked. Conversely, degraded areas that would respond favorably to restoration may be left
41 unattended. For informed land management in the current context of global changes, it is important to
42 identify, *a priori*, how different zones in a given area of interest (e.g. a conservation area) may respond to
43 perturbations. Rigorously and precisely documenting large changes after they happen is too late.
44 Approximately forecasting its potential to occur can help prioritize resources for proactive decisions.

45 To improve the practical forecast of large changes in ecosystems, ecologists have sought to build more
46 operational frameworks and tools to identify from empirical data if a given ecosystem can exhibit shifts,
47 and if so, for which environmental conditions (Scheffer and Carpenter 2003, Andersen et al. 2009, Suding
48 and Hobbs 2009, Ratajczak et al. 2018). However, not all methods can always be applied to a focal
49 ecosystem. Ideally, efforts to identify upcoming shifts would involve documenting temporal responses to
50 changes in environmental conditions, or perturbations (Bestelmeyer et al. 2011, Petraitis 2013), and then
51 applying predictions based on those observations to new locations where environmental changes have yet
52 to occur. Such an approach relies on time-series from either observations or experiments (Scheffer and
53 Carpenter 2003). However, for many locations, obtaining such datasets, or setting up experiments at the
54 appropriate scales can be costly and require perturbation experiments that are often incompatible with
55 management policies. Conservation areas more commonly have inventory data, where descriptive

56 attributes (e.g. abundance of species, soil characteristics, etc.) are surveyed along known environmental
57 gradients (effectively replacing temporal sampling by spatial sampling -- a 'space-for-time' approach).
58 These surveys are often not repeated, resulting in data collected from multiple locations along
59 environmental gradients, but at a single or several close points in time (what we name hereafter 'snapshot'
60 data). As an example, such data could correspond to plant surveys along altitudinal or aridity gradients
61 during a single year. We show here how such data can help land managers prioritize their conservation
62 efforts by predicting where perturbations *may* cause potentially large changes in an ecosystem.

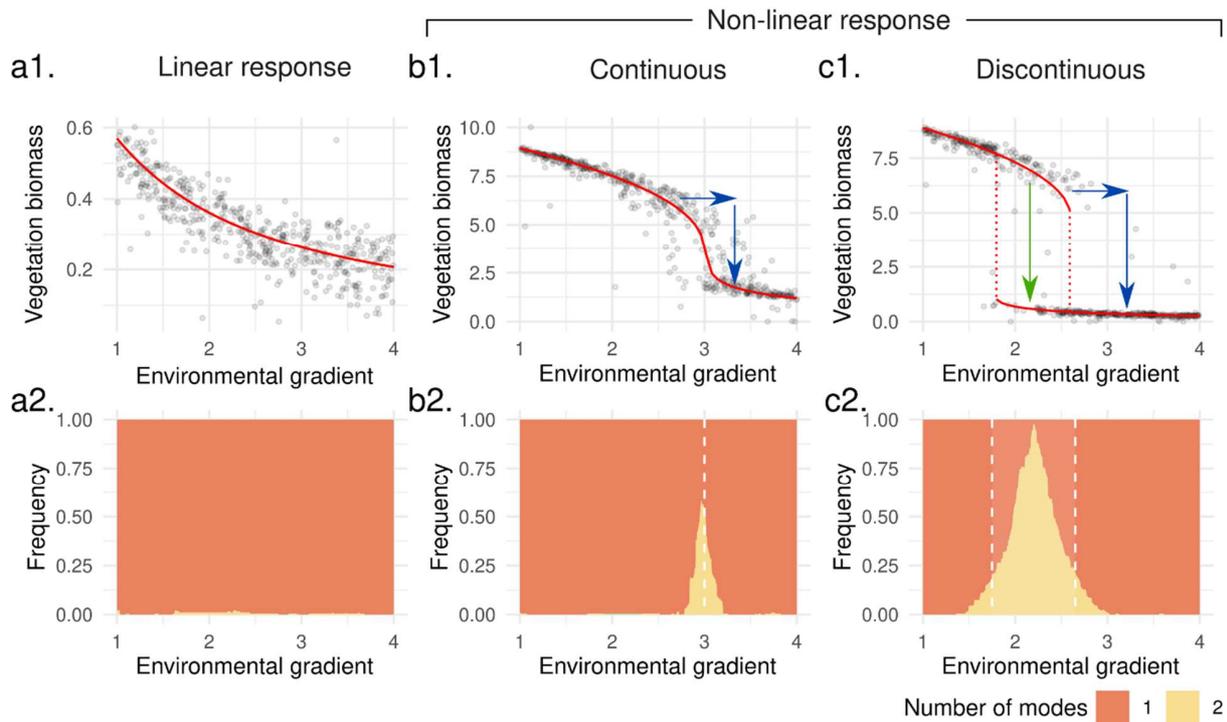
63 Our work focuses on ecologically important subalpine meadows in the Sierra Nevada (California, USA).
64 Many of these meadows are located in two major national parks, Yosemite and Sequoia, and exemplify
65 conservation areas where, due to their remoteness, it is often impractical to regularly monitor for temporal
66 changes, and the use of snapshot data to gain insight on the potential effect of perturbations can be
67 particularly useful. The small-scale species composition of meadow plant communities is known to be
68 tightly linked to water availability (Benedict 1983, Allen-Diaz 1991, Lowry et al. 2011). However, this
69 general response can be altered, for example because of local changes in soil organic matter content
70 (Ankenbauer and Loheide 2017), or because of a locally-increased importance of erosion processes
71 (Klikoff 1965). Due to such local effects, some meadow areas may be more fragile than others to similar
72 perturbations. We show in this study how a novel approach to the analysis of snapshot datasets may help
73 better prioritize conservation and research efforts to protect these habitats.

