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The dimensionality of stability depends on disturbance type

Running title: dimensionality of ecological stability

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52 **ABSTRACT**

53 Ecosystems respond in various ways to disturbances. Quantifying ecological stability therefore
54 requires inspecting multiple stability properties, such as resistance, recovery, persistence, and
55 invariability. Correlations among these properties can reduce the dimensionality of stability,
56 simplifying the study of environmental effects on ecosystems. A key question is how the kind of
57 disturbance affects these correlations. We here investigated the effect of three disturbance types
58 (random, species-specific, local) applied at four intensity levels, on the dimensionality of
59 stability at the population and community level. We used previously parameterized models that
60 represent five natural communities, varying in species richness and the number of trophic levels.
61 We found that disturbance type but not intensity affected the dimensionality of stability and only
62 at the population level. The dimensionality of stability also varied greatly among species and
63 communities. Therefore, studying stability cannot be simplified to using a single metric and
64 multi-dimensional assessments are still to be recommended.

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67 **Keywords:** Community model, persistence, resistance, invariability, recovery, extinction,
68 disturbance intensity, disturbance type, individual-based model

69 **GLOSSARY**

70 **State variables** are variables used to quantify stability properties of a system, i.e. a
71 population or a community in the context of this study. Examples of state variables are
72 abundance (population level) and species richness or total abundance (community level).

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73 **Resistance** is the degree to which a state variable is changed following a disturbance
74 (Pimm 1984), here measured as the difference between a perturbed and a control system at the
75 first sampling after the treatment (Hillebrand *et al.* 2018).

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76 **Recovery** is the capacity of a system to return to its undisturbed state following a
77 disturbance (Ingrisch & Bahn 2018), here measured as the degree of change in a state variable of
78 a perturbed compared to a control system at the last sampling (Hillebrand *et al.* 2018).

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79 **Persistence** is the existence of a system through time as an identifiable unit (Pimm 1984;
80 Grimm & Wissel 1997), measured by the time during which a system maintains the same state
81 (i.e., state variables within certain ranges) before it changes in some defined way (Donohue *et al.*
82 2016).

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83 **Invariability** reflects the temporal constancy of a state variable following the
84 disturbance, usually measured as the inverse of temporal variability of a state variable (Wang *et*
85 *al.* 2017). Higher invariability indicates higher stability (Donohue *et al.* 2013).

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86 **Disturbance** is a change in the biotic or abiotic environment that alters the structure and
87 dynamics of a system (Donohue *et al.* 2016).

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88 **Stability** is a multidimensional concept that tries to capture the different aspects of the
89 dynamics of the system and its response to perturbations (Donohue *et al.* 2016). Here, we
90 consider the following stability properties: resistance, recovery, persistence, and variability.

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91 The **dimensionality of stability** (DS) depends on the strength of correlations among
92 stability properties. Low correlation corresponds to high dimensionality. If dimensionality is
93 high, a single stability measure cannot be used as a sole indicator of the overall system stability
94 (Donohue *et al.* 2013).

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95 INTRODUCTION

96 Understanding the response of populations, communities, and ecosystems to fast, human-induced
97 environmental changes is a key challenge (Carpenter *et al.* 2011; Higgins & Scheiter 2012;
98 Scheffer *et al.* 2015; DeLaender *et al.* 2016). However, quantifying the stability of natural
99 systems is challenging because stability is a multidimensional concept and requires measuring
100 several stability properties such as *resistance*, *recovery*, *persistence*, and *invariability* (see
101 Glossary, Pimm 1984; Grimm & Wissel 1997; Donohue *et al.* 2016). Correlation among these
102 properties manifests the dimensionality of stability (DS): if the stability properties strongly
103 correlate, the dimensionality is low, and *vice versa* (Donohue *et al.* 2013; Hillebrand *et al.* 2018,
104 Fig. 1a,b). Theory underpinning DS is still in its infancy (Donohue *et al.* 2013) and relevant
105 empirical evidence is only beginning to accumulate (Donohue *et al.* 2013; Hillebrand *et al.*
106 2018). A key question is whether DS depends on the kind of underlying disturbance. Donohue *et*
107 *al.* (2013) showed that when disturbed by consumer removal, DS increased in marine shore
108 communities. At present it is unclear if such conclusions can be extrapolated to other kinds of
109 disturbance.

110 There are many kinds of disturbance. Disturbance properties include: duration, spatial
111 extent, intensity, frequency, and type (Turner 2010). According to their *duration*, two extreme
112 classes of disturbance can be distinguished: pulse disturbances (e.g. fire or flooding) occur over a
113 short time scale, relative to the typical speed at which a system changes, and press disturbances
114 (e.g. global warming or exploitation) represent a constant, long-term change. Disturbance
115 *intensity* reflects how much individuals / biomass are affected by an event over a period of time
116 (Turner 2010). Disturbance *frequency* reflects how often disturbance events occur within a given

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117 time period. Examples of disturbance *types* are local vs. global, and selective vs. non-selective
118 disturbances (De Laender *et al.* 2016).

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119 Despite increasing understanding of how disturbances affect each single stability
120 property, we know little of how the kind of disturbance affects the relationships among multiple
121 stability properties, i.e. the dimensionality of stability (Donohue *et al.* 2013). Yet, such
122 knowledge is crucial for guiding efforts to monitor and manage natural systems. Indeed, if
123 several stability properties correlate strongly irrespective of the properties of disturbances acting
124 on them, the stability of the overall system reduces to one dimension (i.e. low DS, Fig. 1a). This
125 means that monitoring schemes could be optimized by quantifying only a few stability
126 properties. ~~Vice-versa~~ Alternatively, if a system's stability properties are poorly correlated (i.e.
127 high dimensionality), inferring the system's overall stability requires measuring all ~~of~~
128 ~~the~~ properties (Fig. 1b). Therefore, management of natural systems would profit from knowing
129 how DS is influenced by different disturbance properties. For example, an increase of
130 dimensionality with disturbance intensity would undermine the main assumption for detecting
131 tipping points (Dakos *et al.* 2012; Dai *et al.* 2015) through early warning signals (e.g. coefficient
132 of variation, temporal autocorrelation), which usually manifest the variability of a system.

