A novel integration of Dynamic Bayesian Networks and Non-Additive modelling to study ecological resilience

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1 EXTENDED ABSTRACT

Ecological resilience is defined by an ecosystem's ability to resist disturbance, while undergoing change to retain the same structure, function, and feedbacks [Folke et al., 2004, Mittelbach et al., 1995, Neubert and Caswell, 1997, Tilman and Downing, 1994]. Understanding the dynamics that regulate ecological resilience is becoming increasingly important in today's world, as ecosystems are facing multiple pressures on global, regional, and local scales [Scheffer et al., 2001]. If pressures exceed a threshold, this may trigger a regime shift where a system undergoes a step change to another state that can last for substantial periods of time. Given this, developing the means to predict the onset of ecological regime shifts has been of paramount importance in the field of ecology [Hooper et al., 2005].

To date, two promising approaches have emerged in the study of ecological resilience. Recent work with Bayesian networks has shown their power in successfully revealing ecological network structures of complex systems [Mitchell et al., 2021, Hui et al., 2022]: such network understanding shows great promise for the understanding of mechanisms underlying resilience. On the other hand, novel non-additive modelling frameworks have been developed and successfully applied to large marine ecosystems, which allowed for the direct quantification of ecological resilience, and the approximation of a folded stability landscape of the system under study [Vasilakopoulos et al., 2017, Ma et al., 2021, Damalas et al., 2021]. So far, research on network structure and the direct quantification of resilience have been largely segregated. However, connecting these two fields may offer novel insight in the study of ecological resilience. For example, combining the direct quantification of resilience along with the associated network structure of ecosystems as they respond to disturbance may offer novel insight in the early warning signals of regime shifts.

Here, we propose a novel 2-step modelling process to study ecological resilience: (1) we apply a dynamic Bayesian Gaussian Mixture ($\mathrm{BGM_D}$) Bayesian network model proposed by Grzegorczyk et al. [2011] to reveal the network structure of ecosystems, with changepoint processes to account for temporal structure; and (2) we apply the Integrated Resilience Assessment (IRA) framework proposed by Vasilakopoulos et al. [2017] to quantify and approximate ecological resilience of ecosystems under study. We apply this process to rocky shore boulder communities, a system that has been shown to demonstrate multiple stable states. To test the effect of disturbance, we manipulated boulders in the following manner: five boulders were left unchanged (control), and five boulders had 20 Topshells added (disturbance). Through experimental manipulation and combined modelling, we aim to address the following: (1) identify critical transitions in our communities; (2) assess ecological resilience of rocky shore boulder communities; and finally (3) investigate the network structure of our ecosystem as it responds to disturbance.

The application of our $\mathrm{BGM_D}$ to our rocky shore system revealed fundamental links that were consistent with prior experimental knowledge of competitive and grazing relationships. In our control group, the $\mathrm{BGM_D}$ revealed a core feedback loop between Topshells and green seaweed. This was consistent with prior knowledge as Topshells have been documented to graze on green seaweed patches [Norton et al., 1990]. Additionally, the feedback loop between these two species makes intuitive sense: green seaweed provide food for Topshells, while Topshells graze on green seaweed. This feedback loop fundamentally regulates stability within this system, where there is a balance between grazers and green seaweed. On the other hand, the network revealed in our disturbance group showed a vastly different species interaction network. While the feedback loop between Topshells and green seaweed was still present, there was now an additional feedback loop between Topshells and Fucus species. Additionally, both networks identified a changepoint process. In our control condition, there was a change point identified at week 8. In our disturbance condition, two changepoints were identified at week 2 and 6. This implies that both conditions exhibited some form of a shift. The

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nature of this shift can therefore be further explored via the IRA modelling.

Upon applying the IRA model to our data, a folded stability landscape was approximated, along with two fitted attractors that represented alternative regimes. In the control condition, most observations were primarily within the resilient green zone. There were a few observations that deviated into the non-resilient zone, before ‘shifting’ into the lower attractor. This likely represented natural grazing pressure over time and corresponded with the revealed change point process in our $\mathrm{BGM_D}$ for our control. On the other hand, the disturbance condition clearly demonstrated a regime shift. All replicates started in the resilient zone, before reaching the tipping point of the upper fitted attractor. This led to an abrupt shift in system state into the lower fitted attractor. Here, the changepoints were consistent with the $\mathrm{BGM_D}$ for our disturbance condition, where week 2 corresponded with the replicates at the tipping point, and week 6 represented the replicates at the upper end of the lower attractor. Importantly, the approximate trajectory of the system states over sampling showed a clear deviation from the control condition, suggesting a critical shift in system state.

Here, we demonstrate the potential of combining network-based approaches with non-additive modelling when studying regime shifts and resilience. The $\mathrm{BGM_D}$ model showed strong potential in revealing dynamic ecological networks, which accurately captured crucial feedback loops that are essential in regulating system stability. Importantly, the ability to detect any fundamental changes to these core feedback processes may provide crucial information in the shifts in internal dynamics. Additionally, the revealed changepoint processes allow us to identify if there were shifts in our system, and where this shift is located. On the other hand, the IRA model revealed resilience dynamics of our boulder system, along with the structure of the critical transitions in our system. Through this novel integration of the $\mathrm{BGM_D}$ and IRA model, two critical features can be achieved: (1) the dynamic network structure of the studied system can be revealed, which provides important insight into the internal dynamics of systems as they respond to disturbance; and (2) the stability landscape reveals previously unknown resilience dynamics of a system, along with the structure of critical transitions, which can be related to revealed network structure to help elucidate mechanisms behind resilience and regime shift.

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