ECOLOGY LETTERS

*Ecology Letters*, (2019) doi: 10.1111/ele.13226

LETTER

# The dimensionality of stability depends on disturbance type

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**Abstract**

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

**Keywords**

Community model, disturbance intensity, disturbance type, extinction, individual-based model, invariability, persistence, recovery, resistance.

*Ecology Letters* (2019)

## INTRODUCTION

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

There are many kinds of disturbance. Disturbance properties include: duration, spatial extent, intensity, frequency and type (Turner 2010). According to their *duration*, two extreme classes of disturbance can be distinguished: pulse disturbances (e.g. fire or flooding) occur over a short time scale, relative to the typical speed at which a system changes, and press disturbances (e.g. global warming or exploitation) represent a constant, long-term change. Disturbance *intensity* reflects how much individuals/biomass are affected by an event over a period of time (Turner 2010). Disturbance *frequency* reflects how often disturbance events occur within a given time period. Examples of disturbance *types* are local vs. global, and selective vs. non-selective disturbances (De Laender *et al*. 2016).

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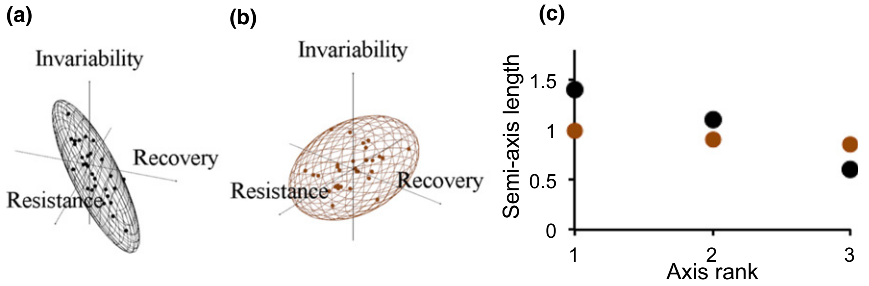

**Figure 1** Schematic representation of the dimensionality of stability. (a and b) Hypothetical multidimensional ellipsoids reflecting systems with low (a, black) and high (b, brown) dimensionality, and their respective semi-axis lengths (c), reflecting the amount of variation along each axis. The axes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

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

DS can be decomposed into pair-wise correlations among underlying stability properties (Donohue *et al.* 2013; Hillebrand *et al.* 2018; Pennekamp *et al.* 2018). We generally expect positive pair-wise correlations between invariability, resistance, recovery and persistence. For example, at the population level, invariability and persistence are expected to correlate positively, because the higher the temporal constancy in population size, the more likely the population is to persist (Ginzburg *et al.* 1982; Inchausti & Halley 2003). Similarly, at the community level, the higher the temporal constancy in community composition, the more likely this community is to persist in its unchanged state. For arguments of why we expect other stability properties to correlate positively, see Table S1 in Supporting Information. Because pair-wise correlations are 'constituents' of DS, they are expected to depend on the same factors as DS: disturbance properties and the level of organization. Indeed, the sign of a pair-wise correlation between stability properties was shown to change when, instead of a single disturbance, two disturbance types were applied simultaneously to yeast populations (Dai *et al.* 2015). Also, pair-wise correlations measured at the community and ecosystem level differed in plankton communities disturbed by reduced light availability (Hillebrand *et al.* 2018). Understanding whether pair-wise correlations are affected similarly across different disturbance types and study systems would facilitate more efficient monitoring of the stability of natural systems.

Here, we used process-based, spatially-explicit models to assess how the intensity and the type of disturbance affect DS at the population and community levels. Our models are well-tested and structurally realistic, and represent five different communities: a species-rich temperate grassland community, a temperate forest, an algae community, a boreal predator-prey system, and a host-pathogen system. The modelled communities varied in species richness (2 up to 86 species) and number of trophic levels (one or two). At both levels of organization we measured four stability properties: resistance, recovery, persistence and invariability (Glossary, Fig. 2a–c, Table S2). We applied three disturbance types at four intensities. We distinguished disturbances that (1) affect individuals selectively depending on their species identity, (2) affect individuals selectively depending on their location, and (3) affect all individuals similarly, irrespective of species identity or location (Fig. 2d,e and f). We tested the following hypotheses:

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

H2: All investigated stability properties exhibit positive pair-wise correlations (Table S1).

