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IDEA AND PERSPECTIVE

Landscape modification and nutrient-driven instability at a distance

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Abstract

Almost 50 years ago, Michael Rosenzweig pointed out that nutrient addition can destabilise food webs, leading to loss of species and reduced ecosystem function through the paradox of enrichment. Around the same time, David Tilman demonstrated that increased nutrient loading would also be expected to cause competitive exclusion leading to deleterious changes in food web diversity. While both concepts have greatly illuminated general diversity-stability theory, we currently lack a coherent framework to predict how nutrients influence food web stability across a landscape. This is a vitally important gap in our understanding, given mounting evidence of serious ecological disruption arising from anthropogenic displacement of resources and organisms. Here, we combine contemporary theory on food webs and meta-ecosystems to show that nutrient additions are indeed expected to drive loss in stability and function in human-impacted regions. Our models suggest that destabilisation is more likely to be caused by the complete loss of an equilibrium due to edible plant species being competitively excluded. In highly modified landscapes, spatial nutrient transport theory suggests that such instabilities can be amplified over vast distances from the sites of nutrient addition. Consistent with this theoretical synthesis, the empirical frequency of these distant propagating ecosystem imbalances appears to be growing. This synthesis of theory and empirical data suggests that human modification of the Earth is strongly connecting distantly separated ecosystems, causing rapid, expansive and costly nutrient-driven instabilities over vast areas of the planet. Similar to existing food web theory, the corollary to this spatial nutrient theory is that slowing down spatial nutrient pathways can be a potent means of stabilising degraded ecosystems.

Keywords
Connectivity, global change, nutrients, stability, theory.

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INTRODUCTION

The growing demand for food is producing ecologically homogenised agroecosystems that now dominate over one-third of the Earth's habitable land surface (Bruinsma and FAO, 2003; Nyström *et al.*, 2019). Human wastewater, fossil fuel emissions, deforestation and agricultural intensification for crops and livestock have vastly increased nutrient flows between terrestrial and aquatic ecosystems (Fig. 1a–d). Because homogenised agricultural landscapes lack the extended storage capacity formerly provided by extensive networks of wetlands, nutrients flow rapidly from crop fields, often equipped with tile drainage, to channelised streams before reaching rivers, lakes and oceans. Collectively, these landscape modifications increase and accelerate the movement of nutrients across the land and water (Bennett *et al.*, 2001; Raymond *et al.*, 2008; Aufdenkampe *et al.*, 2011; Elser and Bennett, 2011; Nyström *et al.*, 2019). This heightened connectivity means that the impacts of local activity rapidly propagate 'downstream', causing farm nutrients and chemicals to accumulate in vast quantities in lakes and oceans where other movement vectors such as ocean currents distribute them globally.

The spatial homogenisation of landscapes broadly increases across-ecosystem connections whereby distant ecosystems become increasingly connected, such that anthropogenic disturbance in one location can have rapid, and often amplified, impacts elsewhere (see landscape example in Fig. 1; Box 1 for definitions). These flows, for example are now understood to be responsible for massive algal blooms resulting in ecosystem dead zones and are striking examples of regional ecological degradation and instability (Diaz and Rosenberg, 2008; Huisman *et al.*, 2018; Ho et al. 2019). Nutrient additions have increased globally, with *c.* 2-fold increases in reactive nitrogen (N) and phosphorus (P) use over the last half century (Galloway *et al.*, 2008; Cordell *et al.*, 2009; Macdonald *et al.*, 2011; Steffen *et al.*, 2015) (Fig. 1b) resulting in increasing nitrogen loads to lakes and coastal oceans (Fig. 1d).

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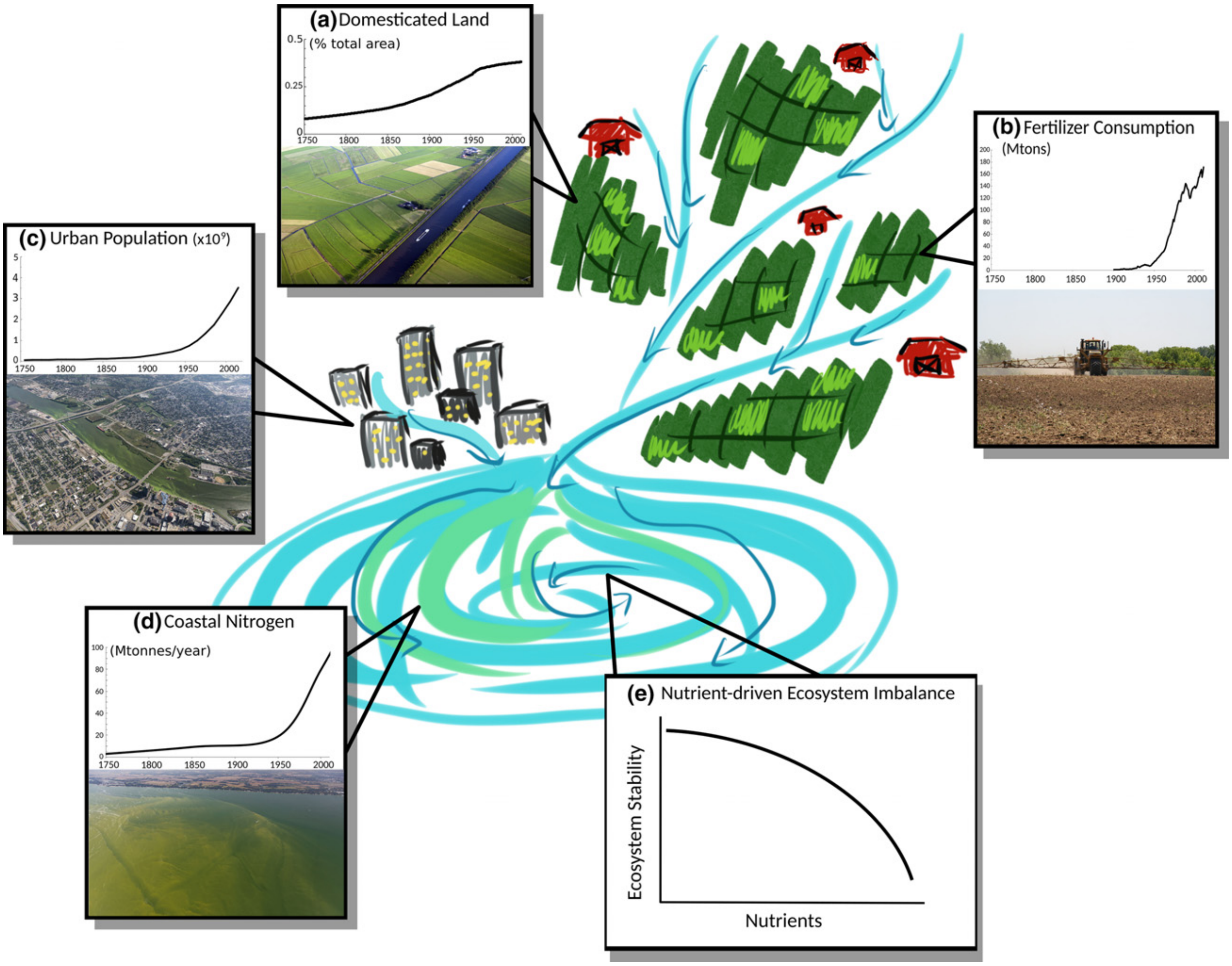

Figure 1 Picture of an increasingly common set of multiscale influences on ecosystems. Natural land is being developed into agricultural land at an increasing rate (inset a). A highly agricultural landscape that removes natural spatial heterogeneity as it is made into one large agro-ecosystem producing a homogenised regional scale system. Globally this landscape modification has been accompanied by an increasing use of nutrients on farms (inset b). Increasing human population is increasing urban populations globally (inset c), and land modification on generic farms reduce or remove riparian buffers, tile drains fields and channelises streams (inset a) – all activities that ramp up the loading and movement of sediment including nutrients from the field to the creeks, to the streams, rivers and finally lakes and oceans where nutrients accumulate (inset d). This threatens the ecological balance of these terminal ecosystems (i.e. instability takes place at a distance from local actions), often with nutrient-driven instabilities such as harmful algal blooms and dead zones (inset e). The form of instability can be variance-driven or mean-driven instability (Box 1and 2). Data from: Steffen*et al.*,2015. Great Acceleration Data http://www.igbp.net/globalchange/greatacceleration.4.1b8ae20512db692f2a680001630.html Photo credits: (a) Peter Prokoschhttp://www.grida.no/resources/1698; (b) P177 https://www.flickr.com/photos/48722974@N07/4478367887; (c) Aerial Associates Photography, Inc. by Zachary Haslick; (d) Aerial Associates Photography, Inc. by Zachary Haslick.

These trends are likely to continue, with an estimated 50% increase in food demands by 2050 as the human population exceeds 9 billion (Vitousek *et al.*, 2009; Eisenhauer *et al.*, 2012; Springmann *et al.*, 2018). As the problem intensifies, so does the need to understand how it might unfold and why the magnitude of impact is so powerful, both of which inform potential avenues for remediation. To advance understanding we begin to link three fundamental bodies of ecological theory: consumer–resource dynamics due to the Paradox of Enrichment (Rosenzweig, 1971), species replacement due to nutrient-mediated competitive exclusion (Tilman, 1982), and spatial dynamics represented by recent advances in meta-ecosystem theory (Loreau *et al.* 2003; Gounand *et al.*, 2018).

