Temporal changes in native-exotic richness correlations during early post-fire succession

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ABSTRACT

The relationship between native and exotic richness has mostly been studied with respect to space (i.e., positive at larger scales, but negative or more variable at smaller scales) and its temporal patterns have rarely been investigated. Although some studies have monitored the temporal trends of both native and exotic richness, how these two groups of species might be related to each other and how their relative proportions vary through time in a local community remains unclear. Re-analysis of early post-fire successional data for a California chaparral community shows that, in the same communities and at small spatial scales, the native-exotic correlations varied through time. Both exotic richness and exotic fraction (i.e., the proportion of exotic species in the flora) quickly increased and then gradually declined, during the initial stages of succession following fire disturbance. This result sheds new light on habitat invasibility and has implications for timing the implementation of effective management actions to prevent and/or mitigate species invasions.

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1. Introduction

A major indicator of ecosystem health is the level or degree of invasion by exotic (i.e., introduced, nonnative, or alien) species (Williamson, 1996; Lu et al., 2015). A common practical approach to computing this indicator is to assess the native-exotic richness relationship, which reflects the interactions between these two groups of species or the impact of exotics on natives (Sax, 2002; Shea and Chesson, 2002; Figueroa et al., 2011). The vast majority of past research on biotic invasions has focused on spatial patterns, including the positive relationship between native and exotic richness at larger spatial scales and negative association at smaller scales (but see Shea and Chesson, 2002; Sandel and Corbin, 2010). A recent synthesis further revealed that, even over small spatial scales, the correlations between natives and exotics are not only inconsistent, but may be highly variable (Guo, 2015). Because the importance of time has become increasingly recognized, recent efforts have studied the temporal patterns of exotic richness and/or abundance in terms of density, cover, or biomass (Tognetti et al., 2010; Tognetti and Chaneton, 2012) and interactions between individual exotic species and the native plant community (Kulmatiski, 2006; Tognetti et al., 2010; Martín-Forés et al., 2016).

With accumulated data concerning biological invasions during the past several decades, a growing number of studies have examined temporal trends in native and exotic species richness (Rejmánek, 1989; Heard et al., 2012; McLane et al., 2012; Clark et al., 2013). Since both native and exotic species richness is likely to be controlled by resource availability, which varies more drastically after major disturbances (Davis et al., 2000), potential changes in the native-exotic relationship would be better examined during succession (Rejmánek, 1989; Davis et al., 2000; Anderson, 2007).

Earlier studies on habitat invasibility or degree of invasion have used the number of exotic species present in a community as an indicator of change (reviewed by Rejmánek, 1989; Levine and D'Antonio, 1999; Lonsdale, 1999). More recent studies have used the exotic fraction (i.e., proportion of exotic species among the invaded flora) or the native-exotic richness relationship as another indicator (Sax, 2002; Sandel and Corbin, 2010; Clark et al., 2013; Guo et al., 2015). Since exotic richness in the same community often changes through time, some observed inconsistencies in spatial patterns (i.e., positive, negative, and no relationship between native and exotic species) at smaller scales could be caused by successional dynamics. First, if the study area supports the same type of community but covers a mosaic of patches that are in different stages of succession (e.g., burned at different times or with different severity), the native-exotic richness relationship would be spatially variable. Second, even at the same location (or patch), the

native-exotic relationship could vary because of succession and/or long-term continuing invasion by additional exotic species facilitated by ongoing human activities and climate change.

To assess how the exotic species richness fraction varies through time, I re-analyzed an existing successional dataset from the Santa Monica Mountains of southern California, USA, where fire is frequent and serves as a major promotor for exotic species invasion (Grace and Keeley, 2006; Keeley, 2006). I then examined the ways in which natives and exotics might be related to each other during succession and also made comparisons with corresponding spatial patterns. I hypothesized that the same community may show different native-exotic correlations and degrees of invasion (exotic fraction), at different points in time during early post-fire succession. After disturbance, the richness of both native and exotic species should first increase because of facilitation and/or increased availability of resources and then decline when accumulated biomass leads to resource limitation (Fig. 1; Shugart, 1984; Guo, 2003; De Miguel et al., 2010; Martín-Forés et al., 2016). Although exotic species richness usually follows the same trend as overall species richness after disturbances, how the exotic fraction may change remains an open question. A specific goal is to provide empirical evidence that, even at the same location, native-exotic correlations can change drastically during a short period of time, thus shedding new light on successional dynamics that will aid ecosystem managers in addressing species diversity-community invasibility challenges.