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

## METHODS

### Study systems

We used models representing the dynamics of the following communities: temperate forests (Bohn *et al.* 2014), a marine algal community (Baert *et al.* 2016a), a species-rich temperate grassland (May *et al.* 2009), a boreal predator-prey system of mustelids and voles (Radchuk *et al.* 2016a), and a temperate host-pathogen system of classical swine fever (CSF) virus affecting wild boar populations (Kramer-Schadt *et al.* 2009; Lange *et al.* 2012). All of these models had previously been parameterized to mimic the conditions of the respective natural

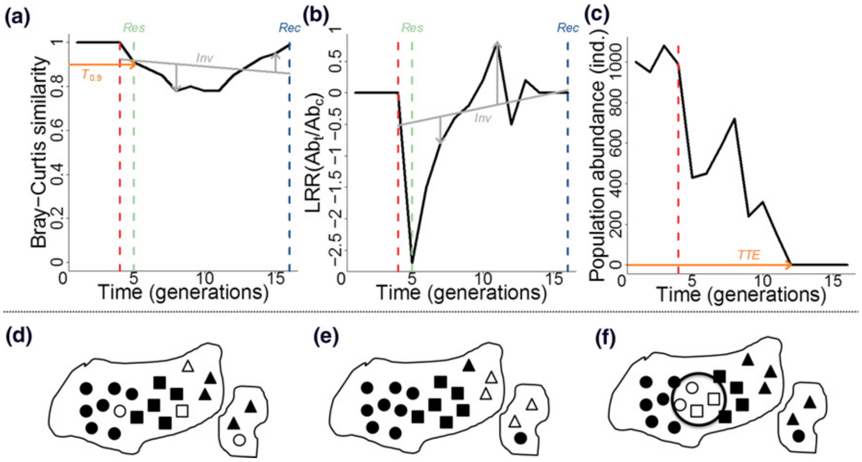

**Figure 2** (a–c) Four stability properties measured at the community (a) and population (b and c) level in this study. Red vertical dashed line highlights the time step at which the disturbance (= treatment) occurs (for demonstration purpose here generation 4). Resistance (*Res*) and recovery (*Rec*) at the community level are measured as $BC\left(\frac{Comp_t}{Comp_c}\right)$, where *BC* is Bray–Curtis similarity, and $Comp_x$ is community composition in either control (x = c) or treatment (x = t), measured at the time steps indicated by green (*Res*) and blue (*Rec*) vertical dashed lines, respectively. Resistance and recovery at the population level are measured as $\ln\left(\frac{Ab_t}{Ab_c}\right)$, where $Ab_x$ is abundance in either control (x = c) or treatment (x = t), measured at the time steps indicated by green (*Res*) and blue (*Rec*) vertical dashed lines, respectively. The grey solid line depicts a fitted model that is used to assess invariability (*Inv*), for demonstration purpose only two residuals are highlighted. An orange arrow shows how (a) $T_{0.9}$ at the community level and (c) TTE (time to extinction) at the population level are obtained. Persistence at the population level is calculated as: $Perc_{pop} = \frac{TTE}{T_{\max}}$; and at the community level: $Perc_{com} = \frac{T_{0.9}}{T_{\max}}$, where $T_{\max}$ is the maximum duration (here 16 generations) (for more details see Methods and Table S2). (d–f). Disturbance types used in this study: random (d), rare species removal (e) and spatially-structured disturbance (f). Each disturbance type is shown at 20% disturbance intensity. A two-patch system is depicted with each symbol representing an individual and the shape reflecting the species identity. Empty symbols indicate the individuals that would be removed under each disturbance. A circle in (f) shows a radius of a spatially-structured disturbance type.

communities (Table S3). All models have three aspects in common: (1) they are spatially explicit, describing the location of habitat patches and movement of individuals among them; (2) they include demographic stochasticity; and (3) the smallest modelled entity is the individual (except for the model simulating an algae community, which is based on Lotka-Volterra equations with a dispersal component; Text ST1). In addition to demographic stochasticity, two models (a host-pathogen model and a model of temperate forests) also include environmental stochasticity. Temperate grassland was modelled in two ways: using the original IBC-grass model (May *et al.* 2009) and a modified version that incorporates intraspecific trait variation (from now on referred to as Grassland ITV, Crawford *et al.* 2018). We thus used six models that represented five study systems. An advantage of using models that have been previously developed is that those models have already been tested and verified for natural systems. We provide short summaries of the main processes included in each model in the Supplementary Methods, and more detailed descriptions of the models in the Supplementary Texts T1-T5.

