Environmental Science and Policy 89 (2018) 300–314

Contents lists available at ScienceDirect

Environmental Science and Policy

journal homepage: www.elsevier.com/locate/envsci

Social-ecological drivers and impacts of invasion-related regime shifts: consequences for ecosystem services and human wellbeing

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ARTICLE INFO

Keywords:
Biological invasions
Environmental management
Global change
Invasive alien species
Novel ecosystems
Resilience
Transformation

ABSTRACT

There are growing concerns that increasing global environmental pressures could lead to the exceedance of critical ecological thresholds that could trigger long-lasting regime shifts that will affect the structure and function of ecosystems and the broader social-ecological systems in which they are embedded. Biological invasions are a major driver of global change, and a number of invasive species alter key ecological feedbacks in ways that lead to regime shifts, with consequences for biodiversity, ecosystem services, livelihoods and human wellbeing. We present four case studies, chosen to represent a diverse range of ecosystems and invasive taxa, to illustrate invasion-driven regime shifts in a variety of social-ecological systems globally. The case studies are: i) wattle trees (Australian *Acacia* species) in fynbos shrublands in South Africa; ii) Nile perch (*Lates niloticus*) in Lake Victoria in East Africa; iii) chestnut blight fungus (*Cryphonectria parasitica*) within broad-leaved forests of eastern North America; and iv) the floating macrophytes salvinia (*Salvinia molesta*) and water hyacinth (*Eichhornia crassipes*) in East Sepik Province of Papua New Guinea. For each case we identify the social and ecological drivers and feedbacks underlying the shift, the impacts on ecosystem services and human wellbeing, and the management options for reducing impacts. We discuss the value of using causal-loop diagrams to improve our understanding of the complex dynamics of shifts, and explore how concepts associated with regime shifts can inform guidelines for enhancing adaptive governance of biological invasions. Identifying species that have the potential to generate high-impact regime shifts, understanding the diversity of consequences for different environments and stakeholders, and developing robust management methods to reduce impacts and restore systems to improve social-ecological resilience and reduce vulnerability are priorities for further research.

1. Introduction

Biological invasions are a major driver of human-induced global change in the Anthropocene. Some invasive species cause rapid, substantial and long-lasting changes to the structure and function of ecosystems – so-called regime shifts – that are very difficult or impossible to reverse (Scheffer et al., 2001; Gaertner et al., 2014; Hui and Richardson, 2017). Such shifts have major implications for biodiversity and can cause extinctions and large-scale community change (Clavero and García-Berthou, 2005; Hejda et al., 2009; Downey and Richardson, 2016). They can also substantially alter or change the supply of ecosystem services (Pejchar and Mooney, 2009; Le Maitre et al., 2011; Vaz et al., 2017a), and have significant impacts on human wellbeing and livelihoods, through their effect on factors such as human health and agricultural productivity (Shackleton et al., 2007, 2018a). An improved understanding of the conditions under which invasive species may trigger such far-reaching changes to social-ecological systems, the implications of these shifts for ecosystems and people, and options for integrated management of these changes are urgently needed (Millennium Ecosystem Assessment (MA), 2005; Pejchar and Mooney, 2009; Kueffer, 2013; Gaertner et al., 2014). Such advances are crucial for building resilience and adaptive capacity (Folke, 2006; Brooks et al., 2005), in ways that both reduce the likelihood of such shifts (Chaffin et al., 2016) and increase the capacity to deal with unexpected regime shifts if they do occur.

Biological invasions arise due to human-mediated movement of species to new environments and the subsequent interactions of these species with the recipient ecosystems (Hui and Richardson, 2017). Species are introduced both accidently (e.g., in ballast water, or through seeds with imported goods) and intentionally (e.g., as

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https://doi.org/10.1016/j.envsci.2018.08.005
Received 2 March 2018; Received in revised form 7 August 2018; Accepted 7 August 2018
1462-9011/