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133 DS can be decomposed into pair-wise correlations among underlying stability properties
134 (Donohue *et al.* 2013; Hillebrand *et al.* 2018; Pennekamp *et al.* 2018). We generally expect
135 positive pair-wise correlations between invariability, resistance, recovery and persistence. For
136 example, ~~at the population level~~ invariability and persistence are expected to correlate positively
137 at the population level, because the higher the temporal constancy in population size, the more
138 likely the population is to persist (Ginzburg *et al.* 1982; Inchausti & Halley 2003). Similarly, at
139 the community level, the higher the temporal constancy in community composition, the more

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140 likely this community is to persist in its unchanged state. For arguments of why we expect other
141 stability properties to correlate positively, see Table S1 in Supporting Information. Because pair-
142 wise correlations are ‘constituents’ of DS, they are expected to depend on the same factors as
143 DS: disturbance properties and the level of organization. Indeed, the sign of a pair-wise
144 correlation between stability properties was shown to change when, instead of a single
145 disturbance, two disturbance types were applied simultaneously to yeast populations (Dai *et al.*
146 2015). Also, pair-wise correlations measured at the community and ecosystem level differed in
147 plankton communities disturbed by reduced light availability (Hillebrand *et al.* 2018).
148 Understanding whether pair-wise correlations are affected similarly ~~by across disturbances~~
149 ~~irrespective of different~~ disturbance types and study systems would facilitate more efficient
150 monitoring of the stability of natural systems.

151 Here, we used process-based, spatially-explicit models to assess how the intensity and the
152 type of disturbance affect DS at the population and community levels. Our models are well tested
153 and structurally realistic, and represent five different communities: a species-rich temperate
154 grassland community, a temperate forest, an algae community, a boreal predator-prey system,
155 and a host-pathogen system. The modelled communities varied in species richness (2 up to 86
156 species) and number of trophic levels (one or two). At both levels of organization we measured
157 four stability properties: resistance, recovery, persistence, and invariability (Glossary, Fig. 2a-c,
158 Table S2). We applied three disturbance types at four intensities. We distinguished disturbances
159 that i) affect individuals selectively depending on their species identity, ii) affect individuals
160 selectively depending on their location, and iii) affect all individuals similarly, irrespective of
161 species identity or location (Fig. 2d,e,f). We tested the following hypotheses:

162 H1: At each level of organization, DS depends on disturbance type and intensity.

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163 H2: All investigated stability properties exhibit positive pairwise correlations (Table S1).

164 H3: At each level of organization, the pair-wise correlations depend on disturbance type

165 and intensity.

166 **METHODS**

167 **Study systems**

168 We used models representing the dynamics of the following communities: temperate
169 forests (Bohn *et al.* 2014), a marine algal community (Baert *et al.* 2016a), a species-rich
170 temperate grassland (May *et al.* 2009), a boreal predator-prey system of mustelids and voles
171 (Radchuk *et al.* 2016a), and a temperate host-pathogen system of classical swine fever (CSF)
172 virus affecting wild boar populations (Kramer-Schadt *et al.* 2009; Lange *et al.* 2012). All of these
173 models had previously been parameterized to mimic the conditions of the respective natural
174 communities (Table S3). All models have three aspects in common: 1) they are spatially explicit,
175 describing the location of habitat patches and movement of individuals among them; 2) they
176 include demographic stochasticity; and 3) the smallest modelled entity is the individual (except
177 for the model simulating an algae community, which is based on Lotka-Volterra equations with a
178 dispersal component; Supplementary Text T1). In addition to demographic stochasticity, two
179 models (a host-pathogen model and a model of temperate forests) also include environmental
180 stochasticity. Temperate grassland was modelled in two ways: using the original IBC-grass
181 model (May *et al.* 2009) and a modified version that incorporates intra-specific trait variation
182 (from now on referred to as Grassland ITV, Crawford *et al.* 2018). We thus used six models that
183 represented five study systems. An advantage of using models that have been previously
184 developed is ~~because that~~ those models have already been tested and verified for ~~respective~~
185 natural systems. We provide short summaries of the main processes included in each model in
186 ~~the~~ Supplementary Methods, and more detailed descriptions of the models in the Supplementary
187 Texts T1-T5.

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189 Disturbances

190 The previously published versions of the models, parameterized to reflect a stochastic
191 quasi-equilibrium state (Nolting & Abbott 2016), were used as a control (no disturbance). We
192 implemented disturbance as a one-time (pulse) removal of individuals. We implemented three
193 types of disturbance (Fig. 2d, e, f): *random disturbance* affected individuals randomly,
194 irrespective of their species identity and location. This disturbance type reflects a non-selective
195 disturbance (De Laender *et al.* 2016). The *rare species removal disturbance* reflects the
196 assumption that the rarest species are most extinction-prone (Solan *et al.* 2004) and is applied to
197 species inversely to their population abundance ranks. This disturbance type was not possible in
198 the wild boar - virus model (Supplementary Methods). The *spatially-structured disturbance*
199 mimicked a localized disturbance by randomly selecting a point for the centre of the disturbance
200 and then gradually increasing the disturbance radius around this point until the disturbance
201 affected the target number of individuals (as defined by the disturbance intensity). We have
202 implemented disturbance types via removal of individuals because this is a generic process that
203 is inherent to several real-world disturbances, such as habitat fragmentation, hunting, culling and
204 pollution. Using removal of individuals allows for comparability of results among the models as
205 they differ in their processes. Therefore, removal of individuals was the best compromise among
206 the relevance of the disturbance type and comparability of results among the systems.

207 Each disturbance type was implemented at four intensities, reflecting increasing
208 proportions of the community that were removed (0.1, 0.2, 0.3 and 0.4 respectively). An upper
209 bound of intensity was chosen via preliminary tests scanning a larger range of intensities, which

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210 showed that at a disturbance intensity > 0.5 , all species in our 2-species systems went extinct,
211 complicating the measurements of all stability properties.

212 We ensured the comparability of the results in terms of the temporal scales among our
213 study systems by scaling the duration of the simulation runs to the average generation length of
214 all the species in the community (Pimm 1984). We used 30 average generations of the control as
215 a ‘burn-in’ phase, after which either the control or one of the disturbance type scenarios were run
216 for the next 60 generations, which was enough for majority of the species to attain either
217 previous or a new stochastic quasi-equilibrium state (based on Gelman-Rubin diagnostics,
218 Supplementary Figs. S1-S3, Supplementary Methods). The disturbance was applied in the first
219 time step immediately after the ‘burn-in’ phase. We ran 30 replicates of each of the 13 scenarios
220 (the control plus three disturbance types crossed with four levels of disturbance intensity) to
221 account for the stochasticity inherent in the models. These 30 replicates were sufficient to
222 capture effects that are due to disturbances and not merely a result of stochasticity
223 (Supplementary Methods and Figs. S4-S7). The ‘burn-in’ phase was discarded when calculating
224 the stability properties.

225 **Stability properties**

226 At both the community and population level, we quantified four stability properties:
227 *resistance*, *recovery*, *persistence* and *invariability* (Glossary, Fig. 2a-c, Table S2). We quantified
228 stability properties analogously at both levels of organization. At the community level as state
229 variable we used community composition, and at the population level we used abundance. We
230 here detail how stability properties were measured at the community level, for details on how it
231 was done at the population level please refer to Supplementary Methods.