## Disturbances

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

Each disturbance type was implemented at four intensities, reflecting increasing proportions of the community that were removed (0.1, 0.2, 0.3 and 0.4, respectively). An upper bound of intensity was chosen via preliminary tests scanning a larger range of intensities, which showed that at a disturbance intensity > 0.5, all species in our 2-species systems went extinct, complicating the measurements of all stability properties.

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

### Stability properties

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

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

### Dimensionality of stability

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

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

## Pair-wise correlations

To test whether all pair-wise correlations among stability properties were positive (H2) and affected by the disturbance properties (H3), we calculated Spearman-rank correlation for each pair of stability properties obtained for each of the 13 scenarios at the community level. Similarly, at the population level, Spearman-rank correlation was calculated for each species within each scenario. Next, we transformed these Spearman-rank correlations into Fisher's z scores to improve their normality and to avoid any disproportionate influence of extreme values, and used them as effect sizes in the meta-analysis (Koricheva *et al.* 2013). We fitted mixed-effects meta-analytic models (Gaussian distribution) with the fixed effects of disturbance type (a factor), disturbance intensity (a continuous variable), and an interaction between them. At the community level, the models included the study system and replicate as random intercepts. At the population level, also species identity was included as a random intercept. All meta-analytic mixed-effects models were fitted with the library