74 Theoretically, three broad types of changes in a variable of interest (e.g. productivity) can be observed
75 along an environmental gradient: linear, continuous non-linear or discontinuous non-linear with discrete
76 alternative states (Box 1 panels a1, b1, c1) (Ratajczak et al. 2018). Such variable can be a population-level
77 (e.g. abundance of a focal species), community-level (e.g. species composition) or a more ecosystemic
78 attribute (e.g. productivity), depending on what is most relevant for management. When a linear response
79 is observed, the observed state changes proportionally to changes in environmental conditions along the
80 gradient (panel a1 in Box 1). In contrast, with a continuous non-linear response, small changes in
81 conditions result in an apparent large shift as an ecological threshold is crossed (panel b1 in Box 1). A
82 specific case arises when the response exhibits alternative states (panel c1 in Box 1), a case in which
83 several discrete states can be observed for a range of environmental conditions along the gradient. These
84 states can arise from differences in an environmental variable not captured by the main gradient (e.g.
85 different local soil types), or because ecological processes make the ecosystem persist in one of several
86 contrasted states despite similar environmental conditions. In this latter case, the discrete states are
87 effectively alternative stable states, which can arise due to a variety of ecological mechanisms, such as
88 priority effects, or reinforcing feedbacks (Beisner et al. 2003, Petraitis 2013). Regardless of the ecological

89 origin of non-linear responses along a gradient, for practical conservation purposes, the areas where such
90 responses are observed can be considered more fragile, either because they are susceptible to larger shifts
91 than elsewhere, or because the community types in those areas strongly depend on a specific, narrower set
92 of environmental conditions not reflected in the main gradient. Finding ways to identify where they occur
93 is thus essential for informed management.

94 Previous studies have suggested approaches to identify the ranges of external conditions where discrete
95 states are observed, based on detecting distinct ecosystem states in time series (Livina et al. 2010,
96 Vasilakopoulos and Marshall 2015) or ecosystem data along spatial gradients (Hirota et al. 2011, Scheffer
97 et al. 2012). These approaches have mostly been used for cases where a single, well-known index (e.g.,
98 tree cover), characterizes the observed ecosystem state. When the latter cannot be adequately
99 characterized by a single index, it is more challenging to visualize discontinuous changes in data
100 (Magurran et al. 2010), and fewer statistical tools are available to identify discrete states. Yet many cases
101 of interest to both conservation and ecological theory require identifying discontinuous changes in
102 complex multi-species communities. For example, when focusing on changes in species compositions, the
103 observed state is accurately characterized by a set of species abundances, which cannot be reduced into a
104 single index without losing information (Barros et al. 2016). We show here how non-linear responses can
105 be detected along environmental gradients by applying such previous approaches to inventory data. We
106 apply our work to detect areas in subalpine meadows that could be more fragile to upcoming
107 perturbations, and discuss the implications of such fragility for the local conservation of habitats and
108 species.

109



111

112 Proof of concept model: to illustrate the link between multimodality in observations and the type of
 113 response of an ecosystem along a gradient, we can consider a simple model of ecosystem dynamics (Noy-
 114 Meir 1975, May 1977), which can produce different types of deterministic ecosystem responses (red lines)
 115 along an environmental gradient. When a linear response is observed (a1), the average ecosystem state
 116 (which could here represent the vegetation biomass; red line, y-axis) changes proportionally to the
 117 changes in environmental conditions (x-axis). This is not the case for non-linear responses (b1, c1), where
 118 large changes in the observed state can arise following small changes in the environmental conditions
 119 captured by the gradient (blue arrows), or between alternative states after a perturbation (green arrow).

120 We modified the model to have similar dynamics, but subjected to typical sources of ecological noise. We
 121 retained the final state of a set of independent simulations with varying parameters to simulate a sampling
 122 scheme that would lead to snapshot data (i.e. sampling independent instances of the same system in
 123 different environmental conditions, but at a single point in time). This dataset is represented by the black
 124 points in panels a1, b1, c1, each point corresponding to one observation. Using a moving-window
 125 approach, we can investigate how the distribution of these observations changes along the grazing
 126 gradient, and thereby characterize how their ‘modality’ relates to the type of ecosystem response (panels
 127 a2-c2). Wherever the observations tend to exhibit two modes along the gradient, their distribution is better
 128 described by a density with two modes, and thus the frequency of counts for two modes increases (see
 129 *Methods* for details about this approach). As this arises in the vicinity of non-linear responses (panels b2
 130 and c2), modality can be used as a criterion to identify ranges of environmental conditions where apparent
 131 non-linear responses occur.

132 It is important to note that a non-linear response along a gradient does not mean that intrinsic ecological
 133 processes drive the response: external variables not captured by the main gradient could also explain such
 134 a pattern (e.g. different soil types producing alternative states). More information about the model is
 135 provided in Supplementary Material S2.

136 2 Methods

137 2.1 Data source

138 We used a dataset resulting from a study documenting meadow plant communities in 47 meadows located
139 in Yosemite and Sequoia National Parks in 2011 and 2012 (Lee et al. 2017). Meadows were situated
140 between 2517m and 3355m a.s.l. and had an area between 0.42ha and 22.1ha. Data were collected for
141 each meadow from 2x2m plots, regularly spaced (20 m intervals) along belt transects that were oriented
142 perpendicularly to the main meadow drainage, spaced 40 m apart and ran from meadow edge to meadow
143 edge. Volumetric water content of the top 12 cm of soil was obtained for all plots using a handheld TDR
144 soil moisture probe. In every third plot, ocular cover estimates of all plant species were recorded in 8
145 25x25cm sub-plots, and averaged to estimate the relative abundance of each species in the plot. In
146 addition, ocular estimates of the cover of 28 variables describing the local water regime, upper soil
147 characteristics and disturbance by herbivores were measured (e.g. cover of bare ground, rock bed, etc., see
148 Supplementary Material S1). Overall, sampling resulted in 2860 plots with soil moisture and local
149 environmental conditions; of these, 1287 also had species composition recorded.

150 We focused on the variations of a community-level attribute, the species composition of vegetation
151 communities, along the natural moisture gradient in the meadows. Decades of work show that moisture is
152 a key factor in determining meadow species composition, as within a meadow, plant species sort along the
153 gradient (Allen-Diaz 1991, Lowry et al. 2011). We checked that this aspect of meadows was also captured
154 by our dataset (Supplementary Material S2, section 2), and used water content as the main gradient. We
155 attenuated the effect of year-to-year variations in precipitation on the measurements of the moisture
156 gradient by standardizing the measured water content within year. As a result, in what follows, water
157 content values are given in standard deviations (s.d.) to the annual mean.

158 2.2 Analyzing changes in modality along a gradient

159 When a set of observations is unimodal, observations tend to cluster around a single mean. For example, a
160 unimodal set of observations of a given species' abundance can be effectively characterized by a mean
161 abundance, from which most observations would deviate only slightly (Figure 1a). When a set of
162 observations is multi-modal, observations cannot be well-summarized by a single mean and instead,
163 several, different clusters are present in the data. This could for instance be the case when a species is
164 either locally very rare or very abundant (these abundances being *modes*, Figure 1b), but rarely observed
165 with intermediate abundances.

