



Original research article

Ecosystem process interactions between central Chilean habitats

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ARTICLE INFO

Article history:

Received 18 December 2014

Received in revised form 13 April 2015

Accepted 14 April 2015

Available online 20 April 2015

Keywords:

Acacia caven

Ecosystem process

Espinal

Functional trait

Matorral

Silvopastoral system

ABSTRACT

Understanding ecosystem processes is vital for developing dynamic adaptive management of human-dominated landscapes. We focus on conservation and management of the central Chilean silvopastoral savanna habitat called “espinal”, which often occurs near matorral, a shrub habitat. Although matorral, espinal and native sclerophyllous forest are linked successional, they are not jointly managed and conserved. Management goals in “espinal” include increasing woody cover, particularly of the dominant tree *Acacia caven*, improving herbaceous forage quality, and increasing soil fertility. We asked whether adjacent matorral areas contribute to espinal ecosystem processes related to the three main espinal management goals. We examined input and outcome ecosystem processes related to these goals in matorral and espinal with and without shrub understory. We found that matorral had the largest sets of inputs to ecosystem processes, and espinal with shrub understory had the largest sets of outcomes. Moreover, we found that these outcomes were broadly in the directions preferred by management goals. This supports our prediction that matorral acts as an ecosystem process bank for espinal. We recommend that management plans for landscape resilience consider espinal and matorral as a single landscape cover class that should be maintained as a dynamic mosaic. Joint management of espinal and matorral could create new management and policy opportunities.

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1. Introduction

Understanding ecosystem processes is essential to developing conservation and management interventions. Ecosystem processes are broadly controlled by the distribution of functional traits, habitat modification by species, and abiotic inputs controlling primary productivity (Crain and Bertness, 2006; Fischer et al., 2006; Mouillot et al., 2011; Maestre et al., 2012). Anthropogenic transformations due to agriculture, forestry and climate change, as well as natural successional processes, affect ecosystem processes by creating heterogeneity (Loreau et al., 2001; Fischer et al., 2006). Within habitat mosaics, each habitat type may harbor components of biodiversity, abiotic inputs and physical substrates needed for different ecosystem processes (Loreau et al., 2003; Fischer et al., 2006). Ecosystem processes, and their inputs, also travel beyond their immediate spatial distributions via biotic and abiotic fluxes and interactions (e.g. Rand et al., 2006; Alongi, 2008). Thus landscape-scale heterogeneity may contribute to providing more inputs for more ecosystem processes, yet many studies show that it can also reduce overall functioning due to island and matrix effects (Loreau et al., 2001, 2003; Fischer et al., 2006).

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One possible explanation for these contrasting outcomes is that successional linked mosaic patches may increase overall functioning within the landscape, while mosaics not linked by a successional pathway may more frequently show decreased functioning as a result of fragmentation (Odum, 1969). By successional, we refer broadly to all endogenous habitat changes, including shifting mosaics, while by non-successional we mean land cover change created and maintained through high levels of disturbance and human niche construction, such as cropland or urban areas. Successional pathways between habitat types imply spatiotemporal dispersal of nutrients, propagules, and/or ecosystem functions at a landscape scale. Thus, when habitat types are linked via successional processes, the functional “insurance” effect of diverse taxon dispersal across landscapes (Loreau et al., 2003) may be facilitated, compared to habitat types not linked by succession. This is because cropland, for example, acts as a successional sink. Ecosystem processes leading to succession, e.g. seed dispersal, may enter cropland but the cropland is either physically inhospitable or maintained through anthropogenic disturbance in a state far from natural succession, until abandonment. While the flux of ecosystem functions across anthropogenically maintained mosaics with cropland, plantations, cities, etc. is of particular interest to conservationists taking an ecosystem services perspective, many semi-natural production systems, such as rangelands, silvopastoralism and agroforestry, can be managed for natural successional mosaics (Fischer et al., 2006).