Almost 50 years ago, Michael Rosenzweig warned that increased nutrient loading and higher resultant productivity could lead to ecosystem destabilisation and species loss (Rosenzweig, 1971) – the exact challenges we are seeing today. This concept, known as the paradox of enrichment (hereafter POE), centred on the irony that the initial benefit of nutrients for higher productivity eventually destabilises an ecosystem by disrupting the interaction between consumers and their resources. In simple systems with a single species of consumer and a single species of prey (resource), high levels of nutrient loading drive extreme cycles in abundance. At high enough enrichment, the oscillatory dynamics cause one species or the other to dip to dangerously low population densities and would therefore go locally extinct in a stochastic world. This

Box 1. Key Definitions

DENDRITIC RIVER NETWORK

Branching pattern of connections that directionally transports water across landscapes.

INSTABILITY

Any form of dynamic that threatens the persistence of a species (i.e., a species reaches dangerously low densities), often measured by coefficient of variation ($CV = \sigma/\mu$) or strength of attraction to an equilibrium in theoretical models. Local minima on an attractor allow one to assess stability as they detail when populations are at dangerously low densities from oscillations as well as follow the loss of an equilibrium. For more detailed definitions and concepts behind a general loss in stability of a dynamical system see Box 2.

EQUILIBRIUM

A steady state where all densities are balanced such that gains equal losses.

ATTRACTOR

An equilibrium or non-equilibrium state (e.g., cycle) to which solutions are attracted after a transient.

BIFURCATION

A **bifurcation** occurs when a small smooth change made to the parameter values (the **bifurcation** parameters) of a system causes a sudden 'qualitative' or topological change in its behavior.

CYCLIC OR VARIANCE-DRIVEN INSTABILITY

Variability driven by population cycles with potential for a species to approach low densities and go locally extinct at the cycle's minima. Caused generically by Hopf bifurcations in dynamical systems models, where a stable equilibrium turns into limit cycles.

STRUCTURAL OR MEAN-DRIVEN INSTABILITY

Decreasing densities of species, or set of species, which results in the eventual total loss of an equilibrium (i.e., a species mean density declines to zero). Even in simple ecosystem models nutrient increases tend to drive a fundamental change in ecosystem structure that re-routes whole carbon pathways (e.g., increased inedible resources, increased detritus). All such changes are driven by losses of key species that tend to be caused by **transcritical, saddle node or pitchfork** bifurcations in dynamical systems models. In ecological models, transcritical bifurcations are generic for loss of a species, although ecosystem feedbacks can also readily yield saddle node bifurcations that lead to alternate states. See Box 2 for more details.

PHASE TRANSITION

A qualitative change in the state of a system (e.g. equilibrium) under a continuous change in an external parameter (e.g., increased nutrient flux, and/or nutrient loading).

FOOD WEB OR ECOSYSTEM MODULE

Building blocks of a whole food web or ecosystem model, generally describing the simplified structure of interactions between major components or guilds within the system. Here, the base ecosystem module includes a consumer, a resource, detritus and nutrients and includes nutrient recycling.

oscillatory dynamic has been referred to as *oscillatory or variance-driven instability* (Gellner *et al.*, 2016; see Box 2 for details). This mechanism has been verified by highly controlled trials in some simple experimental microcosms (Luckinbill, 1973, 1979; Fussmann *et al.*, 2000), but is rarely confirmed by empirical research in more complex natural settings (although see Tilman and Wedin, 1991). Instead, empirical results suggest shifts in ecosystem states without oscillations (Morin and Lawler, 1995; Isbell *et al.*, 2013). Here, the effects of nutrient loading appear to favour dominance by some species (e.g. harmful algal blooms; HABs) that push the mean densities of other organisms to functional extinction. In food webs, this process involves the competitive displacement of one kind of prey resource by a second variety that is better adapted to high nutrient conditions (Tilman, 1982). We refer to this as *structural or mean-driven ecosystem instability* as it tends to restructure whole carbon pathways in ecosystem models, see Box 2; (Huisman *et al.*, 2018; Ho et al. 2019). This common field result suggests a second mechanism for ecological destabilisation through enrichment, broadening Rosenzweig's initial concept of the paradox of enrichment.

Although ecology has historically sought to explain ecosystem stability through local processes, recent meta-ecosystem theory suggests that coupling ecosystems across large spatial scales by organismal migration and material transport may play a key role in determining ecosystem stability (Levin, 1995; Callaway and Hastings, 2002; Gounand *et al.*, 2014; Marleau *et al.*, 2014; Gravel *et al.*, 2016). With the growing empirical evidence of heightened connectivity of nutrients, POE can now be recast as a more general nutrient theory for global ecology. This recast version of POE integrates multiple scales of ecosystem connectivity allowing us to better explain some of the most striking examples of ecosystem imbalance and degradation. One important feature is that increased ecosystem connectivity often occurs in dendritic river networks, where flows are directional, and nutrient

Box 2. Enrichment and Instability

TWO GENERAL FORMS OF LOSS OF STABILITY: VARIANCE (CYCLIC) AND MEAN-DRIVEN (STRUCTURAL) LOSSES IN STABILITY

Broadly speaking, stability can be lost in an ecological model via wild oscillations or the complete loss of an equilibrium (Fig. B.2a). In 1971, Michael Rosenzweig pointed out that numerous models produced something he coined the paradox of enrichment (Resenzweig, 1971). The idea was simple, he found that changes in carrying capacity (a surrogate for increased nutrients), all else being equal, tended to alter the structure of consumer-resource interactions such that they drove wildly oscillating population dynamics (via a Hopf bifurcation; Fig. B.2a). During these wild cycles (say where nutrient levels are at the red star), the argument goes, population densities of either consumer or resource occasionally plunge to near zero density (see dashed red line which is the persistence line Fig. B.2c for example), which increases the likelihood of consumer or resource collapse in a stochastic world (e.g., drought). The paradox therefore was seen as increased nutrients, somewhat counterintuitively, could lead to collapse of C or R or both. This loss of stability has been more recently referred to as variance-driven or cyclic instability for the simple reason that it would be expected to largely inflate the standard deviation in a coefficient of variation (referred to as CV in literature) stability calculation (where CV = SD/μ). Clearly this variance-driven route to instability is not the only form of instability that threatens the persistence of interacting species. Generally speaking, as we vary some parameter there is the possibility that instead of oscillations the varying parameter can push an internal equilibrium (i.e., all species > 0 densities; Fig. B.2b) to a situation where one species is excluded (i.e., the mean density of one species goes to zero as for the time series example where nutrients are at the red star level; Fig. B.2d). Since the interior equilibrium is lost, system level stability is clearly breached. This tends to occur via several possible bifurcations, most notably transcritical or saddle node in ecology (Grover, 1995; Scheffer *et al.*, 2001). Note, since in the above example one of the species at equilibrium (i.e., not deterministically varying over time) is pushed to zero densities this is an example of mean-driven loss in stability (CV inflates as mean goes to zero) and signals the complete **loss** of an interior equilibrium. Often, as in the edible-inedible resource case discussed below, this can completely alter the structure of energy flow in the ecosystem.

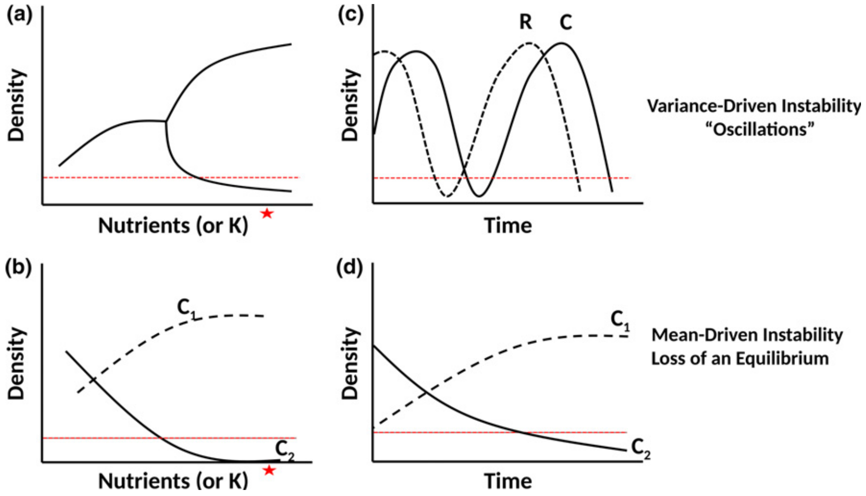

Figure B2 Time series of two different instabilities (loss of persistence of an interaction or set of interactions). (a) of an oscillatory loss of stability (variance-driven as mean is high) produced by a deterministic or stochastic Hopf, and; (b) a mean-driven loss of stability associated with the complete loss of an equilibrium through a bifurcation such as a transcritical or saddle node.

concentrations amplify dangerously downstream. The dendritic network is effectively 'space filling', and like a lung, efficiently transports localised inputs (e.g. particle-bound P) into distant waterbodies before ultimately ending in oceans where global current systems move them over vast scales. Our empirical understanding suggests that local land modification enhances the already significant connectivity of directional transport networks (Raymond *et al.*, 2008), intensifying ecosystem connectivity and accelerating the build-up of nutrients that destabilise biological processes at great distances (Diaz and Rosenberg, 2008).

