**Introduction**

Ecological stability is a well-studied concept that encompasses many different definitions of stability such as resistance and resilience to perturbations, temporal variability of populations and communities, and community resistance to invasion or extinction (Ives and Carpenter 2007, Donohue et al. 2013). Many mechanisms contribute to ecological stability, however it is unclear if a mechanism contributes similarly to different definitions of stability because we do not have a complete picture of the relationship between different definitions of stability.

Integrating research on ecological stability is challenging because different attributes of stability are typically studied in isolation preventing direct comparisons of different aspects of stability (RW.ERROR - Unable to find reference:966, Ives and Carpenter 2007, Donohue et al. 2013), and theoretical and empirical approaches tend to study different aspects of stability. For instance, theoreticians typically seek to understand mechanisms contributing to asymptotic stability (i.e. resilience) derived from the community matrix, a measure of stability not easily measured by empiricists. Empiricists typically measure the temporal variability of populations and communities relative to repeated perturbations, or community resistance to invasion or extinction (Donohue et al. 2013, Arnoldi 2016). The difference in focus has hindered the integration of theoretical work with empirical work, and the integration between empirical studies that measure different aspects of stability (Donohue Arnoldi et al. 2016, (Ives and Carpenter 2007).

Paragraph on expected relationship between different stability measures. (CJ?,CP?) Temporal stability is based on ongoing repeated perturbation, and assumes a non-equilibrium view of the world. We understand how population CVs and community CVs relate. We also know what underlying mechanisms are likely important: asynchrony, statistical averaging, and possibly weak interactions. Ongoing repeated perturbation …… and response of populations and communities. We expect popn and community CV to be partially correlated, but other factors such as asynchrony might make these measures uncorrelated (Jiang and Pu argument). Asymptotic stability …..

Paragraph on weak interaction effect - outline evidence for weak interactions in both theoretical work and empirical work. Do they work the same way in terms of how they stabilize the system (SS?).If different components of stability are related as indicated by Donohue et al. (2013), those stability components might also share a similar underlying mechanism. One important community attributes that have been identified as broadly important for ecological stability are weak interactions. Weak interactions appear to stabilize communities by reducing the strength of stronger interactions and reducing the magnitude of population oscillations through time (McCann, deRuiter, 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 and Tang 2012).

In this study we focus specifically on (Pfister et al. 2014) exploring the relationship between two aspects of stability: temporal variability, typically measured empirically as the CV of a population or community variable over time (add references) and theoretical stability derived from the community matrix (May 1972, Pimm 1984, Allesina and Tang 2012). First we explore the relationship between these different attributes of ecological stability by estimating multiple measures of stability from the same experimental study of plankton communities. Second, we explore how species richness and the prevalence of weak interactions, two factors that have been repeatedly shown to be important for different aspects of ecological stability, affect these different measures of stability.

Using time-series plankton data collected from an aquatic mesocosm experiment, we first calculated temporal variability of plankton populations and communities (CVs). With the same time-series data we used a multivariate-autogressive modeling approach (MAR) to calculate community matrices (Hampton et al, Ives et al). The community matrices generated from the MAR approach also allows us to calculate stability metrics such as asymptotic resilience as well as provides estimates of the relative interaction strengths in the community. We predict that:

1. Temporal stability of populations (but not communities) are expected to be mathematically more stable. (Do we still predict this?).
2. Weak interactions enhance both forms of ecological stability. (Do we still predict this?)
3. Species richness is positively correlated with weak interactions.
4. Species richness is positively correlated with temporal stability due to previously identified mechanisms, but
5. The number of weak interactions, as determined through the MAR approach and resulting community matrices analyses, increases with species richness of the food webs.

TABLE 1: Stability measurements

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| --- | --- | --- |
| 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 |

**Methods:**

1. Overview of the approach - taking experimental data on plankton ecosystems and using MAR to derive community matrices and stability. (AD)
2. Describe the experiment and time-series data collection. (AD)
3. Describe the MAR approach. (CP, CJ) (composite vs average)
4. Describe how the data were prepared for MAR and analyzed using MAR. (AD, CP, CJ)
5. Simulations?

**Results:**

1. A) No consistently strong relationship between theoretical and empirical measures of stability in the tank mesocosm experiment. (Figure 1: 6 paneled figure of PCV, CCV vs RESIL, REACT, INVAR).

B) However, simulations of randomly generated matrices within bounds set by our empirically based matrices, suggest that some relationship between empirical and theoretical stability could exist because in all cases there was a significant correlation between empirical and theoretical CV’s. The lack of a relationship between observed empirical CVs and theoretical measures of stability could be explained by the following:

- the relationship between theoretical and empirical stability is too too weak to detect (lowish R2s) with our sample size of 18 compositions.

- the empirically based matrices contain a pattern of interactions that are not captured in randomly generated matrices, and this pattern does not generate a relationship between empirical and theoretical

- Other variables are important in determining CCVs and PCVs in the empirical system such as real environmental noise that is different from the simulated environmental noise, or asynchrony between species.

