IDEA AND PERSPECTIVE

On the dimensionality of ecological stability

Ian Donohue,[1,2]* Owen L. Petchey,[3] José M. Montoya,[4] Andrew L. Jackson,[1,2] Luke McNally,[1,2] Mafalda Viana,[1,2] Kevin Healy,[1,2] Miguel Lurgi,[4,5] Nessa E. O'Connor[6] and Mark C. Emmerson[6]

Abstract

Ecological stability is touted as a complex and multifaceted concept, including components such as variability, resistance, resilience, persistence and robustness. Even though a complete appreciation of the effects of perturbations on ecosystems requires the simultaneous measurement of these multiple components of stability, most ecological research has focused on one or a few of those components analysed in isolation. Here, we present a new view of ecological stability that recognises explicitly the non-independence of components of stability. This provides an approach for simplifying the concept of stability. We illustrate the concept and approach using results from a field experiment, and show that the effective dimensionality of ecological stability is considerably lower than if the various components of stability were unrelated. However, strong perturbations can modify, and even decouple, relationships among individual components of stability. Thus, perturbations not only increase the dimensionality of stability but they can also alter the relationships among components of stability in different ways. Studies that focus on single forms of stability in isolation therefore risk underestimating significantly the potential of perturbations to destabilise ecosystems. In contrast, application of the multidimensional stability framework that we propose gives a far richer understanding of how communities respond to perturbations.

Keywords

Ecosystem function, ellipsoid, extinction, invasion, multidimensional stability, persistence, resilience, resistance, robustness, variability.

Ecology Letters (2013)

INTRODUCTION

Understanding the factors that determine the stability of biological communities has been a focal point of ecological research for decades (e.g. MacArthur 1955; May 1972; Pimm 1984; McCann 2000; Montoya *et al.* 2006; Ives & Carpenter 2007; Allesina & Tang 2012). One challenging aspect of stability is its many components, including asymptotic stability, resilience, resistance, robustness, persistence and variability (Table 1; Pimm 1984; Ives *et al.* 1999). Thus, ecological stability is touted as a multifaceted and complex concept (Orians 1975; Pimm 1984; Ives & Carpenter 2007). This perception has been compounded by the propagation of a wide variety of terms for describing similar aspects of stability (Pimm 1984; Grimm & Wissel 1997). Progress in the field has been hampered further by a lack of comparability among studies and a disparity between the components of stability that most frequently comprise the focus of either theoretical or empirical studies. The former tend to concentrate on mathematical asymptotic stability (May 1974; Pimm 1984; Allesina & Tang 2012); a binary measure (communities are either stable or unstable at an equilibrium point) which itself has many forms (Logofet 2005). On the other hand, empirical studies typically measure the temporal variability of some aggregate feature of populations or communities (typically as the coefficient of variation of

their biomass or abundance; e.g. Steiner *et al.* 2005; Tilman *et al.* 2006; Table 1) to characterise their stability.

In spite of its multidimensionality, the few studies that measured multiple components of ecological stability simultaneously considered them as independent and therefore analysed them separately (e.g. France & Duffy 2006; O'Gorman & Emmerson 2009). It is likely, however, that components of stability are related (Harrison 1979; Pimm 1984). For example, communities with high temporal variability in abundance are expected to have low robustness (the number of secondary extinctions caused by the initial loss of a species; Table 1) due to an increased extinction risk in species with small population sizes (Pimm & Redfearn 1988; Lande 1993). Theoretical research (Harrison 1979) has also suggested that pairwise relationships between components of stability could vary; the resistance of populations to perturbations (the magnitude of change in their abundance or biomass in response to a perturbation; Table 1) may correlate either positively or negatively with their resilience [the length of time taken to return to their pre-disturbance state, also referred to as 'elasticity' (e.g. Orians 1975)], depending on the nature of intrinsic population growth rates and their sensitivity to the environment. However, remarkably little is known about the form or strength of correlations among multiple components of ecological stability, or the potential causes or consequences of those rela-

[1]*School of Natural Sciences, Trinity College Dublin, Ireland*
[2]*Trinity Centre for Biodiversity Research, Trinity College Dublin, Ireland*
[3]*Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland*
[4]*Instituto de Ciencias del Mar, Agencia Consejo Superior de Investigaciones Científicas, Barcelona, Spain*

[5]*Centre for Ecological Research and Forestry Applications (CREAF), Universitat Autònoma de Barcelona, Bellaterra, Spain*
[6]*School of Biological Sciences, Queen's University Belfast, Belfast, UK*
Correspondence: E-mail: ian.donohue@tcd.ie

Table 1 Description of our measures of stability, based primarily on the definitions of Pimm (1984)