Here, we spatially extend ecosystem theory to examine how human-mediated increases in nutrient transport can drive widespread long-distance ecosystem instability by integrating POE dynamics and nutrient-mediated competitive exclusion with elevated connectivity. We define instability as any dynamic outcome that threatens the persistence of species (i.e. via variance or mean-driven ecosystem instability; detailed in

Box 2) and alters ecosystem processes due to shifts in the structure and function of food webs (e.g. large detrital loads that can cause bacterial-driven oxygen depletion). We first argue that a synthesis of existing theory suggests that nutrient enhancement should commonly generate ecosystem instability through either cycle-driven or structural changes in ecological equilibria. To highlight this and place it within an ecosystem context, we then employ a set of ecosystem models with advective movement of either nutrients, resources or consumers within a simple dendritic network. We find that increases in nutrient transport (e.g. tile drainage, channelisation, climate-derived extreme pulses of local precipitation) or large-scale resource or consumer movement (e.g. ocean circulation, migration) amplify the likelihood of ecological instability (e.g. detrital take over). We then discuss empirical examples that suggest this phenomenon is happening and appears to be increasing globally. We end by suggesting that management of connectivity within directional dendritic networks (Peterson *et al.*, 2013a; Galiana *et al.*, 2018) could mitigate these costly ecological imbalances at regional and global scales. Specifically, our theoretical framework suggests that well-placed landscape-scaled management practices (e.g. 'slow nutrient pathways' within a spatial network) can act as potent stabilisers of distant ecosystem imbalance, in a manner akin to the stabilising role weak interactions play in food web theory (May, 1973; Gellner and McCann, 2016).

A BRIEF REVIEW OF NUTRIENT-STABILITY THEORY

Rosenzweig suggested that increasing carrying capacity, a surrogate for nutrient enrichment, can drive population instability by transforming a stable equilibrium into a cyclically unstable one (termed a Hopf bifurcation; see Box 2), such that steady-state dynamics give way to consumer–resource oscillations (Rosenzweig, 1971). More recent elaborations of food web theory largely agree with this insight (McCann, 2011; Murdoch, Briggs, and Nisbet, 2013), with one important caveat – any biological structure or process that reduces energy flow between consumer and resource can inhibit the expression of the cyclic instability (e.g. Rip and McCann, 2011). As an example, any form of interference that reduces consumer growth – either through the functional response or as intraspecific competition – dampens the expression of instability (Jensen and Ginzburg, 2005). These theoretical results suggest variance-driven instability may be rare; however, macroecological analyses suggest that oscillatory dynamics are surprisingly common in time series (e.g. up to 50% in arctic time series; Kendall *et al.*, 1998). Alternatively, competitive modification of food web components (mean-driven ecosystem instability) can cause ecosystem malfunction through the addition of an inedible, or less edible, resource (Tilman, 1982; Abrams and Walters, 1996; Vos *et al.*, 2004). These results are related to the more general concept of keystone predation (Holt, 1977; Leibold, 1996) and intraguild predation (Holt and Polis, 1997), finding that high productivity generally reduces prey diversity via mean-driven processes. Here, instead of boom and bust cycles in abundance, the less edible resource (e.g. primary producers laden with secondary chemical compounds) takes up the excess nutrients and flourishes. The flourishing less edible prey ultimately outcompetes the edible resource driving it to extinction (termed a transcritical bifurcation in dynamical systems theory; Grover, 1995). Note, the result of less edible takeover is a specific instance of competition theory (Tilman, 1982; Chase and Leibold, 2003). This alternative route to POE leads to a loss in stability expressed as the complete replacement of the original ecological equilibrium with a new equilibrium due to a phase transition to a new state (Scheffer *et al.*, 2001; Carpenter, 2005; see Box 2). Ecosystem theory predicts large detrital accumulations in the new steady state as high resource pools die off and ultimately lead to the accumulation of large detrital pools, something we see frequently in the empirical examples (e.g. build-up of dead plant material in enriched grasslands; Tilman and Wedin (1991)). Below, we will spatially follow nutrients and detritus in the theory as large detrital build-up is arguably an outcome of ecosystem imbalance.

In the 1990s Gary Polis and others championed the notion that nutrient and resource subsidies across ecosystem boundaries alter the structure and function of local ecosystems (Polis and Strong, 1996; Polis *et al.*, 1997; Leroux and Loreau, 2008). These ideas produced theory that showed, for example that nutrient subsidies can lead to dynamic outcomes that are stabilising in the sense that they reduce boom and bust dynamics; however, they also drive strong top-down suppression such that consumers can often reduce their resources to low densities or extinction (Huxel and McCann, 1998; Takimoto *et al.*, 2002). This is not the destructive oscillations predicted by Rosenzweig's POE, but rather another nutrient-driven loss of an equilibrium (i.e. mean resource densities suppressed to extinction). The problem of nutrient run-off has also inspired models that predict alternate states in lakes and coastal ecosystems (Scheffer *et al.*, 2001; Carpenter, 2005). Here, though, the loss of an equilibrium is due to an abrupt shift to a new alternate ecosystem state through a saddle-node bifurcation. More recently, this nutrient theory has progressed to analysing meta-ecosystems whereby the coupling among ecosystems creates feedbacks that can propagate instabilities (Gounand *et al.*, 2014, 2018). This cross-ecosystem research has added to DeAngelis' seminal contributions that showed ecosystem models readily produced instability and POE (DeAngelis, 1992). Intriguingly, one of the findings from meta-ecosystem research is that the paradox of enrichment, or strong consumer–resource oscillations, can be driven by nutrients coming from a neighbouring ecosystem – this is the first theoretical suggestion that nutrients can spatially propagate instability across ecosystems (Gounand *et al.*, 2014).

A SYNTHETIC META-ECOSYSTEM MODEL: NUTRIENTS AND CONSUMERS CONNECTED IN SPACE

In order to integrate the theory discussed above, we use a spatial ecosystem model (Fig. 2a–c). The base of this model is a fundamental ecosystem module that includes a detrital pathway and a consumer–resource interaction (Fig. 2b; as in DeAngelis, 1992). This model is consistent with the clearest experimental evidence of the POE (Fussmann *et al.*, 2000). The ecosystem module serves two main purposes: (1) it allows