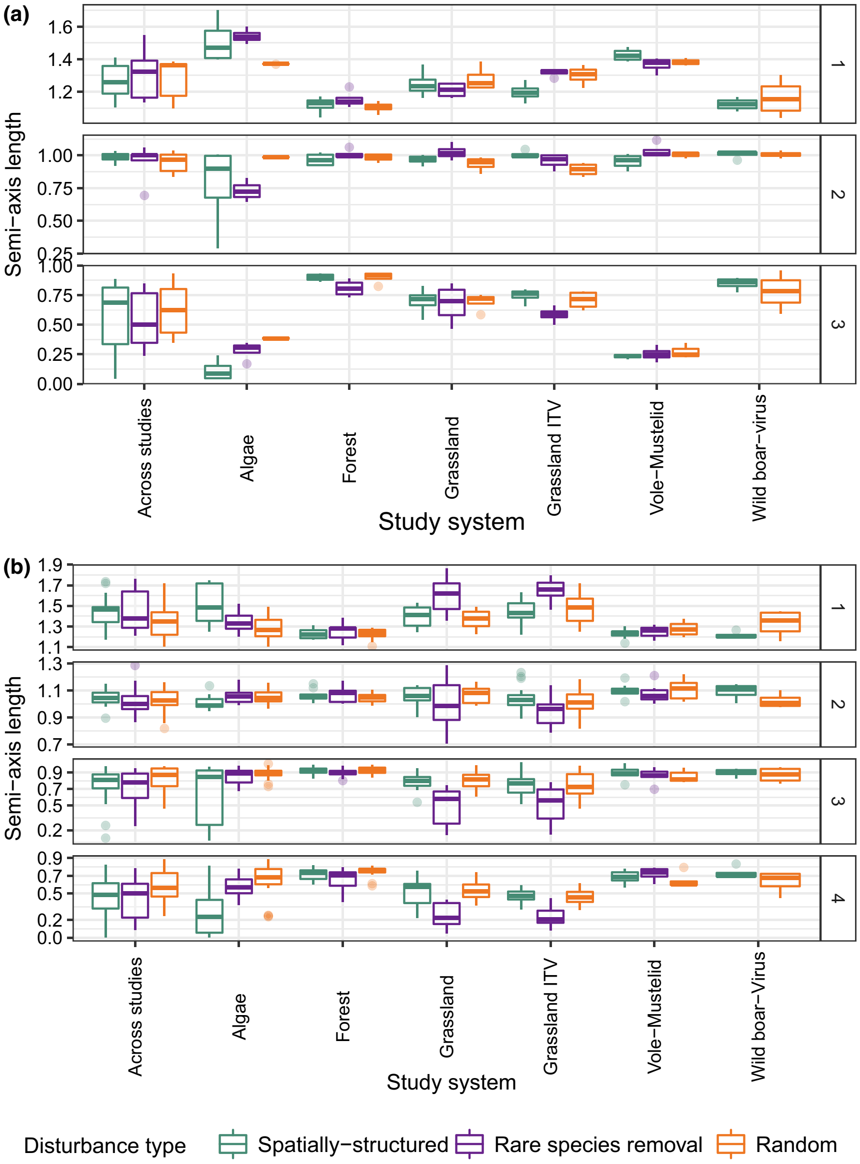

**Figure 3** At the community level (a) disturbance type did not affect semi-axis lengths, whereas at the population level (b) semi-axis lengths were affected by the disturbance type. High DS was found under random disturbance, as indicated by the semi-axis lengths of the 1st rank on average shorter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

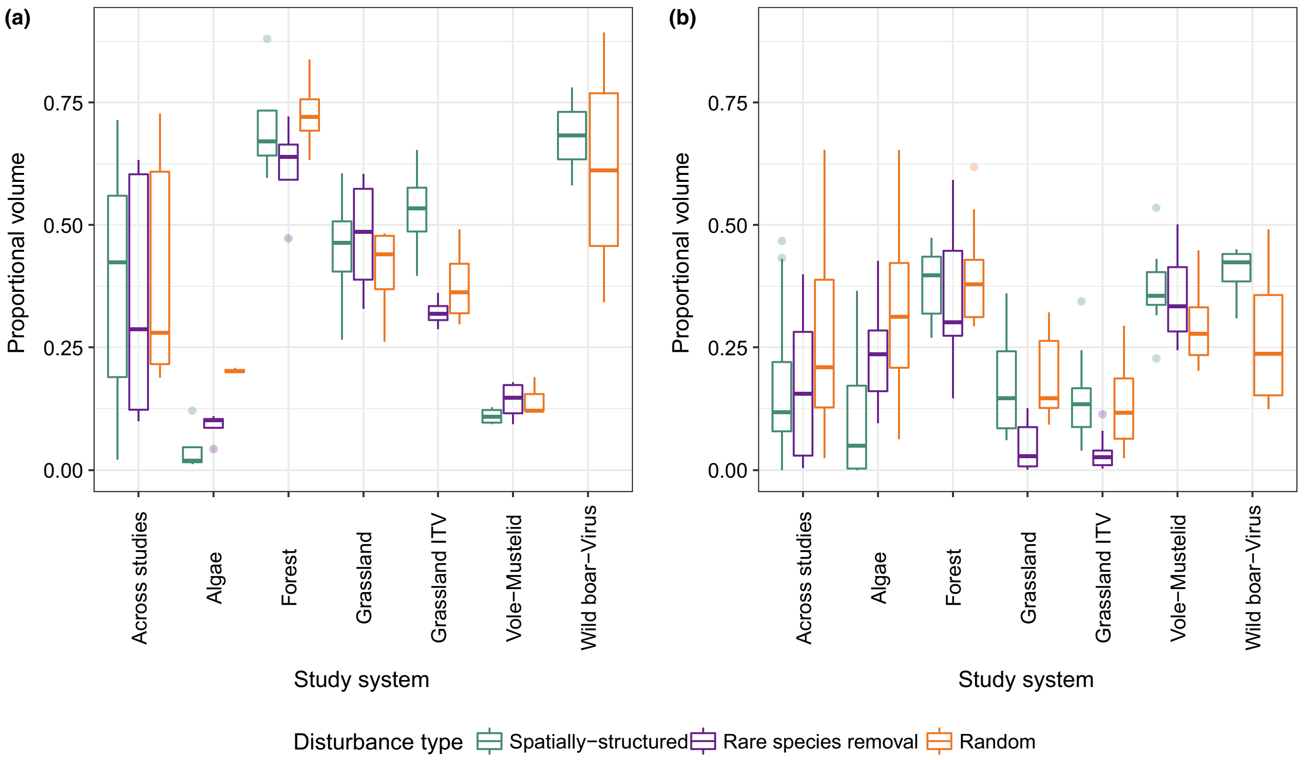

**Figure 4** Disturbance type did not affect proportional ellipsoid volumes at the community (a), but did affect them at the population (b) level: random disturbance increased the dimensionality of stability, as visible from larger ellipsoid volume. We observed large variation among study systems in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

*metafor* in R (Viechtbauer 2010). All analyses were conducted in R 3.4.2 (R 2017).

