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Linking the ball-and-cup analogy and ordination trajectories to describe ecosystem stability, resistance, and resilience

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Citation: Lamothe, K. A., K. M. Somers, and D. A. Jackson. 2019. Linking the ball-and-cup analogy and ordination trajectories to describe ecosystem stability, resistance, and resilience. Ecosphere 10(3):e02629. 10.1002/ecs2.2629

Abstract. The ball-and-cup diagram for conceptualizing ecosystem stability, resistance, and resilience is often presented as a ball rolling around within and between two or more cups. This analogy has a long history in ecology and has been used to illustrate ecosystem changes over time where the magnitude of changes required to push the ball from one cup to another represents a regime shift to an alternative state. Another approach for visualizing ecosystem stability, resistance, and resilience involves ordinations of repeated measures of community data or environmental variables and tracking trajectories over time in ordination space. Interestingly, the two approaches have not been linked in a meaningful way. Here, we provide a conceptual link between trajectories of ecological change in ordination space to the ball-and-cup analogy and show how distance-based measures calculated from ordination scores can be used to quantitatively classify and evaluate the relative stability and resilience of ecological systems.

Key words: ball-and-cup; ecosystem stability; multivariate; ordination; resilience; resistance.

Received 16 January 2019; accepted 1 February 2019. Corresponding Editor: Dawn M. Browning.

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Introduction

The ball-and-cup diagram is commonly used by scientists and engineers to illustrate complex topics across a variety of scientific disciplines (e.g., ecology, evolution, engineering; Fig. 1). Among the first to use the ball-and-cup analogy was Sewall Wright in a presentation at the sixth International Congress of Genetics in 1932 on shifting balance theory (Wright 1931, Ruse 1996, Kaplan 2008). In his presentation, Wright used the ball-and-cup metaphor to describe an evolutionary fitness landscape, where the cup-shaped landscape is comprised of adaptive peaks that represent high-fitness collections of genotypes and valleys representing genotypes of relatively low fitness (Kaplan 2008). A ball mapped onto the fitness landscape and its trajectory across the landscape over time provided a measure of change in adaptive capacity of a population.

Willems (1970) was among the first to interpret the ball-and-cup diagram in an ecological context. In his perspective, the ball represented the current ecosystem state (see Table 1 for definitions of italicized words) and the cup represented a basin of attraction (Peterson et al. 1998, Walker et al. 2004) based on the normal range of variation for that ecosystem. One-or-more neighboring cups represent alternative stable states in the stability landscape (Walker et al. 2004, Scheffer 2009) for that ecosystem. Willems (1970) used this analogy to describe ecosystem stability, and

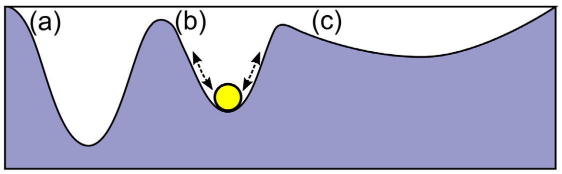

Fig. 1. Ball-and-cup heuristic. The yellow ball represents the current ecosystem state, and the cup-shaped landscape represents all possible ecosystem states within some normal range of variation for that ecosystem. Two alternative states (a, c) to the current basin of attraction (b) are depicted where (a) has steeper walls and a deeper cup than (c).

this diagram has since been used to describe ecosystem responses to disturbance (Hurd and Wolf 1974, Godron and Forman 1983, Hamilton and Haeussler 2008) including resistance (Hirst et al. 2003, Walker et al. 2004), resilience (Holling 1973, Bagchi et al. 2017), stability (Forman and Godron 1986, DeAngelis and Waterhouse 1987), and regime shifts (Scheffer and Carpenter 2003, Osland et al. 2016).