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232 *Resistance* was measured as Bray-Curtis similarity of the community composition
233 between treatment and control at the first sampling after treatment (time step 1, Hillebrand *et al.*
234 2018). *Resistance* ranges between 0 and 1 with 1 reflecting maximum resistance (100%
235 similarity between treatment and control). *Recovery* reflects the degree of restoration of the
236 system at the end of the time series and was measured as Bray-Curtis similarity of the
237 community composition between treatment and control at the final sampling (time step 60,
238 Hillebrand *et al.* 2018). Analogously to resistance, recovery ranges between 0 and 1, with 1
239 reflecting a full recovery. *Persistence* was measured as the time during which the community
240 composition in a treatment remains within 90% of the Bray-Curtis similarity with the
241 composition of the control community. We scaled the original persistence values (min = 1, max
242 = 60) by dividing them by their theoretically possible maximum (60), so that persistence ranges
243 from 0 (the similarity between the treatment and control is < 0.9 in the first time step) to 1
244 (maximum persistence, a system remains within 90% of similarity during the whole period).
245 Temporal *invariability* (Wang *et al.* 2017) was measured as the inverse of standard deviation of
246 residuals from the linear model regressing the Bray-Curtis similarity between the treatment and
247 control communities on time (Hillebrand *et al.* 2018). When temporal invariability is higher, i.e.
248 when community composition fluctuates less around the average trend, the stability is higher. In
249 Supplementary Methods we explain the choice of 1) Bray-Curtis similarity as a particularly
250 suitable state variable for measuring stability at the community level (Donohue *et al.* 2013;
251 Hillebrand *et al.* 2018) and 2) the threshold of 90% of Bray-Curtis similarity to measure
252 persistence.

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253 Dimensionality of stability

254 We quantified DS using multidimensional ellipsoids based on the covariance matrices
255 among all stability properties (Donohue *et al.* 2013). The covariance matrices were constructed
256 using the 30 replicates per scenario (at the community level) and per species nested within each
257 scenario (at the population level). Since disturbances may affect both the volume and the shape
258 of such ellipsoids (Donohue *et al.* 2013, Fig. 1a-c), we considered both. We used semi-axis
259 lengths to characterize the shape of ellipsoids. The semi-axis length a_i was measured as $a_i =$
260 $\lambda_i^{0.5}$, where λ_i is the i^{th} eigenvalue of the covariance matrix for a given scenario (i.e. a
261 combination of the disturbance type and intensity) at the community level and for each species
262 within each scenario at the population level. Ellipsoid volume was calculated as $V =$
263 $\frac{\pi^{n/2}}{\Gamma(\frac{n}{2}+1)} \prod_{i=1}^n (\lambda_i^{0.5})$, where n is the dimensionality of the covariance matrix. Prior to the calculation
264 of the ellipsoid volume, each set of semi-axis lengths was standardized by dividing all of them
265 by the maximum length within a set, so that the maximum standardized length equalled 1. This
266 allowed us to calculate the largest volume that was theoretically possible (i.e. all of the
267 standardized semi-axis lengths are 1), which reflects a perfect spheroidal shape and, therefore,
268 high DS. By dividing the actual ellipsoid volume by the theoretical maximum, we obtained a
269 proportional volume. This proportional volume varies between 0 (a ‘cigar’-like shape of
270 ellipsoids, Fig. 1a), and 1 (a perfect sphere, Fig. 1b), reflecting low and high DS, respectively.
271 Characterization of multidimensional ellipsoids based on covariance matrices relies on the
272 assumption of linear relationships among stability properties (Supplementary Methods). In our
273 case this assumption is satisfied for most study systems and disturbance types (e.g. Figs. S8-
274 S15).

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275 To test the effect of disturbance properties on DS (H1) we fitted generalized mixed-
276 effects models (Gamma distribution) with either ellipsoid volume or semi-axis length (per each
277 rank, Fig. 1c) as a response (Supplementary Methods). As fixed effect predictors we included
278 disturbance type (as a factor) and intensity (as a continuous variable). At the community level,
279 we included study system as a random slope and at the population level, the random slope
280 structure consisted of the species nested within the study system. We tested for the significance
281 of fixed-effect terms using likelihood-ratio tests (LRT), but in our interpretations focused on
282 effect sizes, because our study is based on simulations and virtually anything can become
283 significant given enough replicates. At the community level, there was no variation in
284 persistence for at least one disturbance type in the three study systems (persistence was 0 in all
285 replicates of a rare species removal disturbance in both grassland systems and it was 1 in all
286 replicates of random disturbance and rare species removal of the algae system). This precluded
287 calculation of semi-axis lengths and ellipsoid volumes using all four stability properties (i.e. four
288 dimensions) for these study systems. Therefore, we first fitted models using all four dimensions
289 with only three study systems (forest, vole-mustelid, and wild boar-virus), and then used three
290 dimensions (excluding persistence) to fit models with all six study systems. The results from
291 both analyses are qualitatively the same. The results based on three dimensions are presented in
292 the main text, and those based on four dimensions in Fig. S16, Tables S4 and S5.

293 **Pair-wise correlations**

294 To test whether all pair-wise correlations among stability properties were positive (H2)
295 and affected by the disturbance properties (H3), we calculated Spearman-rank correlation for
296 each pair of stability properties obtained for each of the 13 scenarios at the community level.
297 Similarly, at the population level, Spearman-rank correlation was calculated for each species

298 within each scenario. Next, we transformed these Spearman-rank correlations into Fisher's z
299 scores to improve their normality and to avoid any disproportionate influence of extreme values,
300 and used them as effect sizes in the meta-analysis (Koricheva *et al.* 2013). We fitted mixed-
301 effects meta-analytic models (Gaussian distribution) with the fixed effects of disturbance type (a
302 factor), disturbance intensity (a continuous variable), and an interaction between them. At the
303 community level, the models included the study system and replicate as random intercepts. At
304 the population level, also species identity was included as a random intercept. All meta-analytic
305 mixed-effects models were fitted with the library *metafor* in R (Viechtbauer 2010). All analyses
306 were conducted in R 3.4.2 (R 2017).