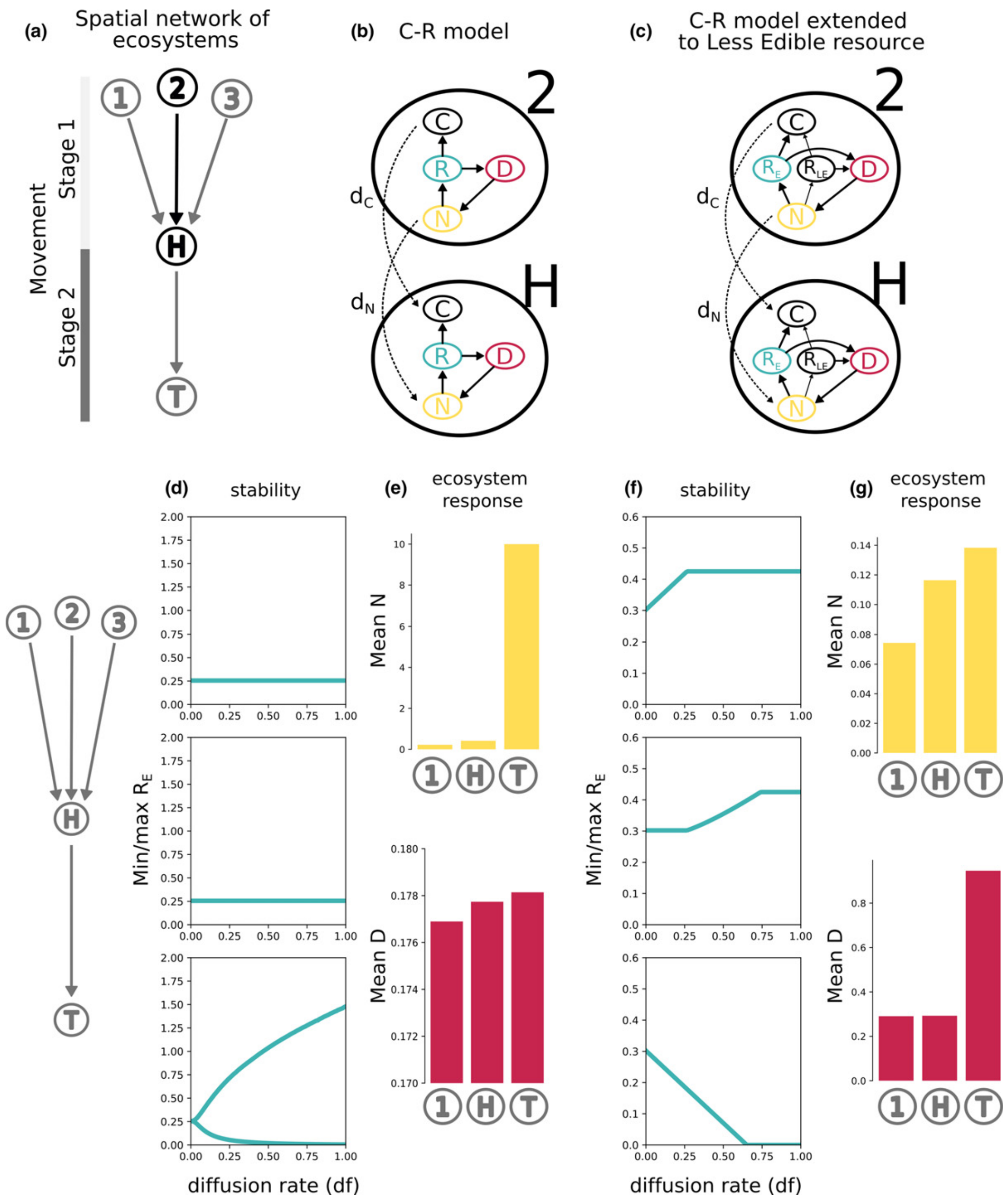

Figure 2 Simple dendritic or directionally connected model with multi-stage movement and an ecosystem model in each node (a). All nodes are considered 'fast' and so all have high and equivalent nutrient loading, I_N, and all nodes are changed with changes in nutrient diffusion, d_N. The spatial arrangement with initial nodes (1, 2 and 3), an intermediate hub node (H) and a terminal node (T) is shown in Fig. 2a; whereas a standard C-$R_E$ecosystem module (b), and the same ecosystem model extended to consider edible resources (R_E) and less edible resources (R_{LE}) are shown (c). d) Local max and min solution of the edible resource, R_E, over a range of nutrient diffusion rates (d_N) for initial, hub and terminal nodes. Results show oscillatory instability in terminal node (POE) relative to other nodes (bottom panel Fig. 2d). e) Nutrient dominated movement results from C-R model show inflated nutrients and detritus in the terminal node under high nutrient movement rates ($d_N = 0.80$). f) Local max and min solution of edible resource,R_E, over a range of nutrient diffusion rates for the initial, hub and the terminal node for the standard ecosystem model with both edible and less edible resources. This latter (C) result differs from the POE cyclic instability in that it shows that the takeover by inedible resource coupled to the generalist consumer ultimately pushes$R_E$through a transcritical bifurcation (see Box 1for bifurcation definitions). This loss in stability is of a different flavour than the classic POE but nonetheless is a loss that fundamentally alters the ecosystem due to nutrient increases and nutrient transport. (g) Nutrient dominated movement results from C-R model shown in flated nutrients and detritus in the terminal node under high nutrient movement rates (d_N; left most panel C).– Fig 2a *parameters. All nodes* –I_N=0.25, $r = 0.05$, $e = 0.80$,$f = 0.05$,a_N=0.60,b_N=0.04, $d = 0.10$,a_R=0.20,h_R=0.005,m_R=0.10,m_C=0.001.Fig 2b. *All nodes* –I_N=0.25, $r = 0.05$, $e = 0.80$, $f = 0.05$,$a_{N,E}$=0.40,$b_{N,E}$=0.04,$a_{N,\leq}$=0.07,$b_{N,E}$=0.047, $d = 0.10$,$a_{R,E}$=0.15,$h_{R,E}$=0.005,$a_{R,E}$=0.05,$h_{R,\leq}$=0.005,$m_{R,E}$=0.10,$m_{R,\leq}$=0.11,m_C=0.001.

us to follow the fate of nutrients and detritus locally and regionally; and (2) it allows us to monitor the local and regional stability properties of one of the major building blocks of food webs (i.e. consumer–resource interactions). Importantly, the consumer–resource sub-system of this module will allow us to synthetically bridge our model results to the historical theory discussed above (McCann, 2011; Murdoch *et al.*, 2013). While we employ a simple base module, we see it as a significant starting point for interpreting whole food web effects on the landscape. Qualitative general results from consumer–resource theory have been recently shown to scale coherently to whole food webs (Gellner and McCann, 2016). We also extend our spatial model to include less edible basal resources (Fig. 2c) and consumer interference (in mortality and foraging; Supporting Information S4) to show how food webs can alter the form of instability instigated by increased nutrients.

To understand the role of spatial networks on local, regional and global scales we assume a simple spatial unidirectional dendritic network (Fig. 2a) and a terminal node. The simple spatial network can be considered to have two stages of movement allowing us later to relate this theory to empirical results, which are often defined by multiple stages of movement and connectivity (Fig. 2a). As an example, the spatial model can mimic a simple dendritic network linking agricultural run-off from streams to rivers (stage 1 movement) and rivers to a terminal larger waterbody (stage 2 movement). Similarly, one can envision the spatial model as a network linking terrestrial nutrient flows to the ocean (stage 1 movement) and a second stage whereby ocean currents move the nutrients at intercontinental scales (stage 2 movement).

For simplicity, we assume that each spatial node has two potential parameter configurations: an unmodified pristine state with lower nutrient loading (I_N) and reduced flows between spatial nodes (d_N or d_R or d_C) or a modified state with high nutrient loading and high flow rates between neighbouring nodes. When each node in the entire grid is in the modified state, we are examining the impact of a homogenised landscape (identical parameters in each node). This simplification is motivated by agriculture but also importantly allows us some level of tractability in an otherwise extremely complex system of equations (see Supporting Information S2 and S3). In order to study stability, we employ local maxima and minima of population dynamics as it allows us to rapidly assess changes in population variation (i.e. consistent with classical POE) and it also simultaneously allows us to visualise structural changes in equilibria. This equilibrium-tracking allows us to monitor where we have instability through the complete loss of an interior equilibrium. The local maxima and minima thus allow us to see where enrichment in space drives cyclic instability (high variance with dangerously low minima) as well as changes in mean-driven ecosystem instability (Gellner *et al.*, 2016).

In what follows, we look at how increasing rates of movement through the nutrient-subsidised nodes impact the dynamics of the ecosystem module in space. We first do this by increasing movement rates for nutrients and looking at the spatial structure of attractor solutions, as well as the maxima and minima stability metrics. For this consumer–resource base case, we then show that common extensions beyond the Rosenzweig-MacArthur that include less edible resources, consumer interference (consumer self-regulation and ratio dependence) tend to yield nutrient-driven instability via exclusion of the edible resource and runaway detrital loads, not the paradox of enrichment. Finally, towards creating a general framework for nutrient-driven instability that match empirical research we extend these experiments briefly to discuss resource and consumer movement scenarios. Note, in all movement scenarios we are always considering increased local nutrient inputs (high I_N) in the modified nodes on the landscape, so our model experiments always link nutrients to spatial stability.

HOMOGENISED LANDSCAPE WITH HIGH LOCAL NUTRIENT LOADING: NUTRIENT MOVEMENT (ALL PARAMETERS THE SAME; EXPERIMENTALLY INCREASING NUTRIENT MOVEMENT RATE)

We first consider the case of a homogenised spatial model (all nodes are equivalent with high nutrient loading, I_N) and we look at how altering the spatial connectivity of this landscape (via increasing diffusion rates, d_N, of the nutrients) influences model solutions to the base C-R ecosystem in space (module in middle Fig. 2a and b; model 1 in methods, Supporting Information S1). With the results in tow, we then consider a simple realistic food web extension that includes less edible resources (Fig. 2c; model 2 in methods, Supporting Information S1).

Our first result is that under a homogenised modified landscape with nutrient movement dominating the connections between ecosystems, the terminal node in a directed spatial network eventually garners the most nutrients and detritus (ecosystem response; Fig. 2e for diffusion rate $d_N = 0.80$). In this simple unidirectional flow model nutrients tend to build up in the terminal cell when flow rates between nodes grow (when at equilibrium this produces a surge of nutrients and detritus (i.e. mean values of N and D that increase to maximum values in terminal node; Fig. 2e) in the dendritic network). In essence, the dendritic network under high connectivity yields a strong spatial inflation of mean nutrients and detritus. This inflated flux of nutrients across the landscape, consistent with the original POE, suggests that local land modification drives the greatest instability ultimately in the terminal node (Fig. 2d; see Supporting Information S2 for qualitative proof that this generally occurs) as seen expressed with the increasing local max and local min of edible resources for a given diffusion rate, d_N (Fig. 2d). Note, the role of consumer interference, as is well known, overrides this result (Supporting Information S4). That is consumer density-dependent mortality, or ratio-dependent foraging, mute variance-driven instability such that it is generally not expressed (Jensen and Ginzburg, 2005; McCann, 2011; Murdoch *et al.*, 2013).

While an interesting result in and of itself, food webs are clearly not as simple as the ecosystem module above. One common natural component of many aquatic ecosystems is the presence of resources (e.g. algae) that are relatively inedible (Fig. 2c; model 2 in methods; Supporting Information S1). This has the potential to change the stability result above, or at least change the expression of instability. Fig. 2g shows the ecosystem results for this model with the nutrients and detritus again showing increases in the terminal node under high movement rates. Fig. 2f also shows local maxima and minima for an initial node, the hub node and the terminal node for edible resource densities. Again, there is a standing wave of nutrients and detritus (Fig. 2g) but this time the edible resource is ultimately pushed to local extinction directly (i.e. edible resource in terminal node hit zero densities in a transcritical bifurcation; Fig. 2f bottom panel) – this is the second form of instability and different from the POE version above (Box 2). In the POE the dynamics drive wild oscillations with average consumer, C, densities increasing and average resource, R, densities staying steady. The oscillation in the POE case never actually reaches 0 but approaches it – in the real world, these would very likely lead to local extinction of C, or both R and C. Instead, in this latter case, the mean density of edible resource (R_E) is pushed lower until the equilibrium solution intersects with the $R_E = 0$ axis. Effectively, less edible resources stabilise cyclic instability but give way to mean-driven ecosystem instability (i.e. high biomass of less edible resource). The responses of both less edible resources, R_{LE}, and detritus, D, grow to high densities in the terminal node (see Supporting Information S3). High detrital biomass, D, correlates to high bacterial loads and increased oxygen consumption potentially threatening critical ecosystem function – aspects of biology not modelled in consumer–resource models. Intriguingly, employing any form of consumer interference (consumer density-dependent mortality or ratio dependence; sensu Yodzis, 1994), reduces the likelihood of POE type dynamics (see Supporting Information S4) and in doing so increased the relative propensity for exclusion as the dominant instability outcome to enrichment as well as increased detrital loads in the terminal node. Again, nutrient-driven instability still tends to occur at a distance from the local nutrient application but under these conditions generally expressed as mean-driven instability (see Supporting Information S4).