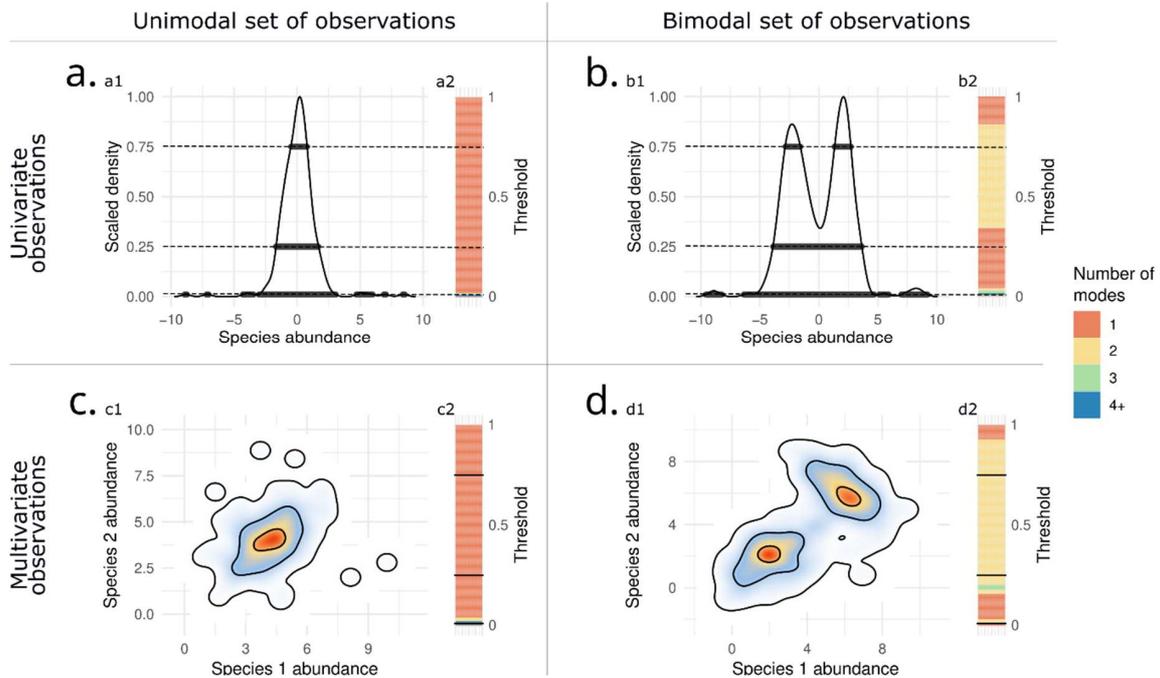
166 Characterizing the multimodality for a set of observations can be done using the density of observations.
167 The density is a function that captures the relative frequency of different observed values: those that are
168 more frequent in a given set of observations will have higher density values. Conversely, values that are
169 scarcely observed correspond to lower density values. This results in local peaks ('modes') in the density
170 around values that are frequently observed in a given set of observations. A unimodal set of observations
171 will tend to have a single peak in its density, i.e. most observations cluster around a single, average value
172 (Figure 1 a, c). A multi-modal set of observations will have a density with multiple well-defined peaks
173 (Figure 1 b, d). Computing the density of a given set of observations, and estimating the number of well-
174 separated peaks in it is thus a natural way to characterize the number of modes in a set of observations (its
175 *modality*, Silverman (1981), Müller and Sawitzki (1991)).

176 For each subset of observations, we computed its density, and considered n_{cut} thresholds regularly spaced
177 between zero and the maximum value of the density. For each threshold, we considered a "horizontal
178 slice" of the density and counted the number of observed disjunct parts of the density above the threshold
179 (λ -clusters *sensu* Müller and Sawitzki (1991), see Figure 1). This number of clusters provides an estimate
180 of the number of well-separated modes in a given density above a certain threshold (Müller and Sawitzki
181 1991, Fisher 2001, Scott 2015). For a given density, i.e. a set of observations, this process yields a set of
182 n_{cut} integer values, each corresponding to an estimated number of modes. How these counts vary along an
183 environmental gradient informs about changes in the modality of the distribution of states. A typical
184 example could be that of a density switching from unimodal to bimodal around a certain value of the
185 environmental gradient, which would be reflected in a higher number of counts for two well-separated
186 modes.

187 This non-parametric method can be applied to univariate densities (Figure 1, top; Box 1), which
188 corresponds to the case where the state of the system is defined by a single value. It can also be applied to
189 multivariate densities, obtained through multi-dimensional kernel density estimation (Figure 1b), which
190 makes it applicable to cases where each observation is multi-dimensional (e.g. when each observation
191 consists of abundances of individual species). It only depends on a single parameter (the density
192 bandwidth) and it is more robust to outliers than previous approaches for the detection of multimodality
193 (Fisher 2001). n_{cut} only affects the precision of computations, and was set to a large value to identify
194 differences in height of the density (we used 512 here, which was enough to detect changes in modality
195 along the gradient).

196 Given a fixed set of observations, this procedure allows estimating the number of modes in the density,
197 but it needs to be adapted to investigate change in this number along a gradient. To do so, we adopted a

198 moving-window approach. We chose a window size w , here corresponding to a range of water content
 199 values, and estimated the number of modes for each subset of observations falling within this range, each
 200 time 'moving' the window by a small amount along the gradient. This allows determining how the
 201 number of modes (i.e. the *modality*) of observations change along an environmental gradient.



202
 203 Figure 1: Principle of the measure of modality based on synthetic data. With univariate observations (i.e.
 204 that are described by a single variable such as the abundance of a single species), the density can be
 205 represented as a one-dimensional function of that variable (a1, b1). This function may have one peak, and
 206 thus be unimodal (a1) or two and be bimodal (b1). When an observation is multivariate (c1, d1), i.e. when
 207 two or more variables are used for each observation, such as abundances of several species, the density is
 208 represented as a two-dimensional plot (c1, d1) along these variables, where red values represent high
 209 density values. Again, multivariate densities can be unimodal (c1) or multi-modal (d1). To estimate the
 210 number of modes, we can consider the number of disjunct parts of a given density with values above a
 211 certain threshold (dashed lines, a1, b1 and continuous lines in c1 and d1). Doing so for a range of
 212 thresholds between zero and the maximum value of the density yields a majority of counts for one mode
 213 for unimodal densities (red area in panels a2, c2). For bimodal densities, the same analysis yields an
 214 increased number of counts for two modes (yellow areas, b2, d2). Note that very low thresholds identify
 215 spurious clusters because of outliers in the density, but this effect only concerns a reduced number of
 216 threshold values, so the influence of outliers on this estimate of modality is minimal. Data was generated

217 by drawing samples out of a univariate or multivariate Gaussian distribution (a,c), or a mixture of two
218 Gaussian distributions (b,d; see Supplementary Material S2 section 5 for the distribution parameters).