Around the same time that the ball-and-cup analogy was being introduced in ecology, ecologists were beginning to use multivariate approaches to quantify community and ecosystem responses to disturbance (Allen and Skagen 1973, Holmes et al. 1979). For example, ordinations of species community composition data enabled ecologists to illustrate how communities were changing over time (i.e., temporal trajectories of communities in ordination space), whether impacted by disturbance or not (Lake et al. 2007, Smith 2012, Matthews et al. 2013). Like the ball-and-cup analogy, ordinations are routinely used to illustrate ecological responses to disturbance (Boulton et al. 1992) and provide a canvas for explaining concepts such as resistance and resilience (Seidl et al. 2016, Lamothe et al. 2017), stability (Bloom 1980, Hughes 1990), and regime shifts (Warwick et al. 2002, Daufresne et al. 2007).

Despite a parallel history in ecology, the links between the ball-and-cup diagram and ordinations are not well established. As such, our objective was to identify similarities between the two paradigms and to demonstrate how to quantitatively distinguish different community or environmental trajectories based on movement in ordination space as they relate to the ball-and-cup analogy. Below, we first provide an overview of both visual approaches. Following this introduction, we demonstrate a conceptual framework relating the ball-and-cup analogy (Fig. 1) to ordination trajectories representing ecosystem trends through time (Fig. 2). Finally, we demonstrate

Table 1. Glossary of terms used to describe, or are described by, the ball-and-cup diagram.

Term	Definition
Alternative stable state	Alternative combinations of ecological systems that may persist at a given space and time†
Basin of attraction	A region in state space in which an ecosystem tends to remain‡
Ecosystem state	An all-encompassing term for the various structures and processes that characterize the conditions of an ecosystem at a given space and time
Ordination space	The spatial arrangement of data points in a plot of the first several ordination axes
Press disturbance	Environmental disturbances that may arise sharply and then reach a constant level that is maintained§
Pulse disturbance	Short-term and sharply delineated environmental disturbances§
Regime shift	A relatively sudden, fundamental change in the structures and processes that characterize the conditions of an ecosystem at a given space and time¶
Resilience	The capacity of an ecosystem to absorb disturbance and reorganize while undergoing change so as to retain essentially the same functions, structures, identity, and feedbacks‡
Resistance	The ease or difficulty of changing the system‡
Stability	The ability of a system to return to an equilibrium state after a temporary disturbance#
Stability landscape	Various basins of attraction and the boundaries that separate them in which an ecosystem can reside‡
Ecological threshold	The break point between two basins of attraction‖

† Beisner et al. (2003).
‡ Walker et al. (2004).
§ Lake (2000).
¶ Scheffer and Carpenter (2003).
# Holling (1973).
‖ Walker and Meyers (2004).

how measures of distance in ordination space can be used to characterize community or environmental trajectories over time, providing a quantitative tool to compare ecosystem changes, and then we link this quantitative approach back to the ball-and-cup analogy. Overall, we demonstrate how relating ordinations to the ball-and-cup diagram allows ecologists to develop conceptual hypotheses for complex, ecosystem dynamics that have a quantitative visual underpinning and can be directly measured.

Ball-and-Cup Heuristic for Understanding Ecological Processes

The ball-and-cup analogy provides a relatively simple heuristic tool that can be used to illustrate complex ecological concepts in a tangible way (Fig. 1). In the analogy, the position of the ball represents the current ecosystem state (i.e., state variable) which is constrained by the system parameters which include the characteristics of all of the biophysical structures that occur at a given space and time (i.e., the cup; Fig. 1b). Neighboring cups represent alternative states that the ecosystem could occupy where the shape of each cup results from interactions between different environmental variables or processes associated with that cup (Fig. 1a, c; Walker et al. 2004, Briske et al. 2017). The steepness and height of the walls of each cup represent barriers to the movement of the ball to alternative states. A deep cup with steep walls indicates greater *resistance* to movements of the ball (Fig. 1a), whereas a shallow cup with gently sloped walls indicates less resistance to change (also known as engineering resilience: Fig. 1c; Briske et al. 2017). The width of the basin of the cup is important for ecological resistance (Gunderson 2000, Briske et al. 2017), where wider cups make it less likely for the ball to jump into a neighboring cup (i.e., a regime shift; Scheffer and Carpenter 2003). Regime shifts are typically characterized by abrupt, or saltatory, changes in state variables (deYoung et al. 2008), where novel internal feedbacks can maintain potentially undesirable long-term alternative states.

