N-dimensional hypervolumes to study stability of complex ecosystems (Barros et al. 2016) - *Read in detail!*

Although our knowledge on the stabilising role of biodiversity and on how it is affected by perturbations has greatly improved, we still lack a comprehensive view on ecosystem stability that is transversal to different habitats and perturbations. Hence, we propose a framework that takes advantage of the multiplicity of components of an ecosystem and their contribution to stability. Ecosystem components can range from species or functional groups, to different functional traits, or even the cover of different habitats in a landscape mosaic. We make use of n-dimensional hypervolumes to define ecosystem states and assess how much they shift after environmental changes have occurred. We demonstrate the value of this framework with a study case on the effects of environmental change on Alpine ecosystems. Our results highlight the importance of a multidimensional approach when studying ecosystem stability and show that our framework is flexible enough to be applied to different types of ecosystem components, which can have impor- tant implications for the study of ecosystem stability and transient dynamics.

Introduction

- Ecosystem components range from species/functional groups through to habitat types and structure

- Ecosystems are changing and we need to understand there responses

- Stability is multifaceted...

- Biodiversity-Ecosystem Functioning (BEF)

    - Understanding how biodiversity maintains and promotes productivity

- Fewer studies have looked at perturbation-biodiversity

    - Functional diversity can change across environment /disturbance gradients

    - Relationship of ecosystem function and biodiversity

- **Ecosystem stability is no easily summarised by a single metric**

    - Using multiple components should provide better results...

    - Components often have temporal oscillations..

        * In 2D these converge on a point...

        * in 3D (and n-dimensions) it becomes more complex $\Rightarrow$ N-Dimensional Hypervolumes!

- N-Dimensional Hypervolumes

    - These oscillations become a trajectory in n-dimensional space

    - A cloud of points...

    - If conditions are disturbed than the trajectory will change $\Rightarrow$ new hypervolume

    - They can be used to test departure from a stable state

    - Also convergence on new stable state or return to old (i.e. different measure of stability can be tested)

- Choosing components (Choice of components depends on the kind of study)

    - Stability of biodiversity at community scale

        * Time series of species abundances

        * Community weighted means (CWMs) and varience (CWVs) of functional traits

    - Larger Scale

        * Taxonomic functional traits

        ∗ Phylogenetic diversity metrics

    – Ecosystem Mosaics

        ∗ Proportions of habitat patches

The Framework!

- Step 1 - Choice of Components

    – Their example contructs n-dimensional hypervolumes in time-series of n-ecosystem traits at equilibrium.

    – My study will also look at space

- Step 2 - Data Treatment and Hypervolume calculation

    – Number of dimensions must be fixed to maintain comparability

    – Need comparable units (centred and scaled)

    – Not correlated!! (Look at PCAs, PCoAs etc to get around this?)

    – Try not to exceed 5-8 variables to avoid disjointed and holey hypervolumes

    – Hypervolume calculations follow a multi-dimensional kernal density estimator procedure. See Blonder et al. (2014)

- Step 3 - Comparing hypervolumes and analysis of community changes

    – Sufficiently large changes in environmental conditions should produce shifts in community structure. $\Rightarrow$ These should be seen in the constructed hypervolumes...

    – Three possible measures

        ∗ Overall similarity $\Rightarrow$ Overlap

        ∗ Changes in mean values of components $\Rightarrow$ Distance between centeroids

        ∗ Changes in Variance $\Rightarrow$ Changes in hypervolume size

- Step 4 - Complementary metrics for more detailed analysis

    – Hypervolume comparisons don't really tell you what changed so there is need for further analysis looking at the specific components used...

    ### Working Example

    – Based on simulated data (Don't really understand this!)

    – Habitats under climate change (CC) and land use change (LUC)

    – calculated hypervolume every 15 years of simulation

    – used actual abundances instead of relative - not interested in dominance/structural changes.

        ∗ This also meant the differences between hypervolumes were bigger (easier to see)

    – hypervolume overlap was significantly affected by CC & LUC

    – hypervolumes on traits and on Plant Functional Diversity (PFDs)

    – Trait hypervolumes tended to be smaller

Discussion

- Environmental changes impact biodiversity at many levels

- Need to measure contribution of different taxanomic, functional or landscape entities