219 2.3 Empirical data analyses

220 Classical univariate synthetic indices (*e.g.* total species richness or total cover) fail to capture the response
221 of meadow vegetation communities to environmental parameters (Lee et al. 2017). We thus defined the
222 state of meadow vegetation communities as the set of relative abundances of all species in a given plot
223 (Barros et al. 2016). Each single observation had thus a dimension equal to the total number of species in
224 the dataset (257). Because carrying kernel density estimation cannot be done on data with this many
225 dimensions (typically, computational costs become too high after 5-10 dimensions (Blonder et al. 2014),
226 we summarized the variations of vegetation species compositions to a few axes using an ordination. In
227 principle, using Principal Coordinate Analysis (also named metric Multi-Dimensional Scaling) is the
228 method of choice as it preserves dissimilarities between sites in the resulting axes. However, empirically it
229 often produces strong arch artefacts on vegetation data, in particular when species turnover is high along a
230 gradient (Legendre and Legendre 2012). Non-metric multidimensional scaling could be considered as an
231 alternative but, because it preserves only the ranks of the original dissimilarities between sites, the
232 resulting axes summarizing species turnover cannot be used quantitatively. We therefore chose a
233 Correspondence-analysis-based method – Detrended-Correspondence Analysis – which (i) produces axes
234 that can be used as quantitative variables and (ii) is less subject to arch-like artifacts. We carried out
235 sensitivity analyses to confirm that our results were robust to the choice of dimensionality reduction
236 method (Supplementary Material S2, section 4).

237 We used the two first axes of the DCA and measured changes in the modality of observations along the
238 moisture gradient using the previously-described approach. We set the window size to 1 and used the
239 bivariate diagonal density estimation kernel [0.70, 0; 0, 0.62], as obtained from automatic bandwidth
240 selection (function *bw.nrd* in R). Because the sample size affects the shape of the density (and thus the
241 counts of modes), we always computed densities using a fixed number of observations (150). Because
242 there were often more samples falling within a window of water content, we repeated the analysis 100
243 times for each window, using a random subsample of 150 observations.

244 Based on results from the previous analysis, patterns identified two ranges of water content with increased
245 support for two well-separated modes, dry areas and wet areas. We extracted these subsets from the
246 dataset and investigated soil attributes that could underpin their more bimodal distributions. We refer to
247 dry areas for sites where water content was below -1 s.d. and wet areas for those where water content was
248 above 1 s.d. Because the multimodality analysis suggested a dominance of two discrete plant community

249 types, we clustered each subset into two groups based on species composition, using hierarchical
250 clustering with a Ward distance on a Bray-Curtis distance matrix. We contrasted the environmental
251 covariates of each group to discuss possible underlying mechanisms for this apparent non-linear response
252 along the water-content gradient. We used two-sample Mann-Whitney tests (*wilcox.test* in R) to contrast
253 the distribution of each plot's characteristics across groups, adjusting p-values for multiple tests using the
254 Benjamini-Hochberg correction.

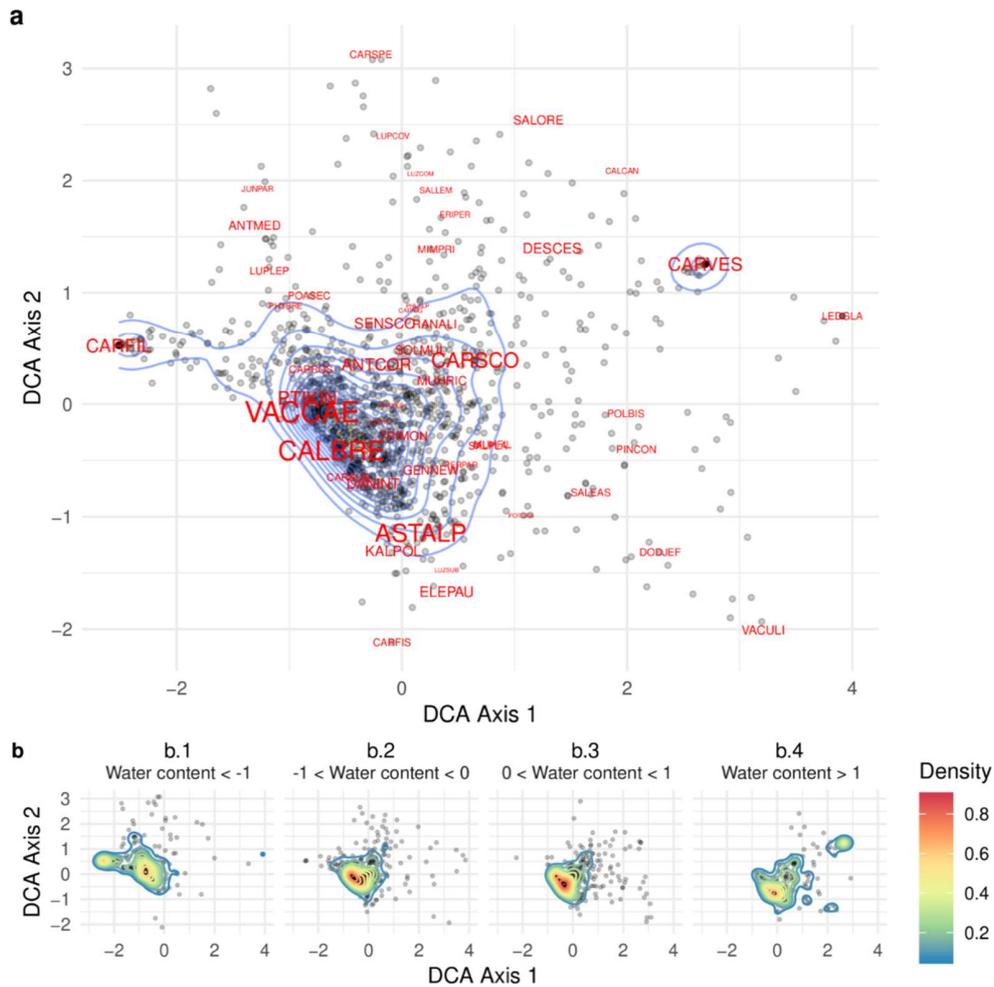
255 Because the sampling was regularly spaced in meadows, we computed for each meadow an estimate of
256 the proportion of area with increased multimodality as the proportion of plots laid in that meadow with a
257 measured standardized water content above 1 or below -1. To map in space where this increase of
258 modality occurred, we interpolated the standardized soil water content within meadows over a regular grid
259 of points using ordinary kriging (using a spherical variogram for each meadow separately). We then
260 modelled the empirical relationship between water content and the proportion of counts for more than one
261 cluster as a one-dimensional generalized additive model. We used this empirical relationship to infer from
262 the interpolated water content the proportion of counts for more than one cluster, and used it as an index
263 of meadow areas with apparent non-linear responses (Supplementary Material S2, section 6). Analyses
264 were conducted in R (version 3.6.1, R Core Team 2019), along with the R package 'vegan' v2.5 (Oksanen
265 et al. 2018), 'gstat' v2.0.3 (Pebesma 2004) and 'mgcv' v1.8.28 (Wood 2004).