The stability landscape can be dynamic and may affect the behavior of the ball. Press disturbances (e.g., nutrient loading in aquatic ecosystems) can cause long-term changes to the shape of the stability landscape whereby the cups become shallower, with gently sloped walls (Rydzak et al. 2006). Natural processes such as seasonal changes in hydrologic flow regimes, plant community succession, and cyclic predator–prey interactions can also alter the shape of the cup (Walker et al. 2004). Similarly, pulse disturbances (e.g., floods, wildfire) can cause

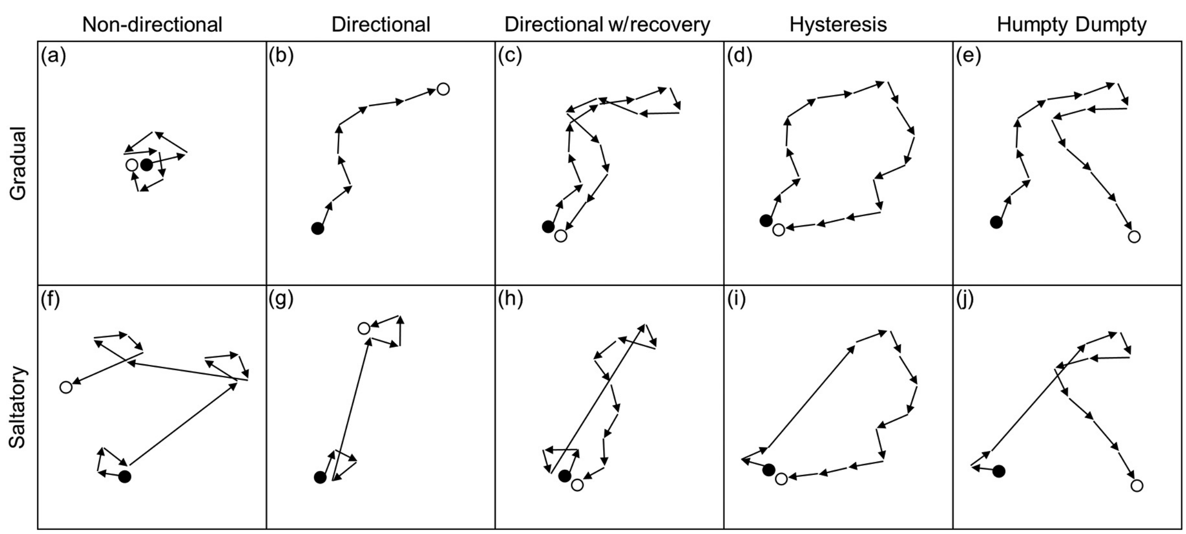

Fig. 2. Trajectories of ecosystems over time in an ordination. These example ecosystem trajectories can result from ordinations of repeated measures of community composition or environmental variables. Filled circle is initial observation; open circle is final observation; and arrowheads are positions of intervening observations.

short-term changes to the shape of the stability landscape as well as the position of the ball. Changes to the cup-shaped landscape not only reflect changes in ecosystem conditions but can also increase the chance of a regime shift (i.e., change ecosystem resilience), and may prevent the possibility of recovery by, for example, removing a keystone or foundation species. A well-developed quantitative theory exists to mathematically describe the shape and behavior of the stability landscape and its influence on movement of the ecosystem state between coexisting alternative stable states (Freidlin and Wentzell 2012, Zhou et al. 2012, Nolting and Abbott 2016, Zhou and Li 2016).

Ecosystem Trajectories Over Time

Ordination techniques (ter Braak 1994, Legendre and Legendre 1998) have commonly been used to illustrate how ecosystems change over space and time. The term "ordination" simply means to arrange observations in a particular order, and here, ordinations are used to reduce the dimensionality of the data while maintaining and explaining as much of the variation as possible. To illustrate this concept (Fig. 2), we use principal component analysis to ordinate repeated observations of community composition (e.g., species abundance) as it represents the simplest and best-known ordination approach (ter Braak 1994, Legendre and Legendre 1998). Note that depending on the question, our approach can be similarly applied to environmental characteristics such as water chemistry parameters as community composition and environmental conditions are both important components of ecosystems and changes within them can lead to changes in ecosystem trajectories (i.e., movement in ordination space) over time.