2. Methods

I used early post-fire successional data (1994–1997) from a southern California chaparral community in the Santa Monica Mountains to examine temporal changes of native-exotic richness correlations in the plant community. This chaparral community was burned during November 1993, just before the normal rainy season. The study site was located at a 310-acre University of California Nature Reserve, surrounded by extensive natural areas which are protected by various conservation management organizations. Established for research, teaching, and public service, the reserve had no major catastrophic disturbance events (i.e., natural or anthropogenic) during the study period. Soils are primarily loams or clay loams, but texture and other soil properties vary substantially across the study site. Prior to the fire, vegetation was dominated (~100% cover) by evergreen chaparral, with dense stands of *Quercus berberidifolia* Liebm. and a mixture of shrubs such as *Arctostaphylos glandulosa* Eastw., *Adenostoma fasciculatum* Hook. & Arn. and *Ceanothus megacarpus* Nutt. (Keeley, 1996; Potts et al., 2010).

In March 1994, permanent plots (n = 30) and quadrats (n = 60) were established at three locations, one on the north-facing slope and two on the south-facing slope of the study site. Each location was divided into 10 contiguous permanent plots (each 10 × 10 m). Within each plot, two 1 × 1 m permanent quadrats were placed in opposite corners. Vegetation data were collected from May to July of 1994–1997, during the seasonal peaks of herbaceous biomass. In each permanent quadrat, foliar cover for each species was measured and number of individuals per species and total number of species were determined. At the end of each field season, aboveground plant materials were cut at ground level from different sets of neighboring quadrats (1 × 1 m), one to four meters away from the permanent quadrats. Harvested plant materials were then sorted by species, oven-dried, and weighed. For details about the field sampling, see Guo (2001). The number of species for all native and exotic plants based on their growth forms were also separately counted on each permanent plot.

For purposes of this study, the temporal patterns of native vs. exotic plant richness and exotic fraction, as well as the temporal native-exotic richness relationships, were examined using regression analyses, based on data from both north-facing and south-facing slopes. Exotic fraction was calculated as the proportion of exotic species richness relative to species richness of the entire flora. Mixed effects models were used to evaluate the effects of aspect (north-facing vs. south-facing slopes), time (years after fire), and their interaction on temporal changes in native and exotic richness as well as exotic fraction using SAS Proc MIXED (SAS Institute, 2014).

3. Results

Similar to findings from many other successional studies, early post-fire data for chaparral in the Santa Monica Mountains showed that both native and exotic plant species richness increased during the first two years after fire and then gradually declined. This overall trend in species richness was consistent with predictions in Fig. 1. Results of the mixed effects modeling revealed significant differences in patterns of native richness, exotic richness, and exotic fraction through time (i.e., across successional years). In addition, slope aspect (north-facing vs. south-facing) and the Aspect × Year interaction significantly affected native richness, but not exotic richness and exotic fraction (Table 1; Fig. 2).

During the first four years after fire, the native-exotic relationship changed with time, at the same location and spatial scale (e.g., the same permanent plots). Specifically, the native-exotic richness correlations were non-significant in the first post-fire year, positive during the second year, and non-significant again in the third year (Fig. 2 upper). During this same period, exotic fraction exhibited similar variation as the total number of exotic plant species; that is, it initially increased after fire then gradually declined as native species regained dominance at the site (Fig. 2 lower).

