Integrating theoretical and empirical definitions of ecological stability

***Background***

Ecological stability is complex and multifaceted, fueling vigorous research into ecosystem attributes that contribute to stability. However, the integration and synthesis of stability research is difficult because relationships between different definitions of stability are not always understood or easily compared, and theoretical and empirical studies tend to focus on different aspects (Ives & Carpenter 2007; Donohue et al. 2013).

A few studies have attempted to synthesize our understanding of ecological stability by exploring the relationships between different forms of stability (Ives & Carpenter 2007; Donohue et al. 2013; Arnoldi et al. 2016). A central challenge identified by these studies is that different attributes of stability are typically studied in isolation. Donahue et al. (2013) addressed this challenge by conducting a field experiment on marine rocky shores in which they measured different aspects of ecological stability. They found that the different measures of stability tended to be correlated with one another but that some correlations were stronger than others. Specifically, they found that higher temporal variability (CV) was associated with higher compositional turnover and a greater number of extinctions, but resistance (size of the change in species abundances after a perturbation) and the number of invasions were lower in more temporally variable communities (Donohue et al. 2013). (Importantly, they also found that various aspects of ecological stability responded in unique ways to different scenarios of biodiversity loss, cautioning against using only one measure of stability to understand the consequences of biodiversity loss or other perturbations.)

Not only do single studies rarely integrate different measures of stability, but theoretical and empirical approaches also tend to study different aspects of stability. Theoreticians typically focus on asymptotic stability such as the resistance and resilience of a community matrix to single perturbations, whereas empiricists more often measure temporal variability of populations and communities relative to repeated perturbation (Donohue et al. 2013, Arnoldi 2016). The difference in focus has hindered the integration of results from theory and experiments (Arnoldi et al. 2016, (Ives & Carpenter 2007).

***Overview of our study***

In this study, our primary goal is to integrate different definitions stability by measuring multiple stability types from an aquatic mesocosm experiment. We will accomplish this in part by using the MAR approach to build community matrices from the data in order to estimate a variety of different stability metrics. Additionally, we seek to determine if different community and food web attributes contribute similarly to different measures of stability. Specifically, we will focus on the following questions:

Q1) Should different aspects of stability (e.g. CV vs resilience/eigenvalue) relate to one another theoretically, and what do the data actually show? (literature review, MAR modeling and math approach, data exploration)

Q2) What attributes of food webs (e.g. connectance, weak interactions) are important for ‘stability’, and for what types of stability? (See Table below: literature review)

Q3) What food web attributes can we measure from our community matrices from MAR and how will we quantify or measure them? (literature review, brainstorming).

Q4) After identifying a set of hypotheses we can test with our data (Q3), and then conducting statistical tests of those hypotheses, what conclusions can we make?

**Question 1: How do different elements of stability (Table 1), relate to one another?**

We will compare different definitions of stability that are measured from the same experimental aquatic mesocosm communities (Question 1). Using time series data, we measured temporal variability, expressed as the coefficient of variation (CV), of both populations (CV of the biomass of individuals species of zooplankton) and communities (CV of total zooplankton biomass). Through multivariate-autoregressive models (MARs), we also generated community matrices that are used to calculate additional measurements of stability such as asymptotic resilience (the asymptotic rate of return to equilibrium after a perturbation). By estimating stability measurements that include measurements typically the focus of empirical studies (CV’s) and theoretical work (asymptotic resilience as measured by the dominant eigenvalue), we can explore how different definitions of stability are related). For example, is asymptotic stability (Eig) related to temporal stability (CV) of communities or populations? What would we expect and why? I am especially interested in the connection between theoretical measures derived from the community matrix versus the temporal CVs (e.g. Ives, Arnoldi).