1. A) Some relationships exist between empirical stability and interaction strength, but these relationships are not consistent. (Figure 2, 21 paneled figure?? PCV, CCV vs mean intx, top-down, bottom-up, off-diagonal, comp?).

b) Theoretical simulations suggest that there should be no significant relationship between interaction strength and empirical stability, however the data suggest there should be. This could be explained by:

- the empirical data contain patterns of interactions that are not captured in the simulations that allow for weak interactions to have an effect

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1. A solid relationship between theoretical stability and interaction strength. (Figure 3, 21 paneled figure?? RESIL, REAC, INVAR vs mean intx, top-down, bottom-up, off-diagonal, comp?)

**Discussion: (~4 paragraphs)**

1. Empirical and theoretical stability are not strongly correlated in this study, with the exception of PCV vs Reactivity showing a slight positive correlation, as we predicted. The remaining trends between different stability measures are all positive, but generally not significant.
2. Empirical stability is generally associated with weak interactions, but not always.
3. Theoretical stability is strongly associated with weak interactions.
4. Complexity, or species richness, is weakly or not associated with all measures of stability.

**Conclusions: (~2 paragraphs?)**

Caution should be used when applying results derived from purely theoretical measures of stability derived from the eigen value of the community matrix to traditional empirical measures such as CVs. While some trends indicate some relationship, the CVs appear unrelated or not strongly related to theoretical measures. (although simulations support a relationship between the two different types of measures….)

Perhaps it is not surprising that theoretical and empirical measures are not strongly related. They are capturing different elements of the system - one is an equilibrium view of the system and one is a stochastic view. (The one measure that most closely captures the stochastic view is reactivity …)

Importantly, we found that weak interactions in experimental plankton communities play an important role in enhancing stability with respect to measures that are derived from the community matrix, and a slightly less consistent but still important role in enhancing stability as expressed by the CVs. This is somewhat surprising given the lack of strong congruence between theoretical and empirical measures of stability. However, we know from previous work that weak interactions are important for enhancing theoretical stability, and also empirical stability (although less so ….?).

In summary, we did not show strong relationships between theoretical and empirical measurements of stability. However, we did find strong support for the role of weak interactions as a stabilizing force for both empirical and theoretical measures of stability.

So what community attributes are associated with weaker interactions? Adding more species to a community tends to reduce the average interaction strength because off-diagonal (interspecific) elements tend to be weaker then diagonal elements (intraspecific), so as you add species the number of weaker interactions tends to increase and reduces the overall mean interaction strength of the community. However, species richness is not strongly associated with stability of any type. Therefore, weak interactions appear to be every important for enhancing stability and future work should focus on what features of communities lead to fewer strong and many weak interactions as these features will be useful in predicting the stability of ecosystems to both single perturbations (e.g. theoretical stability) and repeated perturbations (e.g. empirical stability).

Allesina and Tang (2012)

They found that in some cases weak interactions are stabilizing and in others they are destabilizing. In particular, they found that predator-prey interactions are destabilizing when many weak interactions are present or realistic structure is imposed but are stabilized if strong predator-prey dynamics prevale. We sort of found support for this because we did not find any significant effect of interaction strength of top-down interactions (Figure 3). But, Allesina argues that other weak interactions are stabilizing (competitive interactions, when weakened, can be stabilizing which we find support for in Figure 3). I think he measured the strength of predator-prey interactions as the absolute value of the top-down AND bottom-up interactions. (pg 1, column 2, 2nd paragraph).

Our results suggest that, as a general rule, weak interactions (or lower mean interaction strength) tends to be associated with more stable systems, despite several studies that suggest that weak interactions must be present in particular structures or patterns to be stabilizing (Wootton and Stouffer 2016, Allesina and Tang).

References

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Ives AR, Carpenter SR. 2007. Stability and diversity of ecosystems. Science 317:  58-62.

May RM. 1972. Will a large complex community be stable? Nature 238:  413-414.

Pfister CA, et al. 2014. Detecting the unexpected: A research framework for ocean acidification. Environmental Science & Technology 48:  9982-9994.

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Extra language that might be useful:

Intro paragraph (or discussion) on details of weak interaction effect.

Additional work on the weak work has further that there seems to be something unique about the structure of weak interactions within natural food webs that is stabilizing. For example, de Ruiter et al. (1995) used empirical data on soil food webs found that food webs with many weak and few strong interactions exhibited stabilizing characteristics, but when the same data was put in matrices randomly it appeared to be less stable. Therefore, even though theoretical and real food webs had the same number of strong and weak interactions and the same mean interaction strength, the matrices based on real food webs were more stable (deRuiter et al. 1995). Natural communities appear to be more stable because of the patterning of weak interactions within real food webs natural pattern that isn’t being replicated in theoretical matrices (Allesina and Tang, Wootton and Stouffer 2016).

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