Our second major result, then, is that nutrient-driven instabilities (i.e. loss in persistence of a species) in a highly modified homogenised landscape can occur at a distance through different types of instability (bifurcations). No matter which path leads to instability (e.g. Hopf versus transcritical), they have similar consequences for ecological systems – high local nutrient inputs shunted rapidly across a homogenised landscape drive instability and ecosystem imbalance (e.g. high detrital loads) in a distant terminal node. Furthermore, all cases above suggest that the increase in nutrients and their speed of transport over time lead to a phase transition to a new ecosystem state (at the onset of the nutrient-driven bifurcations). Note, our simple ecosystem models generically produce transcritical outcomes but alterations to these models with positive feedbacks (e.g. discussed cogently by Scheffer *et al.* (2001)) would change these results to abrupt transitions to alternate states. Nonetheless, the general result holds – nutrients propagated rapidly drive phase shifts to a different equilibrium (e.g. a detritus-dominated equilibrium state) at great distances. If consumer interference dominates interactions then we expect the loss of equilibria to dominate instability or collapse at a distance (Supporting Information S4). These instabilities caused by rapid spatial movements of nutrients resonate with non-spatial ecological network results in that high flux through a food web, or strong interaction strengths, generally drive instabilities (see Box 3) suggesting that high flux scenarios in spatial or ecological networks are instability generators. Research on ecological networks has found that weak interactions can prevent these potent instabilities (structural energy deflection; see Box 3) and so this immediately suggests that a similar spatial result may hold for highly modified landscapes.

HOMOGENISED LANDSCAPE WITH HIGH LOCAL NUTRIENT LOADING: RESOURCE OR CONSUMER MOVEMENT

Clearly, physical or biotic mechanisms can drive resource or consumer movement (examples discussed in empirical section below). For completeness, we consider how altering the spatial connectivity of this landscape (via increasing movement rates of either the resource d_R, or movement rates, d_C, of the consumer alone) influences the model solutions across space using the homogenised spatial model, (all nodes are equivalent with high nutrient loading, I_N). Note, in this uni-directional flow model resource movement and consumer movement act identically to a subsidy at equilibrium in that the equilibrium at any node is not dynamically linked in space (see Supporting Information S2 and S3). Thus, the results from constant subsidy theory apply here (Huxel and McCann, 1998; Huxel *et al.*, 2002). Under a homogenised landscape with resource movement we generally find that the resource movement alone can be stabilising as it removes oscillatory dynamics (Huxel and McCann, 1998)), but elevates consumer densities while resources are largely held in check (see Supporting Information S5 for both the base model and the inedible resource model). Again, as in all other cases, here consumer and detrital densities are elevated most in the terminal node (Supporting Information S4). As found in subsidy theory (Huxel and McCann, 1998), this result does not display a complete loss of stability (bifurcation), but nonetheless resource movement drives either a highly inverted biomass pyramid, or the relative proliferation of less edible resources both accompanied by large detrital biomasses (Fig. S5A, Supporting Information S5). These results resonate with existing theoretical arguments that resource subsidies can be stabilising (remove variance-driven instability) but result in top heavy webs that can strongly suppress resources and threaten persistence via mean-driven extinction (Huxel and McCann, 1998; McCauley *et al.*, 2018).

Similar but stronger resource suppression results occur for consumer movement. Under a homogenised landscape with consumer-movement dominating the connections between ecosystems, the terminal node in a directed spatial network garners the most consumers. What we see here then, akin to our first experiment, is the spatial inflation of consumers in the terminal node (Supporting Information S5). This is another example of mean-driven loss of stability but this time through consumer spatial inflation – the terminal node inflation of C ultimately suppresses R and drives the loss in stability through the loss of the interior equilibrium (i.e. R_E is removed).

Box 3. Non-spatial muting of enriched food web networks: structured energy deflection

It is informative to look at results from ecological networks to understand the outcome for stability in directional spatial networks. We briefly discuss ideas from food web theory that allow us to interpret how food web structure can mute the ecological instabilities discussed in Box 2. Specifically, the notion that weak interactions can stabilize both modular and whole food webs relies, to some extent, on the notion that certain common food web structures can re-route energy away from a strong interaction and in doing so stabilize a food web (where stability here can mean reduce CV either through reducing variance (*SD*) or reduce CV by increasing the mean (μ)). As an example (Fig. B.3.a), McCann et al. (1998) performed simple experiments where adding a weak interaction strength to a key interaction (e.g., reducing attack rate) on a wildly oscillatory food web module rapidly reduced the size of the oscillation, even potentially fully stabilizing the system (e.g., becomes stable equilibrium; CV = 0). Here, we introduce a relatively inedible competitive consumer 2 into a wildly oscillatory P-C-R system and note it deflects energy away from a strongly interacting food chain. In doing so, it reduces the CV and stabilizes the dynamics. We will refer to this form of ecological network stabilization as structural energy deflection and note while it works in non-spatial ecological networks there is clearly room for a spatial analog as theory suggests high nutrient and energy flux in space ought to generally drive instability (we show that indeed it does). This deflection of energy also can similarly impede the loss of an equilibrium (see Box 2). As an example, we have a subsidy model driving strong top-down impacts on an intermediate consumer (Fig. B.3.b). This top down suppression with enough subsidy can remove the intermediate C1 (a form of mean-driven instability associated with a loss in equilibrium). If we introduce to this same subsidy a weak food chain (Fig. B.3.b), the subsidy is deflected away from top predator 1 (some portion going to the weak predator 2), removing the pressure on the intermediate consumer 1 and impeding the loss of stability (consumer 1 is relieved of top-down suppression). Again, as above, weak energy deflection away from the strong interaction removes the instability. Note, while this structural deflection works in non-spatial ecological networks we conjecture that this same general form of material or energy deflection can play a potent role in stabilizing spatially connected food web networks but rather than deflecting energy into weaker species or food web pathways (as above) nutrient and material flow on the landscape is deflected in space away from strong nutrient pathways and thus inhibiting high nutrient aggregations in space.

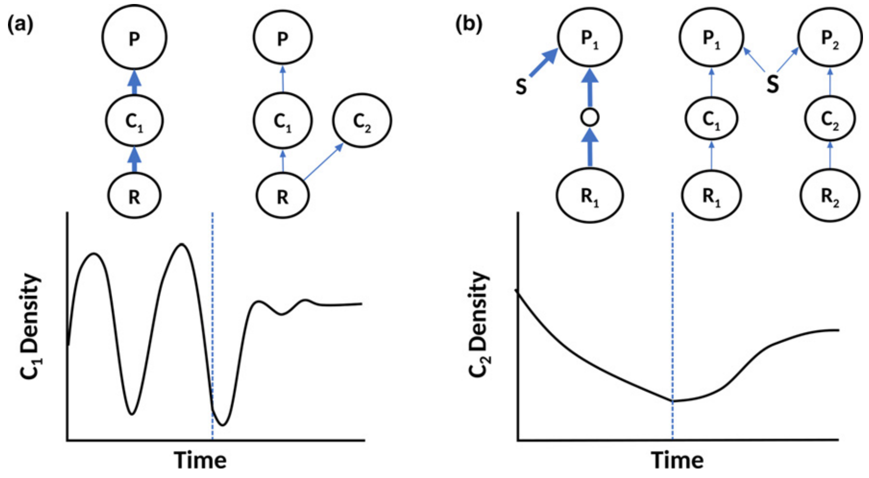

Figure B3 Ecological network, or food web, structures that can mute the two forms of instability. (a) Weak or inedible consumer mutes oscillatory P-C-R, and; (b) Weak food chain introduced and it deflects subsidy away from top predator in the strong food chain, and in doing so releases consumer suppression muting the loss of instability due to a complete loss of an equilibrium.

In summary, our theoretical synthesis suggests that the loss of stability on a modified homogenous landscape tends to occur first in the terminal node. This instability tends to include increased nutrient and detrital loads as well as losses in stability due to either variance-driven instability (via oscillations) or mean-driven instability (via exclusion). Finally, including inedible resources, consumer interference and other forms of movement (e.g. resources or consumers) tend to push mean-driven instability as the most likely empirical outcome.