TABLE 1: Stability measurements

|  |  |  |
| --- | --- | --- |
| Stability type | Meaning | Measure |
| Asymptotic resilience (Arnoldi et al. 2016)  Return rate (Ives et al. 2013) | Rate of return to equilibrium (assuming linear, deterministic model) following a disturbance | Largest (dominant) eigenvalue of community matrix  (max λB) |
| Rate of convergence of the transition distribution to the stationary distribution | The rate at which the transition distribution returns to the stationary distribution (which is not a stable point in a stochastic model). This is related to asymptotic resilience, but not completely (Ives pg. 309) | max λBXB  (Max eigenvalue of the Kronecker product?) |
| Variation along the dominant eigenvector | The best one dimensional estimate for the multidimensional system. Larger means less stable. | 1/(1-eig^2) |
| Variance of the stationary distribution (Ives et al. 2013) | Measures the size of the stationary distribution relative to the size of the distribution of process (environmental variation) errors. A measure of how much species interactions amplify environmental variability | Det (B) 2/p Determ. of a matrix (B) the products of all eigenvalues, p is the # of sp. in the matrix. |
| Intrinsic Stochastic invariability | Stochastic variability (Vs) is the maximal system response to a white noise or a sequence of uncorrelated shocks, determined by computing the spectral norm of the covariance matrix (Figure 3, Arnoldi et al. 2016 | Is = 1/(2Vs)  Where Vs = function of covariance matrix |
| Intrinsic deterministic variability | The inverse of the maximal amplitude gain over all single-frequency periodic signals - basically looking at the maximum system response to different frequencies and directions of perturbations | ID = 1/VD  Where VD = deterministic variability which is the maximum system response |
| Reactivity or Initial resilience (Arnoldi et al. 2016). High initial resilience is equivalent to non-reactivity | Instantaneous displacement after a perturbation. Initial resilience is positive when the system is non-reactive. | -tr(Σ)/tr(V∞)  max λB’B |
| Temporal variability | popn and comm variability through time | CV: time series data |

**Question 2: What attributes of food webs (e.g. connectance, weak interactions) are important for ‘stability’, and for what types of stability?**

We also want to understand how different community and ecosystem attributes affect different aspects of stability (Question 2). If aspects of ecological stability are related (see Question 1 and Donohue et al. 2013), we would predict features that influence one form of ecological stability will also be important for a different form of stability. However, if different measures of ecological stability are unrelated then different community or ecosystem attributes will be differentially important. Various features of food webs have been identified as influencing stability (e.g. connectedness, species richness, number of weak interactions), but we still do not know the extent to which these features affect different aspects of stability. We plan to review the features, determine what type of stability they have been shown to influence, and make predictions about how and if they are expected to influence other aspects of stability.

Two important mechanisms/attributes that have been identified as broadly important for ecological stability are weak interactions and species richness. Many studies show weak interactions appear to stabilize communities or are more common in stable communities (McCann 2000, deRuiter et al. 1995, Wootton and Emmerson 2005, Kokkoris et al. 2002 - see Allesina last two references for these full citations), but at least one study has found that weak interactions can also destabilize communities (Allesina & Tang 2012). Species richness has also been shown to enhance temporal stability. The temporal stability of populations and communities tends to increase more diverse ecosystems, particularly at aggregate levels such as the biomass of trophic levels or groups, due to compensation and portfolio effects. This result has been supported by both theoretical work (Loreau et al, Lehman and Tilman, Loreau, Doak et al, DeAngelis and…), and experimental work (Tilman, Downing et al, Petchy, Steiner, et al). There are additional features of communities and food webs that are also likely important for ecological stability.

Below is a preliminary set of predictions that we will expand upon or modify after completing a review of the literature.

1. Temporal stability of populations and communities (lower CV) are also mathematically more stable (resistant and resilient, as defined by the Eigen values of the community matrix). (actually not sure here about this prediction - still need to read more literature).
2. Species richness is positively correlated with multiple types of stability.
3. Weak interactions enhance multiple forms of ecological stability.
4. The number of weak interactions, as determined through the MAR approach and resulting community matrices analyses, increases with species richness of the food webs.

**Question 3: What food web attributes can we measure from our community matrices from MAR, and how will we quantify or measure them? (literature review, brainstorming).**

Once we have a list of important community features that are thought to influence stability, we will work to determine what features we can measure from our community matrices. For example, how do we measure ‘weak interactions’ or ‘connectance’ from the community matrices we have generated? We will generate a list of features that are thought to be important for ecological stability that can be measured or estimated from our data.