Measure of stability	Description	Method of quantification
Variability (temporal and spatial)	The variability of community biomass or, less frequently, abundance in time or space (Cottingham *et al.* 2001; Ives & Carpenter 2007). Higher variability equates to reduced stability.	*Temporal variability*: quantified as coefficient of variation (CV) of total algal cover (e.g. Pimm 1984; Tilman *et al.* 2006; O'Gorman & Emmerson 2009) in experimental plots over time. To test whether our measures of variability were confounded with any particular positive or negative shifts in algal cover over the duration of the experiment, which may be caused by, for example, transient dynamics or seasonality, we detrended variability in total algal cover (see Tilman *et al.* 2006). This was done by deriving the standard deviation of the residuals from the linear regression of total algal cover of each plot on month and dividing this by the respective mean total algal cover to obtain the detrended community-level temporal CV. Analyses of the raw and detrended data produced qualitatively consistent results (Tables S1 and S2 in Supporting Information). For clarity, we present in the main text results from the analyses of the raw data. *Spatial variability*: quantified as the CV of total algal cover (e.g. Pimm 1984; Tilman *et al.* 2006; O'Gorman & Emmerson 2009) in experimental plots in space. The CV of algal cover in space (spatial CV) was quantified from measurements of total algal cover among the plots within each experimental treatment on each census. We detrended spatial variability in total algal cover by deriving the standard deviation of the residuals from the linear regression of total algal cover of plots within treatments on month and dividing this by the respective mean total algal cover to obtain the detrended community-level spatial CV. Analyses of the raw and detrended data produced qualitatively consistent results (Tables S1 and S2). For clarity, we present in the main text results from the analyses of the raw data.
Compositional turnover	The extent of change in community composition over time, thus integrating elements of invasions, extinctions, resistance and variability. The reciprocal of persistence (Pimm 1984). Less stable communities experience higher rates of compositional turnover.	Quantified for each experimental plot as the Jaccard similarity in algal community composition (calculated from species presence/absence data) between consecutive surveys (after the commencement of experimental manipulation).
Number of extinctions (robustness)	Corresponds to the number of secondary extinctions caused by the initial loss of a species. Sometimes referred to as structural robustness (Solé & Montoya 2001; Dunne *et al.* 2002; Allesina *et al.* 2009; Dunne & Williams 2009).	Quantified for each plot as the number of algal taxa that were observed in plots prior to experimental manipulation but were absent at the end of the experiment.
Number of invasions	Based on the concept of persistence. Communities that are more difficult to invade are more persistent and vice versa (Pimm 1984).	Quantified for each plot as the number of algal taxa that were observed in plots at the end of the experiment but were absent prior to experimental manipulation.
Resistance	The extent of change in community structure caused by a perturbation (Pimm 1984). Corresponds to MacArthur's (1955) definition of 'stability'. Also referred to as 'inertia' by Orians (1975). More resistant communities show less structural change.	Measured as the inverse of the Euclidean distance from each experimental plot to the centroid of the unmanipulated uncaged treatment at the end of the experiment [based on Bray-Curtis similarity matrices calculated from log (x + 1)-transformed algal cover data]. This provides a holistic measure of the extent of change in algal community structure over the duration of the experiment, over and above natural background dynamics. The resistance of the caged plots with no experimental consumer removals did not differ statistically from the inverse of the distance of the uncaged plots to their treatment centroid ($t_3 = 0.24$, $P = 0.82$).

tionships. That is, there is no general framework that integrates across the different dimensions of stability.

The primary question about multidimensional ecological stability is how correlated or independent are the various components of stability (Box 1)? Few and weak correlations among stability components (Box 1a) imply that simultaneous quantification of multiple components of stability is necessary and suggests that different processes and mechanisms could be responsible for different components of stability. Alternatively, many strong correlations among several components of stability (Box 1b, c, d) imply that the effective dimensionality of ecological stability is low. This makes ecological stability less complex than if correlations were weak. Finding strong correlations (i.e. low effective dimensionality) implies that similar processes and mechanisms underlie multiple components of ecological stability and/or that there are causal connections among components of stability.

A second question about multidimensional stability is whether the effective dimensionality of stability changes in the face of major perturbations, such as biodiversity loss. This could be explored, for example, by simulating the loss of different predator species and their prey both separately and together (Fig. 1), with a focus on consumer species conceivably capturing effects most realistically because species at higher trophic levels tend to suffer higher extinction rates (Duffy 2003) and exert disproportionately large effects on the structure and functioning of ecosystems (Paine 1966; Mittelbach *et al.* 1995; Estes *et al.* 2011). The loss of different functional groups of consumers may also trigger shifts in the relationships among different components of ecological stability. For example, empirical studies have shown that predators are key contributors to ecosystem robustness (Paine 1966; Terborgh *et al.* 2001; Estes *et al.* 2011), whereas intermediate consumers such as grazers can regulate the spatial variability of their prey (Hillebrand 2008).

In this article, we develop the concept of ecological stability in a multidimensional framework and explore the two key questions about the interrelationships among different stability measures. As an example of how this framework can be applied, we conducted a manipulative field experiment on marine rocky shore communities