Each of the time-trend scenarios presented in Fig. 2 can be observed in an ordination plot (Lamothe et al. 2017). In each panel, a dot or arrowhead represents the ecosystem state (here, community composition) at a given space and time (i.e., an observation). The distance between successive observations represents the magnitude of the change in community composition for that system over time. The ecosystem trajectories can vary in direction and magnitude. For example, ecosystems can be undergoing gradual, non-directional, or idiosyncratic change over time, representing a stable community demonstrating natural variability in composition (Matthews et al. 2013, Matthews and Marsh-Matthews 2016; Fig. 2a). In this scenario, sequential observations are close together and the magnitude of change over time (perhaps stochastic) is relatively small with a lack of directionality (Fig. 2a).

Alternatively, ecosystems can demonstrate saltatory change, characterized by leaps rather than gradual transitions (Matthews et al. 2013). Saltatory, non-directional movement (Fig. 2f) can represent the situation where multiple large pulse disturbance events occur (e.g., natural disaster, species invasion) causing several dramatic shifts in species composition. Directional changes, or movement away from previous location in ordination space, can also be observed as either gradual (Fig. 2b) or saltatory (Fig. 2g). Although often seen as a relatively sudden event (Fig. 2g), gradual, directional changes (Fig. 2b) can result in regime shifts (Walker and Meyers 2004, Hughes et al. 2013), for example, the shift from a grass-dominated to shrub-dominated landscape (Folke et al. 2004, Walker and Meyers 2004). Saltatory, directional patterns in ecosystem trajectories may occur due to the sudden appearance of species such as species invasions (Lamothe et al. 2017) or due to the loss of species from disturbances like drought (Bogan and Lyle 2011).

Recovery is depicted as movement of the community composition back toward a historical state. When recovery from disturbance is possible, it is often gradual and relatively slow (Hughes et al. 2013, Palmer et al. 2013), where rates of return vary based on the local ecosystem and may not return to a historical condition altogether (i.e., Humpty Dumpty model; Lake et al. 2007; Fig. 2e). As such, we always depict recovery as gradual transitions back to the historical state whether the recovery is occurring after initial gradual (Fig. 2c) or saltatory (Fig. 2h) movements away from the historical state. Hysteresis occurs when multiple ecosystem states co-exist despite identical environmental conditions due to the legacy of historical conditions (Beisner et al. 2003; Fig. 2d, i). A common example of hysteresis occurs in shallow lake ecosystems, where a clear-water, macrophyte-dominated state or a turbid, phytoplankton-dominated state