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307

308 **RESULTS**

309 **Effect of disturbance properties on the dimensionality of stability**

310 At the community level, neither disturbance type nor intensity affected DS (as measured
311 by semi-axis lengths, Fig. 3a & Fig. S17a; and ellipsoid volumes, Fig. 4a & Fig. S18a; Table S4).
312 However, study systems varied in their DS, as measured by semi-axis lengths (Table S6, Fig. 3a)
313 or ellipsoid volumes (Fig. 4a). While grassland and forest communities were characterized by
314 high DS (Fig. 4a), corresponding to spheroid-looking stability ellipsoids (Fig. S19a,b), vole-
315 mustelid and algae communities had low DS, corresponding to a ‘cigar’-like ellipsoids.

316 At the population level, the disturbance intensity did not affect DS (Fig. S18b), while
317 disturbance type did (Table S4). Random disturbance increased DS (Fig. 4b). This was also
318 reflected in the differences among semi-axis lengths: under random disturbance, the semi-axis
319 lengths of the 1st rank were shorter ~~compared to~~ than for other disturbance types, and the semi-
320 axis lengths of the 3rd and 4th order were longer than for ~~compared to~~ other disturbance types
321 (Fig. 3b). At the population level, DS varied among study systems and species (Fig. 4b, Table
322 S5).

323 **Pair-wise correlations between stability properties**

324 At the community level, pair-wise correlations were on average positive (supporting H2)
325 and three out of six correlations were affected by disturbance properties (supporting H3, Fig. 5a).
326 ~~The Correlation correlation~~ of recovery with resistance and ~~of~~ recovery with invariability
327 depended on the disturbance type, with positive correlations s under random disturbance and very
328 weak correlations s (around 0) under spatially-structured disturbance. ~~The Correlation correlations~~

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329 between invariability and persistence became weaker and approached 0 as disturbance intensity
330 increased.

331 At the population level, two pair-wise correlations were on average negative, three were
332 positive, and one correlation was close to 0 (Fig. 5b-d). All pair-wise correlations were affected
333 to a certain degree by disturbance type (Table S7). Additionally, disturbance intensity interacted
334 with disturbance type in its effect on one correlation (invariability with recovery, Fig. 5c) and
335 affected another one (invariability with resistance) in an additive way (Fig. 5d). There was no
336 coherent pattern in how disturbance type modulated different pair-wise correlations.

337 **DISCUSSION**

338 We tested whether the correlation structure among stability properties was affected by ~~the~~
339 disturbance properties across five communities, differing in species richness and number of
340 trophic levels. ~~Contrary to our expectation (H1). At the community level,~~ we did not find an
341 effect of ~~the~~ disturbance properties on the dimensionality of stability- (DS) at the community
342 level~~(DS, H1)~~. At the population level, DS was higher under random disturbances. Additionally,
343 at both levels of organization DS varied largely among study systems. At the community level,
344 as expected (H2), we found generally positive correlations among different stability properties.
345 In contrast, at the population level, the sign and magnitude of correlations were highly
346 heterogeneous. Finally, pair-wise correlations at both levels depended on the disturbance
347 properties, mainly on disturbance type, supporting our hypothesis (H3), although the effect sizes
348 were smaller at the community level.

349 **Dimensionality of stability at the community and population level**

350 We did not find any effect of disturbance properties on DS at the community level.
351 However, our findings reveal high heterogeneity in DS among study systems. For 4 of the 6
352 study systems, community stability was a highly-dimensional concept (Fig. 4a), suggesting that
353 monitoring these systems requires measuring multiple stability properties. A promising avenue
354 for future research would be investigating whether – and what – properties of a system predict its
355 DS. At the community level, our findings indicate that such candidates of system properties as
356 species richness and number of trophic levels do not discriminate the systems with low and high
357 DS (Fig. S20a,b). Indeed, our two species-poor systems (‘vole-mustelid’ and ‘wild boar-virus’)
358 exhibited strikingly different DS (Fig. 4a). Similarly, we observed both high and low DS in
359 communities with either one (e.g. ‘algae’ vs ‘grassland’) or two trophic levels (‘vole-mustelid’

360 vs 'wild boar-virus'). Taken together our results indicate that, although DS does not depend on
361 disturbance properties, measuring multiple stability properties is necessary until we can establish
362 whether and what system properties underlie DS.

363 Similarly to the community level, DS was highly context-dependent at the population
364 level: in addition to variation among disturbance types, we also found high heterogeneity among
365 study systems and species (Table S5), with the highest dimensionality under random disturbance.
366 Although this type of disturbance may seem of little relevance to real-world applications, it is
367 closely mimicked by the application of certain chemicals (Roessink *et al.* 2006; DeLaender *et al.*
368 2016), and therefore its effects on DS deserve further investigations. Interestingly, our findings
369 indicate that species-poor systems may generally have higher DS (Fig. S20d). Since population
370 invariability is known to be lower in species-rich systems (Gonzalez & Descamps-Julien 2004;
371 Jiang & Pu 2009; Gross *et al.* 2014), it is likely that species richness modulates the relations of
372 population-level invariability with other stability properties. However, as we did not
373 experimentally manipulate species richness in this study, this is a hypothesis to be tested by
374 future research.

375 Reflecting the context-dependence of DS, all pair-wise correlations between population
376 stability properties depended on the disturbance type, and additionally two out of six depended
377 on the disturbance intensity (Fig. 5b-d). These results corroborate earlier analytical derivations
378 (Harrison 1979) that showed that the relation between population resilience and resistance
379 depends both on density-dependence and on the environmental sensitivity of the population
380 growth rate. In fact, the high heterogeneity found in the meta-analytic models testing the context-
381 dependence of the pair-wise correlations between population stability properties (Table S8)
382 points towards species-specific differences which may be due to differences in density

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383 dependence (as found by Harrison 1979) or any other species-specific properties (e.g. population
384 growth, carrying capacity).

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385 From a monitoring perspective, the context-dependence of the correlative structure
386 among stability properties at the population level (H3) means that quantification of population
387 stability as a whole requires measurements of multiple stability properties unless the context-
388 dependence of these properties was established beforehand. Even though this may sound like a
389 daunting task, it is already a well-established practice within population viability analysis
390 (Beissinger & Westphal 1998; Pe'er *et al.* 2013). In such studies, multiple stability properties
391 such as time to extinction, minimum viable population size, mean population size, etc. are jointly
392 reported as a rule (Pe'er *et al.* 2013).

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393 **Across-system differences in dimensionality of stability and plausible** 394 **mechanisms**

395 We did not find any effect of disturbance type on DS at the community level but higher
396 DS was observed for random disturbances at the population level. Although these general results
397 hold across the five different study systems, the largest heterogeneity in DS was revealed among
398 study systems. As mentioned above, this heterogeneity cannot be explained by system properties
399 as species richness and number of trophic levels. Two general mechanisms behind the responses
400 of ~~system's~~ DS to disturbance can be distinguished: changes in the intensity of species
401 interactions and changes in the degree of stochastic dynamics of the system. Although we have
402 not experimentally manipulated these mechanisms here, we discuss the revealed differences in
403 DS among systems in light of these mechanisms.