Box 1 The dimensionality of ecological stability
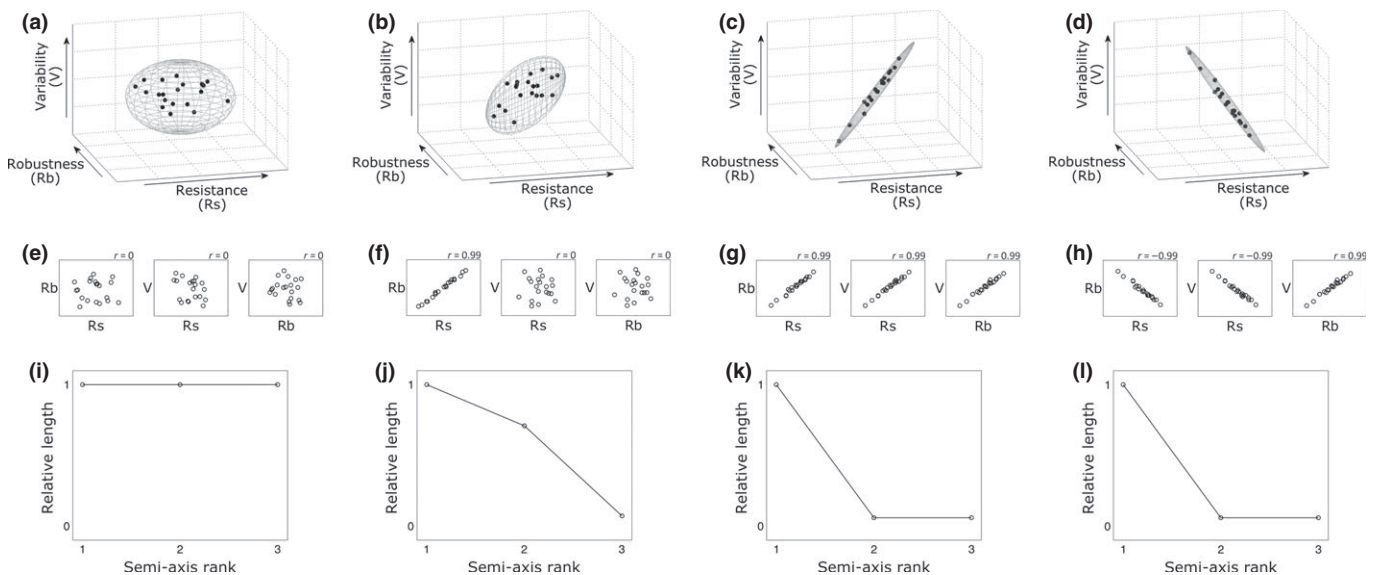
Four scenarios illustrating a spectrum of possible relationships among three different dimensions of stability; variability (V), resistance (Rs) and robustness (Rb) are used in this example, though in reality there will often be more than three components: (a, e, i) the three components of stability are independent, ecological stability is a relatively complex phenomenon with relatively high effective dimensionality; (b, f, j) two components of stability are strongly correlated and both independent of the third; (c, g, k) all measures of stability are strongly and positively correlated, ecological stability is a relatively simple phenomenon, with low effective dimensionality; (d, h, l) all measures of stability are strongly correlated, but some of those correlations are negative; ecological stability again has low effective dimensionality. The relationships among the three components of stability for the four scenarios are illustrated as ellipsoids in multidimensional stability space in (a-d) [(a) spherical, (b) 'frisbee'-shaped and (c, d) 'cigar'-shaped], which were constructed using the covariance matrix of stability measures (see *Methods*); as sets of pairwise scatterplots in (e-h), with associated Pearson correlation coefficients (*r*), and using the relative (to the dominant axis) lengths of ellipsoid semi-axes in (i-l). The relative length of any ellipsoid semi-axis is proportional to the amount of variation along that axis, meaning that the distribution of relative lengths among axes defines the dimensionality and shape of the ellipsoid. Similarly, the volume of the ellipsoid describes the total variation in stability, while changes in ellipsoid orientation indicate shifts in the relative magnitude and/or form of correlations among stability measures. The orientation of the ellipsoid in (c) is orthogonal to that in (d) (i.e. the angle between the dominant eigenvectors of each ellipsoid is 90°).
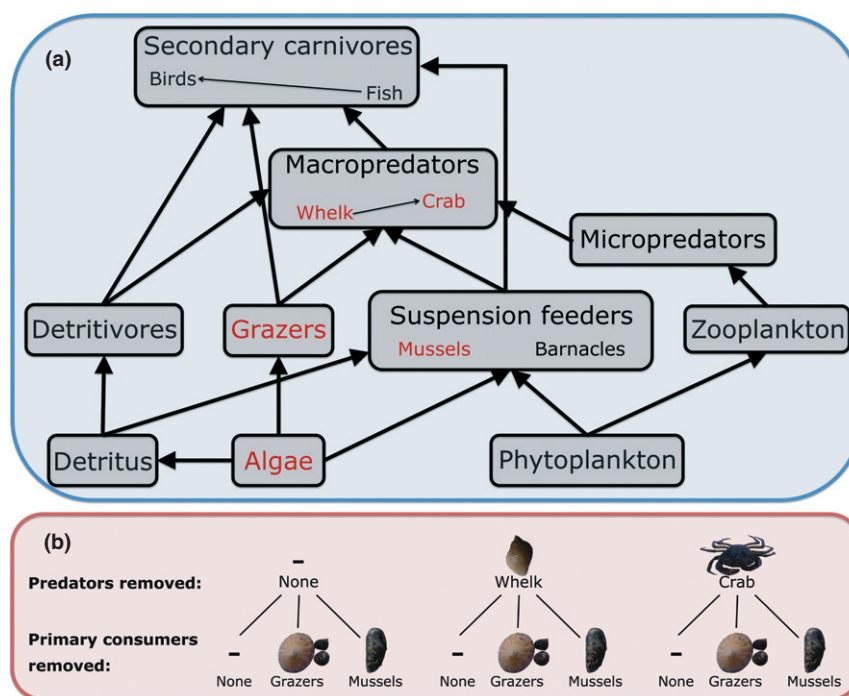
Figure 1 (a) Simplified trophic interaction network on moderately exposed rocky shores (adapted from Little *et al.* 2009). Highlighted in red are consumers whose presence was manipulated (see *Methods*). We quantified the effects of these experimental species extinctions on multiple components of the stability of macroalgal communities (also highlighted in red). (b) Our experimental design comprised two fixed factors: 'predators removed' and 'primary consumers removed', each comprising three levels (predators removed: no removal, whelk removed and crab removed; primary consumers removed: no removal, grazers removed and mussels removed). Comparison of the resulting nine treatments enabled us to quantify the individual and combined effects of consumer species loss across multiple trophic levels on the stability of macroalgal communities.

comprising primary producers, primary consumers (prey) and predators. Six measures of stability were quantified (Table 1), representative of a range of components of ecological stability. We hypothesised that ecological stability has relatively low effective dimensionality but that the loss of different species can trigger distinct shifts in the strength and nature of relationships among stability components and increase the effective dimensionality of stability. To maximise the ecological realism of our results, we conducted the experiment in a natural ecosystem containing established communities structured by a diverse range of both trophic and non-trophic interactions (Díaz *et al.* 2003; Naeem 2008).

METHODS

Our experimental site was located on the mid to low shore at Rush (53°31.4' N, 6°04.9' W) on the east coast of Ireland on a moderately exposed flat rocky reef containing networks of patches of bare rock, mussels, barnacles and macroalgal stands. Each plot contained approximately 50% mussel cover prior to the random allocation of treatments (range 45–55%). There was no difference in macroalgal communities (Table S3 in Supporting Information) among treatments at the commencement of the experiment (PERMANOVA; Pseudo-$F_{9,30} = 0.81$, $P = 0.82$).