Table of candidate hypotheses

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Food web features that affect stability** | **Can we calculate these features from community matrices?** | **What measure or type of stability is affected?** | **Prediction** | **References** |
| Connectance |  |  |  |  |
| Weak interactions |  |  |  |  |
| Species richness |  |  |  |  |
| Top down, bottom-up interactions |  |  |  |  |
| Etc. |  |  |  |  |

**Question 4: After identifying a set of hypotheses we can test with our data (Q3), and then conducting statistical tests of those hypotheses, what conclusions can we make?**

**Background Reading**

**Introduction to the experimental pond system:**

(Downing et al. 2008; Downing, A.L. Brown, B.L., Leibold, M.A. 2014; Brown et al. 2016)

**General introduction to ecological stability & the diversity-stability debate:**

(McCann et al. 1998; McCann 2000; Loreau et al. 2002; Ives & Carpenter 2007)

**More advanced papers that involve comparing different aspects of stability:** (Donohue et al. 2013; Arnoldi et al. 2016)

**The weak interaction effect and diversity-stability:**

(May 1972; Pimm 1984; de Ruiter et al. 1995; McCann et al. 1998; Kokkoris et al. 2002; Wootton & Emmerson 2005; Allesina & Tang 2012)

Food Web Book Chapters by de Ruiter et al.

**Measuring interaction strength:**

(Wootton & Emmerson 2005)

**Introduction to the Jacobian Matrix and Food webs:**

Morin, Peter. 1999. Community Ecology textbook.

CH 5 Food Webs

CH 7 Multi-species interactions

Appendix: Stability

Case, Ted. 2000. An Illustrated Guide to Theoretical Ecology textbook.

CH 13 Stability of Predator-Prey Systems

CH 15 Multi-species communities

(May 1972; Pimm 1984)

**Introduction to MAR method:**

(Ives et al. 2003; Hall et al. 2009; Hampton et al. 2013)

References

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

Arnoldi, J., Loreau, M. & Haegeman, B. (2016). Resilience, reactivity and variability: A mathematical comparison of ecological stability measures. J.Theor.Biol., 389, 47-59.

Brown, B., Downing, A. & Leibold, M. (2016). Compensatory dynamics stabilize aggregate community properties in response to multiple types of perturbations, 1-13.

de Ruiter, P. C., Neutel, A. & Moore, J. C. (1995). Energetics, patterns of interaction strengths, and stability in real ecosystems, 269, 1257-1260.

Donohue, I., Petchey, O. L., Montoya, J. M., Jackson, A. L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N. E. & Emmerson, M. C. (2013). On the dimensionality of ecological stability. Ecol.Lett., 16, 421-429.

Downing, A.L. Brown, B.L., Leibold, M.A. (2014). Multiple diversity-stability mechanisms enhance population and community stability in aquatic food webs, 95, 173-184.

Downing, A. L., Brown, B. L., Perrin, E. M., Keitt, T. H. & Leibold, M. A. (2008). Environmental fluctuations induce scale-dependent compensation and increase stability in plankton ecosystems, 89, 3204-3214.

Hall, S. R., Becker, C. R., Simonis, J. L., Duffy, M. A., Tessier, A. J. & Caceres, C. E. (2009). Friendly competition: Evidence for a dilution effect among competitors in a planktonic host-parasite system. Ecology, 90, 791-801.

Hampton, S. E., Holmes, E. E., Scheef, L. P., Scheuerell, M. D., Katz, S. L., Pendleton, D. E. & Ward, E. J. (2013). Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. Ecology, 94, 2663-2669.

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

Ives, A., Dennis, B., Cottingham, K. & Carpenter, S. (2003). Estimating community stability and ecological interactions from time-series data. Ecol.Monogr., 73, 301-330.

Kokkoris, G. D., Jansen, V. A. A., Loreau, M. & Troumbis, A. Y. (2002). Variability in interaction strength and implications for biodiversity, 71, 362-371.

Loreau, M., Downing, A., Emmerson, M., Gonzalez, A., Hughes, J., Inchausti, P., Joshi, J., Norberg, J. & Sala, O. (2002). A New Look at the Relationship between Diversity and Stability. In: Biodiversity and Ecosystem Functioning: Synthesis and Perspectives (eds. Loreau, M., S. Naeem & P. Inchausti). Oxford University Press, pp. 79-91.

May, R. M. (1972). Will a large complex community be stable?, 238, 413-414.

McCann, K., Hastings, A. & Huxel, G. R. (1998). Weak trophic interactions and the balance of nature, 395, 794-798.

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

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

Wootton, J. T. & Emmerson, M. (2005). Measurement of interaction strength innature, 36, 419-444.