404 Changes in the intensity of species interactions could explain the link between
405 disturbances and DS. Indeed, previous research demonstrated that inter- and intra-specific
406 interactions affect community stability (McCann 2000; Thébault & Loreau 2005; Barabás *et al.*
407 2016). Moreover, the effect of changes in species interactions on DS may differ depending on
408 the primary type of interactions within a system (competitive vs. trophic), because vertical
409 diversity was shown to modulate the biodiversity – stability relationship (Reiss *et al.* 2009;
410 Radchuk *et al.* 2016b)+Wang and Brose’s Ecology Letters from last year (‘vertical diversity
411 hypothesis’). Indeed, in our simulations, the removal of a rare species ~~removal in from~~
412 communities driven by competitive interactions (algae, grassland and forest systems) resulted in
413 lower DS (Table S9) both at the community and population level. The mechanism underlying the
414 lower DS in these communities after removal of rare species (Table S9) may be an increasing
415 strength of competitive interactions among the remaining species.

416 Stronger competitive interactions presumably occurring after removal of rare species,
417 may in turn lead to more deterministic dynamics of the system. The degree of dynamic system
418 behaviour may itself affect DS. Indeed, ~~a~~ more stochastic population dynamics likely results in
419 weaker pair-wise correlation among stability properties, thus leading to higher DS. In support of
420 this expectation, we found increased DS after a spatially-structured disturbance in systems
421 consisting of two strongly interacting species at different trophic levels (Table S9). Such two-
422 species communities are presumably more prone to stochastic effects than multispecies
423 communities, and therefore exhibit the above-described behaviour. To closer inspect the relation
424 between system stochastic behaviour and DS, we used population abundance and community
425 ~~evenness the following~~as proxies of the influence of demographic stochasticity ~~at the on~~
426 populations and ~~community communities~~level, respectively: ~~population abundance and~~

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427 ~~community evenness~~ (Supplementary Methods). Overall, we found an increase in DS under
428 higher stochasticity at both population and community levels (Fig. S21-S22). However, the
429 responses varied among disturbance types, study systems and species (for the population-level
430 DS; Figs S23-S24). ~~Importantly, these findings have to be treated with caution because~~ Clearly,
431 we did not experimentally vary stochasticity, as this was not the goal of our study. ~~and Future~~
432 future research in this direction is warranted.

433 The change of system behaviour from stochastic to deterministic and vice versa may also
434 be caused by dispersal. Dispersal plays an important role in stochastic community assembly
435 (Chase 2007) and has recently attracted attention in the context of metapopulation and
436 metacommunity stability (Dai *et al.* 2013; De Raedt *et al.* 2017; Gilarranz *et al.* 2017; Zelnik *et*
437 *al.* 2018). Further, functional diversity, in particular response diversity and correlations among
438 effect and response traits were suggested as mechanisms potentially explaining pair-wise
439 correlations between stability properties (Pennekamp *et al.* 2018). Additionally, some of the
440 observed differences in system responses may be due to the model type used and not especially
441 because of the system-specific characteristics. Thus, models such as the Lotka-Volterra model
442 (used for the algae community) result in more deterministic community dynamics compared to
443 individual-based models that incorporate more stochasticity at different levels and processes.
444 Indeed, the algae model showed a strikingly clear response as compared to other systems (Table
445 S9, Fig. 4a), which may be explained by deterministic system behavior.

446 Challenges and future research

447 Our study identified several challenges associated with measuring DS. ~~for example Amongst~~
448 those are: quantifying the relationships among stability properties that are non-linearly related;
449 choosing appropriate state variables to measure stability properties; choosing specific stability

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Commenté [FDL2]: Not clear what we mean here.

450 properties at each level of organization; deciding on the disturbance types and intensity levels. A
451 wide variety of stability properties is used in the literature, and different approaches to
452 quantifying them are available (Grimm & Wissel 1997; Ingrisch & Bahn 2018). For example, we
453 have chosen to measure resistance at the first time step after disturbance. An alternative would be
454 to measure resistance at the time step when the response is the strongest, which, naturally, will
455 differ among species and systems. Comparison of how existing stability properties and methods
456 to measure them perform under different conditions and unification of such approaches ~~must be~~
457 an avenue for future research (Ingrisch & Bahn 2018). Further, we here focused on disturbance
458 by removing individuals mainly for the sake of comparability of results among systems and
459 models. What the implications of other disturbance types are, in particular the addition of
460 individuals (stocking) and habitat fragmentation ~~are~~, and how they compare to the removal of
461 individuals, remains to be tested.

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462 Further, a future research agenda on DS should include: a mechanistic (?) investigation of
463 interactions among disturbance types, developing approaches to quantify non-linear responses of
464 systems to disturbance, and non-linear trade-offs among dimensions of stability. Importantly,
465 understanding ~~the mechanistic mechanisms~~ underpinnings of the responses of DS requires that
466 future experiments on real and *in-silico* systems manipulate potential mechanisms, generally the
467 strength and sign of species interactions, and the stochasticity of the system's dynamics (which
468 may be achieved by manipulating response diversity, dispersal abilities and environmental
469 sensitivities of the species in the community). ~~[What I cut may be a bit too evident] Preferably,~~
470 ~~such experiments would use a factorial design combining several tentative mechanisms of DS,~~
471 ~~while measuring population or community dynamics at a fine temporal resolution.~~ For such
472 experiments the use of modelling studies, as done here, seems ~~indispensable~~ useful ay forward,

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473 because collection of such data empirically is feasible only in micro- and mesocosm settings
474 (Baert *et al.* 2016b; Garnier *et al.* 2017; Karakoç *et al.* 2018; Pennekamp *et al.* 2018).
475 Importantly, although measuring DS was rather easy in our modelling study, empirical studies
476 may be limited because of the difficulty to measure multiple stability properties in natural
477 systems.

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478 There is a large, continually growing literature on stochastic population, community and
479 metacommunity ecology, which considers relationships between (usually only two) different
480 stability properties at different levels of organisation, and includes age-, stage- and spatial
481 structure (e.g. Petchey *et al.* 1997; Ovaskainen & Hanski 2002; Inchausti & Halley 2003; de
482 Mazancourt *et al.* 2013; Arnoldi *et al.* 2016; Wang & Loreau 2016). We here point out avenues
483 for extending the current research and underline that both empirical and theoretical efforts are
484 needed.