## RESULTS

### Effect of disturbance properties on the dimensionality of stability

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

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

### Pair-wise correlations between stability properties

At the community level, pair-wise correlations were on average positive (supporting H2) and three of six correlations were affected by disturbance properties (supporting H3, Fig. 5a). The correlation of recovery with resistance and of recovery with invariability depended on the disturbance type, with positive correlations under random disturbance and very weak correlations (around 0) under spatially structured disturbance. The correlation between invariability and persistence became weaker and approached 0 as disturbance intensity increased.

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

## DISCUSSION

We tested whether the correlation structure among stability properties was affected by disturbance properties across five

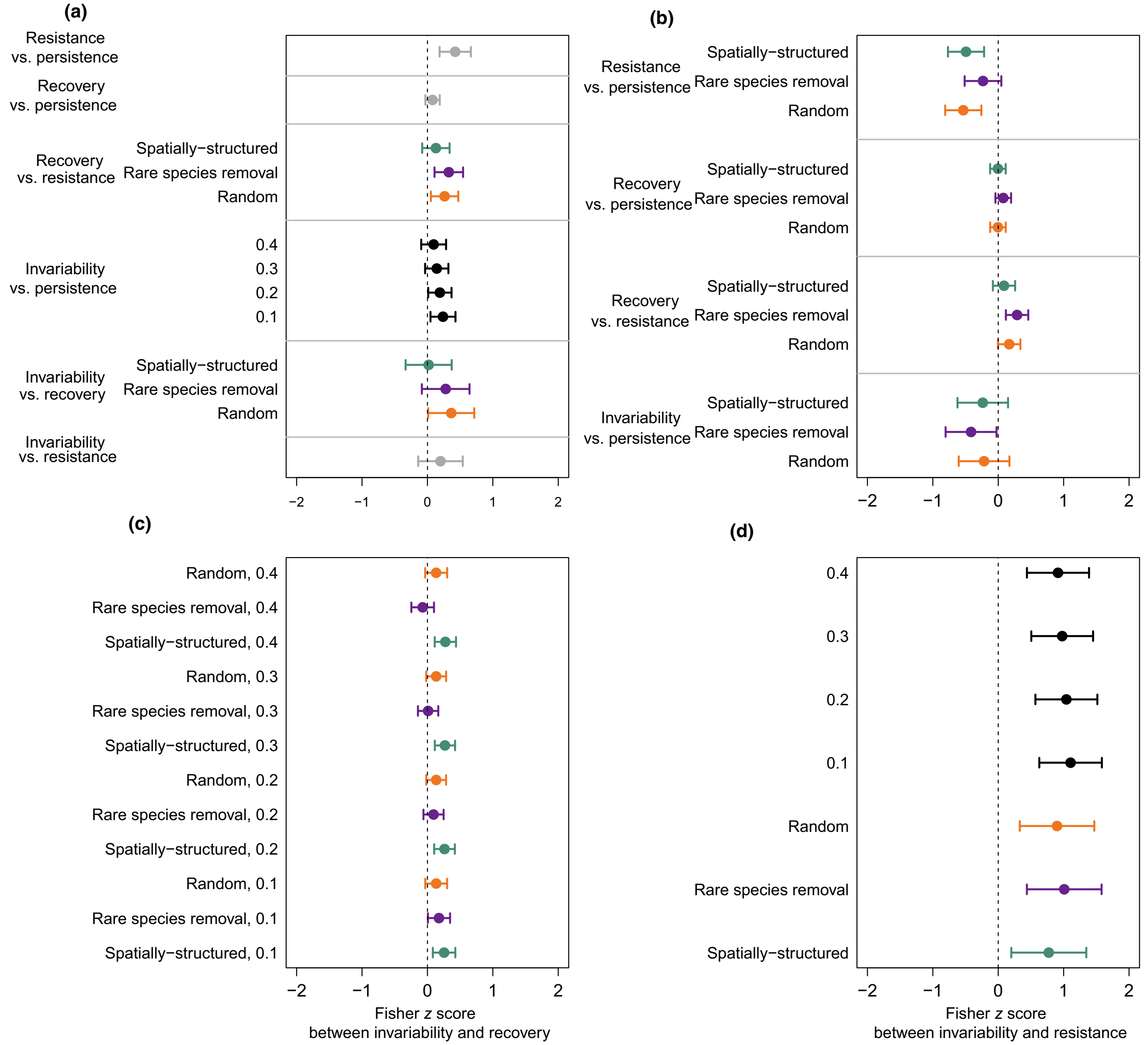

**Figure 5** Effects of disturbance type and intensity on Fisher's z scores representing all pair-wise correlations between stability properties at the community (a) and population (b–d) level. At the community level, majority of correlations were positive (a), whereas at the population level, the sign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

communities, differing in species richness and number of trophic levels. Contrary with our expectation (H1), we did not find an effect of disturbance properties on the dimensionality of stability (DS) at the community level. At the population level, DS was higher under random disturbances. Additionally, at both levels of organization DS varied largely among study systems. At the community level, as expected (H2), we found generally positive correlations among different stability properties. In contrast, at the population level, the sign and magnitude of correlations were highly heterogeneous. Finally, pair-wise correlations at both levels depended on the disturbance properties, mainly on disturbance type, supporting our hypothesis (H3), although the effect sizes were smaller at the community level.

### Dimensionality of stability at the community and population level

We did not find any effect of disturbance properties on DS at the community level. However, our findings reveal high heterogeneity in DS among study systems. For 4 of the 6 study systems, community stability was a highly-dimensional concept (Fig. 4a), suggesting that monitoring these systems requires measuring multiple stability properties. A promising avenue for future research would be investigating whether –