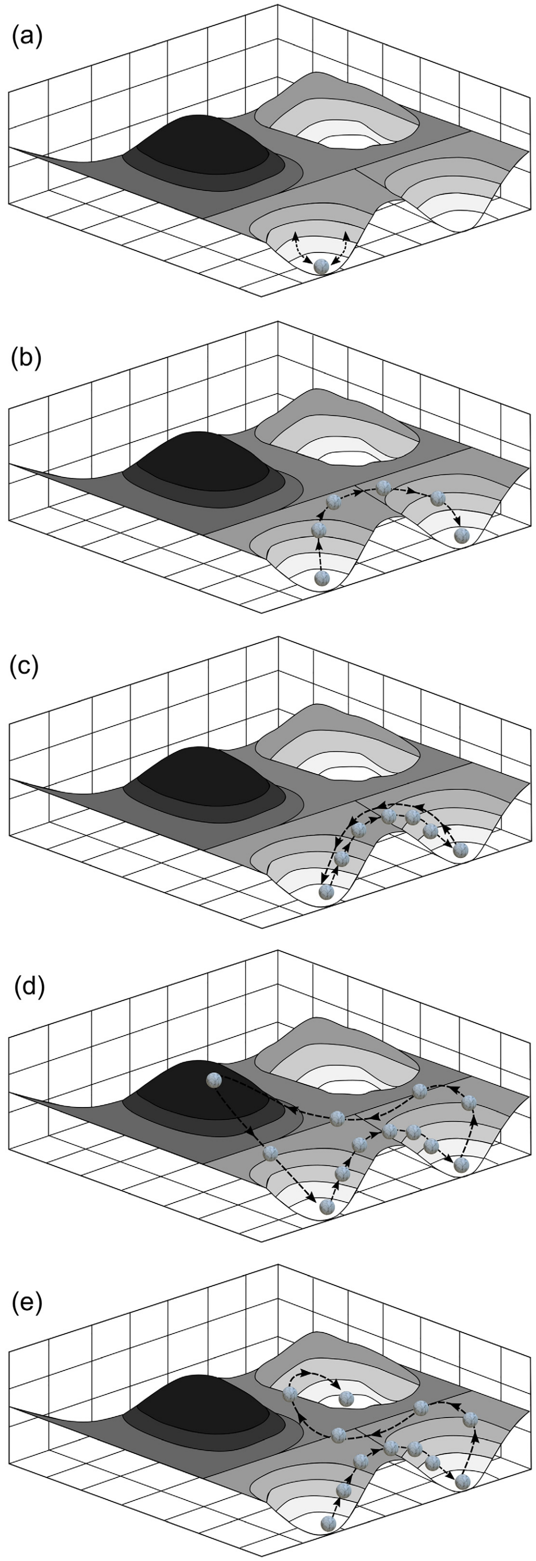

Fig. 3. Linking the ball-and-cup and ecosystem

can be observed at moderate levels of nutrient input, depending on lake history (Ibelings et al. 2007). As such, the return trajectory following a pulse or press perturbation can follow a novel path (Fig. 2d); however, it is also possible that the recovery trajectory is simply a reversal of the impact trajectory (Wernberg et al. 2016; Fig. 2c, h).

Finally, in the English nursery rhyme, Humpty Dumpty, it states "Humpty Dumpty sat on a wall, Humpty Dumpty had a great fall, and all the king's horses and all the king's men, couldn't put Humpty Dumpty together again." In an environmental context, the impact of disturbance on ecological systems may be so severe that novel feedbacks develop and recovery to the historical state does not occur (Fig. 2e, j). For example, long-term patterns of rising ocean temperature (i.e., press disturbance) and a recent heat wave (i.e., pulse disturbance) led to the transformation of a temperate Australian kelp forest into a seemingly subtropical state (Wernberg et al. 2016); increased water temperature promoted a 400% increase in biomass of scraping and grazing fishes more typical of coral reef systems, and these fish decimated standing kelp stocks and suppressed recovery of the kelp forest.

Conceptual Links Between the Ball-and-Cup Analogy and Ecosystem Trajectories

Both the ball-and-cup analogy and ecosystem trajectories in ordination space are useful frameworks for visualizing change (or lack thereof) in ecosystem structure and function and can be used to demonstrate similar concepts. In Fig. 3, we provide examples of how the ball-and-cup analogy can be aligned with ecosystem trajectories described in Fig. 2. For example, communities demonstrating gradual, non-directional trajectories in ordination space (Fig. 2a) can be represented as a ball located within a deep cup with steep walls (Fig. 3a). In this description, the cup-landscape contains all the possible combinations

(Fig. 3. *Continued*)
trajectory analogies. The balls represent observations of community composition, and the arrows indicate the directionality of movement across the cup-shaped landscape.

of, for example, species abundance data where peaks represent an unstable community structure and valleys represent stable composition. Changes in the composition of the observed community over time will result in movement of observations in ordination space. In the first example where the system is demonstrating gradual, non-directional trajectories, the ball situated within the landscape will show modest, stochastic changes over time, potentially indicating stability and resistance to the impacts of disturbance.