We perturbed our experimental plots by simulating the loss of two predator species [whelk (*Nucella lapillus*) and crab (*Carcinus maenas*)] and two groups of their primary consumer prey [mussels (*Mytilus edulis*) and molluscan grazers, comprising principally *Patella vulgata*, *Littorina littorea* and *Gibbula umbilicalis*] over 14 months using

wire mesh cages (Fig. 1a). Experimental manipulations mimicked as closely as possible natural patterns at the experimental site. The stainless steel mesh cages used to manipulate the presence of target consumers (0.9 mm wire diameter, 3.33 mm aperture, 61% open area) measured 35 × 35 cm and were 12 cm high, allowing for algal growth and recruitment. This cage design has been used extensively and successfully to manipulate consumer presence on rocky shores with no consequences for algal community structure (O'Connor & Crowe 2005; O'Connor & Donohue 2013). The cages allowed immigration and recruitment of primary producers and many epibenthic consumers, including primary consumers and small predators (e.g. amphipods, polychaetes and Nemertea). We thereby caused the local extinction of key components of a larger intertidal food web in an open experimental system without removing all consumers from a given trophic level. The fences were attached to the shore by drilling holes into the rock and securing them with stainless steel screws and washers. Roofs were also made from the stainless steel mesh and were fixed to the tops of the fences with cable ties. Cages and treatments were checked and maintained regularly (approximately every 2 weeks) and cages were scrubbed routinely with a wire brush to remove any algae.

To test for any experimental artefacts caused by the presence of the cages, we compared the structure and stability of macroalgal communities in unmanipulated (i.e. with all consumer species present) caged and uncaged communities. We found no difference in any response variable between the caged plots and the uncaged procedural controls (Table S4), demonstrating that the presence of the experimental cages had no significant effect on the structure or stability of algal communities.

Our experimental design comprised two crossed fixed factors, with three levels in both [loss of predators (no predators removed, whelk removed, crab removed) and loss of primary consumers (no primary consumers removed, grazers removed, mussels removed)], resulting in a total of nine caged treatments (Fig. 1b). Each of our experimental treatments was replicated four times. Mussels and molluscan grazers were removed manually from treatments to simulate loss of these species. Although mussels do not consume benthic macroalgae, they comprise important consumers of macroalgal propagules (Santelices & Martínez 1988). They also have strong non-trophic interactions with macroalgae arising primarily from competition for space on the shore (Lubchenco & Menge 1978; O'Connor 2010) and these interactions vary in the presence of grazers (Crowe *et al.* 2011). Predators were placed in the plots as required for the treatment at a density of one individual per plot. Crabs found on the shore and used in the experiment had a carapace width of 3–6 cm. This size range of crab feeds mainly on mussels and small grazers (Rangeley & Thomas 1987). Although larger crabs have been found to feed on whelk (e.g. Hughes & Elner 1979), no predation by crabs upon whelk was observed during our experiment.

We quantified the extent of cover and composition of macroalgal communities on each plot with a 25 × 25 cm double-strung quadrat four, seven, ten and fourteen months after the commencement of the experiment. The quadrat was placed in the middle of each plot to avoid sampling edge effects and the cover and composition of algae estimated by identifying all species present under each of 64 intersections. Species of macroalgae present within the quadrat but not recorded under an intersection point were noted and assigned a value of 1% cover. Given that algal cover varied along vertical as well as horizontal axes, total algal cover within experimental plots frequently exceeded 100%.

Algal communities on rocky shores are highly dynamic and can change dramatically within a few months, particularly at the scale of individual plots (Figure S1), driven by dynamic interactions between environmental fluctuations and biological interactions (e.g. Hawkins & Hartnoll 1983). Consequently, by focusing our efforts on primary producers, we maximised the probability of detecting relatively rapid shifts in stability (Borrvall & Ebenman 2006). We quantified the following six measures of the stability of macroalgal communities, representing a range of components of ecological stability (Pimm 1984): the temporal and spatial variability of total algal cover; the compositional turnover of algal communities over time (the reciprocal of persistence); the number of extinctions (structural robustness) and invasions (another measure of persistence) of algal taxa and the resistance of algal communities to perturbations. These components of stability and the methodologies used to quantify them are described in Table 1.

We waited 4 months before commencing our measurements to ensure establishment of experimental treatments and to avoid transient dynamics. Analyses of effect sizes of our experimental manipulations for a number of stability components indicate a lack of consistent directional shifts in stability (Figure S2), which would be expected were the communities still undergoing transient dynamics. Further, detrending the data to remove any particular positive or negative shifts in algal cover on variability over the duration of the experiment had no effect (Table 1), while significant effects of our experimental manipulations on algal community structure were found on every sampling occasion after experimental manipulation (Table S5).

Pairwise relationships among stability components were quantified using Pearson correlation coefficients. We used principal components analysis (PCA), based on standardised data (calculated by subtracting the means and then dividing by the standard deviations to remove differences in scales of measurement), to examine the effective dimensionality of stability. Unlike the other measures of stability, spatial variability was not associated with individual experimental plots and could not be incorporated in the PCA.

We used modified Mantel tests to compare the volume, orientation and shape of ellipsoids in multidimensional stability space (see Box 1). Ellipsoids were constructed from the matrix of pairwise covariances between components of stability. All measures of stability were standardised (as described above for PCA) to remove differences in scales of measurement prior to the construction of ellipsoids. As spatial variability was not associated with individual experimental plots and could not be used in the calculation of covariance matrices, ellipsoids were quantified in five rather than six dimensions. We generated null distributions of effect sizes using a series of permutation analyses, where we reassigned each observation to a treatment group randomly without replacement 10^4 times. We focused our analytical comparisons of ellipsoids on tests for effects of the loss of primary consumer species. This was done to maximise the number of samples used to construct the ellipsoids and because the loss of primary consumers affected every measure of stability in some way and was the only factor that had significant main effects in the absence of interactions.