4. Discussion

Higher native species richness on the north-facing slope is not surprising and corresponds with earlier studies (Keeley and Keeley, 1981; Guo, 2001; Grace and Keeley, 2006). However, plots on both slopes show similar levels of exotic species richness and exotic fraction, which may imply that both slopes experienced similar levels of disturbance and propagule pressure across early succession years. Nevertheless, mixed effects modeling reveals that both native and exotic richness as well as exotic fraction vary significantly with time during early succession as expected based on related studies (Westman, 1981; Keeley, 1996; Anderson, 2007;
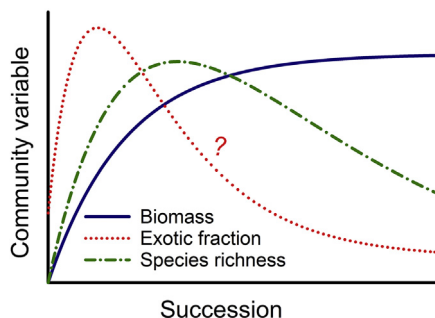

Fig. 1. Hypothetical temporal trajectories in species richness (native, exotic, or both, depending on specific ecosystems), biomass, and exotic fraction associated with native-exotic relationship during succession (see Shugart, 1984; Guo, 2003). Note that the changes in exotic fraction may be different from that of exotic richness, as it reflects the relative value of exotic vs. native richness in a particular flora.

Table 1
Results from mixed effects modeling of effects of slope aspects (north-vs. south-facing slopes), sampling year, and the aspect x year interaction on native richness, exotic richness, and exotic fraction on Santa Monica Mountains, southern California, USA. *P < 0.05, **P < 0.01, ***P < 0.001.

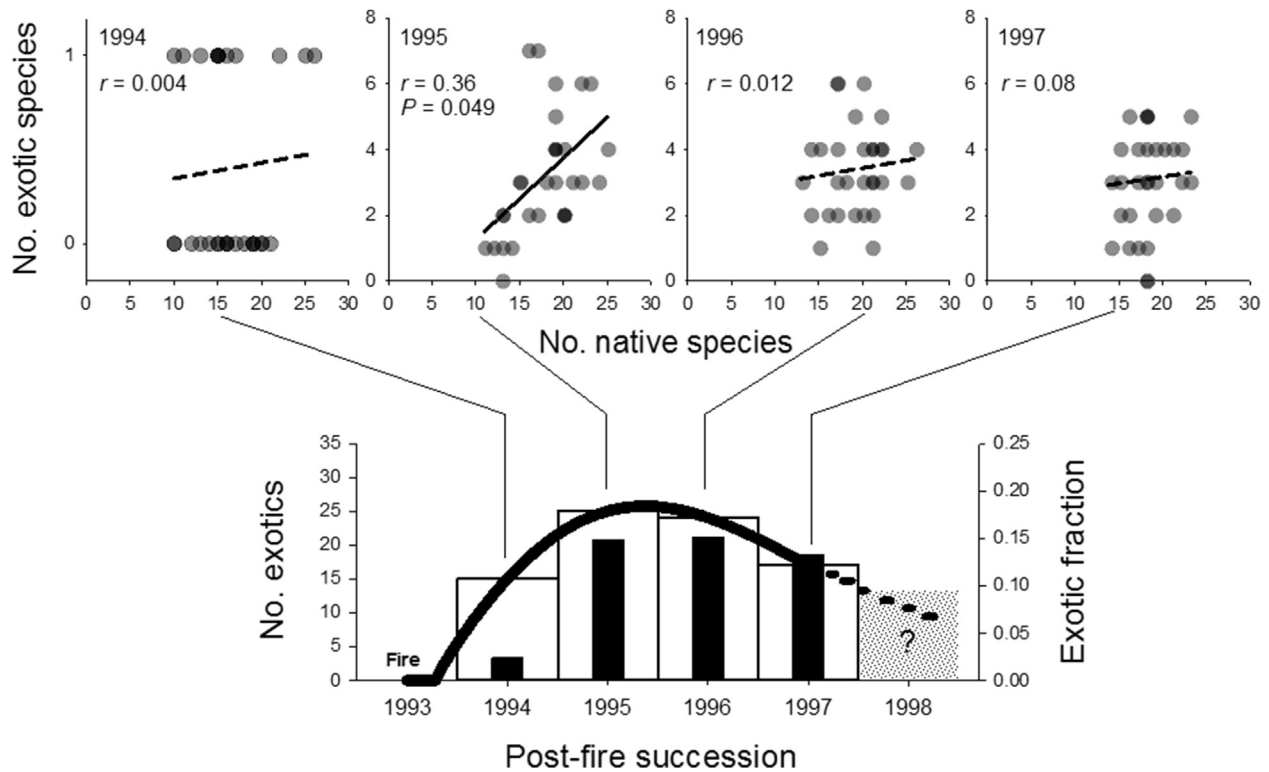|		Native richness	Exotic richness	Exotic fraction
Source	df	F	F	F
Aspect	1, 116	26.53***	1.85	0.69
Year	1, 116	19.47***	38.17***	40.00***
Aspect X Year	1, 116	26.50***	1.86	0.70