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485 Conclusions

486 We used process-based models developed and parameterized to reflect a range of natural
487 systems to test the effect of disturbance properties on the dimensionality of stability measured at
488 the population and community level. Our findings indicate that in the majority of cases
489 monitoring of population and community stability will require quantification of multiple stability
490 properties, and the use of a single proxy is not justified (Donohue *et al.* 2013; Hillebrand *et al.*
491 2018). Moreover, we also show that the correlations among stability properties may differ
492 depending on the level of organization, which was demonstrated only once until now by
493 Hillebrand *et al.* (2018), ~~who considered~~ who compared the community ~~and~~ and ecosystem
494 levels. We believe that our study will catalyze the emerging research on the relations among
495 stability properties measured at different organization levels, and temporal and spatial scales,

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496 which in turn will lead to the development of a comprehensive theory of community and
497 population dynamics further from their equilibrium.

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641

FIGURES

642 Figure 1. Schematic representation of the dimensionality of stability. (a,b) Hypothetical
 643 multidimensional ellipsoids reflecting systems with low (a, black) and high (b, brown)
 644 dimensionality, and their respective semi-axis lengths (c_x), reflecting the amount of variation
 645 along each axis. The axes are ranked from the one that explains most variation to the one with
 646 the least variation (Donohue et al. 2013).

647 Figure 2. (a-c) Four stability properties measured at the community (a) and population (b,
 648 c) level in this study. Red vertical dotted line highlights the time step at which the disturbance (=
 649 treatment) occurs (for demonstration purpose here generation 4). Resistance (Res) and recovery
 650 (Rec) at the community level are measured as $BC\left(\frac{Comp_t}{Comp_c}\right)$, where BC is Bray-Curtis similarity, and
 651 $Comp_x$ is community composition in either control ($x = c$) or treatment ($x = t$), measured at the
 652 time steps indicated by green (Res) and blue (Rec) vertical dashed lines, respectively. Resistance
 653 and recovery at the population level are measured as $\ln\left(\frac{Ab_t}{Ab_c}\right)$, where Ab_x is abundance in either
 654 control ($x = c$) or treatment ($x = t$), measured at the time steps indicated by green (Res) and blue
 655 (Rec) vertical dashed lines, respectively. The grey solid line depicts a fitted model that is used to
 656 assess invariability (Inv), for demonstration purpose only two residuals are highlighted. An
 657 orange arrow shows how (a) $T_{0.9}$ at the community level and (c) TTE (time to extinction) at the
 658 population level are obtained. Persistence at the population level is calculated as: $Perc_{pop} =$
 659 $\frac{TTE}{T_{max}}$; and at the community level: $Perc_{com} = \frac{T_{0.9}}{T_{max}}$, where T_{max} is the maximum duration (here 16
 660 generations) (for more details see Methods and Table S2). (d-f). Disturbance types used in this
 661 study: random (d), rare species removal (e) and spatially-structured disturbance (f). Each
 662 disturbance type is shown at 20% disturbance intensity. A two-patch system is depicted with

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663 each symbol representing an individual and the shape reflecting the species identity. Empty
664 symbols indicate the individuals that would be removed under each disturbance. A circle in (f)
665 shows a radius of a spatially-structured disturbance type.

666 Figure 3. At the community level (a) disturbance type did not affect semi-axis lengths,
667 whereas at the population level (b) semi-axis lengths were affected by the disturbance type. High
668 DS was found under random disturbance, as indicated by the semi-axis lengths of the 1st rank on
669 average shorter compared to other disturbance types, and the semi-axis lengths of the 3rd and 4th
670 order longer compared to other disturbance types. We observed large variation among study
671 systems in their semi-axis lengths. Results are shown for disturbance intensity = 0.2 (since there
672 is no effect of intensity). The semi-axis lengths are shown for each rank separately (1-3 for the
673 community and 1-4 for the population level). The dots show outliers. Study systems are
674 described in Table S3, different colours reflect different disturbance types: spatially-structured,
675 rare species removal and random disturbance.

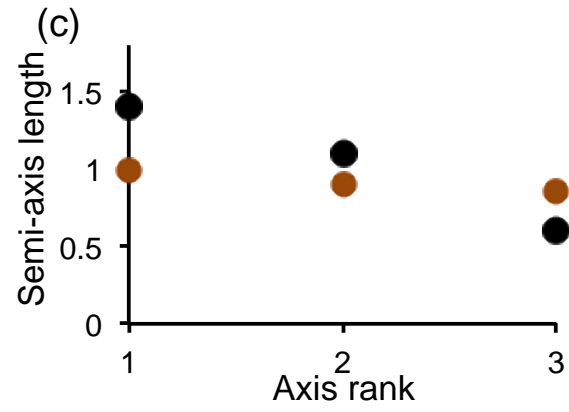
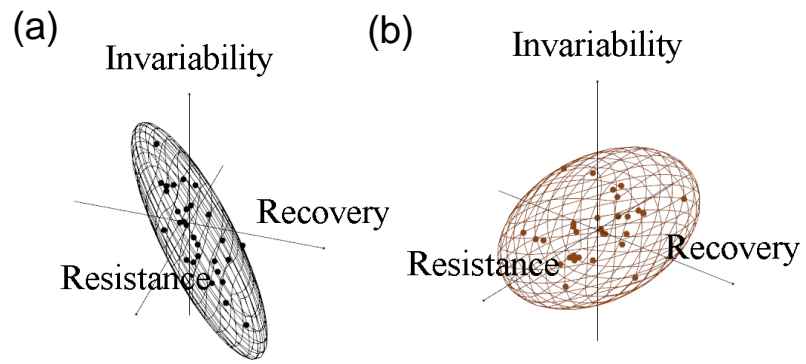
676 Figure 4. Disturbance type did not affect proportional ellipsoid volumes at the
677 community (a), but did affect them at the population (b) level: random disturbance increased the
678 dimensionality of stability, as visible from larger ellipsoid volume. We observed large variation
679 among study systems in their ellipsoid volumes, especially at the community level. Results are
680 shown for disturbance intensity = 0.2 (since there is no effect of intensity). At the maximum
681 proportional volume (= 1) DS is highest, corresponding to a perfect sphere. The lower the
682 proportional volume the lower is DS, with ellipsoid shape changing via a 'frisbee'-looking to a
683 'cigar'-like shape. Ellipsoids at the community and population level are calculated using three
684 and four dimensions, respectively (see Methods). Abbreviations are as in Fig. 3.

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685 Figure 5. Effects of disturbance type and intensity on Fisher's z scores representing all
686 pair-wise correlations between stability properties at the community (a) and population (b-d)
687 level. At the community level, majority of correlations were positive (a), whereas at the
688 population level, the sign and magnitude of correlations were highly heterogeneous (b-d).
689 Disturbance type affected two out of six correlations at the community level and all correlations
690 at the population levels. Shown are the effect sizes (and their 95 % CI) from the model that
691 described the data the best. For those correlations not affected by tested variables the effect size
692 obtained with the model including the intercept only is shown (i.e. the effect across all study
693 cases). Abbreviations are as in Fig. 3.
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Figure 1.