266

267 Results

268 We used a proof-of-concept model (Box 1) to investigate how the modality of observations, i.e. how many
269 peaks in the distribution are identified, changes along gradients for different types of ecosystem responses:
270 linear, non-linear continuous and discontinuous. Simulations show that, in the case of a single ecosystem
271 state along a gradual/linear ecosystem response, the distribution is predominantly characterized by a single
272 mode, while multimodality arises when the state changes non-linearly with environmental conditions (Box
273 1, panels b2, c2).

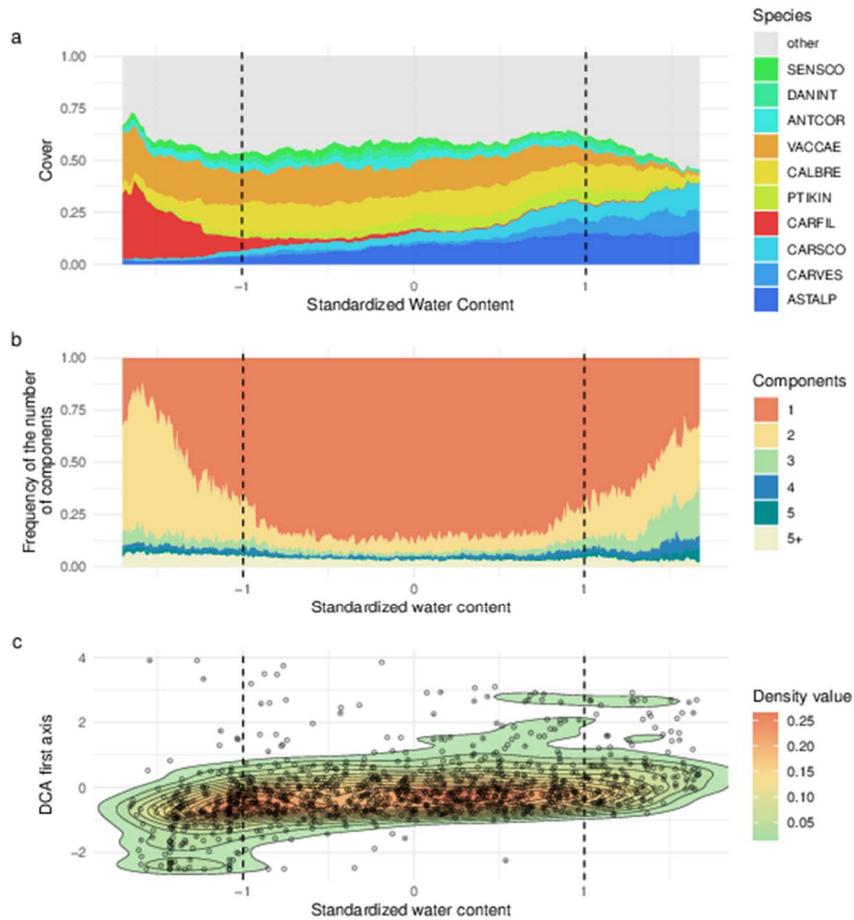
274 The vegetation composition of the sites of our data set was summarized to the two first axis of a
275 Detrended-Correspondence Analysis (Figure 2). The analysis of changes in modality in DCA scores along
276 the moisture gradient highlighted ranges of the moisture gradient with an increased modality in the species
277 composition of the meadows (Figure 2): dry areas and wet areas. In these two ranges of the water gradient,
278 we found an increased count for two well-defined modes (Figure 3b), highlighting an apparent non-linear
279 response of species composition to changes in water content.



280

281 Figure 2: Detrended Correspondence Analysis results on the subalpine dataset (a). The distribution of each
 282 point in the two axes is based on similarity of species composition (two close points tend to have a more
 283 similar composition). Species labels indicate points (plots) where a given species is the most abundant,
 284 with font size being proportional to the overall abundance of the species in the dataset (see supplementary
 285 materials2 for a list of species codes). The bottom panels (b1-4) show the same graph, but only with
 286 points comprised within different ranges of water content. Increased modality (i.e. multimodality) can be
 287 observed for water contents below -1 s.d. and above +1 s.d.