Ellipsoid volume (V) was calculated for each treatment group in both the observed and permuted datasets using the formula

$$V = \frac{\pi^{n/2}}{\Gamma(\frac{n}{2}+1)} \prod_{i=1}^{n} (\lambda_i^{0.5})$$

where λ_i is the ith eigenvalue of the covariance matrix for a given treatment and n is the dimensionality of the covariance matrix of standardised stability measures. We tested the significance of pairwise differences in observed volumes between treatments by comparison with the null distribution of differences from the permuted data. The orientations of the dominant eigenvector (v_1) for each treatment were compared in a similar pairwise manner. The smallest angle (ϑ) between the dominant eigenvectors ($v_{1,i}$ and $v_{1,j}$) of treatments i and j is a function of their dot product by the equation

$$\vartheta = \min([\cos - 1(V_{1,i} \cdot V_{1,j})], [\pi/2 - \cos - 1(V_{1,i} \cdot V_{1,j})])$$

The null distribution of angles between eigenvectors was created using the permuted null dataset and observed values compared against it to test for significance. As angles are inherently dyadic and positive, we used one-tailed tests to test for pairwise differences in orientation between treatments. Finally, we compared the shape of ellipsoids by using the distribution of the semi-axis lengths ($a_i = \lambda_i^{0.5}$). We standardised each set of ellipsoidal semi-axis lengths by dividing by their maximum. Pairwise comparisons of differences in relative lengths for semi-axes were then evaluated against the respective null distributions of differences.

We tested for effects of our experimental manipulations on individual components of stability using analysis of variance (ANOVA) after first ensuring homoscedasticity with Cochran's test. Each of the spatial variability, number of extinctions and detrended temporal variability of algal communities were square-root transformed to homogenise variances prior to analysis (Tables S1 and S2).
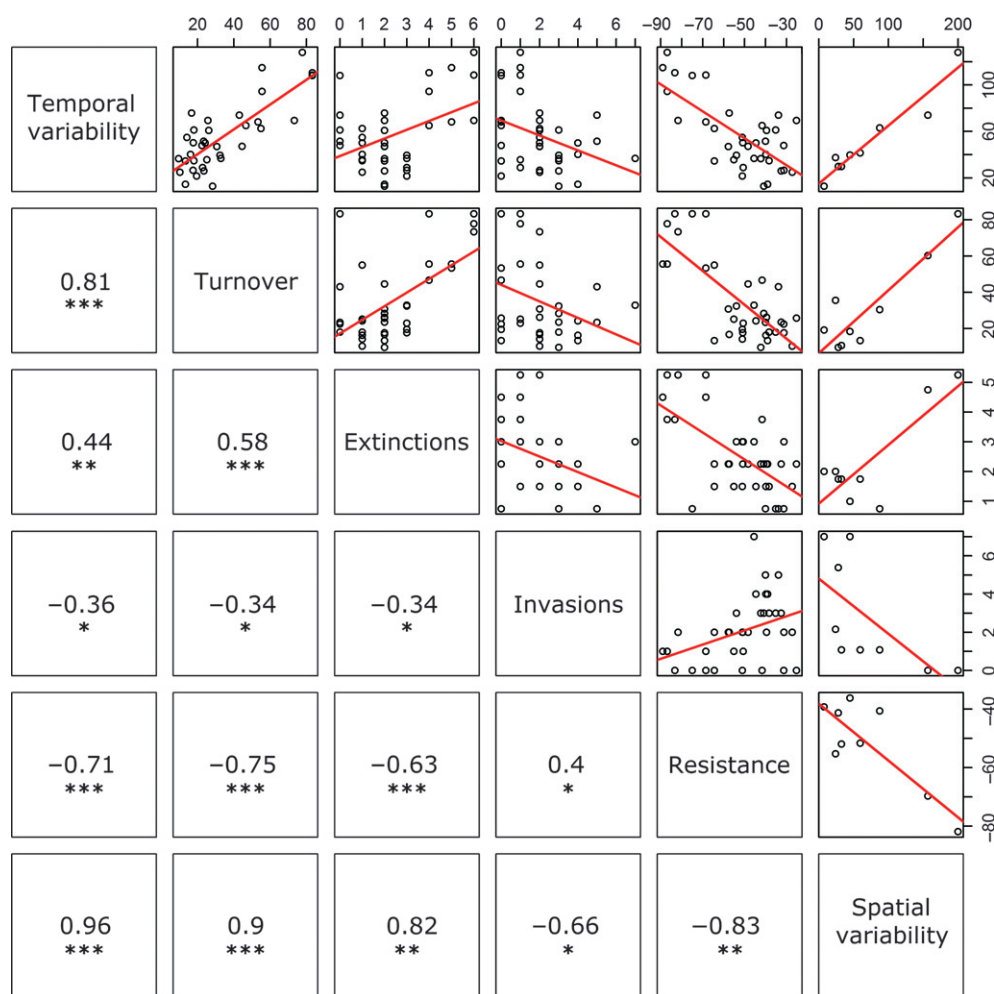
Figure 2 Pairwise relationships among multiple components of ecological stability. Scatterplots and associated Pearson correlation coefficients for the pairwise relationships between each of our measures of stability at the among-community ecological scale. As spatial variability was quantified as the variability among plots within each of our nine experimental treatments (see *Methods*) and could not therefore be associated with individual plots, we used the mean treatment value for each measure of stability in all pairwise correlations involving spatial variability. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 2 Results of principal components analysis (PCA) of multidimensional stability in our experimental plots. Spatial variability was omitted from this analysis as it could not be associated with individual plots

Principal component	Eigenvalue	% Variation	Cumulative% variation
1	3.21	64.2	64.2
2	0.774	15.5	79.7
3	0.593	11.9	91.5
4	0.254	5.1	96.6
5	0.169	3.4	100