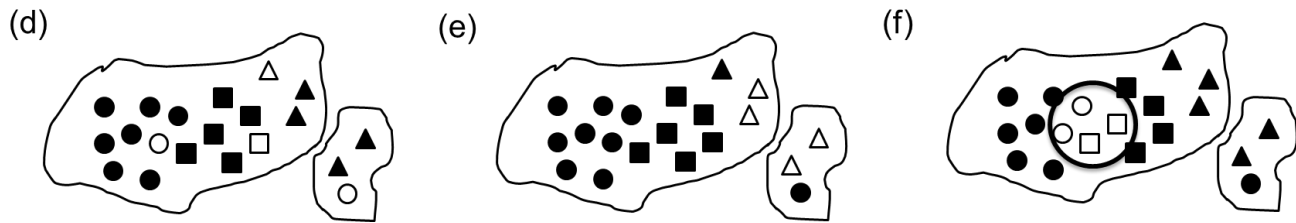
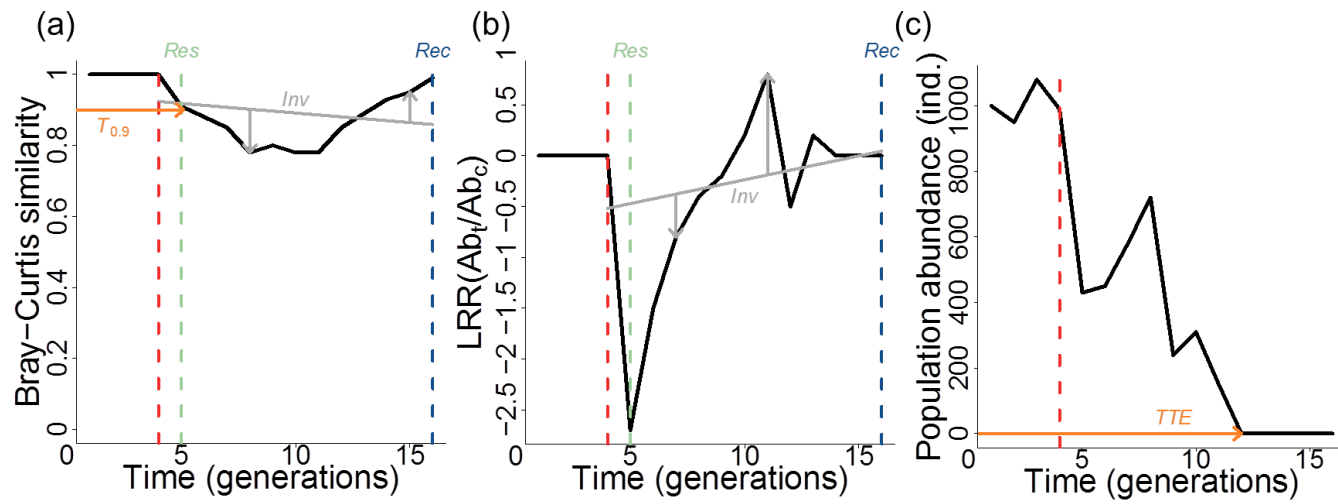
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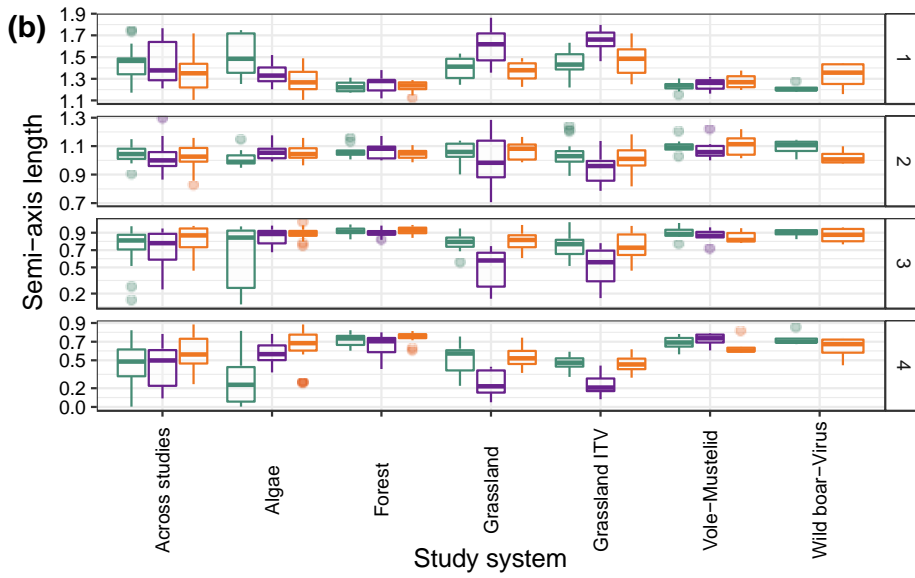
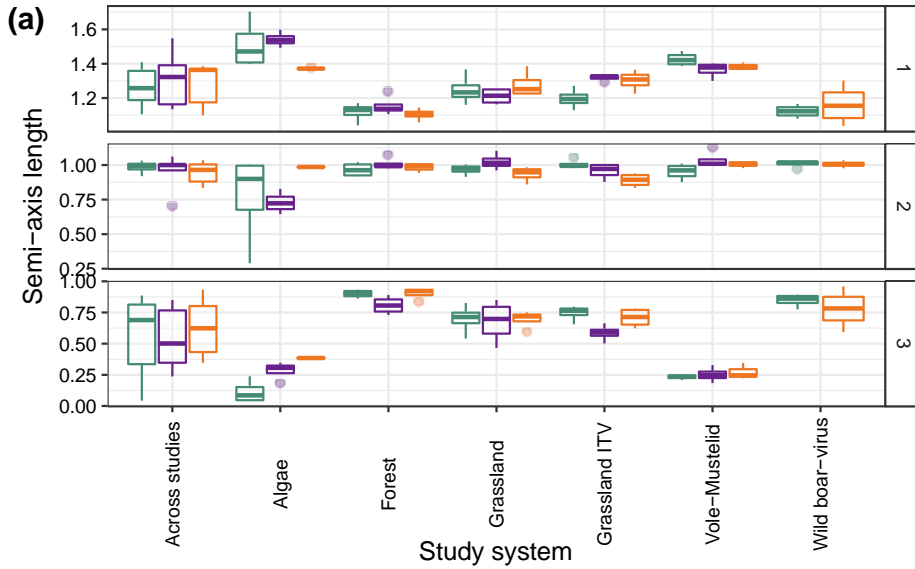
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700 Figure 2.