Fig. 2. Temporal variation in the native-exotic richness correlations (upper), exotic richness (lower − open bars), and exotic fraction (lower − solid bars) measured on the permanent plots through time. The solid curve indicates the diversity trend for all species through time. Data from early (first four years) post-fire succession of a chaparral community (burned in 1993) on Santa Monica Mountains in southern California (Guo, 2001).

Tognetti et al., 2010; Han et al., 2016; Hanan et al., 2016) (Table 1, Fig. 2).

This study, along with a recently published study by Martín-Forés et al. (2016), helps to fill a knowledge gap by showing that, just as native-exotic correlations vary across communities and spatial scales, they also vary through time, even when the spatial scale is constant. In early post-fire California chaparral succession, exotics—especially short-lived herbs—usually emerge first, followed by native and exotic perennials, and then dominant native species—especially shrubs. Consequently, native-exotic relationships in the same community are expected to vary accordingly; that is, a positive association during early stages when habitat is relatively open, potentially becoming negative in late stages when stand density increases and shrub dominance is re-established (Fig. 1)(Rejmánek, 1989). This study indicates that in this particular California chaparral community, although the overall temporal patterns in native and exotic species richness are similar during early post-fire succession (Figs. 1 and 2; Guo, 2001), when the rates of change differ between native and exotic species, their temporal correlations also change.

Clearly, varying native-exotic correlations in different developmental stages of the same community should be treated as an important cause of inconsistencies in small-scale invasion patterns (Martín-Forés et al., 2016). This causal mechanism has been mostly missing from the major factors previously identified in spatial studies. Long-term continuing invasion under global change would further increase the number of exotic species in many regions and habitats with time, thus altering the native-exotic relationships. Previous research reports that disturbance usually increases the chances of exotic invasion and establishment (Williamson, 1996). Yet, disturbances occur at different levels of intensity and each level may impose different effects on both native and exotic species. Disturbance at intermediate levels could facilitate the coexistence of natives and exotics by reducing dominance and competition (Guo, 2003; Figueroa et al., 2011). Therefore, although native diversity could enhance invasion resistance to some degree, it may not be sufficient to expel exotic species and form negative native-exotic richness correlations. This is especially the case when in early succession, some exotic species may actually be beneficial by reducing soil erosion or reducing animal predation on native species. Species-rich habitats resist invasion through occupying both the number of niches and the fullness (in abundance and distribution) of each niche.

Two related issues deserve further attention. First, like many

spatial studies of native-exotic correlations, the correlations may not necessarily show causality. Both groups of species may only show similar responses to changes in area and other environmental conditions associated with the succession process. In addition to altering microclimate and soil conditions, invasion mechanisms affecting succession include germination or re-sprouting of previously existing/resident species and colonization of new species from neighboring areas through seed dispersal after fire. Second, most data and associated studies only show the patterns in aboveground vegetation, and belowground patterns and processes have mostly been ignored. In reality, the seeds of many exotic (and native) plants are present belowground in seed banks, and overall patterns in the entire (aboveground and belowground) community may not be consistent with what can be seen only in aboveground vegetation.

In summary, while native-exotic richness correlations for California chaparral depend on time during early succession, these patterns remain largely unexamined or unconfirmed in other regions and ecosystems (Iannone et al., 2015). Exotic richness and fraction (of usually short-lived herbs) typically show sharp increases right after disturbances and gradually decline as native species (mostly woody shrubs) become dominant. This finding has significant practical relevance, in terms of when and where to implement management actions that mitigate the expansion of invasive species more efficiently (Keeley, 2006).

Author contribution

Qinfeng Guo conceived the model, performed the research, and wrote the manuscript. The author has approved the final article.

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