and what – properties of a system predict its DS. At the community level, our findings indicate that such candidates of system properties as species richness and number of trophic levels do not discriminate the systems with low and high DS (Fig. S20a,b). Indeed, our two species-poor systems ('vole-mustelid' and 'wild boar-virus') exhibited strikingly different DS (Fig. 4a). Similarly, we observed both high and low DS in communities with either one (e.g. 'algae' vs. 'grassland') or two trophic levels ('vole-mustelid' vs. 'wild boar-virus'). Taken together our results indicate that, although DS does not depend on disturbance properties, measuring multiple stability properties is necessary until we can establish whether and what system properties underlie DS.

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

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

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

### Across-system differences in dimensionality of stability and plausible mechanisms

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

Changes in the intensity of species interactions could explain the link between disturbances and DS. Indeed, previous research demonstrated that inter- and intraspecific interactions affect community stability (McCann 2000; Thébault & Loreau 2005; Barabás *et al.* 2016). Moreover, the effect of changes in species interactions on DS may differ depending on the primary type of interactions within a system (competitive vs. trophic), because vertical diversity was shown to modulate the biodiversity – stability relationship (Reiss *et al.* 2009; Radchuk *et al.* 2016b; Wang & Brose 2018). Indeed, in our simulations, the removal of a rare species from communities driven by competitive interactions (algae, grassland and forest systems) resulted in lower DS (Table S9) both at the community and population level. The mechanism underlying the lower DS in these communities after removal of rare species (Table S9) may be an increasing strength of competitive interactions among the remaining species.

Stronger competitive interactions presumably occurring after removal of rare species, may in turn lead to more deterministic dynamics of the system. The degree of deterministic system behaviour may itself affect DS. Indeed, more stochastic population dynamics likely result in weaker pair-wise correlations among stability properties, thus leading to higher DS. In support of this expectation, we found increased DS after a spatially structured disturbance in systems consisting of two strongly interacting species at different trophic levels (Table S9). Such two-species communities are presumably more prone to stochastic effects than multispecies communities, and therefore exhibit the above-described behaviour. To closer inspect the relation between system stochastic behaviour and DS, we used population abundance and community evenness as rough proxies of the influence of demographic stochasticity on populations and communities, respectively (Supplementary Methods). Overall, we found an increase in DS under higher stochasticity at both population and community levels (Fig. S21-S22). However, the responses varied among disturbance types, study systems and species (for the population-level DS; Figs S23-S24). Clearly, we did not experimentally vary stochasticity, as this was not the goal of our study, and future research in this direction is warranted.