ADDING SPATIAL HETEROGENEITY TO HOMOGENISED SPATIAL NETWORK: SLOW NODES AS A POTENT STABILISING FORCE

We end our development of the theory by considering the case of a heterogeneous spatial model (model 1) – in this model experiment we include both modified nodes with high nutrient loading (I_N) and an unmodified, slow hub node with lower loading and diffusion rate (d_N) into the terminal node. We use

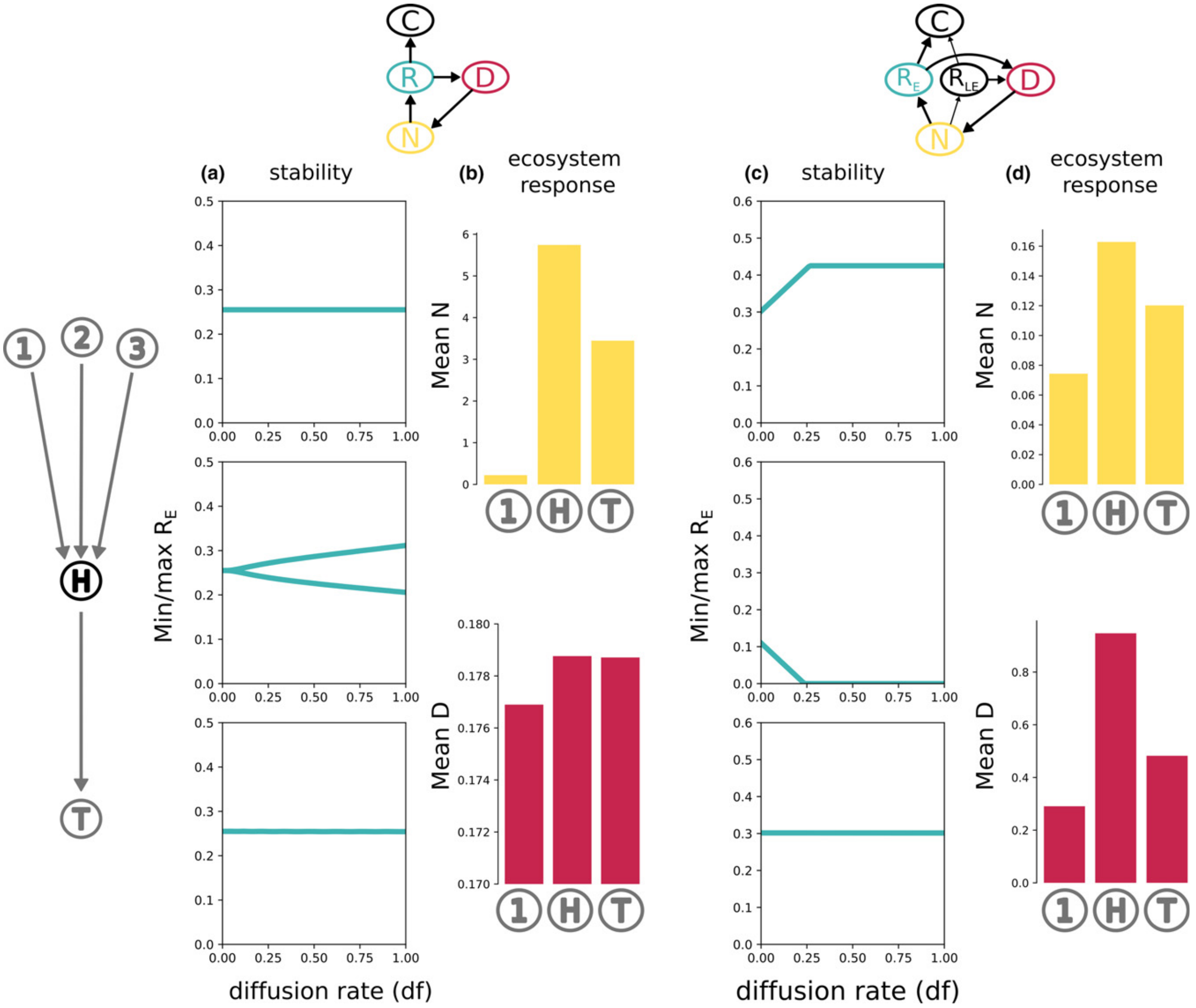

Figure 3 Examples of how landscape heterogeneity that includes a node that slows flow rates or weakens landscape connectivity ultimately drives greater stability at terminal node. For the simple C-R ecosystem model, deterministic min/max solution for increasing nutrient diffusion rates (d_N) in initial, hub and terminal nodes (low$d_N$and$I_N$in the slow hub node) are shown with variance instability now in the hub node (a). While ecosystem response of nutrients and detritus now peak in the slow hub node (middle panel Fig. 2b). Similar results for the extended model 2 (c, stability response; d ecosystem response of N and D). In both cases, the terminal node response is stabilised. In a manner similar to weak interaction theory (Box 3), the heterogeneity limits nutrient movements and alters the distant expression of variance-driven instability as it is most unstable in the slow hub node. Fig. 3a *Parameters: Hub Node –* $I_N=0.09$ *and* $dN = 0.001$ *all other parameters identical to* Fig. 2b*; Fast Node – all parameters identical to* Fig. 2b.Fig. 3b *parameters Hub Node –*$I_N=0.09$ *and* $dN = 0.001$ *all other parameters identical to* Fig. 2c*; Fast Node – all parameters identical to* Fig. 2c.

this model scenario to assess how altering the spatial connectivity of this landscape via increasing diffusion rates, d_N, of nutrients from nodes 1-3 impact the model solutions in space. Here, for the variance-driven instability case above (Fig. 2d), we find that heterogeneity in the rate of diffusion first changes where nutrients and detritus accumulate (Fig. 3b) and stabilise the terminal node (bottom of stability panel Fig. 3a) relative to the purely modified homogeneous case (Fig. 2d). More specifically, heterogeneity can alter where instability is expressed in the network (hub node; Fig. 3a). Fig. 3b shows that nutrient and detritus tends to increase in the now slow hub node, resulting in local instability, which then reduces the flux of nutrients to the terminal node, leaving it relatively stable. Similarly, a slow node can also alter ecosystem responses on the landscape in the less edible model web (model 2; Fig. 3c and d). Note, again nutrients and detritus peak in the hub node in Fig. 3d with the expression of mean-driven instability again altered away from the terminal node to the hub node (Fig. 3c) – slow nodes allow for nutrients and material to be assimilated and accumulated deflecting destabilising build-up in the terminal nodes.

This result highlights that strong connectivity drives instability at great distances, but that altering where the nutrients accumulate on the landscape determines how effectively nutrients can be assimilated preventing their effects from being expressed at the terminal node. Akin to food web theory, increasing the number and location of slow nodes (weak

Box 4. A. Some empirical predictions from nutrient theory

(1) Landscape homogenization with increased loading and nutrient movement will produce instabilities first expressed at terminal nodes
  (a) If inedible species are largely unconsumed, or stabilizing mechanisms (e.g., consumer interference) are ubiquitous, we expect loss of species through mean driven processes (i.e., competitive exclusion not consumer-resource variation-driven instability) to dominate and inhibit variance-driven instability.
  (b) If the consumer species are capable of consuming all resource species, or no species are inedible given the consumer functional group, then variance-driven instability should dominate over mean driven coexistence loss.
  (c) Resource or consumer movement can also amplify nutrient loading at a distance although these heightened resource or consumer densities would be expected to drive mean-driven instability with strong detrital build-ups.
(2) Making the spatial network heterogeneous by slowing down a node connection, or a set of node connections, will lead to a reduction of either form of instability expressed at the terminal node.
(3) The expression of instability at the added slow connection nodes depends on the number of slow nodes added such that: (1) very few slow nodes will potentially increase the instability expression at the now slow local node, and; (2) many slow connections will act to diffusely mute the expression of instability everywhere in the spatial network.

B. SOME OPEN EMPIRICAL AND THEORETICAL PROBLEMS

(1) How do the fractal dendritic properties of spatial networks scale to amplify nutrients and these distant instabilities?
(2) What is the best way within a fractal dendritic spatial network to mute connectivity and reduce distant instabilities while still allowing food production?
(3) How do complex food webs alter the theory presented here?
(4) How does the spatial dendritic network homogeneity or heterogeneity impact stability via the portfolio effect (i.e., spatial averaging of densities that promotes regional stability)?
(5) Use large scale (space and time) empirical monitoring of rainfall, and nutrients across watersheds to ask empirically how a gradient in homogeneity to heterogeneity alters nutrients flows (with modelling)?
(6) What are the optimal number, and placement, of slow nodes (low impact sites) in a dendritic network that maximizes high agricultural production (e.g., high nutrients) and minimizes likelihood of ecosystem instability?

interactions in food webs) on the landscape could reduce the stability of any one node while increasing the stability of the terminal node, and therefore overall regional stability by lessening the distant impacts of nutrient accumulation. This result resonates with the suggestion above, that low spatial flux – akin to weak interactions in ecological networks – can mute spatial instabilities (Box 3). An interesting extension of this work would be to understand how the near fractal pattern of riverine networks might alter stability by buffering flow rates. This issue of buffering flow rates not only relates to curbing distant accumulation of nutrients but has well-established practical implications for global efforts to ‘slow the flow’ of floodwaters (Milly *et al.*, 2002; Poff, 2002). Those efforts seek to combat accelerating flooding with climate change, with flooding compounded by long-established barriers and channelisation networks that, as with nutrients, sought to shunt water downstream as quickly as possible. Our work reinforces how these water management efforts, from field tiling to straightening rivers and modifying wetlands, solve local-scale concerns but are increasingly creating unanticipated regional and global scale impacts. This suggests that dams may act as slow hubs but as is well-known we caution that they also fundamentally alter the habitat structure in ways that are highly detrimental to diversity (e.g. Kominoski *et al.*, 2018).

Collectively, this theoretical framework predicts that land modification with strong local nutrient loading generally lead to distant instabilities (for predictions and future research see Box 4), and that theory suggests that mean-driven distant instabilities may dominate empirically. Furthermore, these theoretical results suggest that distant instabilities are not likely just from nutrient movements (e.g. dead zones) but also can and ought to show up from large-scale directional movement of resources and consumers that integrate local nutrients and move the nutrient imbalances in space leading to collapse. Finally, slow nodes can act as potent stabilisers of the distant impacts. In what follows, we begin to look at emerging empirical examples and trends arguing that they are strongly consistent with theory.