Eigenvectors

Variable	PC1	PC2	PC3	PC4	PC5
Temporal variability	0.478	−0.211	−0.494	0.270	0.640
Compositional turnover	0.502	−0.261	−0.192	0.310	−0.739
Extinctions	0.417	−0.013	0.833	0.304	0.199
Invasions	−0.310	−0.936	0.147	−0.055	0.059
Resistance	0.500	−0.105	0.061	−0.857	0.001

RESULTS AND DISCUSSION

When considering assemblages within plots as a set of local communities that vary in species composition and are exposed to the same relatively weak perturbations (i.e. natural fluctuations in environmental conditions), all pairwise correlations among the six components of stability were significant ($P < 0.05$) and frequently strong ($|r| > 0.7$ for seven of the 15 pairwise correlations; Fig. 2). Temporal and spatial variability, compositional turnover and the number of extinctions were all correlated positively with one another and negatively with the number of invasions and resistance. PCA (quantified here in five dimensions because spatial variability could not be associated with individual plots) revealed that over 64% of the variability among communities in multidimensional stability space could be accounted for in a single dimension, 80% in two dimensions, and 92% in three (Table 2). Without correlations among stability components, we expect these figures to be, respectively, 20, 40 and 60%. The first principal component was related positively to compositional turnover and resistance
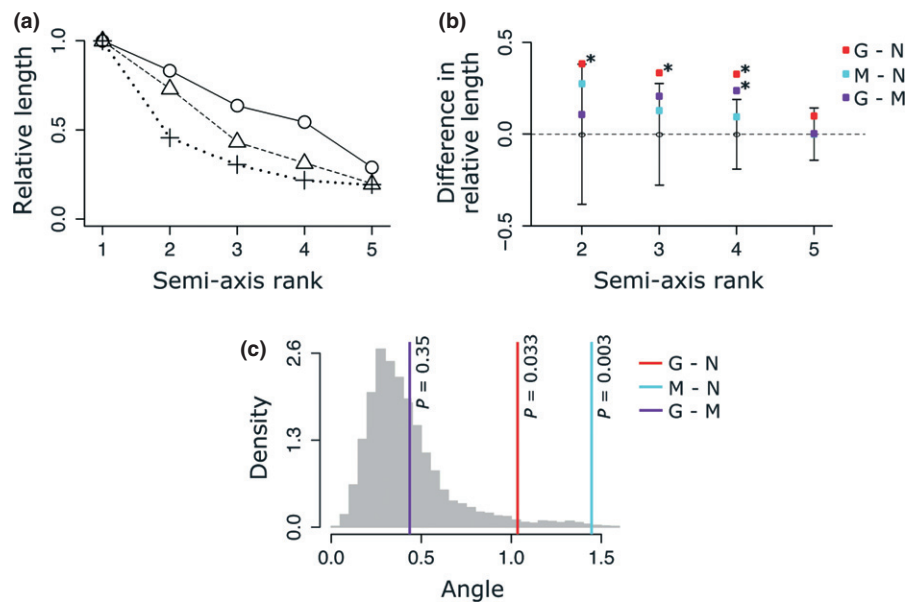
Figure 3 Effects of primary consumer species loss on the shape and orientation of ellipsoids in multidimensional stability space. (a) Relative lengths of ranked ellipsoidal semi-axes where no primary consumers were removed (+), after mussel loss (Δ) and after grazer loss (o). (b) Pairwise differences in relative semi-axis lengths for random permutations of the data (95% CI shown here) and observed treatments [No primary consumers lost (N), Grazers lost (G), Mussels lost (M)]. Semi-axes with significantly (*P* < 0.05) greater relative lengths than the null distribution are highlighted with asterisks. (c) Pairwise differences in the angle (in radians) between dominant semi-axes (i.e. eigenvectors) for random permutations of the data (grey histogram) and observed treatments [No primary consumers lost (N), Grazers lost (G), Mussels lost (M)].
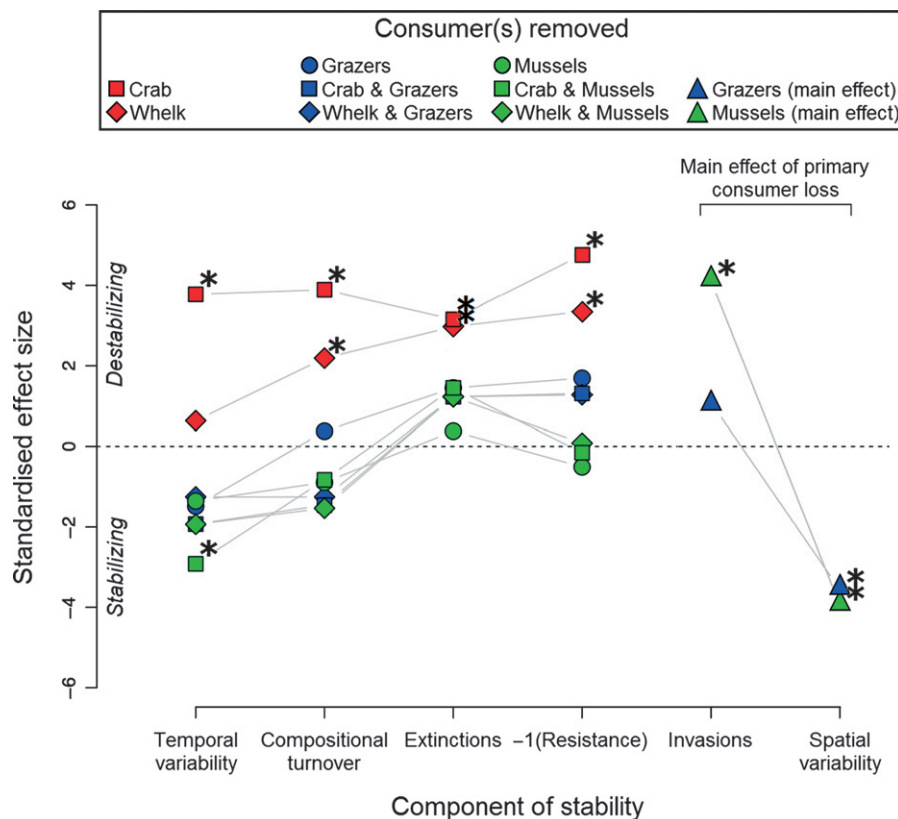
Figure 4 Effects of the loss of different consumer species on individual components of ecological stability. Standardised effect sizes based on the difference between experimental treatments and the corresponding treatment with no species removals. Treatments that differed significantly (*P* < 0.05) from the latter are highlighted with asterisks. The inverse of resistance is shown here so that all positive effect sizes correspond to reductions in stability. As the number of invasions and the spatial variability of algal cover were affected only by the loss of primary consumer species, effect sizes for these components of stability are shown only for the main effect of primary consumer loss.