288

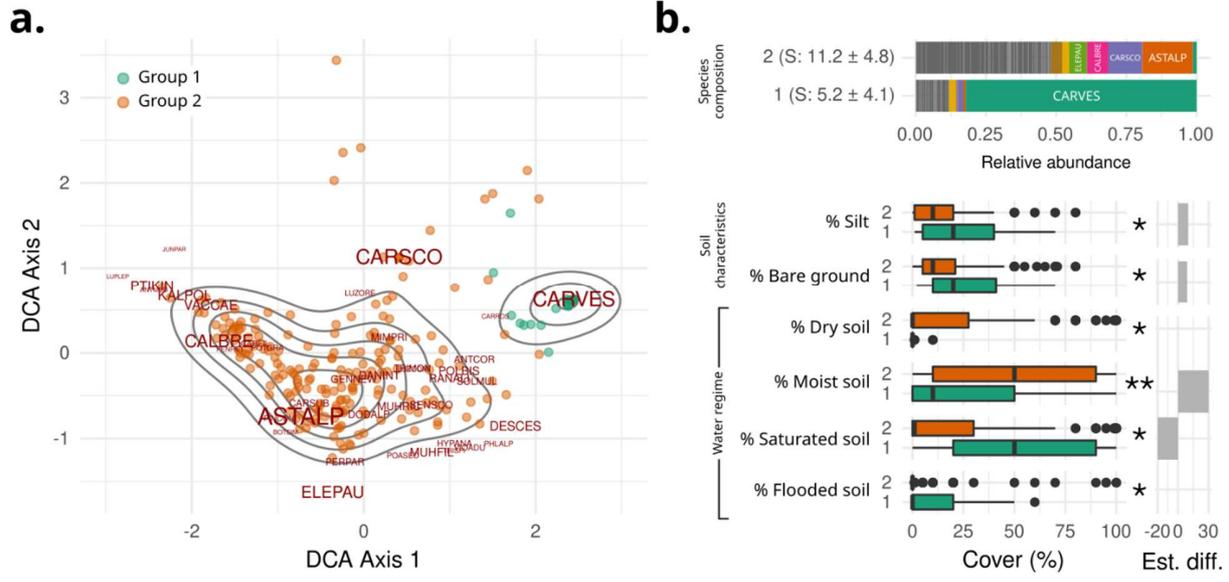


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290 Figure 3: (a) Moving averages (window width: 0.4 s.d.) of the relative covers of the ten most abundant
 291 species in the subalpine meadow dataset along the gradient of soil water content. (b) results of modality
 292 analysis along the same gradient. (c) Changes in the first axis values of the Detrended Correspondence
 293 Analysis (DCA) along the water moisture gradient (each point corresponds to a summarized species
 294 composition), and density contour highlighting local modes.

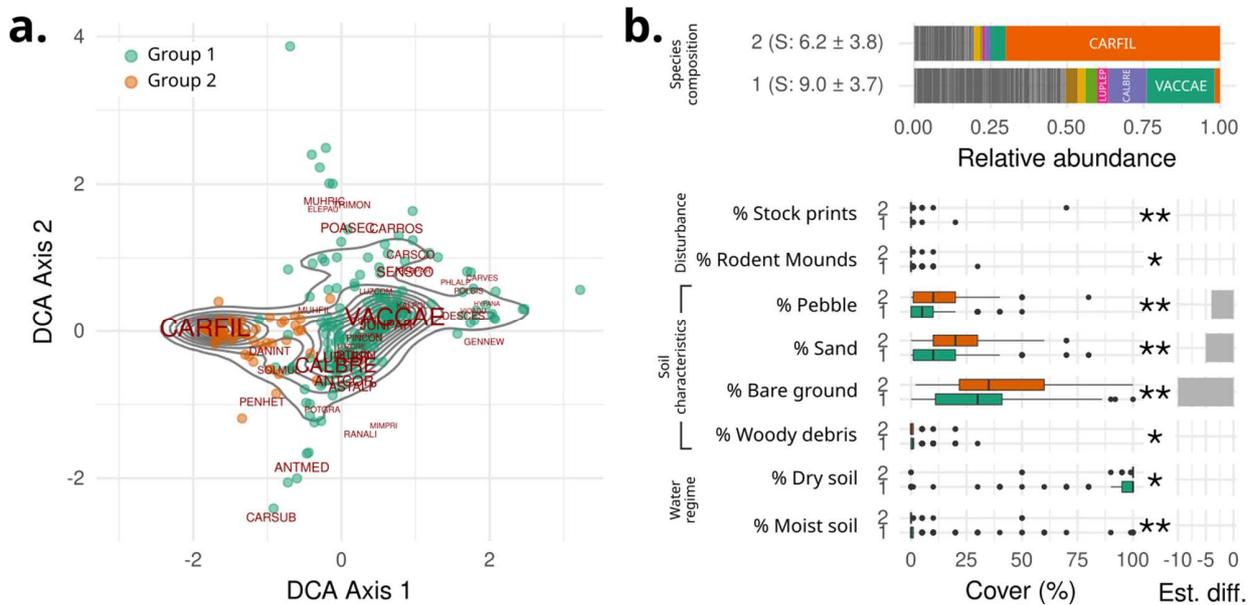
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298 Figure 4: (a) Detrended Correspondence Analysis results on the wet meadow subset. Species labels
 299 indicate where individual species are dominant, with label size proportional to the total abundance of the
 300 species in the subset (see supplementary material S2). A density estimate is added on top of the points. (b)
 301 Differences in species composition, number of species S , and in plot attributes between the two groups
 302 (only attributes with significant differences are shown). Stars represent the significance of a Mann-
 303 Whitney test (one star for $P < 0.05$ and two for $P < 0.01$). The grey bars show the estimated difference in
 304 medians between the two groups.



305
 306

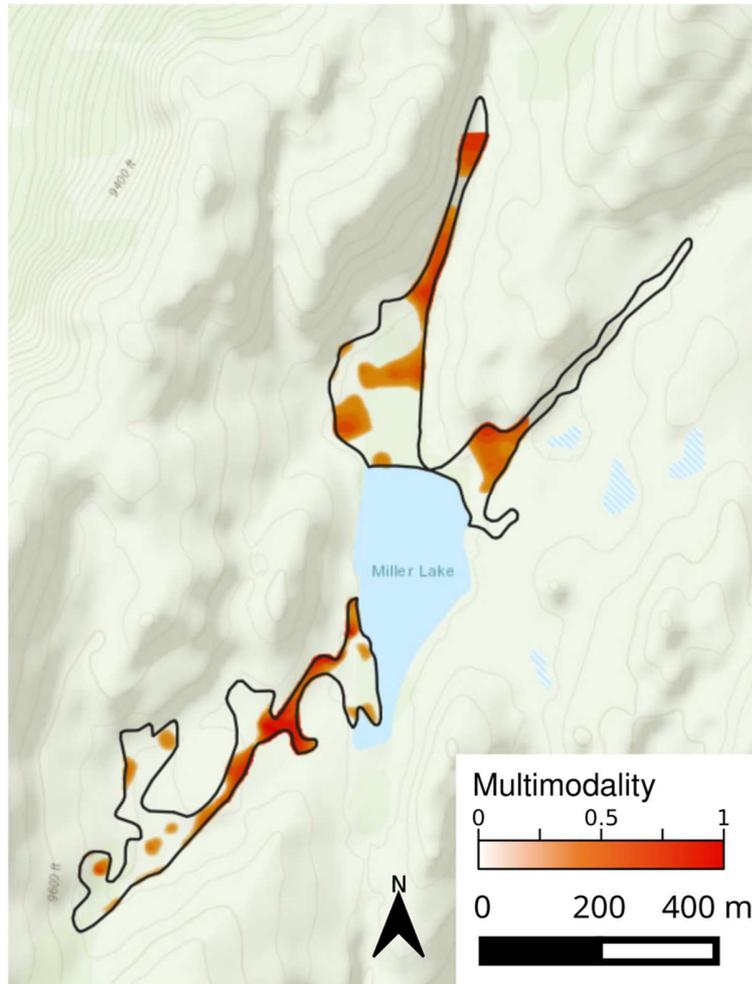
307 Figure 5: (a) Detrended Correspondence Analysis results on the dry meadow subset. Species labels
308 indicate where individual species are dominant, with label size proportional to the total abundance of the
309 species in the subset. (b) Differences in species composition, number of species S , and in plot attributes
310 between the two groups (only attributes with significant differences are shown), stars represent the
311 significance of a Mann-Whitney test (one star for $P < 0.05$ and two for $P < 0.01$). The grey bars show the
312 estimated difference in medians between the two groups.