EMPIRICAL EXAMPLES OF NUTRIENT-DRIVEN ECOSYSTEM IMBALANCE

Empirical data show nutrients are consistently involved in long-distance ecological instability. Although some researchers have argued against the existence of empirical examples of cyclic dynamics from nutrient enrichment (Jensen and Ginzburg, 2005), it is clear that nutrients have impacted ecosystem stability (Diaz and Rosenberg, 2008; Smetacek and Zingone, 2013; Hautier *et al.*, 2014). Indeed, the most obvious and pervasive empirical example is the rising frequency of runaway harmful algal blooms (Diaz and Rosenberg, 2008) (Fig. 4.a). These events are often found in large lakes, seas and oceans

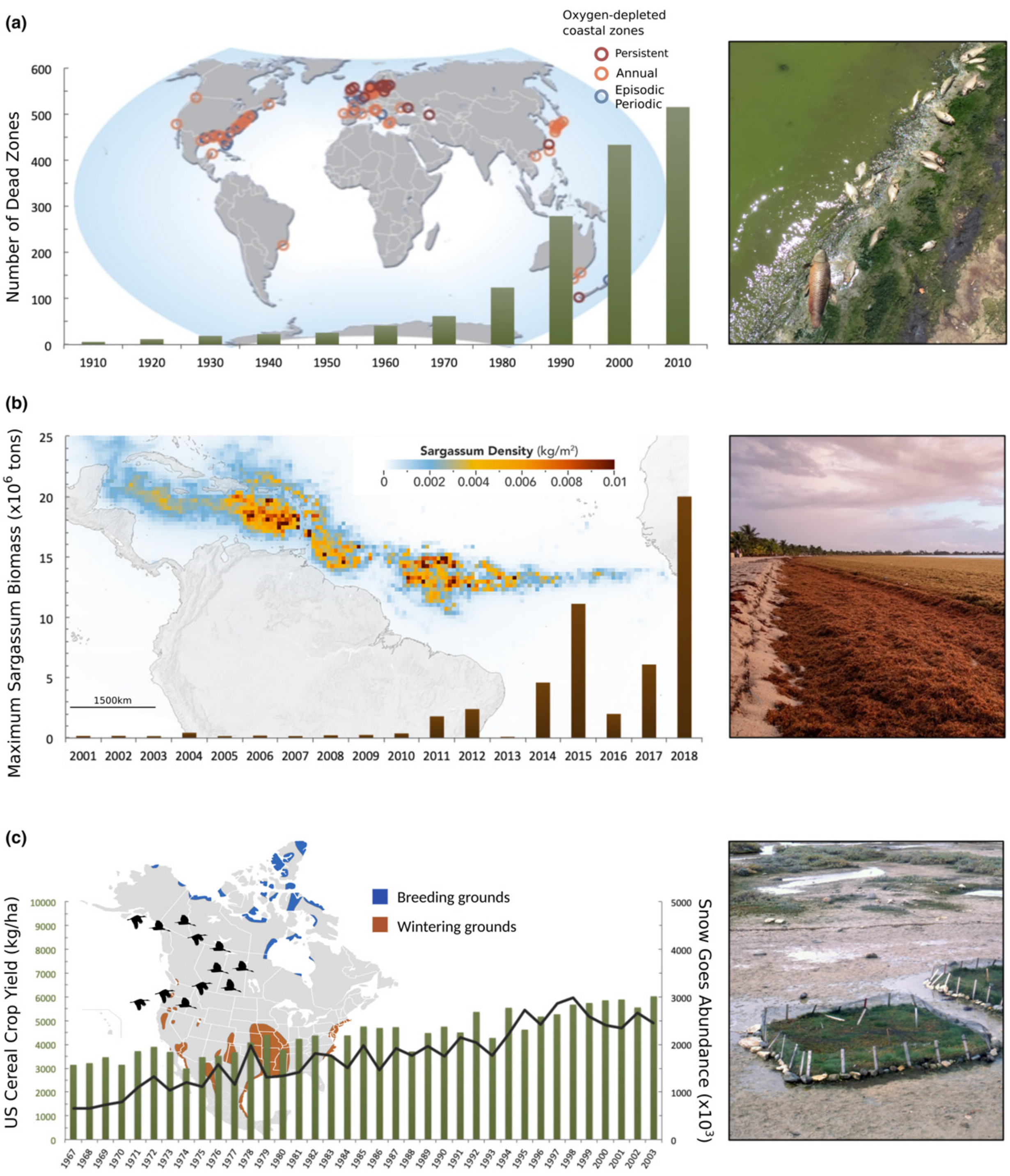

Figure 4 Some examples of nutrient-driven instabilities at a distance. (a) Dead zones of nutrient and climate fuelled runaway plankton followed by deep water bacterial growth that removes oxygen, both in large freshwater lakes and oceans, have been noted to increase in intensity and frequency globally; (b) Similarly, nutrient and climate fuelled macroalgal blooms have also been increasing. In this example,*Sargassum*densities have been magnified by deforestation and nutrient loss off the coast of Brazil resulting in increasing intensity and frequency of blooms that have been swept thousands of kilometre around the ocean landing on terrestrial coastal zones; (c) A terrestrial mobile consumer, snow geese, has grown in step with the use of increased nitrogen on cereal crops in the southern USA to migrate thousands of kilometres North where it denudes whole marshland ecosystems. (a) Map from: Hugo Ahlenius, UNEP/GRID-Arendal. Time series data from: Convention on Biological Diversity Secretariat 2010. Photo credit: Kirsten Macintyre, California Department of Fish and Wildlife. (b) Map from: NASA/Earth Observatory. Data provided by Mengqiu Wang and Chuanmin Hu, USF College of Marine Science. Time series data adapted from: Wang*et al.*,2019. (c) Map from: Cephas, CC BY-SA 3.0https://commons.wikimedia.org/w/index.php?curid = 5980177. Snow geese data from: Jeffries et al. 2004. US Cereal crop yield from: Food and Agriculture Organization. Photo credit: Peter Prokoschwww.grida.no/resources/4428.

(e.g. Lake Erie, Baltic Sea) – effectively terminal nodes of a spatial network (Diaz and Rosenberg, 2008). These dominant inedible algae drive the mean densities of once prolific species (e.g. edible algae) to functional extinction, simultaneously diverting primary production from the rest of the normal food web and completely altering ecosystem structure. This structural or mean-driven instability appears as a competition-driven process whereby edible algae are reduced in density over time and replaced by inedible algae due to increased levels of nutrient loading and enhanced nutrient coupling on the landscape. In its most extreme form, this mean-driven ecosystem destabilisation can lead to dead zones, where top consumers in the aquatic food web have gone locally extinct. This empirical result resonates with the abrupt loss of an equilibrium or equivalently a phase transition to a new diminished ecosystem equilibrium state discussed in the spatial nutrient-stability theory above (particularly model 2).

Harmful algal blooms and aquatic dead zones have been argued to be driven by nutrient run-off from agriculture and urban development, coupled with increased temperatures that further accelerate algal growth rates, suggesting that the rising tide of imbalance may be created synergistically by increasing nutrients and climate change (Diaz and Rosenberg, 2008; Huisman *et al*., 2018; Ho et al. 2019). Yet climate change may do more than increase growth rates. It has been suggested that, on top of the spatial amplification of nutrients in dendritic landscapes, climate change has also been associated with increased temporal variation in meteorological events that can temporally amplify nutrient run-off (e.g. during a large rainfall event) in time and space (Michalak *et al*., 2013). Scientists have argued that in the Lake Erie agricultural basin, the extreme spring rainfalls or snowmelt can rapidly carry off fall or winter-applied fertiliser, creating highly concentrated nutrient pulses that ignite blooms to record levels (Michalak *et al*., 2013; Motew *et al*., 2018). Here, spatial and temporal nutrient inflation combine to intensify the nutrient-driven ecosystem imbalance at a distance.

Interestingly, little work has been done in agriculturally dominated landscapes to look at where in a spatial network we experience blooms or ecosystem imbalance. The empirical results above suggest that wherever we have a slowing down of nutrient transport, which in turn increases nutrient deposition, we may expect increased biotic nutrient assimilation accompanied by nutrient-driven imbalance. Recent work looking for mini-blooms in an urban streams network have found outbreaks of harmful algal blooms where storm events have scoured the streams to set up slow-moving stream pools (Blaszczak *et al*., 2019). Here, the combination of fast, high nutrient transitions into these slow pools, even small ones, are a recipe for resource blooms as rapid nutrient movement reduces efficient biotic assimilation of excess nutrients until it hits the slow pool where nutrients are assimilated, and instability is expressed. Additionally, there can be significant impacts on coastal ecosystems like seagrasses or coral reefs. For example a 30-year long-term data set on nutrients and climate found that while temperature stress causes coral reef bleaching, the impacts are exacerbated by an interaction with nutrient loading (Lapointe *et al*., 2019). Sewage, fertilisers and topsoil from a large region of Florida inflate nitrogen levels entering the Keys hundreds of kilometres away, which then alter the coastal N:P stoichiometry ultimately starving corals of phosphorus, and in turn reducing their temperature threshold for bleaching (Lapointe *et al*., 2019). Note, this case acts as an unintentional ecosystem connectivity experiment. Algae blooms correlate perfectly in time with the sudden speeding up of water movement by the Army Corps of Engineers – an action to reduce hyper-salinity in Florida Bay – suggesting a strong coherence with the ecosystem theory presented here. This result suggests that the cascading impacts of local actions are likely empirically underestimated as they potentially move across many connected ecosystems.