- Analysing Magnitude of Change

    – Size $\Rightarrow$ Variance

- – Mean ⇒ Position of centeroid
- – Similarity ⇒ Overlap
- **N-dimensional hypervolumes do not summarise components as one metric but describe them as an n-dimensional cloud!**
- Assessing type of change
  - – can be informative about what facets of an ecosystem were most affected by ecosystem perturbation
  - – complimentary measures are important though!
- Following changes in time
  - – Since hypervolumes define different ecosystem structures they can be used to test all types of ecosystem stability
    - * Persistence ⇒ Time before change once perturbation starts
    - * Resilience ⇒ Return to state after perturbation
    - * Resistance R ⇒ Amount of change after perturbation
    - * Variabiltiy ⇒ Variation before vs after perturbation
  - – Implications for ecosystem services
  - – Small overlaps may still indicate changes in ecosystem state. I think this study saw overlaps = 0 this is not as likely on real data!.
- Advantages of hypervolumes
  - – Ecosystems are made up of a multiplicity of components
  - – Allows for detec tion of finer changes
  - – negates problems with habitat mosaics and ecotone interactions
  - – Can be used to predict future responses and resilience to extreme events/perturbations

Predicting ecosystem stability from community composition and biodiversity (de Mazancourt et al. 2013) - *Intro and Discussion*

Second, is it really useful to lump together everyone born between 1984 and 1993 into one group? I was born in 1989 (yes, yes, I am peak millennial, I came out of the womb holding an avocado trying to get a discount on a train ticket). I tried to talk to a colleague born in 1993 recently about Snapchat, and before she finished explaining how the new update had ruined the âĂIJstoryâĂİ function, my bones had turned to dust like the Nazi in Indiana Jones and the Last Crusade. I donâĂŹt necessarily feel a sense of âĂIJmillennial solidarityâĂİ, except when millennials are being attacked by tabloids for being too sensitive (ie showing a level of compassion for people who donâĂŹt look like them).

As biodiversity is declining at an unprecedented rate, an important current scientific challenge is to understand and predict the consequences of biodiversity loss. Here, we develop a theory that predicts the temporal variability of community biomass from the properties of individual component species in monoculture. Our theory shows that biodiversity stabilises ecosystems through three main mechanisms: (1) asynchrony in speciesâĂŹ responses to environmental fluctuations, (2) reduced demographic stochasticity due to overyielding in species mixtures and (3) reduced observation error (including spatial and sampling variability). Parameterised with empirical data from four long-term grassland biodiversity experiments, our prediction explained 22âĂŞ75% of the observed variability, and captured much of the effect of species richness. Richness stabilised communities mainly by increasing community biomass and reducing the

strength of demographic stochasticity. Our approach calls for a re-evaluation of the mechanisms explaining the effects of biodiversity on ecosystem stability.

Introduction

- Ecosystems undergo temporal stressors which impact their stability

- It seems intuitive that biodiversity increases stability with different species compensating for each other when lost. But there has been lots of debate about the relationship of diversity and stability since the 1970's

  - This is mainly because while diversity increases stability of overall biomass it decreases stability of individual species abundances

- A number of theories have been developed to explain diversities stabilising effect on aggregate ecosystem properties.

  1. Statistical approach based on phenomenological relationships

  2. A stochastic approach describing population dynamics but not specifically species interactions

  3. A general population dynamical approach

  4. Specific models of interspecific competition

- these all kinda describe whats going on but not a mechanism! $\Rightarrow$ This is still contentious

- These are not able to predict ecosystem stability from the properties of component species

- This study comes up with a new theory to do just that...

Theoretical Model

- Discrete-time version of Lotka-Volterra model incorporating environmental and demographic stochasticity

- Description of model (not really important for me)

- Lots of maths and results...

Discussion

- Their model explained 22-75% variance in the aboveground community biomass in 4 long-term experiments

- Summed species covariances are unlikely to provide a mechanistic explanation for community stability

- Asynchrony of species environmental responses is the basic mechanism of the 'insurance hypothesis'

- Their model also shows these. Asynchronous species responses $\Rightarrow$ Greater community stability

- Reduced demographic stochasticity $\Rightarrow$ increased community biomass

  - Species richness increases community biomass, though complimentary species or selection of more productive species $\Rightarrow$ known as overyielding

  - Their study when tested on empirical data showed this was happening...

- Effect of diversity on ecosystem stability through reduced observation errors

  - If species biomasses are measured individually, the higher the diversity the more the error will even out across the whole community biomass...

  - Common species weigh more on the variability than rare species.

  - Maybe this is just a methodological problem?

  - all this stuff is based on experiments in monocultures...

Network spandrels reflect ecological assembly (Maynard et al. 2018) - *Intro and Discussion*

Ecological networks that exhibit stable dynamics should theoretically persist longer than those that fluctuate wildly. Thus, network structures which are over-represented in natural systems are often hypothesised to be either a cause or consequence of ecological stability. Rarely considered, however, is that these network structures can also be by-products of the processes that determine how new species attempt to join the community. Using a simulation approach in tandem with key results from random matrix theory, we illustrate how historical assembly mechanisms alter the structure of ecological networks. We demonstrate that different community assembly scenarios can lead to the emergence of structures that are often interpreted as evidence of 'selection for stability'. However, by controlling for the underlying selection pressures, we show that these assembly artefacts or spandrels are completely unrelated to stability or selection, and are instead by-products of how new species are introduced into the system. We propose that these network-assembly spandrels are critically overlooked aspects of network theory and stability analysis, and we illustrate how a failure to adequately account for historical assembly can lead to incorrect inference about the causes and consequences of ecological stability.