Systems demonstrating directional scenarios (Fig. 2b, g) could indicate an ecosystem undergoing a regime shift (Fig. 3b). Here, disturbance forces the ball into a neighboring cup characterized by potentially novel feedbacks that support a different suite of ecosystem structures and processes. Ecosystem recovery can be represented several ways in the ball-and-cup analogy (Fig. 3). In Fig. 3c, the ecosystem state demonstrates gradual directional change into an alternative cup, but subsequently moves back to the original cup using the same historical path (Fig. 2c). Here, the landscape remains static (or stable) with ecosystem conditions reflecting historical conditions during the process of recovery (Fig. 3c). Hysteresis (Fig. 2d) is illustrated in Fig. 3d where the ecosystem moves to a neighboring cup and its recovery path differs from its original path (Beisner et al. 2003). Finally, a community or ecosystem can change from an initial state to an alternative state, and just when one might expect recovery, the ecosystem shifts into another different alternative state due to novel feedbacks (i.e., Humpty Dumpty; Figs. 2e, j, 3e). Although not depicted in the figure, perturbations to the ball and the landscape can also occur simultaneously, creating a complex, dynamic situation that is difficult to predict.

Quantitative Framework for Classifying Ball-and-Cup Trajectory Scenarios

Ecosystem trajectories can be classified quantitatively using a distance-based approach with a suite of statistical metrics (Laliberté and Legendre 2010, Timpane-Padgham et al. 2017) and these results can be linked to the ball-and-cup analogy. In Fig. 4, we illustrate the approach using a fictional example where the data consist of 10 repeated samples of species compositions collected at each of six different sites (i.e., communities). Distances were calculated between repeated observations for a given site within ordination space (Fig. 4a) to represent changes in species composition over time.

To distinguish the different patterns of change over time as gradual or saltatory (Fig. 2 rows), distances between sequential observations in an ordination (Fig. 4a) can be calculated and compared within a given community trajectory (Fig. 4b). Each distance represents the change in ecosystem composition over a single time-step. When a distance is exceptionally large compared to other distances in that time series (i.e., the distance is an outlier), we consider this condition to represent a saltatory change (Fig. 4b; Community 2). Although there are many outlier detection approaches that vary in their sensitivity to extreme values (Dixon 1950), these types of methods can be used to identify saltatory changes over time. In Fig. 4b, we identify a saltatory change (yellow point for Community 2) using 1.5× the inter-quartile range.

To distinguish between the different directional scenarios presented in Fig. 2 (columns), the distances of each observation to a baseline were calculated for each community and plotted over time. Here, we define the baseline as the first observation in the temporal sequence of each community (Fig. 4c); however, other baselines can be used (Anderson and Thompson 2004, Milner et al. 2016). We can extend this distance-based approach by comparing the distances between all observations in the time series for a given sampling site or community and plotting these distances as a function of their time lag (Collins et al. 2000, Lamothe et al. 2018; Fig. 4d–f). Here, distances are calculated between all observations for an individual site in the ordination. In our example, each site was sampled 10 times, so there would be a total of 45 distances, where 9 distances are calculated between sequential observations (e.g., observations 1 and 2, observations 2 and 3), 8 distances between observations that span 2 time-steps, 7 distances between observations that span 3 time-steps, and so on. We can then plot those individual distances as a function of their respective time lag (Fig. 4d–f), where a time lag of 1 represents sequential observations, a time lag of 2 represents the differences between observations separated by 2 time-steps,