313

314 In wet areas (plots with water content above 1 s.d.), the two groups defined based on species composition
315 were contrasted. One was dominated by *Carex vesicaria* (*CARVES*), while the other was a more mesic
316 community that included *Oreostemma alpigenum* (Figure 4a, b-top). The *C. vesicaria*-dominated group
317 represented 25% of all the plots in wet areas and had different water regime-related attributes: a more
318 saturated and less moist soil, as well as a higher observed cover of silt and bare ground (Figure 4b). The
319 covers of dry and flooded soils were significantly different between the two groups but the estimated
320 effect size was close to zero.

321 In dry areas (plots with water content below -1 s.d.), one of the two groups was dominated by *Carex*
322 *filifolia* (*CARFIL*) (10% of plots in dry areas), while the other was dominated by more mesic plants (e.g.
323 *Vaccinium caespitosum* (*VACCAE*); *Calmagrostis brewerii* (*CALBRE*); Figure 5a). The *C. filifolia*-domi-
324 nated group had a higher ocular cover of coarse particles (sand, pebble) and bare ground (Figure 5b). It
325 also showed a significant difference in water-regime attributes (cover of dry and moist soil), and
326 disturbance attributes (stock prints, rodent mounds), although they had a very small estimated cover
327 difference (below 10^{-4}).

328 Overall, the proportion of area with increased multimodality in meadows represented on average 22% of a
329 given meadow area of (across surveyed meadows, this number reached from 0 to 77%) and could be
330 identified on maps based on the spatial interpolation of soil moisture (Figure 6).



331

332 Figure 6: Example of spatial use of a multimodality index (the empirical support, between zero and one,
 333 for more than one community type for a given soil moisture level, see *Methods*). Zones in red represent
 334 areas where non-linear responses to changes in soil water content are present, and could thus be more
 335 fragile to perturbations.

336

337 Discussion

338 Our analysis revealed that in wet and dry areas of meadows, there was no smooth response of vegetation
 339 composition to the moisture gradient but instead, discrete vegetation types were present. These types were
 340 associated with contrasted local soil characteristics. As a result, current and upcoming perturbations may
 341 have an unexpected effect in these areas because general changes in moisture regime may alter the

342 specific environmental factors on which vegetation states depend. Reviewing the factors that co-varied
343 with species composition (Figure 4 and 5) helps identify specific environmental variables and potential
344 ecological processes that are critical to the conservation of these habitats, and provide informed possible
345 scenarios for their response to current perturbations in the Sierra Nevada.

346 **Flagging potentially fragile meadow regions.**

347 In wet areas of the meadows, a *Carex-vesicaria*-dominated community contrasted with a more diverse
348 mesic-wet meadow community. While both communities co-occurred in regions of similar average
349 surface soil moisture (as measured by 12 cm TDR probes); the *C. vesicaria*-dominated community had a
350 larger amount of flooded or saturated soil and more silt, which are typical characteristics of streamside
351 flooded pools where *Carex spp.* dominate (Baldwin and Hickman 2012). The mesic-wet community had
352 a more diverse species composition, and occurred more frequently outside of areas with standing water.
353 Here, the discrete vegetation states seemed to depend on the absence or presence of standing water,
354 despite the fact that average, empirically measured surface soil moisture was similar. Local changes in
355 water regimes could thus have a strong effect on species composition – or vice versa. These local changes
356 can arise following changes in regional climate (see below), but may also be caused by local factors.
357 Grazing for example has been shown to increase run-off through compaction of the soil (Kauffman and
358 Krueger 1984, Ostoja et al. 2014), which could diminish the probability of creation of areas of standing
359 water in meadows. However, given the overall low levels of grazing, and the relatively small importance
360 of stock disturbance in our dataset (Figure 4, 5), their potential impacts are most likely minor within parks
361 compared to regional-scale perturbations (Holmquist et al. 2014, Lee et al. 2017).

362 In dry meadow areas, our analysis identified a *Carex filifolia*-dominated community contrasting against a
363 more diverse mesic community which both occur in areas of similar empirically measured soil moisture.
364 The *C. filifolia* community was observed to have coarser upper soil particles (sand, pebble), and a higher
365 amount of bare ground. The two vegetation states differed significantly in visible disturbance by
366 herbivores and water regime. This difference is consistent with the fact that dry communities are known to
367 respond to external parameters such as rodent disturbance, erosion processes and soil nutrients (Klikoff
368 1965). Differences in local soil surface conditions that are not captured by the main gradient could thus
369 explain the presence of different discrete states. However, these local soil conditions are likely tied to the
370 vegetation state as plant-soil feedbacks have been shown to exist in these areas. For example, sods formed
371 by mesic meadow species can improve local microhabitat conditions by trapping smaller soil particles
372 which hold nutrients and water during the dry season (Wood 1975, Ankenbauer and Loheide 2017). These
373 plant-soil feedbacks could be strong enough to impair a rapid regrowth of the vegetation after soil
374 disturbance, so that an acute disturbance of dry areas could have much longer-term effects than expected

375 (e.g. through trampling). It is unknown whether such feedbacks could be strong enough to impair the
376 vegetation regrowth completely following disturbance (effectively underpinning alternative stable states).
377 However, the evidence as a whole highlights the need to adopt a conservation perspective that takes into
378 account the possibility of long-term, poorly-reversible degradation: based on the available evidence, mesic
379 communities in dry areas are likely to be very fragile to upcoming changes in conditions and recovering
380 from acute degradation following an extreme event would likely take decades, if possible at all without
381 restoration efforts (Ratliff and Westfall 1992).