On a similar empirical note, *Sargassum* – a pelagic macroalga – has risen in density over the last eight years and appeared almost magically stretching across the tropical Atlantic Ocean (Wang *et al*., 2019). Over this time period, the macroalgae have been accumulating in vast quantities on beaches throughout the Caribbean and Central America to the consternation of coastal tourism. The origin and reason for this large-scale spatial bloom was unclear until recent work using global satellite imagery revealed yet another ecosystem imbalance at a distance (Wang *et al*., 2019). Land cleared in Brazil, and subsidised with nutrients for agricultural development, increased the landscape connectivity and, in turn, water flows with the nearby ocean becoming the recipient of excess nutrients. Furthermore, this increased connectivity is exacerbated by climate change producing extreme rainfall events and flooding of the Amazon basin (Wang *et al*., 2019). In turn, the pelagic macroalgae harness these human-driven inputs and bloom off the coast in the plume of the terrestrial-derived nutrient runoff (Fig. 4.b). As modelled in the theory section above, there are arguably two major stages to this ecosystem connectivity with the first-stage driving nutrients from a denuded landscape into the pelagic waters off the coast where *Sargassum* multiplies (Fig. 4b). The bloom (i.e. the resource) is then connected in the second stage of movement by large-scale oceanic currents that sweep the resource at massive spatial scale (thousands of kilometres) to distance coastal regions (Wang *et al*., 2019; Fig. 4.b). This is a poignant case of local actions on the land being coupled to nearby coastal ocean ecosystems, with oceanic conveyor belts carrying the impacts over the Atlantic basin, Caribbean Sea and Gulf of Mexico, causing ecosystem imbalance at a distance. This macroalgal ecosystem instability is not isolated. Other instances include the macroalga *Ulva*, which has experienced runaway growth from nutrient run-off and climate in China (Liu *et al*., 2016) and effluents in Brittany (Charlier *et al*., 2006). Collectively scientists have called these macroalgal blooms green and golden tides and consistent with plankton blooms noted their increasing frequency (Smetacek and Zingone, 2013).

Terrestrial examples also exist that show these distant impacts. Snow geese foraging on cereal crops in the southern USA have attained extremely high densities (Jefferies *et al*., 2004b; Fig. 4c), corresponding in sync with the agricultural use of industrially made nitrogen accelerating in the 1950s near the beginning of the 'Green Revolution'; (Jefferies *et al*. 2004a). Subsidised to high densities from these nutrient-fueled cereal crops, the snow geese migrate thousands of kilometres to the Hudson Bay lowlands during the summer. Here, they collectively overgraze marshlands leaving these once complex ecosystems as denuded hypersaline mud flats (Jefferies *et al.*, 2004a,b). This example emerges as another empirical case of the complete loss of an equilibrium, or mean-driven ecosystem instability (i.e. the marsh sedge resources are totally suppressed) but here the suppression occurs through spatial consumer inflation in the far north triggered by localised nutrient additions thousands of kilometres away to the south. Here, nutrient-driven instability is facilitated by the movement of inflated consumer densities, akin to our theoretical result above. In the case of snow geese, this result is exacerbated by positive feedbacks in the terminal node that make it even harder to potentially remediate these distant impacts of nutrients.

DISCUSSION

Using simple ecological theory, we have shown that ecological systems can become strongly connected over great distances resulting in dramatic ecosystem imbalances. With continued human modification of landscapes and waterways, the speed (e.g. channels) and magnitude (increased local nutrient loading) of this connectivity is increasing. These non-local effects are frequently accompanied by great economic costs to society through the loss of critical ecosystem services, such as loss in water quality, secondary productivity, altered fisheries, tourism and degraded human health (Carpenter and Biggs, 2009). The distant expression of local actions effectively couples cause and effect over space, and in the process makes for 'wicked' environmental problems (Balint, 2011) as they emerge from the cumulative effect of multiple isolated management decisions (e.g. fertilisation, land clearing, river straightening) and across distinctly different political jurisdictions or regions (impacts hundreds to thousands kilometres away – e.g. Great Atlantic Sargassum Belt).

Our theoretical synthesis suggests that factors that increase directional connectivity (advective movement of nutrients or consumers) tend to ultimately inflate the realised nutrient-driven instability in the terminal spatial node. As noted earlier, this spatial amplification of signals may be enhanced by climate variation (e.g. extreme rainfall) if it increases environmental variation that amplifies nutrient transport (Nelson *et al.*, 2013). Arguments for this occurring in the magnification of the Lake Erie dead zone have already been made (Paerl and Scott, 2010). The corollary to the nutrient inflation effect is that any spatial or temporal structure that reduces this hyper-connectivity can remove the distant instability (see Fig. 3 above) by assimilating nutrients before they reach the terminal node. In a complex network, the diffuse assimilation of nutrients within the regional landscape can prevent distant nutrient inflation and costly ecosystem imbalance. We have kept our theory simple with the aim of motivating more detailed work on these directional movements (Box 4) that are major structural attributes of agriculture's interaction with nature's transport systems, such as streams and rivers (Campbell Grant et al. 2007; Fagan, 2002; Grant *et al.* 2007; Peterson *et al.*, 2013b; Moore *et al.*, 2015; Terui *et al.*, 2018). Ultimately, the application of our results will require ecoinformatic approaches that combine detailed local and regional data with spatial modelling to inform how 'slow nodes' can be placed most effectively within a real network.

While we have focused here on the landscape effects of nutrient additions, clearly local nutrient-driven impacts (i.e. on the farm) can still have severe economic and environmental consequences (Carpenter *et al.*, 1998). One might argue that distant effects stall management intervention because they are hidden far from view, or the impacts are observed but the origins unclear (e.g. it took almost a decade to determine the cause of the *Sargassum* bloom). Most fundamentally, however, nutrient-derived instability, local or global, stems from dramatic inefficiencies in how global societies deal with nutrients whether farm applied, or from industry or urban sources (Carpenter *et al.*, 1998; Huisman *et al.*, 2018). For food production, these inefficiencies are part of a massive nutrient retention shortfall where up to 20–30% of applied nutrients can miss their intended target (uptake by maturing crops) and flow off the farm, often because they are applied weeks or months before peak growth that, in turn, makes them susceptible to the loss by extreme rainfall or spring melts (Alexander *et al.*, 2008). Efforts to reduce connectivity may ameliorate distant destabilisation, with local destabilisation possibly the lesser of two evils, but ultimately only reduced nutrient inputs from human-derived sources can truly control the problem (Zhang *et al.*, 2015; Oita *et al.*, 2016).

Here, we have concentrated on the impacts of nutrient loading and its effects on the instability of ecosystems connected by dendritic networks. We focused on exploring the dynamical outcomes (i.e. cycles, loss of interior attractors) and the role nutrients, detritus and consumer movements play in mediating instability. As a result, we did not deal with the role of stabilising portfolio effects whereby nutrients or populations that join different branches of spatial movement can average out variation (Tilman *et al.*, 1998; Schindler *et al.*, 2010; Thompson and Gonzalez, 2016; Thompson *et al.*, 2017). This averaging occurs strongly when different variabilities in different branches are asynchronous. Schindler identified a poignant example with sockeye salmon that return from different streams into a common ocean basin (Schindler *et al.*, 2010). Clearly, future work on these dendritic networks needs to also consider how synchronising forces across the network can disrupt stability. For example regional spatial homogenisation from agriculture likely increases the similarity of abiotic and biotic conditions across the network (e.g. all have high nutrients, all are channelised and fast, all have similar species) resulting in the loss of stability.

There is a growing number of examples of instabilities arising from the coupling of ecosystems across great distances (Diaz and Rosenberg, 2008; Smetacek and Zingone, 2013). Our framework articulates how landscape heterogeneity in nutrient loading and transport can mitigate these instabilities by allowing nutrient flows to be reduced and assimilated before reaching the ultimate end point. Our theoretical synthesis calls for a concerted research effort to understand how spatially complex networks impact ecosystem connectivity and instability, and how it may be managed. Our results speak to the potential for synthesis but much further work is required on more heterogeneous cases as space can drive counterintuitive responses (e.g. see Callaway and Hastings, 2002). The science we summarise here suggests that local actions have global consequences. N and P are both critical drivers of primary production, and support global agriculture and population growth yet ironically, they have also become major ecological pollutants. We have extended the POE from the local to the regional and global scales and suggested how the resulting ecosystem instabilities may be understood and mitigated. Specifically, we find that rapid nutrient transport magnifies ecosystem instability at distant points, but these imbalances can be mitigated by the correct placement of slow nutrient transport nodes in the landscape network. Similarly, imbalances can be magnified by the incorrect placement of fast nodes. Given the social and economic costs of this ecosystem degradation, there is an opportunity to orient research and agricultural policy to manage the considerable environmental externalities arising from coupling of ecosystems. Collectively, this synthesis indicates that the paradox of nutrient enrichment is indeed real as Rosenzweig suggested nearly 50 years ago (Rosenzweig, 1971) albeit this instability may arise most frequently as a structural loss of equilibrium (mean-driven instability).

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AUTHOR CONTRIBUTIONS

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DATA AVAILABILITY STATEMENT

The code to reproduce this study is available as an archived compendium (https://doi.org/10.5281/zenodo.4081347) and the corresponding development repository is available at the following URL < https://github.com/McCannLab/NDID>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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