Ecosystem functions, and the ecosystem services they provide, can be difficult to define and measure, due to their complexity. Underlying ecosystem functions are multiple functional traits belonging to many species with different in spatial and temporal distributions, which together contribute at different rates and in different quantities to ecosystem function dynamics (Bengtsson, 1998; de Groot et al., 2010). Functional traits contribute to ecosystem processes that, in turn, have difficult-to-assess spatiotemporal dynamics. Functional traits and other inputs each have a different strength of contribution to the ecosystem process, a different range and frequency of mobility, and a different lag or residence time at the destination. For example, if seed germination depends on seed production, exozoochory and nurse plant availability, then the spatiotemporal distribution of the seed germination process depends on the spatiotemporal dynamics of shrub seed production, animal movement, and nurse plant distribution. It is unlikely that ecosystem process distributions show a linear decay away from the area of origin (e.g. the seed producing shrubs). Rather, they are likely to distribute in complex and patchy ways. Although there is a great deal of literature on regional and continental-scale spatial mapping of ecosystem services, practical difficulties limit attempts to trace the spatiotemporal dynamics of ecosystem processes at a landscape or patch scale (for related approaches see Jordano et al. 2007; Root-Bernstein et al., 2013a).

In addition, ecosystem processes are often cyclical, such as reproduction, the water cycle, or trophic energy transfer (Fath and Haines, 2007; Scanlon et al., 2005). Because a given functional trait can both cause and be affected by a cyclical ecosystem process, functional traits are not only inputs to processes, but also *outcomes*. The input–outcome relationship is similar to the response-and-effect framework (Suding et al. 2008; Laliberté et al., 2010), but here we focus on the endogenous ecosystem processes underlying succession (Odum, 1969), rather than the functional responses uniquely associated with exogenous factors such as climate change. The functional traits that occur in a habitat as a result of successional processes (outcomes) are rarely studied in relation to functional trait inputs (but see Eldridge et al., 2011).

An additional complication, from a community ecological point of view, may be that counting functional traits alone leaves out many important characteristics of ecosystems that interact closely with other traits, such as properties of the soil. Methods that mix functional traits and other functional non-trait elements fit better with diverse perspectives (e.g. ecosystem engineering, Crain and Bertness, 2006), and can provide good ecological models (e.g. Maestre et al., 2012; Dantas et al., 2013).

We address the concept of ecosystem process interactions with a non-spatially explicit, non-temporally explicit approach, through a case study of the central Chilean mediterranean-climate habitats espinal and matorral (see Fig. 1; Root-Bernstein and Jaksic, 2013; Maestre et al., 2012). Espinal is a savanna dominated by *Acacia caven*, traditionally used as a silvopastoral system (Ovalle et al., 1990; Fuentes et al., 1989). Espinal can be found with or without a shrub understory, and often occurs next to matorral, a dense shrub habitat typical of the foothills of the Andes and the coastal mountain range (Donoso, 1982). The successional relationships between espinal habitats and matorral have been largely ignored after a few early studies (Armesto and Pickett, 1985; Fuentes et al., 1986) and are only recently attracting renewed interest as an element of land cover change (e.g. Hernández et al., 2015; Fuentes-Castillo et al., 2012; Newton et al., 2011). Espinal succession may be characterized as in Fig. 2. Both matorral and espinal have been described as degradations of native sclerophyllous forest (assumed to have been the dominant climax habitat in prehispanic Chile), implying a simple successional model in which forest is degraded, crosses a threshold and rarely recovers (see Ovalle et al., 1990; Aronson et al. 1993; Schulz et al., 2010; van de Wouw et al., 2011). *A. caven* can also be described as a slow-reproducing pioneer species that establishes after anthropogenic disturbance, suggesting that it is not a dead-end degraded state, but rather the initial stage of a successional pathway (Fuentes et al., 1989; Baranelli et al., 1995; Torres et al., 2002; Root-Bernstein and Jaksic, 2013). Espinal can serve as nurse plant habitats, making them important for regrowth of sclerophyllous forests in central Chile (Hernández et al., 2015; Fuentes-Castillo et al., 2012; pers. comm. C. Peña). Within espinal it is often possible to find some sclerophyllous tree species at low density (pers. obs. MR-B). However, anthropogenic disturbances of forest and matorral, and overgrazing of espinal areas preventing tree and shrub recruitment may result in the last part of the cycle, sclerophyllous forest regrowth, rarely occurring.

The lack of a well-studied dynamic functional viewpoint on matorral–espinal–sclerophyllous forest relationships has effects on their conservation and management. The three habitats are formally considered as separate and unrelated, with widely differing protections and management regimes. From an institutional governance perspective, both matorral and

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