382 More broadly, in both wet and dry areas, soil water-related parameters stood out as possible drivers of
383 vegetation shifts. With the increase in frequency and intensity of drought events associated with climate
384 change, snow to rain ratios and total spring snowpack are decreasing across the Sierra Nevada (Knowles
385 et al. 2006, Barnett et al. 2008). These long-term changes in climate dynamics have the potential to
386 extensively alter meadow hydrology, to which the wet and dry plant communities appear to be the most
387 sensitive. As these communities represent on average 20% of meadow areas (up to 77%), this could
388 constitute a significant concern for subalpine meadows across the central and southern Sierra Nevada. The
389 Sierra Nevada has recently experienced an intense drought event (Belmecheri et al. 2015), which included
390 the four driest years (2012-2015) of the last 2000 years (Adams et al. 2015). While the repercussions of
391 the drought have clearly manifested across Sierra Nevada forest ecosystems (Potter 2016), the impacts on
392 meadow ecosystems have yet to be thoroughly evaluated. Monitoring changes and setting up experimental
393 research in potentially fragile areas occur could inform us greatly about such events. Our approach allows
394 planning this next step by creating maps identifying these areas.

395 A workflow to identify and map fragile areas

396 With this work, we showed that investigating snapshot data for changes in modality of ecosystem states
397 can provide information on the potential fragility of specific meadow areas. Importantly, our results show
398 that we may identify these areas more accurately by taking into account the full state of the community
399 (here, species composition) as we would not have detected changes in modality based on simple indices
400 such as richness or total plant cover (Supplementary Material S2). It is a relatively simple analysis that can
401 be carried out on commonly-available inventory data to investigate the possible dynamics of the
402 ecological system under focus. An example workflow could be the following:

403 1. Gather a dataset of observations describing how the state of an ecosystem varies along known
404 influential environmental gradients. This can be done over a relatively short period of time, but the sample
405 size of observations must be sufficiently large (at least 10-50 points per level of the environmental
406 gradient). If no prior knowledge is available to identify main environmental gradients, this can be done

407 based on redundancy analysis or canonical correspondence analysis (Supplementary Material S2, section
408 2).

409 2. When the state is described using a high number of variables (e.g. species abundances), reduce
410 the dimensionality of the dataset (e.g. using Detrended Correspondence Analysis) to 1-5 dimensions
411 (variables). It is noteworthy that reducing the dataset to 2 dimensions or less drastically speeds up the
412 numerical computations.

413 3. Analyze the dataset for changes in modality along the main gradient, to identify areas along the
414 gradient with increased modality, i.e. where apparent non-linear responses are present

415 4. For these areas, use local environmental data to identify the source of increased multimodality.
416 Such increase may arise as a combination of (1) effects of secondary environmental drivers of plant
417 community composition (e.g. different soil types) and (2) intrinsic ecological processes driving non-linear
418 responses (e.g. reinforcing feedbacks, Wilson and Agnew 1992). For conservation purposes, in both cases,
419 these areas may be considered fragile because the local state (e.g. species composition) depends on a
420 narrower set of environmental conditions and/or the response to perturbations may be non-linear (possibly
421 exhibiting ecological shifts).

422 5. Use spatial data to map where these areas are present, *i.e.* where the effect of perturbations may
423 be larger. It is important to note that identifying the ranges of environmental conditions where non-linear
424 responses occur only requires a reduced subset of data. For example, in our work, only 45% of the plots
425 had a recorded species composition. However, the measurement of water content was carried out for a
426 much higher number of plots, which allowed for higher resolution in our maps of community fragility.

427 The measurement of modality is an open area of statistical research (Scott 2015), and other approaches,
428 not based on the use of a density, could be useful to evaluate multimodality in a set of observations
429 (Clarke et al. 2008) and determine the statistical significance of patterns. Computing multivariate densities
430 can be computation intensive, although approximate numerical methods may help (Blonder et al. 2014).
431 Comparing different methods is beyond the scope of this article, but it is important to carry out sensitivity
432 analyses to test for the robustness of the result (e.g. to the bandwidth used, or the method of ordination to
433 reduce dimensionality, Supplementary Information S2, section 4).

434 **Detecting large ecological changes for conservation**

435 The observation of discrete community states does not mean that a given ecosystem necessarily exhibits
436 irreversible shifts between alternative stable states. For example, discrete states can be also due to changes
437 in an environmental parameter not captured by the ones measured. This is probably the case for the

438 different community states observed on the wetter end of the gradient in the data set studied here.
439 Nonetheless, complementing this approach with other sources of evidence can suggest where non-linear
440 and/or poorly-reversible degradation may be possible in a given ecosystem of interest. Such additional
441 knowledge can come from previously-known ecological mechanisms which drive irreversible shifts (*e.g.*
442 known reinforcing feedbacks between vegetation and soil quality like here), historical information about
443 shifts that occurred in the past and appear irreversible, or evidence from independent approaches (*e.g.*
444 experiments, or based on indicators of ecosystem shifts; Dakos et al. 2012, Kéfi et al. 2014, Nijp et al.
445 2019). While no approach by itself is likely to prove the existence of irreversible shifts, from a
446 conservation perspective it is particularly important to consider this possibility when the alternative
447 community is considered to be degraded (*e.g.* because it is poorer in species or because it represents a loss
448 of conservation-critical habitat). It is better to imprecisely predict a poorly-reversible shift than to
449 precisely document it after it happens.

450 As the conditions for the emergence of alternative stable states are quite restrictive, ecosystems probably
451 respond more often to gradual changes in a gradual way than in an abrupt way (*e.g.* because of spatial
452 heterogeneity that favors gradual responses (van Nes and Scheffer 2005)). Cases of irreversible shifts have
453 however been shown to be possible in a broad range of ecosystems and in a response to a number of
454 drivers (lake eutrophication due to increase nutrient loading, coral reef degradation due to warming and/or
455 water pollution, dryland desertification due to increased grazing and/or droughts). Because abrupt
456 ecosystem responses can happen in about any ecosystems and their occurrence depends on a joint set of
457 conditions which are not straightforward to monitor, it is extremely useful to find approaches that allow
458 rapid predictions of where they are most likely to happen. The approach proposed here is promising
459 because it provides a way to do so for species-rich communities (where most theoretical developments so
460 far focus on species-poor models), and because it can be based on data typically gathered in
461 conservation/protected areas.

462

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