The change of system behaviour from stochastic to deterministic and vice versa may also be caused by dispersal.

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

### Challenges and future research

Our study identified several challenges associated with measuring DS. Amongst those are: quantifying the relationships among stability properties that are non-linearly related; choosing appropriate state variables to measure stability properties; choosing specific stability properties at each level of organization; deciding on the disturbance types and intensity levels. A wide variety of stability properties is used in the literature, and different approaches to quantifying them are available (Grimm & Wissel 1997; Ingrisch & Bahn 2018). For example, we have chosen to measure resistance at the first time step after disturbance. An alternative would be to measure resistance at the time step when the response is the strongest, which, naturally, will differ among species and systems. Comparison of how existing stability properties and methods to measure them perform under different conditions and unification of such approaches is an avenue for future research (Ingrisch & Bahn 2018). Furthermore, we here focused on disturbance by removing individuals mainly for the sake of comparability of results among systems and models. What the implications of other disturbance types are, in particular the addition of individuals (stocking) and habitat fragmentation, and how they compare to the removal of individuals, remains to be tested.

Furthermore, a future research agenda on DS should include: a mechanistic investigation of interactions among disturbance types, developing approaches to quantify non-linear responses of systems to disturbance, and non-linear trade-offs among dimensions of stability. Importantly, understanding the mechanisms underpinning the responses of DS requires that future experiments on real and *in-silico* systems manipulate potential mechanisms, generally the strength and sign of species interactions, and the stochasticity of the system's dynamics (which may be achieved by manipulating levels of demographic and environmental stochasticity, response diversity, dispersal abilities and environmental sensitivities of the species in the community). For such experiments the use of modelling studies, as done here, seems a useful way forward, because collection of such data empirically is feasible only in micro- and mesocosm settings (Baert *et al.* 2016b; Garnier *et al.* 2017; Karakoç *et al.* 2018; Pennekamp *et al.* 2018). Importantly, although measuring DS was rather easy in our modelling study, empirical studies may be limited because of the difficulty to measure multiple stability properties in natural systems.

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

## CONCLUSIONS

We used process-based models developed and parameterized to reflect a range of natural systems to test the effect of disturbance properties on the dimensionality of stability measured at the population and community level. Our findings indicate that in the majority of cases monitoring of population and community stability will require quantification of multiple stability properties, and the use of a single proxy is not justified (Donohue *et al.* 2013; Hillebrand *et al.* 2018). Moreover, we also show that the correlations among stability properties may differ depending on the level of organization, which was demonstrated only once until now by Hillebrand *et al.* (2018), who compared the community and ecosystem level. We believe that our study will catalyse the emerging research on the relations among stability properties measured at different organization levels, and temporal and spatial scales, which in turn will lead to the development of a comprehensive theory of community and population dynamics further from their equilibrium.

## ACKNOWLEDGEMENTS

This manuscript was initiated at the session 'Ecological models as tools to assess persistence of ecological systems in face of environmental pressures' organized by VR and SKS at the EcoSummit 2016 conference. We are grateful to Alban Sagouis and four anonymous reviewers for their feedback on the manuscript draft. CS was supported by the BioMove Research Training Group of the German Research Foundation (DFG-GRK 2118/1), MC was funded by DFG Priority Program 1374, "Infrastructure-Biodiversity-Exploratories" (DFG-JE 207/5-1) and JDR by the Research Foundation Flanders (Grant no FWO14/ASP/075). FDL received support from the Fund for Scientific Research, FNRS (PDR T.0048.16). JCS considers this work a contribution to his VILLUM Investigator project "Biodiversity Dynamics in a Changing World" funded by VILLUM FONDEN (grant 16549).

## AUTHORSHIP

All authors discussed and agreed on the experimental design; MC, FB, JDR, CS and VR run the simulations; VR performed the analyses of stability; VR wrote the first draft of the manuscript and all authors contributed substantially to revisions.

## DATA ACCESSIBILITY STATEMENT

The data supporting the results are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ck7k104.

## GLOSSARY

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

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

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

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

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

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

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

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

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Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Ian Donohue
Manuscript received 21 May 2018
First decision made 9 July 2018
Second decision made 8 November 2018
Third decision made 16 December 2018
Manuscript accepted 5 January 2019