Introduction

- Ecological networks tend to be strikingly non-random

    - It is hypothesised that this occurs because selection 'prunes' unstable configurations, resulting in stable patterns

    - for example wildly fluctuating networks would not be expected to persist through time die to stochastic extinctions

- but it could be that these structures are just 'artefacts of assembly' with no inherent connection to stability

- Assembly of biological systems is dictated by two forces

    1. How, when and why variation is introduced into a system.

    2. Selective mechanisms which determine what features persist at what frequencies.

- While selection is a dominant force we must not forget assembly constraints!

    - It is possible for features which appear to have current utility to have been occurred as a by-product of the way the system was formed and have no adaptive origin.

    - dubbed the 'network spandrel' - a nod to cathedral archways which appear to have been selected but are in fact a by-product of construction.

- A 'network spandrel' refers to any network property which emerges as a by-product of how the species joins the community.

- Disentangling whether an empirical pattern has emerged due to assembly constraints or selection is very difficult. Requires experimental, observational and theoretical evidence.

Assembling Ecological Communities

- Again they use the Lokta-Volterra model.

- They set the parameters to reach a steady state

- After each equilibrium is reached they add a new species to the simulated community, then run to equilibrium again. This new species may or may not establish, and may or may not lead to one or more extinctions of other species.

- some stuff about methods, summarised well in fig1.

- lots of results which are interesting but difficult to summarise

Discussion

- Biological systems are not only the result of selection! But also how variation is introduced into systems!

- This study shows that different assembly processes leave different fingerprints on the resulting network giving the appearance of different selective pressures.

- Spandrels reflect the historic processes which shap ed a system (while not specifically saying anything about selection)

- not accounting for spandrels leads to incorrect inferences about selection and stability.

New Approaches for delineating n-dimensional hypervolumes (Blonder et al. 2018)

1. Hutchinson's n-dimensional hypervolume concept underlies many applications in contemporary ecology and evolutionary biology. Estimating hypervolumes from sampled data has been an ongoing challenge due to conceptual and computational issues.

2. We present new algorithms for delineating the boundaries and probability density within n-dimensional hypervolumes. The methods produce smooth boundaries that can fit data either more loosely (Gaussian kernel density estimation) or more tightly (one-classification via support vector machine). Further, the algorithms can accept abundance-weighted data, and the resulting hypervolumes can be given a probabilistic interpretation and projected into geographic space.

3. We demonstrate the properties of these methods on a large dataset that character- ises the functional traits and geographic distribution of thousands of plants. The methods are available in version $\geq$2.0.7 of the HYPERVOLUME R package.

4. These new algorithms provide: (i) a more robust approach for delineating the shape and density of n-dimensional hypervolumes; (ii) more efficient performance on large and high-dimensional datasets; and (iii) improved measures of functional diversity and environmental niche breadth.

<u>Introduction</u>

- Over the last decade there has been a number of studies using n-dimensional hypervolumes as a central concept

- Assuming a system can be characterised by a set of independent axes, these axes would constitute a n-dimensional euclidean space.

- Choosing how to delineate this n-dimensional space is a bit controversial. There has historically been differences when niche-data is used vs trait-data

- All depends on the goals of the analysis

- Hypervolume R package uses a Monte Carlo approach. It can describe complex shapes, measure their volume and perform set operations (to find distance, intersections etc).

- This paper develops the hypervolume concept and better algorithms to delineate them.

<u>New Hypervolume construction methods</u>

- Two methods
  - Gaussian: this kernal decays towards zero in all directions, if you believe the data is an unbiased sample from a probability distribution then use this.
  - Support-vector-machine: provides a smooth fit around the data. Use this if you think the extremes of the data represent the true bounds.

- When calculating hypervolumes the max number of dimensions n should be no more than $\log m$ where m is the number of data points.

- They use a hyperelliptical uniform sampling algorithm

<u>Other New Functionality</u>

- hypervolume_general_model, this effectively maps an n-dimensional hypervolume to on-dimensional Euclidean space.

- Ability to weight data

- Ability to create geographic maps for species distribution modelling

<u>Demonstration Analysis</u>

- Functional trait analysis: Three trait values

- Niche Analysis: Three climatic variables

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