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Mutualistic relationships under landscape change: Carnivorous mammals and plants after 30 years of land abandonment

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Abstract

Little is currently known about the dynamics of mutualistic interactions in relation to land abandonment. Using data from two studies on frugivory and seed dispersal by carnivorous mammals carried out at the same site, and spanning three decades, we show how plant–frugivore interactions change in the long-term after a process of land abandonment in a mountainous area of NW Spain. Over time, the change in the identities of interacting species was small. However, considering the quantitative participation of each species along with the identity and number of strong links, the change was significant. After land abandonment, two successional plant species (rowan and bramble) and a cultivated species (cherry tree) dominated the interactions with carnivores and red foxes replaced pine martens as the main frugivores. The prevalence of cherry tree increased significantly in this sub-web, probably as a consequence of the preference of carnivores for human-selected fruits (higher pulp/seed ratio) and the abandonment of harvesting as a result of the declining human population. Our results suggest that the frequency of interactions between plants and carnivores may be modulated by plant abundance, which in turn is primarily influenced by land abandonment in this scenario, fruit preference by dispersers and the interaction between these two factors. The temporal assessment of plant–animal mutualisms appears to be a valuable tool to predict the course of successional processes. A functional consequence of red foxes as the main frugivore is a higher frequency of long-distance seed dispersal events, which increases connectivity among plant populations, favors colonization and ultimately may shape the course of the successional process. Our study exemplifies the pressing need for more information on the temporal dynamics of ecological interactions in order to understand how they respond to anthropogenic changes such as land abandonment.

Zusammenfassung

Wenig ist über die Dynamik von mutualistischen Interaktionen nach Aufgabe der Landbewirtschaftung bekannt. Diese Studie kombiniert Daten aus zwei Erhebungen zur Frugivorie von Raubsäugern, die im selben Gebiet (Bergland in NW-Spanien) im Abstand von etwa 30 Jahren durchgeführt wurden. Die Identität der interagierenden Arten änderte sich wenig in diesem

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Zeitraum. Es zeigten sich aber bedeutende Änderungen, wenn die quantitative Beteiligung der einzelnen Arten sowie die Identität und Anzahl der starken Interaktionen betrachtet werden. Nach der Landaufgabe dominierten zwei Sukzessionsarten (Eberesche und Brombeere) sowie eine ehemals kultivierte Art (Kirsche) die Interaktionen mit den Raubsäugern, und der Fuchs löste den Baummarder als wichtigster Fruchtfresser ab. Das Vorherrschen der Kirschbäume nahm in diesem Teilnetz signifikant zu, vermutlich als eine Folge der Präferenz der Karnivoren für Kulturfrüchte (höherer Fruchtfleischanteil) und weil die Bäume mit dem Rückgang der Bevölkerung nicht mehr abgeerntet wurden. Unsere Ergebnisse legen nahe, dass die Häufigkeit von Interaktionen zwischen Pflanzen und Karnivoren durch die Abundanz der Pflanzen beeinflusst werden könnte, die ihrerseits hauptsächlich durch die Nichtbewirtschaftung bedingt wird, durch die Präferenzen der Samenausbreiter und die Interaktion zwischen diesen beiden Faktoren. Die zeitliche Bestimmung von Pflanze-Tier-Mutualismen scheint ein wertvolles Mittel zu sein, um den Verlauf von Sukzessionsprozessen vorherzusagen. Eine funktionale Folge von Füchsen als den wichtigsten Früchtefressern ist eine häufigere Ausbreitung von Samen über größere Entfernungen, wodurch die Konnektivität der Pflanzenpopulationen zunimmt, Kolonisierungen begünstigt werden und schließlich der Verlauf des Sukzessionsprozesses beeinflusst wird. Unsere Untersuchung verdeutlicht beispielhaft den dringenden Bedarf an mehr Informationen zur zeitlichen Dynamik von ökologischen Netzwerken, um den Einfluss von anthropogenen Prozessen, wie z.B. die Aufgabe der Bewirtschaftung, auf diese Netzwerke zu verstehen.

Keywords: Plant–animal interactions; Mutualistic networks; Temporal dynamics; Carnivores; Frugivorous mammals; Land abandonment

Introduction

Plant–animal mutualisms are potentially susceptible to global change drivers such as land use changes, overharvesting, invasion of new species, or climate change, owing to their susceptibility to a wide array of factors such as the abundance, behavior or phenology of interacting species (Tylianakis, Didham, Bascompte, & Wardle 2008; Hegland, Nielsen, Lázaro, Bjerknes, & Totland 2009; Holbrook & Loiselle 2009; Kiers, Palmer, Ives, Bruno, & Bronstein 2010; Burkle & Alarcón 2011; Markl et al. 2012).

Land abandonment is recognized as a powerful driving force for landscape change in developed countries (MEA 2005), particularly in rural and mountainous areas where population exodus is the norm (Mac Donald et al. 2000; Munilla, López-Bao, González-Varo, & Guitián 2008). From a global perspective, whereas the common trend is an intensification of agriculture and urbanization of fertile plains and coasts, respectively, we are witnessing land abandonment in mountainous areas (e.g., Mac Donald et al. 2000; Munilla et al. 2008). Both positive and negative effects of land abandonment on biodiversity have been reported (e.g., Benayas, Martins, Nicolau, & Schulz 2007; Russo 2007). However, although the effects of human disturbance on plant–animal interactions have attracted a great deal of attention (Markl et al. 2012), the impact of land abandonment – which takes place over broad temporal scales (i.e., several decades) – on these mutualisms is practically unknown.

When human activities cease in agricultural lands, a secondary successional process (Horn 1974) begins and this involves both natural and human-introduced species (either cultivated, ornamental or alien species) that have a high potential to affect mutualisms (López-Bao & González-Varo 2011; Spotswood, Meyer, & Bartolome 2012). In regions with a temperate climate, in the medium term, the abandonment of mosaic agricultural landscapes favors the increase of secondary forest patches, often comprised of fleshy-fruited species (Jordano et al. 1992; Kuiters & Slim 2003; Guitián & Munilla 2008; see also DeWalt, Maliakal, & Denslow 2003 for an example in tropical regions). Moreover, the remaining human-associated plant species (especially cultivated fruiting trees) will be also affected by land abandonment. For example, these species may benefit from new and altered habitats, thereby becoming dominant and increasing their interaction rates with extant frugivore assemblages and disrupting existing frugivory networks (Lenda et al. 2012; Spotswood et al. 2012).

One of the main handicaps encountered in evaluating the ecological outcome of plant–animal mutualisms is the question of how networks change in space and time (Bascompte & Jordano 2007). However, our understanding of such temporal dynamics remains limited (Olesen, Bascompte, Elberling, & Jordano 2008; Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis 2008; Díaz-Castelazo et al. 2010; Burkle & Alarcón 2011; Olesen, Stefanescu, & Traveset 2011; Burkle, Martin, & Knight 2013). On a temporal scale, the available information suggests that networks may vary in detail regarding the composition of species and interactions (Olesen et al. 2008; Petanidou et al. 2008), but they usually retain basic topological properties such as the number of interacting species, the number of strong links or even the level of connectance (Burkle & Alarcón 2011). A key step toward increasing our understanding of the response of mutualistic networks to environmental variations, and its ecological consequences, is to assess mutualisms on a temporal scale that is large enough to provide for significant environmental changes (several decades). Unfortunately, although empirical evidence for shifts in mutualistic networks on a