(eigenvector loadings of 0.5 in both cases), whereas the second principal component was determined strongly by the number of invasions (−0.94). These results demonstrate that the effective dimensionality of stability can be comparatively low and collapsible to just two or perhaps three dimensions. Thus, ecological stability appears to be less complex, perhaps even considerably so, than it otherwise could be.

Analysis of the shape, volume, and orientation of stability ellipsoids (*sensu* Box 1) reveals that our experimental perturbations changed both the dimensionality and nature of ecological stability. The loss of primary consumer species altered ellipsoid shape, from a 'cigar'-shaped ellipsoid when no primary consumers were lost towards increasingly spheroidal ellipsoids in the absence of mussels and, in particular, grazers (Fig. 3a). In fact, the loss of grazer species increased the relative length of multiple ellipsoidal axes significantly (Fig. 3b), indicating that perturbations can decouple relationships among stability components (Box 1) and, thus, increase the effective dimensionality of stability.

Although reductions in ellipsoid volume after the loss of primary consumers were not statistically significant (Figure S3), we found that the loss of either mussels or grazers, irrespective of the presence or absence of their predators, altered the orientation of ellipsoids significantly (Fig. 3c). So extreme were changes in the nature of interdependencies among components of stability that ellipsoid orientation after mussel loss was effectively orthogonal to that when no primary consumers were removed (Fig. 3c), meaning that the dominant relationships among components of stability shifted to almost the theoretically maximal extent. These findings demonstrate that perturbations can modify the interrelationships among components of stability in many different ways, altering not only the strength of those relationships but also causing potentially dramatic shifts in their form.

In concurrence with these multivariate findings, we found that, while some components of stability responded similarly, others responded in different ways to different perturbations (i.e. the loss of different consumer species; Fig. 4, Table S1). The loss of predator species in isolation, for example, altered four of our six measures of stability significantly; each of the temporal variability of total algal cover (ANOVA, $F_{4,27} = 4.53$, $P = 0.006$), the number of extinctions ($F_{4,27} = 3.81$, $P = 0.014$) and the compositional turnover ($F_{4,8} = 5.43$, $P = 0.021$) of algal taxa increased significantly following the loss of one or either predator species, while multivariate algal community structure also had significantly less resistance ($F_{4,27} = 4.1$, $P = 0.01$) to the loss of either predator species than to any other experimental perturbation (Fig. 4). These destabilising effects of predator species loss occurred when the primary consumer trophic level was intact and disappeared when either grazers or mussels were lost in tandem with either predator, resulting in significant interactions between predator species loss and the loss of their prey (Table S1). In fact, the loss of mussels in combination with crabs even reduced the temporal variability of macroalgal cover significantly (Fig. 4). In contrast, two components of stability were affected solely by the loss of primary consumers irrespective of the presence or absence of their predators (Table S1): the number of invasions of algal taxa increased significantly ($F_{2,27} = 8.05$, $P = 0.002$) following the removal of mussels, whereas the loss of either of the manipulated primary consumer groups reduced the spatial variability of total algal cover ($F_{2,27} = 8.47$, $P = 0.001$; Fig. 4).

Given that different scenarios of biodiversity loss altered different components of stability in disparate ways, our results demonstrate that perturbations can not only modify the shape and orientation of stability ellipsoids but they can also shift the location of communities in multidimensional stability space distinctively along different dimensions of stability. This multifaceted nature of stability cautions against focus on individual forms of stability in isolation, as this could considerably underestimate the potential of different perturbations to alter overall ecological stability.

We have shown that the dimensionality of ecological stability can be considerably lower than one would expect were the various components of stability unrelated. This implies that ecological stability may be a relatively simple concept, or at least not show as high dimensionality as there could be. It remains to be seen how the dimensionality of stability varies across different types of community to the one analysed here. In our experiment, changes in species composition caused changes in the dimensionality of stability and the interrelationships among its components, which suggest that the complexity and nature of stability may not be fixed across communities. In addition, the form of correlations among components of stability is also of great interest. In particular, negative correlations between different components of stability imply some mechanism akin to a trade-off between these components. Such trade-offs would have profound implications for ecosystem management, necessitating the prioritisation of some components of stability (e.g. enhancing agricultural yield reliability by minimising temporal variability in biomass) while accepting reductions in others (e.g. increasing susceptibility to invasion by exotic species). Although there is much to learn about this emerging field, we contend that a multidimensional stability framework gives us a richer understanding of how communities respond to perturbations and is fundamental to support the optimal management of both biodiversity and ecosystem functioning.

Our study adds a new fundamental direction to recent research in developing a deeper and more comprehensive understanding of ecological stability (e.g. McCann 2011; Allesina & Tang 2012). Although we might expect most, if not all, measures of stability to be highly correlated in communities with different compositions, different perturbations are likely to alter and even decouple these strong dependencies in very different ways that are, consequently, difficult to predict. There is, therefore, much need for theoretical development and additional empirical studies both to elucidate mechanisms underpinning relationships among components of stability and to generalise our findings. Whether transient or permanent, changes in the interrelationships among different components of stability comprise one of the major consequences of biodiversity loss and global change.