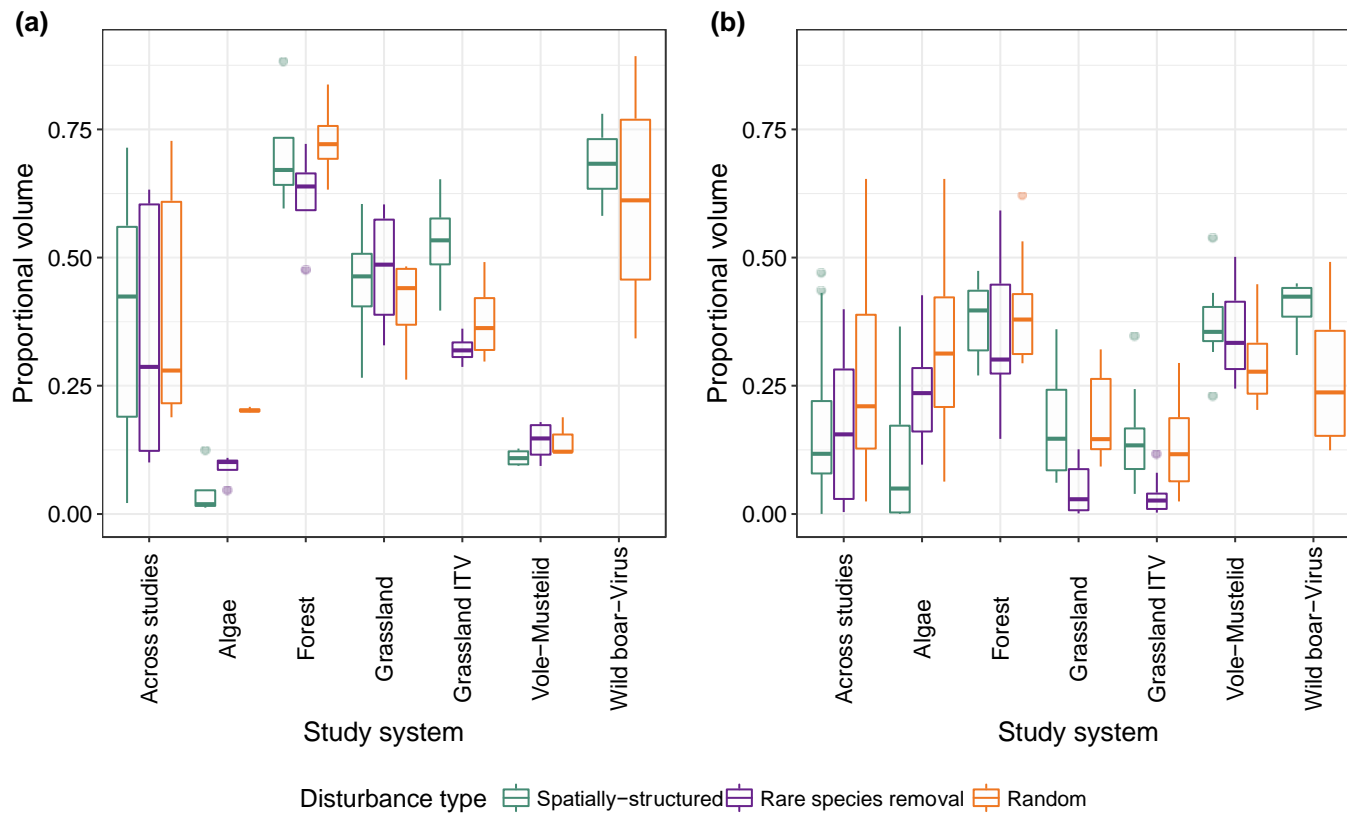
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703 Figure 3.



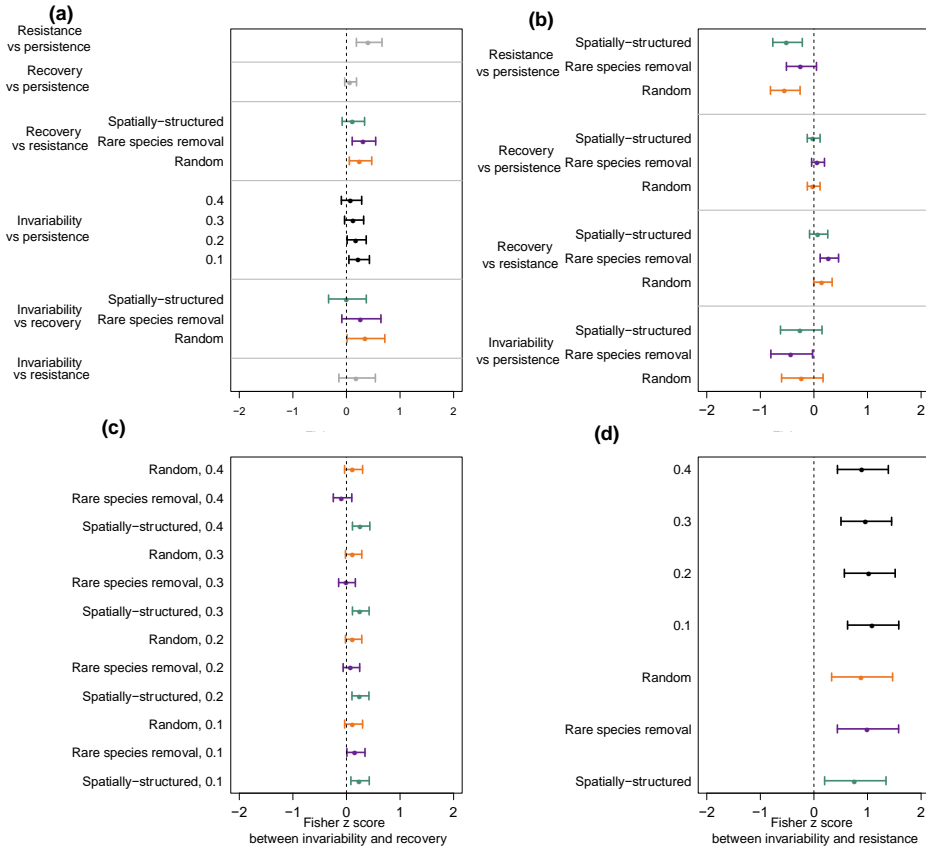
Disturbance type █ Spatially-structured █ Rare species removal █ Random

705 Figure 4.



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707 Figure 5.



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