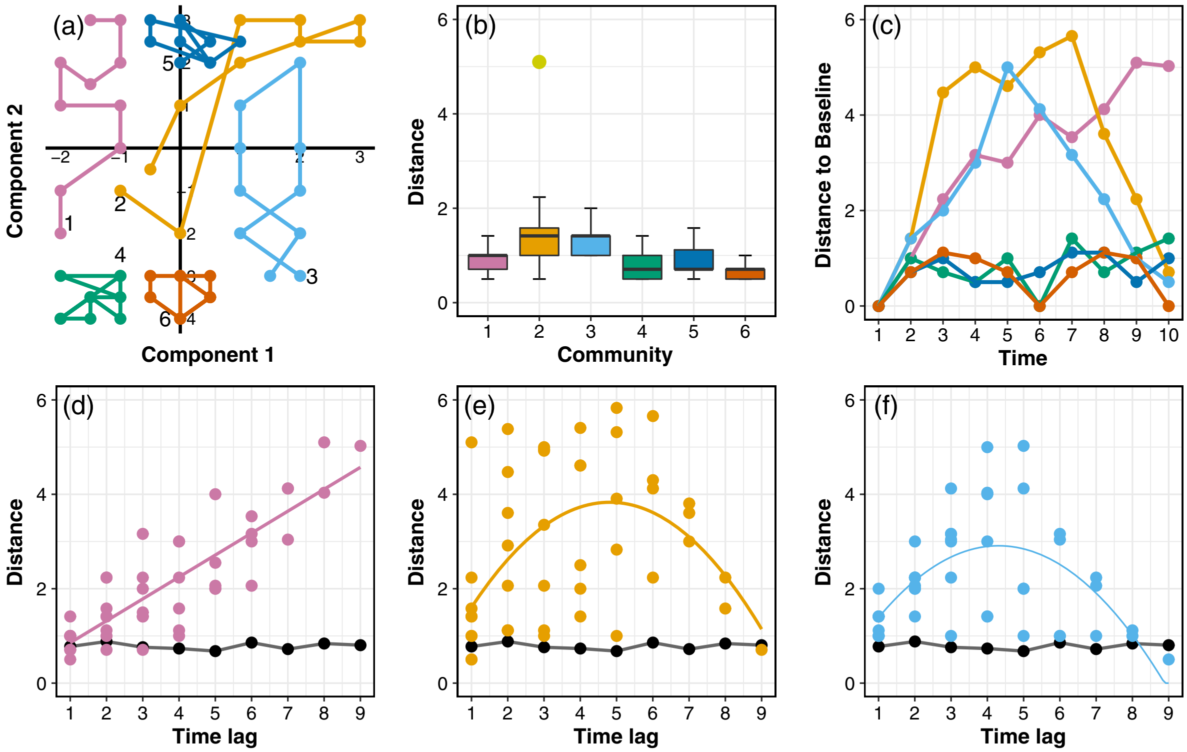

Fig. 4. Distance-based approach for classifying ecosystem trajectories. (a) Fictional example of an ordination of six communities (colors and numbered) observed repeatedly over 10 time-steps. Lines connect sequential observations. (b) Box plot of distances between sequential observations for each of the six communities. Community 2 demonstrates an outlier distance, indicating saltatory change. (c) Distances to the first observation in the temporal sequence plotted over time for each community. (d) Distances between observations vs. time lag for Community 1, (e) Community 2, and (f) Community 3. The black points represent the average distance (+2 standard deviation gray ribbon, or normal range) for Communities 4, 5, and 6 for each time-step.

and so on. Linear models, generalized additive models, or smoothing algorithms (e.g., locally weighted scatterplot smoothing; Cleveland 1979), can then be used to identify the shape of the relationship between distances and time lag for each community. However, the statistical significance of these models should be taken with caution given the lack of independence among distances (Collins et al. 2000) and permutation-based models may provide an alternative for assessing significance.

The distance-based measures for classifying trajectories also permit comparisons between communities. For example, in Fig. 4d–f, we compare individual communities exhibiting directional trajectories to the average of the three communities undergoing gradual, non-directional change over time (i.e., potentially stable reference communities). For these comparisons, we calculate the average distance between observations per time lag for the three communities (i.e., black points Fig. 4d–f) and define boundaries around these measures with 2 standard deviation confidence intervals (i.e., the normal range of variation; Kilgour et al. 1998). By overlaying the trajectories of various communities, we can evaluate the relative magnitude of change in community structure over time.