REFERENCES

Allesina, S. & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483, 205–208.

Allesina, S., Bodini, A. & Pascual, M. (2009). Functional links and robustness in food webs. *Philos. Trans. R. Soc. B*, 364, 1701–1709.

Borrvall, C. & Ebenman, B. (2006). Early onset of secondary extinctions in ecological communities following the loss of top predators. *Ecol. Lett.*, 9, 435–442.

Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecol. Lett.*, 4, 72–85.

Crowe, T.P., Frost, N.J. & Hawkins, S.J. (2011). Interactive effects of losing key grazers and ecosystem engineers vary with environmental context. *Mar. Ecol. Prog. Ser.*, 430, 223–234.

Díaz, S., Symstad, A.J., Chapin, F.S., Wardle, D.A. & Huenneke, L.F. (2003). Functional diversity revealed by removal experiments. *Trends Ecol. Evol.*, 18, 140–146.

Duffy, J.E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.*, 6, 680–687.

Dunne, J.A. & Williams, R.J. (2009). Cascading extinctions and community collapse in model food webs. *Philos. Trans. R. Soc. B*, 364, 1711–1723.

Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.*, 5, 558–567.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011). Trophic downgrading of Planet Earth. *Science*, 333, 301–306.

France, K. & Duffy, J.E. (2006). Diversity and dispersal interactively affect predictability of ecosystem function. *Nature*, 441, 1139–1143.

Grimm, V. & Wissel, C. (1997). Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109, 323–334.

Harrison, G.W. (1979). Stability under environmental stress: resistance, resilience, persistence and variability. *Am. Nat.*, 113, 659–669.

Hawkins, S.J. & Hartnoll, R.G. (1983). Changes in a rocky shore community: an evaluation of monitoring. *Mar. Environm. Res.*, 9, 131–181.

Hillebrand, H. (2008). Grazing regulates the spatial variability of periphyton biomass. *Ecology*, 89, 165–173.

Hughes, R.N. & Elner, R.W. (1979). Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey *Nucella lapillus*. *J. Anim. Ecol.*, 48, 65–78.

Ives, A.R. & Carpenter, S.R. (2007). Stability and diversity of ecosystems. *Science*, 317, 58–62.

Ives, A.R., Gross, K. & Klug, J.L. (1999). Stability and variability in competitive communities. *Science*, 286, 542–544.

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.*, 142, 911–927.

Little, C., Williams, G.A. & Trowbridge, C.D. (2009). *The Biology of Rocky Shores*, 2nd edn. Oxford University Press, Oxford, UK.

Logofet, D.O. (2005). Stronger-than-Lyapunov notions of matrix stability, or how "flowers" help solve problems in mathematical ecology. *Linear Algebra Appl.*, 398, 75–100.

Lubchenco, J. & Menge, B.A. (1978). Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.*, 48, 67–94.

MacArthur, R. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology*, 36, 533–536.

May, R.M. (1972). Will a large complex system be stable? *Nature*, 238, 413–414.

May, R.M. (1974). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, New Jersey, USA.

McCann, K.S. (2000). The diversity-stability debate. *Nature*, 405, 228–233.

McCann, K.S. (2011). *Food Webs*. Princeton University Press, Princeton, New Jersey, USA.

Mittelbach, G.G., Turner, A.M., Hall, D.J., Rettig, J.E. & Osenberg, C.W. (1995). Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. *Ecology*, 76, 2347–2360.

Montoya, J.M., Pimm, S.L. & Solé, R.V. (2006). Ecological networks and their fragility. *Nature*, 442, 259–264.

Naeem, S. (2008). Advancing realism in biodiversity research. *Trends Ecol. Evol.*, 23, 414–416.

O'Connor, N.E. (2010). Shore exposure affects mussel population structure and mediates the effect of epibiotic algae on mussel survival in SW Ireland. *Estuar. Coast. Shelf Sci.*, 87, 83–91.

O'Connor, N.E. & Crowe, T.P. (2005). Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. *Ecology*, 86, 1783–1796.

O'Connor, N.E. & Donohue, I. (2013). Environmental context determines multi-trophic effects of consumer species loss. *Glob. Change Biol.*, 19, 431–440.

O'Gorman, E.J. & Emmerson, M.C. (2009). Perturbations to trophic interactions and the stability of complex food webs. *Proc. Natl Acad. Sci. USA*, 106, 13393–13398.

Orians, G.H. (1975). Diversity, stability and maturity in natural ecosystems. In: *Unifying Concepts in Ecology* (eds van Dobben, W.H. & Lowe-McDonnell, R.H.). Junk, The Hague, The Netherlands, pp. 139–149.

Paine, R.T. (1966). Food web complexity and species diversity. *Am. Nat.*, 100, 65–75.

Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326.

Pimm, S.L. & Redfearn, A. (1988). The variability of population densities. *Nature*, 334, 613–614.

Rangeley, R.W. & Thomas, M.L.H. (1987). Predatory behaviour of juvenile shore crab *Carcinus maenas* (L.). *J. Exp. Mar. Biol. Ecol.*, 108, 191–197.

Santelices, B. & Martínez, E. (1988). Effects of filter-feeders and grazers on algal settlement and growth in mussel beds. *J. Exp. Mar. Biol. Ecol.*, 118, 281–306.

Solé, R.V. & Montoya, J.M. (2001). Complexity and fragility in ecological networks. *Proc. R. Soc. Lond. Ser. B*, 268, 2039–2045.

Steiner, C.F., Long, Z.T., Krumins, J.A. & Morin, P.J. (2005). Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. *Ecol. Lett.*, 8, 819–828.

Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G. *et al.* (2001). Ecological meltdown in predator-free forest fragments. *Science*, 294, 1923–1926.

Tilman, D., Reich, P.B. & Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, 629–632.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).