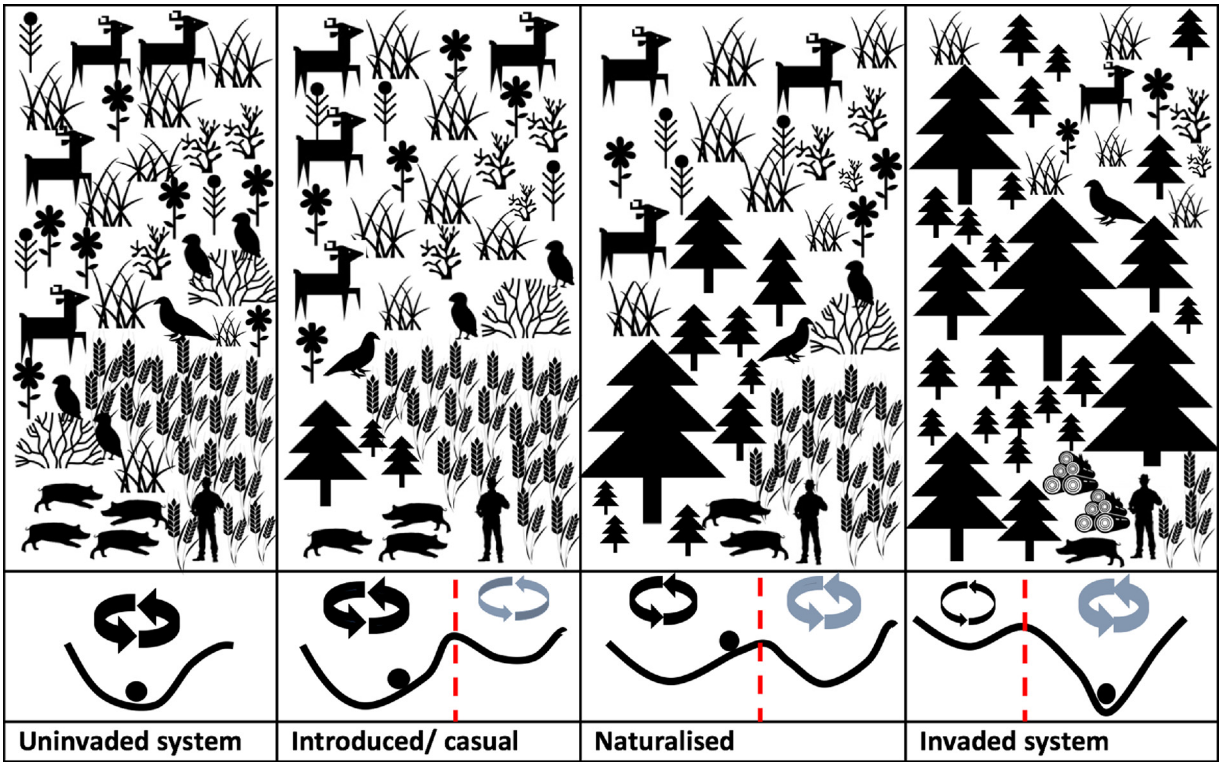

Fig. 1. Example of a hypothetical invasion process that drives regime shifts though altered feedbacks, illustrated with the commonly used ball-and-cup framework. The top panel shows how a hypothetical social-ecological system might change following the introduction of a tree which leads to a reduction in biodiversity and ecosystem services (such as agricultural and ecotourism potential), but also provides new ecosystem services and resources (such as timber), that constitute major alterations (shifts) in the social and ecological components of the system. The lower panel provides a ball-and-cup representation of the alterations in the dominant feedbacks that underlie the regime shift. The black arrows denote the original system feedbacks; new feedbacks introduced by the alien tree are show in blue. The thickness of arrows is proportional to the strength of feedbacks. As the system progresses along the introduction-naturalization-invasion continuum towards a tipping point (threshold separating the two cups - red dashed line), there is a loss of resilience (depth of cup) of the original system state, until a tipping point is reached where a regime shift occurs (ball shifts from one cup to the other) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

ornamentals and pets, for agriculture and forestry) (Essl et al., 2015a). Introduced species face a number of barriers in their new environment and have to survive, proliferate and naturaly disperse (Blackburn et al., 2011). Those that establish, reproduce and develop self-sustaining localised populations are termed naturalised species. When naturalised species spread from original sites of introduction and increase in abundance and spatial scale they are termed invasive alien species (Richardson et al., 2011) (Fig. 1). Only a small proportion of introduced species become naturalised or invasive, and of those that become invasive, only a small number cause regime shifts. Where they do occur, these shifts are highly scale- and density-dependent and can have far-reaching consequences (Gaertner et al., 2014; Hui and Richardson, 2017). Progression along the introduction-naturalization-invasion (INI) continuum can be very rapid, but can also be subject to substantial lags and take several decades or longer (Crooks et al., 1999; Rouget et al., 2016).

Regime shifts are defined as large, persistent (difficult to reverse) changes in the structure and function of social-ecological systems, and are associated with a change in the dominant feedbacks governing system behaviour that lead to a switch between alternative stable states (Scheffer and Carpenter, 2003; Folke et al., 2006; Kinzig et al., 2006; Biggs et al., 2012; Kull et al., 2018). This definition has an ontological basis in resilience/systems thinking, which is the basis of much of our understanding of social-ecological system dynamics (e.g., Adger, 2000; Berks et al., 2003). Regime shifts are usually driven by a combination of external perturbations and slow changes within the system (Andersen et al., 2009; Biggs et al., 2012; Rocha et al., 2015). These perturbations and slow changes can weaken the dominant system feedbacks, reducing the resilience of the current system state, and driving it towards a tipping point. A regime shift occurs once the system reaches a critical threshold (or tipping point/critical transition) where a switch in the dominant feedbacks governing system behaviour significantly alters social-ecological or ecosystem processes and structures (e.g., loss of adaptive capacity, a switch to a new primary livelihood activity and/or a switch in vegetation structure) (Scheffer et al., 2001; Bennett et al., 2005; Kinzig et al., 2006; Biggs et al., 2012; Hammond, 2012; Blythe, 2014; Lade et al., 2013; Kull et al., 2018).

When a species is added to an ecosystem it can act as a primary external perturbation, but it may also interact with other drivers, potentially leading to altered feedback dynamics or to totally novel feedbacks (Biggs et al., 2012; Polasky et al., 2011). Initially, these novel or altered feedbacks are usually weak compared to the dominant feedbacks and energy flows, and the system typically continues to function broadly as before (Fig. 1). However, once an introduced species becomes naturalised, it may start to exert a larger influence on system dynamics. The new or changed feedbacks may become increasingly strong while the system dynamics prior to invasion become weaker and more vulnerable to change and have reduced adaptive and transformation potential (Fig. 1). If the species progresses further along the INI continuum to become a dominant component of the community, it may fundamentally change the ecosystem structure and function and/or livelihood practices, precipitating a social-ecological regime shift or new stable state (Brooks et al., 2004; Lade et al., 2013; Gaertner et al., 2014; Kull et al., 2018). Many shifts are facilitated by multiple or additional social and ecological shocks (e.g., such as fire, drought or flood), altered land-use practices, or by impacts caused directly or indirectly by other invasive species (Hughes et al., 2013; Kull et al., 2018).