Our expectations for community trajectories when plotting distances to a baseline condition over time are similar to plotting distances between observations against their respective time lag (Fig. 5). In unperturbed ecosystems demonstrating natural variability in composition and structure (Fig. 2a), we would expect that the distances to the baseline condition would remain

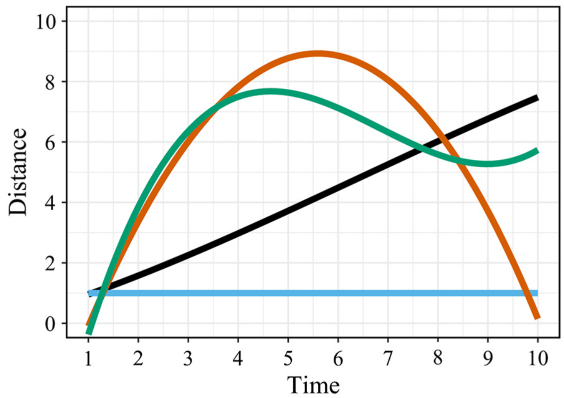

Fig. 5. Example expectations of distances in ordination space over time lags for ecosystems or communities exhibiting non-directional change (blue), directional change (black), directional change with recovery (or hysteresis; orange), and following the Humpty Dumpty model (green).

relatively constant in magnitude over time. That is, when plotted over time, a regression of distances of the observations to their baseline condition should have a slope not significantly different from zero (Fig. 5 blue line). Alternatively, if ecosystems are changing over time (e.g., Fig. 2b or 4a, Community 1), we would expect a positive relationship between distances and time. The slope of this relationship represents a measure of the relative magnitude of change over time (Fig. 5, black line).

For ecosystems recovering from disturbance, patterns of distances plotted over time will depend on when the disturbance occurs relative to the start of the record. For example, if monitoring data exist before, during, and after the disturbance occurred, we would expect that distances over time would be initially small, diverge mid-series, and subsequently return to small distances following a negative quadratic function (Fig. 5, orange line). This scenario is what we might expect if an ecosystem is recovering by following the historical pathway (Fig. 2c) or following patterns of hysteresis (Fig. 2d). In the case of an ecosystem exhibiting the Humpty Dumpty pattern, the trajectory of distances would initially deviate from the baseline, peak mid-series, but would remain distant from the baseline (Fig. 5, green line). However, if predisturbance data are not available, the distances to the baseline condition over time would indicate a system that is undergoing directional change (e.g., Fig. 5, black line).

Conclusions

The ball-and-cup analogy is a useful heuristic to conceptualize how ecosystems change over space and time, particularly in situations where anthropogenic disturbance threatens ecosystem conditions. However, researchers have not linked the patterns of ecological systems in ordination space to the ball-and-cup framework. Distance-based measures provide a straight-forward, statistical approach to classify and visually compare the trajectories of communities or ecosystems over time (Milner et al. 2016, Lamothe et al. 2017). Communities that travel relatively short distances in ordination space over time are considered stable (Fig. 2a) and can be represented conceptually in the ball-and-cup heuristic with the ball remaining within a single cup. Alternatively, communities that lack resistance to change demonstrate movement in ordination space away from a baseline condition (Fig. 2b) and can be represented conceptually with the ball rolling greater distances within the cup and potentially crossing a threshold into a neighboring cup (Fig. 3b). Finally, communities that show resilience by recovering to essentially the original community position will demonstrate unimodal trajectories in distances traveled over time in ordination space, if observations were made before and after a disturbance occurs (Fig. 2d). Conceptually, this scenario would be represented as the ball rolling into a neighboring cup, which is consistent with a large change in community composition away from its historical position on the stability landscape, followed by movement back toward its historical position (Fig. 3d). Overall, linking distance-based measures in ordination space to the conceptual ball-and-cup analogy provides a useful approach with well-known tools for understanding changes in ecosystems over time, allowing ecologists the opportunity to develop ecological hypotheses for complex systems with a quantitative foundation.

Acknowledgments

We thank W. Bill Keller, Marie-Josée Fortin, Brian J. Shuter, Nicholas E. Mandrak, and Rolf D. Vinebrooke for early discussions on the content of this manuscript. We also thank two anonymous reviewers for their valuable comments. All authors acknowledge funding by the Natural Sciences and Engineering Research Council (NSERC) of Canada through the NSERC Canadian Network for Aquatic Ecosystem Services (CNAES). DAJ acknowledges funding by an NSERC Discovery Grant.

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